

FORESTRY SCIENCES

Biology and Ecology of Norway Spruce

Mark G. Tjoelker, Adam Boratyński
and Władysław Bugała
editors



BIOLOGY AND ECOLOGY OF NORWAY SPRUCE

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1. PALEORECORD OF NORWAY SPRUCE

ANDRZEJ ŚRODŃ, KAZIMIERZ TOBOLSKI

The oldest fossil remains of spruce are described under the name *Picea protopicea*, and originate in the upper Cretaceous epoch. Additional fossil specimens of spruce occur in the sediments of the Tertiary (*P. engelri* in Paleogene Baltic amber), and particularly the later Neogene, spanning the Miocene and Pliocene. The fossil evidence indicates a widespread occurrence of spruce taxa with epistomatic needles beginning in the lower Oligocene in the northern hemisphere. Contemporary species of *Picea* possessing this needle type (*P. omorica*, *P. jezoensis*) belong to Tertiary relics in the Mediterranean and sub-Mediterranean mountain regions of Eurasia (MAI 1995). However, species with amphistomatic needles (including *P. abies*) also adapted to changing climatic conditions (continentalization and climate cooling) and consequently occupied large geographic areas during the Quaternary.

According to MAI (1995), both the phylogeny as well as the contemporary occurrence of taxa of this species is characteristic of plants originating with the flora of mesic woodlands of cold temperate climates. During the Triassic, spruce was absent in dry and warm areas. Climate cooling in the late European Triassic was associated with a marked increase in the presence of spruce pollen in sediment cores (*l.c.* p. 216). During the Miocene, spruce played an insignificant role, whereas in the Pliocene it became an important, and sometimes dominant component of forest vegetation. This large difference in the proportion of spruce in pollen diagrams of the Neogene is of stratigraphic significance. In addition to other factors, it permits the separation of Miocene sediments from those of the Pliocene (OSZAST 1973).

The increase in spruce dominance in the Pliocene is a proxy for the large changes that occurred in the species composition of European flora at the threshold of the approaching ice age. In central Europe three other taxa of the species *Picea* were present throughout this period of vegetation change, namely, Serbian spruce (*P. omorica*) as well as two sub-species belonging to Norway spruce *P. abies*: *P. abies ssp. abies* and *P. abies ssp. obovata* – Siberian spruce.

1.1. PALEOBOTANY

Fossil evidence of spruce has been the subject of many paleobotanical studies, revealing much about the history of the taxa belonging to the genus *Picea*. Older studies were based primarily on macroscopic remains, which were largely reproductive organs (particularly cones and seeds) as well as vegetative parts (mainly needles and wood). Less frequent analyses include bud scales (RABIEN 1953; TOMLINSON 1985) and stomata (TRAUTMANN 1953).

Despite the considerable number of macrofossil finds, our current knowledge of the history of spruce is shaped in large part by palynological research. This research method, taking advantage of the diagnostic characteristics of pollen grains, permits an evaluation of the abundance of spruce in the vegetative cover beginning as early as the Neogene and later Pleistocene and Holocene forest assemblages. The characteristic pollen grains of spruce (*vesiculatae*, bearing two air sacs) in central Europe permit the separate identification of *P. abies* and *P. omorica*. Furthermore, as DYAKOWSKA (1964) demonstrates, it is possible to identify variants associated with certain regions of the contemporary geographic range of Norway spruce (LANG 1994).

Traditional methods of presenting the temporal changes in geographic ranges of tree taxa by means of pollen diagrams (cyclograms) have been complemented by the use of isopole and isochrone diagrams. The isopolar method originated with SZAFER (1935) and was developed primarily based on spruce. During the 1980's, spruce isopollen maps were developed for Europe (HUNTLEY and BIRKS 1983), Poland (RALSKA-JASIEWICZOWA 1983), and for the Czech Republic and Slovakia (RYBNIČKOVA and RYBNIČEK 1988).

1.2. THE HISTORY OF SPRUCE IN THE PLEISTOCENE

Macrofossils of spruce, including *P. abies*, are known from several European sites originating in the Neogene and its boundary with the Pleistocene, as well as in sediments of the oldest Interglacial known as the Tegelenian. In southern Poland, in the Pliocene site of Krościenko as well as the sites included in the Pliocene and early Pleistocene in Mizerna, spruce cones and needles have been found and identified as *Picea excelsa* (LAM) LINK *foss.* (ŚRODOŃ 1967b).

Throughout central Europe, spruce regularly occurred in all interglacial periods as well as the warmer interstadials during the Quaternary (ZAGWIJN 1992). The geographic extent of spruce was then much wider than in the Holocene and included areas on the southern shores of the Baltic, North Sea, and the British Isles, including Ireland. The presence and abundance of spruce has been associated with specific positions in the interglacial stratigraphic successions (JAŃCZYK-KOPIKOWA 1991). The dominance of spruce in pollen diagrams during successive interglacials was associated mainly with their waning phases that presumably coincided with a colder and wetter climate.

During the Mazovian Glacial of the middle Pleistocene, Norway spruce was abundant and dispersed throughout Europe (ŚRODOŃ 1967b). During the interglacial period, spruce has been noted in several woodland phases and in two of them was comparatively more abundant than other woodland pollen flora. Analyses of sediments of this interglacial from Podlasie (KRUPIŃSKI 1995) show a widespread occurrence of spruce. The decline in relative abundance of spruce was associated with an increase in the proportion of fir (genus *Abies*). The second period of a marked abundance of spruce was associated with the waning of the Mazovian Interglacial.

During the Eemian Interglacial, a peak in Norway spruce pollen abundance has been noted (E-6 pollen level). In order to emphasize the contribution of this species to vegetation patterns noted in the interglacial succession, this level (r. paz) has been termed *Picea-Abies-Alnus* (MAMAKOWA 1989) and also *Picea-Abies* (TOBOLSKI 1991). Relatively short periods of geographic expansion of spruce during the interglacials were interspersed between long periods of glaciation during which the species likely found protection in mountain refugia in southern Europe. There, under conditions of oscillating and harsh climates and thousands of years of isolation, new variants arose and remain within present-day populations of this species.

In the Brörup Interstadial of the last glaciation, approximately 60,000 years ago, spruce last occupied a geographic area larger than its contemporary range. The highest values of relative abundance in the pollen record occurred in this period, often exceeding 70%, in the Alps and approximately 50% in the Central Massif. Consequently, *P. abies* forests likely dominated the Alps and its northern slopes. A large proportion of Norway spruce pollen, up to 40%, is also found on the coast of the North Sea throughout this period. Near the northwestern shore of the Baltic Sea in Skania (southern Sweden), the proportion of spruce pollen exceeds 20% (TOBOLSKI 1991). At the height of the Vistulian Glacial, Norway spruce was found in refugia scattered along the edges of the Periglacial zone. During this period the range limits were likely closer to the contemporary range limits than in the earlier glacial periods. It is from these refugia that Norway spruce began its migratory expansion as early as the Late Glacial period.

Both Serbian and Siberian spruce played a minor role in the vegetation of the Pleistocene of central Europe. Fossil finds of Serbian spruce were described on the basis of fossil cones, needles, as well as pollen and given the name *Picea omoricoides* (WEBER 1898). WEBER (1898) postulated that these macrofossils belong to an extinct and previously widespread species, and that contemporary Serbian spruce is a relic form of this fossil taxon. Pollen grains identified as *P. omoricoides* are noted most often in the waning sectors of interglacial profiles. These are almost exclusively found along with the pollen of Norway spruce and not only in the sediments of the Tegelenian and Mazovian Interglacial, but also in earlier sediments from the Eemian Interglacial and the Brörup Interstadial of the last glaciation. The range of *P.*

omoricoides expanded extensively in the early phases of the Vistulian Glacial, reaching the Frisian coast and the Jutland Peninsula to the west, whereas in the south, it remained a small component of the vegetation in the foothills of the Alps. Its distribution likely mirrored the unique climate of the early Vistulian period in northwestern Europe, marked by a strong continental climate (TOBOLSKI 1991).

Siberian spruce (*P. abies* ssp. *obovata*) presently occupies vast areas of eastern Europe and Asia. During the Pleistocene its range extended further west, as shown in the occurrence of fossil spruce cones from sites of the Eemian Interglacial in the vicinity of Moscow, Grodno, and northeastern Poland. ŚRODOŃ (1967b) presents evidence phase of a migration of Siberian spruce into present-day Poland during at the waning of the central Polish Glaciation (*l.c.* p. 10). Macrofossil finds demonstrate that near the end of the central Polish Glaciation, a taiga type of forest encroached into central Europe in which Siberian spruce played an important role. It cannot be ruled out that a past westward expansion of Pleistocene Siberian spruce may have played a significant role in the origins of contemporary Norway spruce (ŚRODOŃ 1977).

1.3. HISTORICAL BIOGEOGRAPHY IN CENTRAL EUROPE

Norway spruce migrated into the geographic region of present-day Poland from both a primary Carpathian refugium as well as from a northwestern source. ŚRODOŃ (1967b) describes the proliferation of spruce in Poland in subsequent periods of the Late Glacial and Holocene (Fig. 1.1). LANG (1994) in his monograph on the history of vegetation in Quaternary Europe also depicts the incursion of spruce into present-day Poland. In the Late Glacial the migration and expansion of spruce occurred from several refugia. LANG (1994) identifies three glacial refugia. A major refugium was located in northeastern Europe and included regions of contemporary north-central Russia, a second was located in the Carpathians and another in the northeastern Alps.

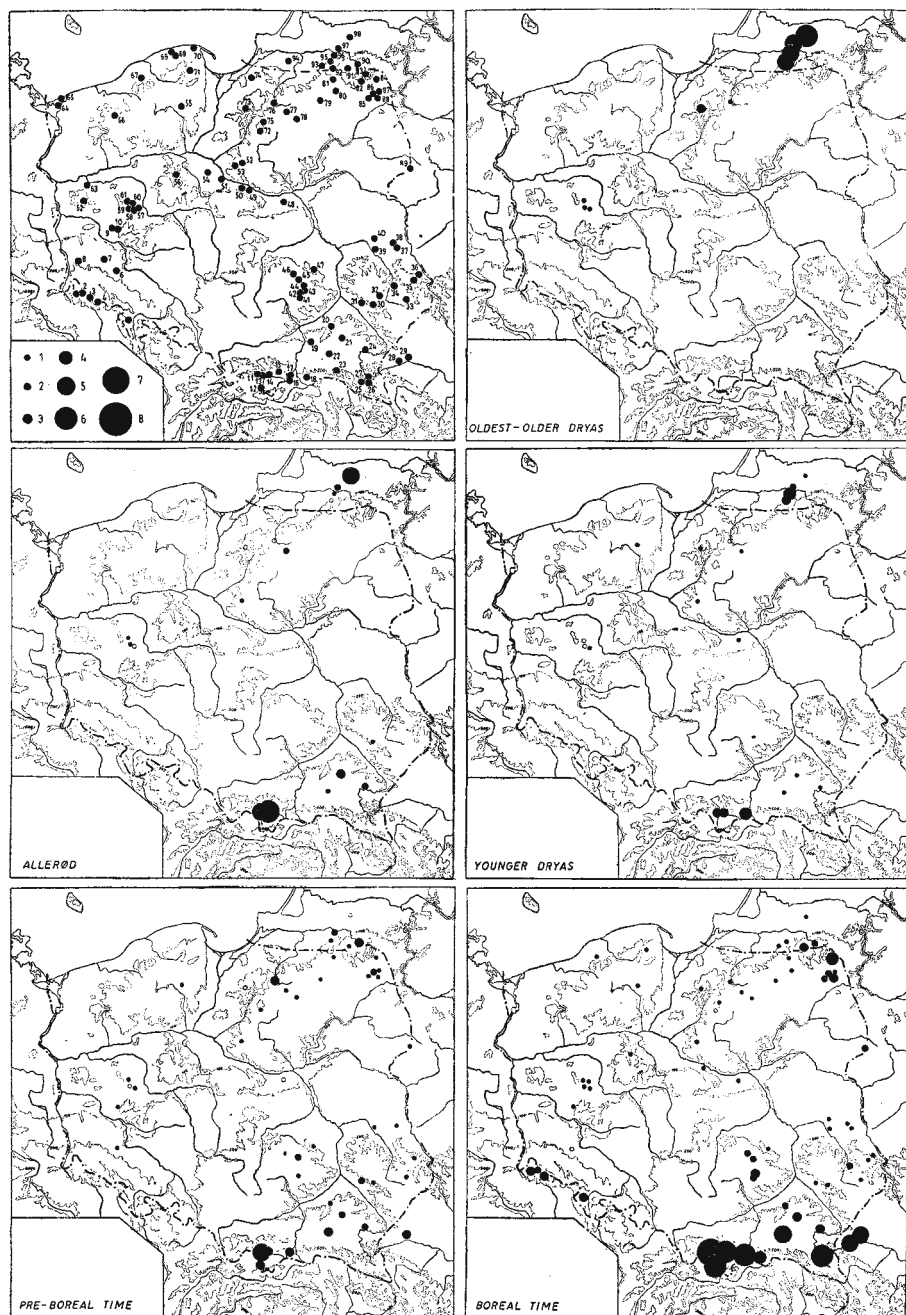
The northern portion of the contemporary range of spruce was likely formed through a northern migration route, which quite early divided into two pathways. One path traversed northern Scandinavia where range expansion occurred somewhat more slowly. This is evidenced by the relatively late proliferation of spruce in the southern part of Norway, at about 500 BC. About 1100 years later (600 A.D.) the range limit of spruce had extended to only approximately one third of its contemporary area (HAFSTEN 1985). In contrast, the wave of spruce migration emanating from the southern migration route arrived in northeastern Poland much earlier than in Scandinavia. The migration of spruce from its Carpathian refugium was apparently much faster, resulting in the presence of Norway spruce, in some places in considerable abundance, in the forests of southern Poland as early as the first half of the Holocene (Fig. 1.1, see also Chapter 5).

Contrasting pathways and rates of migration of spruce that shaped both the northern European and the central-southeastern portions of the species range are illustrated in LANG'S (1994) monograph. In the northern portion, 5000 years ago spruce occupied 51% of its present-day range, and 10,000 years ago, only 22%. The central-southeastern European range of Norway spruce was already 80% occupied 5000 years ago, whereas 10,000 years ago, it occupied 26% of the present day geographic range. Thus, the expansion in geographic range of the central-southeastern portion occurred quite differently from the pattern observed in the north.

Historically Norway spruce expanded into present-day Poland from the Carpathian and northeastern refugia at different times. Spruce initially migrated into Poland from the south. There it occupied numerous sites as early as the late Glacial and during the transition to the Holocene, including the areas of the present-day Carpathian disjunction in the range of spruce (ŚRODOŃ 1990). The migration of spruce from the northeast resulted in the earliest appearance of spruce in Poland near the present-day Suwałki region. There it remained throughout the latter part of the Boreal period of vegetation history. The meeting of the two expanding ranges occurred probably near the end of the Atlantic period.

Without settling either the time or the place where the northern (lowland) range met the southern (mountain) range, the currently accepted view is that there was a continuous expansion of the range of spruce throughout Poland. Range expansion also occurred in the northern Carpathians, where in the Lower Beskid region, an earlier Carpathian disjunction was identified (compare ŚRODOŃ 1967a, b, 1990). The dominance of spruce during the interglacial phases when the climate was cold and humid suggests that the present-day range of spruce, so markedly different from its geographic range during the interglacials, reflects a continuing process of migration. This supposition is reasonable when one considers that the Holocene is also an interglacial period. The climatic conditions are likely close to those prevalent during the past waning Eemian Interglacial and qualitatively support the notion of an expanding range of spruce. In the glacial-interglacial cycle, spruce belongs to the terminocratic group. In the Eemian cycle, spruce attained its dominance during the telocratic phase (BIRKS 1986). However, the last contemporary glacial-interglacial cycle has been marked from as early as the Neolithic by the increasing influence of human activities (TOBOLSKI 1976). Presently, our ability to track migrations is hampered by historical and contemporary changes brought about by human activities that affect the composition and structure of forests and land-use change.

On the basis of the paleorecord of spruce, its presence in the Late Carpathian Glacial is certain. However, spruce occupied the Sudety Mts much later. According to RYBNÍČKOVÁ and RYBNÍČEK (1988) spruce appeared there at relative frequencies of 10 to 25% only 7000 years ago. However, forested areas between the two large areas of the species' contemporary geo-



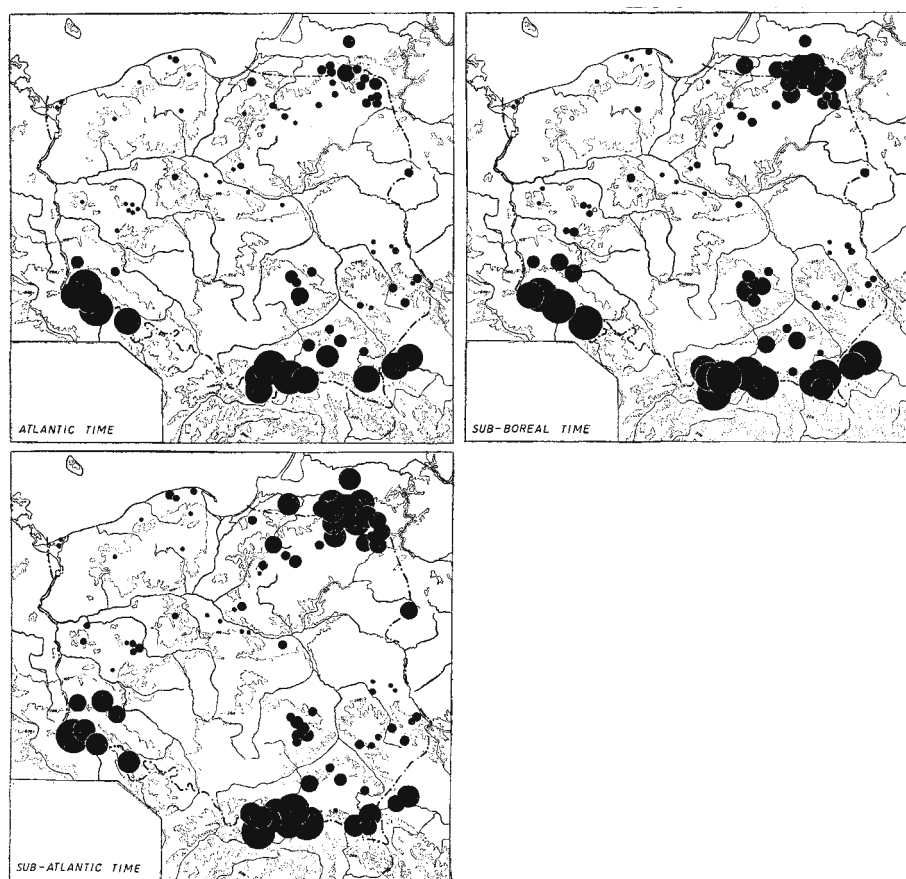


Figure 1.1. Distribution of spruce in the Late Glacial and Holocene periods. Locations numbers are shown on the first panel (ŚRODON, 1967b)

Average values of the proportion of spruce pollen shown by the symbols on the first panel:

1=0.01–0.5%, 2=0.6–1.0%, 3=1.1–3.0%, 4=3.1–5.0%, 5=5.1–10.0%, 6=10.1–20.0%,
7=20.1–30.0%, 8=30.1–60.0%

graphic distribution show a relatively small proportion of spruce during the Holocene. At the same time, it is likely that the low frequency of occurrence of spruce on the central Poland lowlands was the result of non-favorable edaphic conditions in addition to the effects of humans. This migration occurred at a time when conditions were likely suboptimal for the proliferation of spruce. The postglacial expansion of spruce onto the lowlands of central Europe, the formation migration routes in areas subjected to human disturbances, beginning with the waning Mesolithic, remain exciting research challenges in the historical biogeography of Norway spruce.

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2. MORPHOLOGY

TADEUSZ PRZYBYLSKI

The morphology of Norway spruce is linked to its systematics, genetics, and ecology. The species is highly variable and polymorphic, in large part owing to its widespread natural range that extends from the northern parts of Scandinavia and Siberia to southern Europe (see Chapter 4). This natural phenotypic variation is exhibited in crown form, twigs, cones, and bark and depends on environmental and genetic factors.

2.1. HABIT

Norway spruce exhibits an excurrent crown form with marked apical dominance, visible even in individuals of advanced age (Fig. 2.1). The lateral branches typically droop. The maximum height may reach 62 m and maximum diameter at breast height may reach 2 m. The beautiful conical crown shape renders the species a choice Christmas tree throughout Europe. Studies of growth habit and morphology constitute a large body of literature from the early work of SYLVEN (1909) and others from Europe, Asia, and North America, including descriptions of a number of varieties. Variant crown forms are often found in montane populations. Often the crowns appear narrow and cover the entire length of the trunk (Fig. 2.2). Trees possessing narrow crowns in northern and high elevation sites are presumably more efficient in intercepting sunlight at low sun angles for the production of biomass (PULKKINEN and PÖYKKÖ 1990).

2.2 NEEDLES

Norway spruce develops two types of needles. Eight or nine cotyledons are present in germinating seedlings in the first year. True needles are produced throughout the life of the tree and are borne singly and spirally arranged on the twig. The needles are 25 to 35 mm long, about 1 mm wide, and rhomboid in cross section. Needle lifespan averages 4 years in lowland sites and often exceed 5 years or more in high-elevation and high-latitude sites (KAWECKA

1977; WACHTER 1985). The needles are attached to the shoot on woody, peglike projections (sterigmata) that persist on the twig after needle fall. BURGER (1953) noted that a 152 year-old individual had an estimated 25 million needles with total surface area of 1,410 m² and mass of 290 kg. Growing in stands, Norway spruce exhibits a relatively high leaf area index (ratio of leaf area to ground area), estimated at 10.5 in one study (BOLSTAD and GOWER 1990).

2.3. BUDS

The buds of Norway spruce are cylindrical, acute at the top, and covered by red-brown overlapping resinous bud scales. The buds range in length from 2 cm on the terminal leader to 1 mm on the lateral shoots growing in the shade. The arrangement of lateral buds on current-year shoots is irregular and appears as a pseudo-circular array near the top. The differentiation of flower buds (male and female) on the south-facing portion of the tree crown is minimal compared to the north-facing portions (BARABIN 1967).

2.4. SHOOTS

The surfaces of one-year-old twigs have well-developed woody needle bases that persist for many years after needle abscission. Early in development they are reddish-brown and later turn gray. The color of the shoot depends upon the provenance. Lowland populations retain their brownish bark for long periods, whereas individuals from higher altitudes and from the far north exhibit gray-colored bark.

Although the twigs are generally hairless, young shoots of northern provenances of the subspecies *Picea obovata* develop single- or multi-cellular hairs on the epidermis. These hairs typically persist for one year, but may be found on shoots up to three-years old. This trait appears to be largely genetic and has been used to distinguish subspecies and enabled the reconstruction of migration pathways of this species after the last ice age (LINDQUIST 1948).

2.5. MALE CONES

Norway spruce is monocious; both male (staminate) and female (ovulate) cones are borne on reproductively mature individuals. The microsporangiate strobili are formed of inflorescences in clusters of 10–20 and are approximately 2.5 cm in length. The strobili are located on the lower portion of one-year-old shoots between the needles. Their color is highly variable, but mostly yellow to red. They are developed in the middle and lower portions of the tree crown. Each inflorescence contains about ten stamens, each bearing two pollen sacs. Under favorable dry and warm atmospheric conditions, the sacs open and release the pollen grains. The pollen grains have two air sacs



Figure 2.1. Norway spruce habit and form (photo A. BORATYŃSKI)

A, C – growth habit of trees at the upper mountain forest belt; B – dense ramification of the crown; D – trunk of an old tree with typical callus swellings at the branch bases

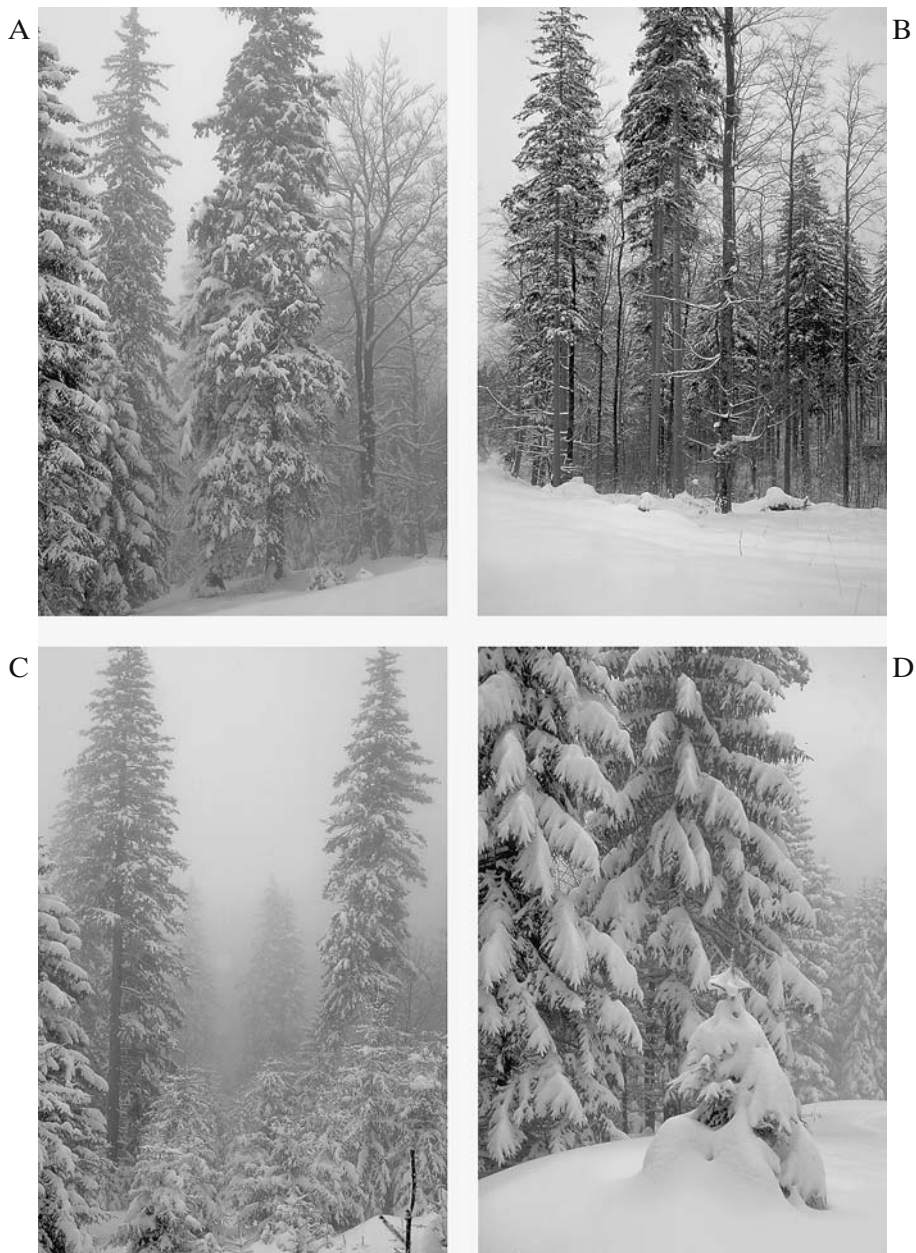


Figure 2.2. Norway spruce trees in the lower montane belt (photo A. BORATYŃSKI)

A–B a single old tree up to 40 m tall in a beech woodland; C–D – old and young Norway spruce

about 150 microns in length (DYAKOWSKA 1959). Pollen differs among provenances and individual trees (ANDERSSON 1954, 1965; DYAKOWSKA 1964). In Bulgaria, PLOSHCHAKOVA-BALEVSKA (1970) noted that flowers and pollen developed one month earlier in the '*erythrocarpa*' than '*chlorocarpa*' varieties. TABOR (1990) observed both male and female strobili in one inflorescence.

2.6. FEMALE CONES

The megasporangiate strobili, 3 to 5 cm in length, are formed as reddish conelets in upper portions of the crown. The cones have two types of bracts, a seed-bearing scale and auxiliary bracts, 3 to 4 mm in length, that are formed at the base of the scales and not visible in the closed cone. Each fertile cone scale bears two embryos, developing into two winged seeds, 4–5 mm long, triangular in shape, and brown to black in color. In mature cones, the scales become lignified and woody. The shape of the cone scales is highly variable among provenances, ranging from a more rounded shape in eastern provenances, resembling the subspecies *obovata*, to an elongated form similar to '*acuminata*' in the western portions of the species range. A number of studies have analyzed cone trait variation in relationship to the geographic distribution of the species (see also Chapter 5). Seed mass varies between 2.68 and 10.0 g per 1000 (ANDERSSON 1965). Seeds of southern provenances tend to have a slightly higher mass than northern and eastern sources (TYSZKIEWICZ 1934b, DUTKIEWICZ 1968).

2.7. BARK

The bark of Norway spruce is relatively thin and scaly, but increases in thickness with tree age. Bark color ranges from gray in northern and montane provenances to brown in lowland and western provenances. Bark thickness also depends on the growth environment of the tree, increasing in thickness on sites with higher insolation (EREMIN 1977).

2.8. ROOT SYSTEM

The root system of Norway spruce lacks a taproot, develops laterally, and is relatively shallow, averaging 40 cm in depth. Most roots are concentrated in the upper 10 cm soil depth in pure stands, but may extend to 35 cm depth in mixed species stands. Consequently, Norway spruce is sensitive to soil moisture conditions and generally occurs on cool, moist sites.

The total length of roots per m² ground area was estimated at approximately 100 m at a stand age of 10 years, and 45 m in the age of 100–110 years (KALELA 1951; ŠIKA 1966). In those studies, 81% of the roots had diameters less than 1 mm and only 2.7% above 2 mm. The biomass of fine roots (less than 1 mm diam-

eter) was estimated at 7,000 to 8,000 kg/ha with a total length of 11 km/ha. The surface area to mass ratio of the roots was estimated at 28–29 m²/kg.

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3. TAXONOMY

WŁADYSŁAW BUGAŁA

3.1. TAXONOMY OF THE GENUS *PICEA*

The genus spruce (*Picea* A. DIETR.) belongs to the family *Pinaceae*, which includes other key taxa of conifers such as pine, fir, and larch. The *Pinaceae* family is divided into the following three subfamilies: *Pinoideae*, which includes the genus *Pinus* only; *Laricoideae*, with the genera *Larix*, *Cedrus*, and *Pseudolarix*; and *Abietoideae*, including the genera *Abies*, *Picea*, *Pseudotsuga*, *Tsuga*, and others. The absence of dwarf shoots is characteristic of the subfamily *Abietoideae* in which the needles are arranged only on long shoots. In contrast, in the subfamily *Pinoideae*, needles occur only on dwarf shoots except for the juvenile primary needles of the seedlings. The subfamily *Laricoideae* exhibits needles on both long and dwarf shoots.

CARL LINNÉ (1753) included all taxa of the *Pinaceae* family, the pines, firs, and spruces in the same genus *Pinus*. He named the two spruce species known at the middle of XVIII century, Norway spruce – *Pinus abies* L. and Caucasian spruce – *Pinus orientalis* L. The Linnean name “*abies*” is valid as the oldest one, according to International Code of Botanical Nomenclature (GREUTER 1994). Consequently, the accepted name of Norway spruce is *Picea abies* (L.) KARST., replacing a long-used name *P. excelsa* LINK (1841, after VOGELLEHNER 1977). The latter binomial was derived from *Pinus excelsa* LAMARC (1778, after VOGELLEHNER 1977). The name *Picea abies* was described and used first by KARSTEN in 1881 (VOGELLEHNER 1977). The genus *Picea* was described and separated from the Linnean genus *Pinus* by A. DIETRICH in 1824, who described Norway spruce under the name *Picea rubra* A. DIETR. (VOGELLEHNER 1977).

Of the several dozen species that belong to the genus *Picea*, many are important forest trees. The exact number of species has been difficult to ascertain, owing to the fact that the spruces are highly variable and frequently form intermediate taxa, possibly of hybrid origin in areas where two or more species occur together. A very high level of intraspecific variation is also characteristic of *Picea abies*.

LINNÉ (1753) recognized and described only two species of spruce. The number of recognized species in the genus has grown with the time, as a result of new discoveries, especially in North America and eastern Asia. Many new species were first described near the end of the 19th and beginning of the 20th centuries. The numbers of species noted in the seminal taxonomic studies of the conifers in the 20th century vary between 24 and 49 (for details see: MAYR 1906; BEISSNER 1909; FITSCHEN 1930; LACASSAGNE 1934; GAUSSEN 1966; HARRISON and DALLIMORE 1966; BOBROV 1970; KRÜSSMANN 1972; SCHMIDT-VOGT 1974; PRAVDIN 1975; REHDER 1977; VOGELLEHNER 1977; ALDEN 1987; FARJON 1990; TAYLOR 1993; FARJON 2001; WENG and JACKSON 2000).

The most recent taxonomic monographs of *Picea* divide the genus into three sections (e.g. GAUSSEN 1966; BOBROV 1970; REHDER 1977; VOGELLEHNER 1977; ALDEN 1987). Alternatively, a more recent classification divides the genus into two sections of two subsections each (FARJON 1990).

Section 1. Picea (=Eupicea WILLK.)

The needles are regularly quadricular in cross-section, frequently almost rhomboidal. The stomata are dispersed regularly along the entire four surfaces of the needle. The cone scales are hard, lignified, and more or less rounded on top. To this section belong *Picea abies* s. l. (including *P. obovata*), *P. orientalis*, many Asiatic species, as for example, *P. asperata* MAST., *P. neoveitchi* MAST., *P. wilsonii* MAST., *P. polita* CARR., *P. maximowiczii* REG., *P. bicolor* MAYR, *P. glehnii* MAST., and *P. koyamai* SHIR. and several North American spruces, such as *P. glauca* VOSS, *P. mariana* BRITT., and *P. rubens* SARG.

Section 2. Casicta MAYR

The needles are irregularly quadricular in cross-section or flattened with stomata present on all four surfaces or only on the lower surface in taxa exhibiting a flattened needle morphology. The cone scales are slender, flexible, with undulate margins, and loosely arranged. To this section belong the species present in North America, such as *Picea sitchensis* CARR., *P. pungens* ENGELM. and *P. engelmannii* ENGELM., and from North-East Asia, the species *P. jezoensis* CARR. and *P. likiangensis* E. PRITZ.

Section 3. Omorika WILLK.

The needles are flattened, dark green on the upper surface, with white or bluish-white rows of stomata on the lower side. The cone scales are closely adherent, thick, inflexible, and rounded. The *Picea omorika* PURK. in Europe and *P. breweriana* WATS. in North America and a few other species from eastern and central Asia belong to this section.

3.2. INTRASPECIFIC VARIATION

Norway spruce exhibits considerable intraspecific variation. The number of described variants in morphology and physiology is the largest among the spruce species. There are about 140 known varieties and forms (cultivars) in addition to described wild types, which differ in cone dimensions or cone scale shape.

3.2.1. Norway spruce and Siberian spruce

One of the most important issues in *Picea abies* taxonomy is the relationship between Norway spruce and Siberian spruce. In 1833 LEDEBOUR described Siberian spruce as a separate species, *P. obovata* LEDEB. This classification is disputed, and it is unresolved whether *P. obovata* should be considered a separate species or only an intraspecific taxon within *P. abies sensu lato*. The main morphological characteristic distinguishing *Picea obovata* from *P. abies sensu stricto* is its comparatively small cone size (4–8 cm in length) and broad, rounded cone scales (Fig. 3.1). The cones of the typical *P. abies* are 10–15 cm long and are characterized by scales that are acute, denticulate, and somewhat flabellate and generally variable. For this reason many taxonomists consider *P. obovata* a separate species (FITSCHEN 1930; LACASSGNE 1934; GAUSSEN 1966; HARRISON and DALLIMORE 1966; KRÜSSMANN 1972; REHDER 1977; FARJON 2001). Russian botanists also treated *P. obovata* as a separate species (SUKATCHEV 1928; KOMAROV 1934; VASILEV and UKHANOV 1949; BOBROV 1970; PRAVDIN 1975). Comparing spruce cones from the Altay Mts in Asia and from the mountains of Europe, TEPLOUKHOV (1868) suggested that *P. obovata* should be considered a geographic variant of *P. abies*. Other taxonomists concur, and Siberian spruce is more recently treated as a subspecies or geographic variety of *P. abies* (L.) KARST. (SCHMUCKER 1942; LINDQUIST 1948; HULTÉN 1949; FRANCO AMARAL 1964; VOGELLEHNER 1977; STASZKIEWICZ 1977). In our taxonomic treatment in this volume, we consider Norway spruce as a species comprised of both *P. abies* and *P. obovata sensu stricto*. The latter taxon is treated as a subspecies of *P. abies* (after VOGELLEHNER 1977 and FARJON 1990):

Norway spruce – *Picea abies* (L.) KARST. subsp. *abies*

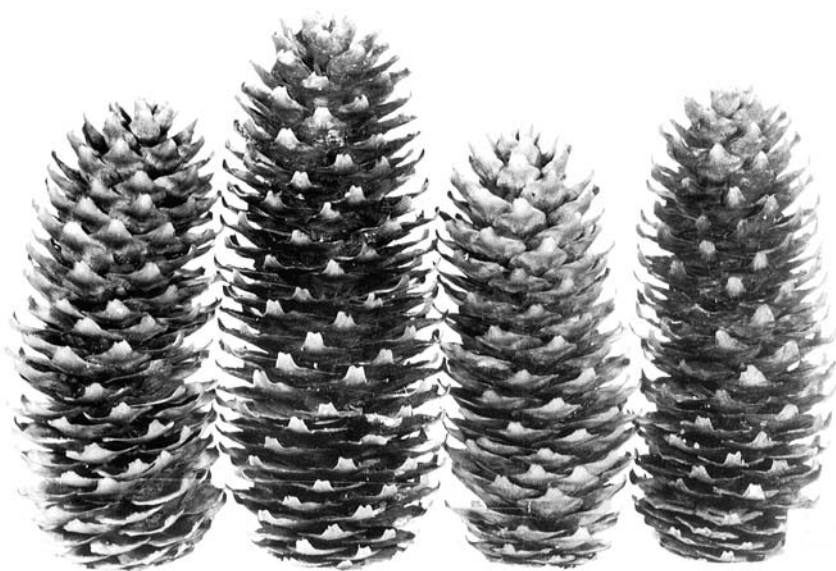
Synonyms: *Pinus abies* L. (1753), *Abies picea* MILL. (1768), *Pinus picea* DU ROI (1771), *Pinus excelsa* LAM. (1778), *Picea rubra* A. DIETR. (1824), *Picea excelsa* LINK (1841), *Picea alpestris* BRUEGG ex STEIN (1887)

Siberian spruce – *Picea abies* (L.) KARST. subsp. *obovata* (LDB.) HULTÉN

Synonyms: *Picea obovata* LDB. (1833), *P. abies* var. *obovata* (LDB.) FELLM. (1869), *Picea excelsa* subsp. *obovata* (LDB.) ASCHERS. et GRAEBNER (1913), *Picea abies* var. *arctica* LINDQ. (1948).

An additional problem concerns the occurrence of Norway spruce specimens with the cones of the *Picea obovata* type in the mountains of central Eu-

A



B

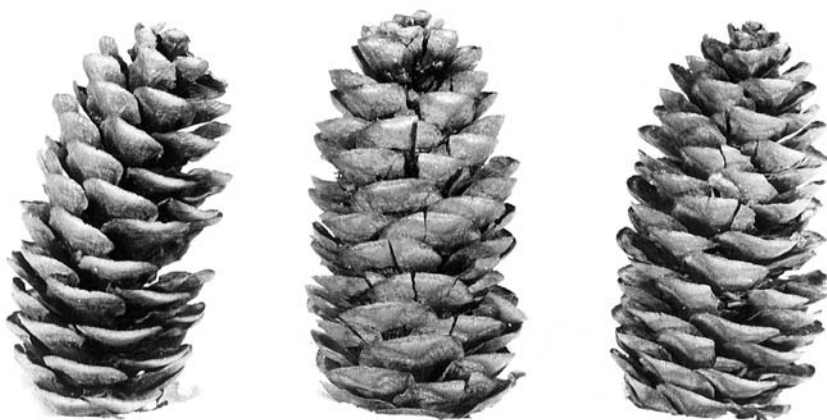


Figure 3.1. Cones of *Picea abies* (photo E. SZUBERT)

A – subsp. *abies*; B – subsp. *obovata*

rope (the Alps, Sudety, Carpathians). One explanation is that these cone characteristics are an adaptation to the high mountain climate conditions (VOGELLEHNER 1977). Another explanation is that populations growing at high altitudes in the mountains of Central Europe are relicts of past migrations of *P. obovata* (BOBROV 1978). During the Holocene this variety (*P. abies* var. *alpestris* or, as other authors prefer, *P. obovata* var. *alpestris*) may have

been replaced by spruce taxa from other glacial refugia with isolated populations surviving only in the highest altitudes, where gene flow took place between populations of European and Siberian origin (BOBROV 1978). The process of introgression is considered one reason for the large degree of variation of the species in Europe.

3.2.2. *Natural varieties of Norway spruce*

3.2.2.1. *Cone variation*

The great variation in shape and form of cones, and especially of cone scales, underpins the description of a dozen or so varieties and forms (SUKATCHEV 1923; PACZOSKI 1925; TYSZKIEWICZ 1934a; MEZERA 1939; LINDQUIST 1948; KORZENIEWSKI 1953; JURKEVICH and PARFENOV 1967; HOLUBČÍK 1969a, b; BOBROV 1970; VOGELLEHNER 1977). The following three taxa are accepted in recent taxonomical reviews of the species.

Picea abies subsp. *abies* var. *picea* (=var. *europaea* TEPL.)

Cones are large, 10–18 cm long. Cone scales range from obovate to rhomboid in shape, flat to somewhat convex, margins lack serration, sometimes with two indentations and slightly flabellate on the top. Scales overlap each other by 2/3 – 3/4 in the cone. This variety predominates in the western Carpathians and Sudety Mts with a frequency of 80–90% (STASZKIEWICZ 1977).

Picea abies subsp. *abies* var. *acuminata* (BECK) JURK. et PARF.

The cones are as large as in the previous variety, 10–18 cm long. The cone scales are slender and elongated (longer than wide), flabellate on the margins, and flexible on the somewhat ligulate tops, mostly adherent, but sometimes strongly reflexed (f. *deflexa* TYSZK.). The scales overlap to about 1/2 below each other in the cone. The variety *acuminata* occurs in populations from the eastern Carpathians and in southern part of the northeastern portion of the species range (JURKIEWICZ and PARFIENOW 1966).

Picea abies var. *alpestris* (BRUEGG.) DOMIN

The cones are smaller, 6–12 cm long. The cone scales are deltoidal or spatulate, erect and wider than long, with rounded tops lacking flabellation and indentation or only slightly serrulate. The scales overlap by more than 3/4 inside each other. The cones of this variety are similar to those of *P. abies* subsp. *obovata*. Individuals with this cone form are present in the highest locales of the mountains of central Europe in the Alps, Sudety, and Carpathians.

Within the above-mentioned varieties a dozen or so forms have been described on the basis of detailed characteristics of the cone scales (MEZERA 1939; JURKIEWICZ and PARFIENOW 1966; HOLUBČÍK 1969b; 1971, 1972). In general, these traits are highly variable and likely instable as a result of gene flow among varieties, and are not useful traits in taxonomic studies.

3.2.2.2. *Macrostrobili variation*

During pollen reception, the female strobili can have various colors. On this basis at least three forms can be distinguished:

- f. *chlorocarpa* PURK., with green strobili
- f. *dichroa* DOMIN, with reddish-green strobili
- f. *erythrocarpa* PURK., with red strobili

3.2.3. *Cultivars*

The great variability of Norway spruce in the wild and its propensity to form morphological variants has resulted in its extensive use in ornamental plantings. To date, about 150 such varieties have been described. Many were found in the wild, such as var. *virgata* or *columnaris*. Numerous dwarf varieties are often fixed teratological forms arising from witches' brooms. The cultivars of *Picea abies* subsp. *abies* are generally divided into three groups: tree-like forms, dwarf forms, and varicolored. Some differ from the typical Norway spruce in their ecological and physiological characteristics. For example, the dwarf forms are drought resistant and grow well on sandy soils. Below are mentioned some of the most commonly planted ornamental forms.

3.2.3.1. *Habit cultivars*

'Columnaris' – the columnar variety. A tree to 20 m in height, characterized by a narrow, dense crown, with short, dense, horizontally arranged branches. Under this name many various varieties can be found in parks and nurseries, originating from various mother plants taken from the forest.

'Cupressina' – the cypress variety. This variety is a tree-like form, attaining a height of about 10 m with a very regular, conical, and dense crown. The branches are upright and arranged on the trunk at an acute angle.

'Inversa' – the inversed variety. This is a slow-growing tree with an inclined trunk and highly elongated, pendent branches. Quite frequently it is procumbent. The growth habit is extremely variable, depending on the inclination of the trunk.

'Viminalis' – the sarmentous variety. This variety is frequent in the wild. The trees exhibit a typical excurrent crown form, attaining more than 20 m in height, and are characterizing by strong, widespread main branches, but flattened and pendulous secondary branches.

'Virgata' – the snake-like variety. Most often this variety is a small tree and rarely occurs as a shrub. Its loose crown is comprised of long (not ramified) snake-like, pendulous shoots. The needles are thick, rigid, and prickly, up to 3 cm long. It was isolated as a wild variety. Individuals occasionally produce cones and viable seed that may produce offspring comprised both normal and more or less 'virgate' individuals.

3.2.3.2. Dwarf varieties

'Barryi' – variety of BARRY. A small, slow-growing tree up to 2 m in height with a broad, conical or irregular crown. The apical shoots are thick and strongly sulcate. The branches are short and densely arranged on the trunk. Needles are short and obtuse.

'Clanbrassiliana' – variety of CLANBRASSIL. Discovered in Ireland in 1790, this is one of the oldest dwarf varieties. It is a low, slow-growing shrub, rarely taller than 1 m, with a dense, slightly flattened crown. It has short (to 1 cm long) needles that are densely arranged on the twig. Numerous dwarf forms are similar and known under the names of 'Pyramidalis Compacta', 'Pygmea' or 'Nana', for example.

'Merkii' – the MERK'S variety (Fig. 3.2). This variety is a stout shrub to about 3–4 m high with a broad, conical, and somewhat irregular crown. It forms numerous main, upright shoots, forming its characteristic crown shape in older individuals. The needles are thin and prickly and markedly shorter on the young shoots than on the older shoots.

'Nidiformis' – the nest form. This is a slow-growing shrub attaining a height of 1 m and characterized by a broad, dense, and flattened crown with a characteristic nest-like depression in the center. The branches form distinct annual whorls. This is a frequently planted variety.



Figure 3.2. *Picea abies* 'Merkii' in the Kórnik Arboretum, Poland (photo E. SZUBERT)

‘Procumbens’ – the procumbent variety. This variety resembles the previous variety, but the crown is broader and more flattened. The lowest branches are suspended above the ground. The needles are arranged in a single plane and are of varying length with the longest needles in the central portion of the shoot.

‘Pygmaea’ – the dwarf variety. A shrub up to 80 cm tall, very slow-growing and densely branched, broadly conical or spherical. The shoots are lightly colored. The dark-green needles are 8–10 mm long. This form is frequently planted.

3.2.3.3. *Color varieties*

‘Finedonensis’ – the yellow-needle variety. This variety is a tree of normal growth habit, but slower growing. The needles on the new shoots in the spring initially appear light yellow in color, but become naturally green within two to three weeks. This is a highly decorative, ornamental variety.

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4. GEOGRAPHIC DISTRIBUTION

KRYSTYNA BORATYŃSKA

4.1. DISTRIBUTION OF THE GENUS

The geographic range of the genus *Picea* A. DIETR. is restricted to the northern hemisphere. Taxa of this genus occur between 71°N latitude in North America and Eurasia to 32°N in North America and 23°N in Southeast Asia (Fig. 4.1). The range is divided into two parts and is considered a classical example of a euroasiatic-North American intercontinental disjunction. Large portions of the range of the genus are occupied by *P. obovata* LEDEB.¹ in Asia, *P. abies* (L.) KARST. in Europe, and *P. glauca* (MOENCH) VOSS and *P. mariana* (MILL.) BRITT. in North America. As a rule, the northern species cover extensive areas and form forests, whereas the southern taxa generally have restricted distributions in the mountains and many are relicts.

Nine spruce species occur in North America (Table 1). *Picea glauca* and *P. mariana* are the most economically important species. These species form forests throughout much of Canada and the northernmost regions of the United States. In the northeastern United State, *Picea rubens* SARG. is also an important spruce species. It grows in the Appalachian Mts up to an altitude of about 2000 m. *P. sitchensis* (BONG.) CARR. occurs in western North America and attains an altitude of 1000 m, while *P. engelmannii* (PARRY) ENGELM. and *P. pungens* ENGELM. occur at altitudes of up to of 3700 m in the Rocky Mts Taxa exhibiting limited ranges in the North America are *P. breweriana* S. WATS in northern California, *P. mexicana* MARTINEZ and *P. chihuahuana* MARTINEZ in northern Mexico. The latter two species mark the southern limit of the range of *Picea* in Central America and attain an altitude of 2800 m in the Sierra Madre (HARLOW and HARRAR 1950; FOWELLS 1965; LITTLE 1971; HARTMUT 1976; WENG and JACKSON 2000).

In Europe the geographic range of the genus is largely comprised of the species *Picea abies*. The remaining European species are *P. obovata* in the northeastern part of the continent (SOKOLOV *et al.* 1977) and a relict *P. omorica*

1 Nomenclature and taxon names after FARJON (1990, 2001).

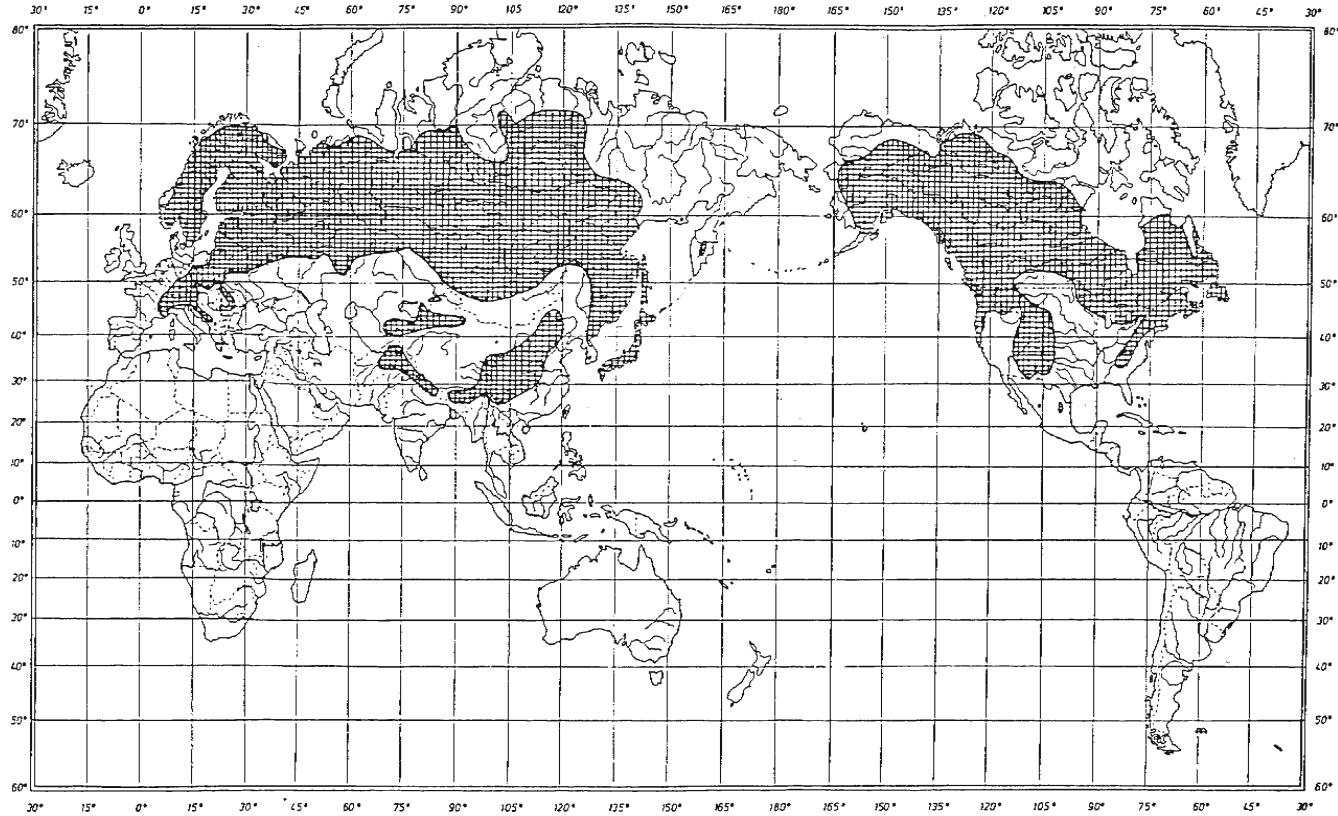


Figure 4.1. Native geographic range of the genus *Picea* (compiled from LITTLE 1971; JALAS and SUOMINEN 1973; HORIKAWA 1976; SOKOLOV et al. 1977; SCHMIDT-VOGT 1977; BROWICZ 1982)

(PANČIĆ) PURK. in the Drin River valley of the Balkan Peninsula, where it grows at altitudes between 600–1400 m (JOSIFOVIĆ 1970, DÉBAZAC 1977).

Picea obovata has the widest distribution in Asia, extending throughout Siberia (SOKOLOV *et al.* 1977). This species occurs at latitudes up to 68–70°N with a northernmost limit in the Khatanga River valley at 72°15'N. It occurs in several taiga forest types together with species of pine, larch, and fir. It co-occurs with *P. jezoensis* (SIEB et ZUCC.) CARRIÈRE in northeastern Asia. Several other species of spruce form forests in the far northeastern regions of Asia, including *P. glehnii* (FR. SCHMIDT) MASTERS, *P. polita* (SIEB et ZUCC.) CARRIÈRE, *P. alcoquiana* (VEITCH ex LINDL.) CARRIÈRE (= *P. bicolor*), and *P. koraiensis* NAKAI (WANG 1961; KURATA 1964; KURATA and HAMAYA 1971; 1974; OHWI 1965; HORIKAWA 1976). The southernmost occurrence of the genus is in Taiwan, where the endemic *P. morrisonicola* HAYATA grows at about 23°N (LI 1975).

More than 30 species of spruce have been reported from eastern and south-eastern China and central Asia (REHDER and WILSON 1916; LEE 1935; BOBROV 1970; CHENG *et al.* 1975; LIU 1982; FARJON 1990, 2001). The taxonomic position of a number these species is not clear. Only a dozen or so of the

Table 1. Global geographic distribution of *Picea* species throughout the northern hemisphere (after data of FARJON 1990, 2001 and BORATYŃSKA 1998)

Region	Species of large areas of distribution	Species of restricted areas
Europe	<i>P. abies</i> (L.) KARST. <i>P. obovata</i> LEDEB.	<i>Picea omorica</i> (PANČIĆ) PURKYNE
North America	<i>P. engelmannii</i> (PARRY) ENGELM. <i>P. glauca</i> (MOENCH) VOSS <i>P. mariana</i> (MILL.) BRITT. <i>P. pungens</i> ENGELM. <i>P. rubens</i> SARG. <i>P. sitchensis</i> (BONG.) CARR.	<i>P. breweriana</i> S. WATS. <i>P. mexicana</i> MARTINEZ <i>P. chihuahuana</i> MARTINEZ
Northern and northeastern Asia	<i>P. jezoensis</i> (SIEB. et ZUCC.) Carr. <i>P. obovata</i> LEDEB.	<i>P. alcoquiana</i> (VEITCH ex LINDL.) CARR. <i>P. glehnii</i> (FR. SCHMIDT) MAST. <i>P. koraiensis</i> NAKAI <i>P. koyamai</i> SHIRASAWA <i>P. maximowiczii</i> REGEL ex MAST. <i>P. polita</i> (SIEB. et ZUCC.) CARR.

Table 1. cont.

Southeastern Asia	<i>P. asperata</i> MAST.
	<i>P. aurantiaca</i> MAST.
	<i>P. brachytyla</i> (FRANCH.) PRITZEL
	<i>P. crassifolia</i> KOMAROW
	<i>P. farreri</i> PAGE et RUSHE.
	<i>P. likiangensis</i> (FRANCH.) PRITZ.
	<i>P. meyeri</i> REHD. et WILLS.
	<i>P. morrisonicola</i> HAYATA
	<i>P. neoveitchii</i> MAST.
	<i>P. purpurea</i> MAST.
	<i>P. retroflexa</i> MAST.
Central Asia (Himalayas)	<i>P. wilsonii</i> MAST.
	<i>P. spinulosa</i> (GRIFF.) HENRY
	<i>P. schrenkiana</i> FISCH et C.A. MEY.
Caucasus	<i>P. smithiana</i> (WALL.) BOISS.
	<i>P. orientalis</i> (L.) LINK

species reported from eastern and central Asia have accepted taxonomic ranks (SCHMIDT-VOGT 1977; FARJON 1990, 2001). Many of these taxa have restricted and geographically isolated ranges. Several are distributed in mountains and occur at the altitudes of 1400–3600 m and are important species in the local forest plant communities.

In central Asia the genus *Picea* is represented by a few montane species. *Picea spinulosa* (GRIFF.) HENRY and *P. smithiana* (WALLICH) BOISS. grow in the Himalayas at altitudes of 1400–3600 m (RAIZADA and SAHNII 1958; WANG 1961; BROWICZ 1982; GRIERSON and LONG 1983; POLUNIN and STANTON 1984) and *P. schrenkiana* FISCHER et MEYER in the Altay at 1400–3000 m (SOKOLOV *et al.* 1977). *Picea orientalis* (L.) LINK is the only species of the genus in the Caucasus and southwest Asia. It grows at elevations of 1000–2000 m and forms extensive mountain forests (DOLUKHANOV and SKHIRELI 1959; COODE and CULLEN 1965; BROWICZ 1982).

4.2. GENERAL DISTRIBUTION OF *PICEA ABIES*

Norway spruce belongs to the Holarctic, European flora. It occurs in the mountain ranges of central and southeastern Europe, the eastern European lowlands, and in the Scandinavian Peninsula (Fig. 4.2). The easternmost range

limit of the species extends to the foothills of the Urals and the westernmost limit is the Alps in France. The northernmost occurrences are from 69°47'N latitude in Norway (HULTÉN 1971; SCHIER 1973) and in the south at 41°45'N in Macedonia and Greece (BORATYŃSKI *et al.* 1992).

Picea abies forms forests in many countries (Figs. 2.2 and 4.3). It is an important forest tree in the mountains of Switzerland, Austria, and Italy (HESS *et al.* 1967; FENAROLI and GAMBI 1976; WELTEN and SUTTER 1982). *P. abies* is important in the Scandinavian countries, in Germany, and in Russia (Table 2). In Germany, Norway spruce grows in the mountain ranges of the southern part of the country (HAEUPLER and SCHÖNFELDER 1989) and is planted as a forest tree in many other regions. The species occurs frequently in the mountain ranges of the Balkan Peninsula, extending to northern Albania and Macedonia. Further to the south, it grows in isolated stands dispersed in western Macedonia, western Bulgaria, and northern Greece (ADAMOVIĆ 1909; HAYEK 1931; STOJANOV 1963; FUKAREK 1981; BORATYŃSKI *et al.* 1992).

Picea abies forests cover large areas in the Carpathians (Fig. 4.3). The species is common in the southern and eastern Carpathians of Romania and the Ukraine (ŠRODOŇ 1947; BELDIE 1967; PROKUBIN 1987). In the western Carpathians in Slovakia and Poland, the species is common in the higher mountain ranges (SVOBODA 1953; KORNAŚ 1957; SOMORA 1958; STUCHLIKOWA and STUCHLIK 1962; ZARZYCKI 1963; JASIEWICZ 1965; JASIČOVA 1966; MYCZKOWSKI *et al.* 1975; TOWPASZ 1975; ZARZYCKI 1981; BIAŁECKA 1982; PAGAN 1992), whereas in the lower mountain ranges it is very rare and may not occur at all. In the Sudety Mts *P. abies* is common and frequently planted (SKALICKÁ and SKALICKÝ 1988; DOSTAL 1989; BORATYŃSKI 1991) (Figs. 2.1 and 2.2). In the northern foothills of the Sudety and Carpathian ranges in central Europe, Norway spruce occurs in the lowlands, where it is less common than in the mountains.

Picea abies is a common forest tree in the Scandinavian Peninsula except for the southern regions of Sweden and the northernmost, arctic regions of Norway (HULTÉN 1971; SCHIER 1973). The taxon, *P. fennica* (REGEL) KOM., has been described in northern Finland and in the Khibiny Mts of the Kola Peninsula at the northern arctic limit of the species. This taxon has an undetermined systematic position and is considered a subspecies or variety of Norway spruce or *P. abies* subsp. *obovata* (JALAS and SUOMINEN 1973).

Specimens intermediate between the typical subspecies *Picea abies* subsp. *abies* and Siberian subspecies *P. abies* subsp. *obovata* are quite common in the eastern European lowlands and in the northern regions of Scandinavia. Thus, delineating the geographic ranges of these two taxa is difficult. The typical *P. abies* is thought to occur only in central Europe, whereas intermediate specimens are found only in the eastern part of the continent (PRAVDIN 1975). The northern lowland range of *Picea abies* attains its southern limit in Belorussia and northern Ukraine (SOKOLOV *et al.* 1977; MEL'NYK 1993). In central Europe, *P. abies* occurs mostly in the mountains, but north of the Alps – Sudety –

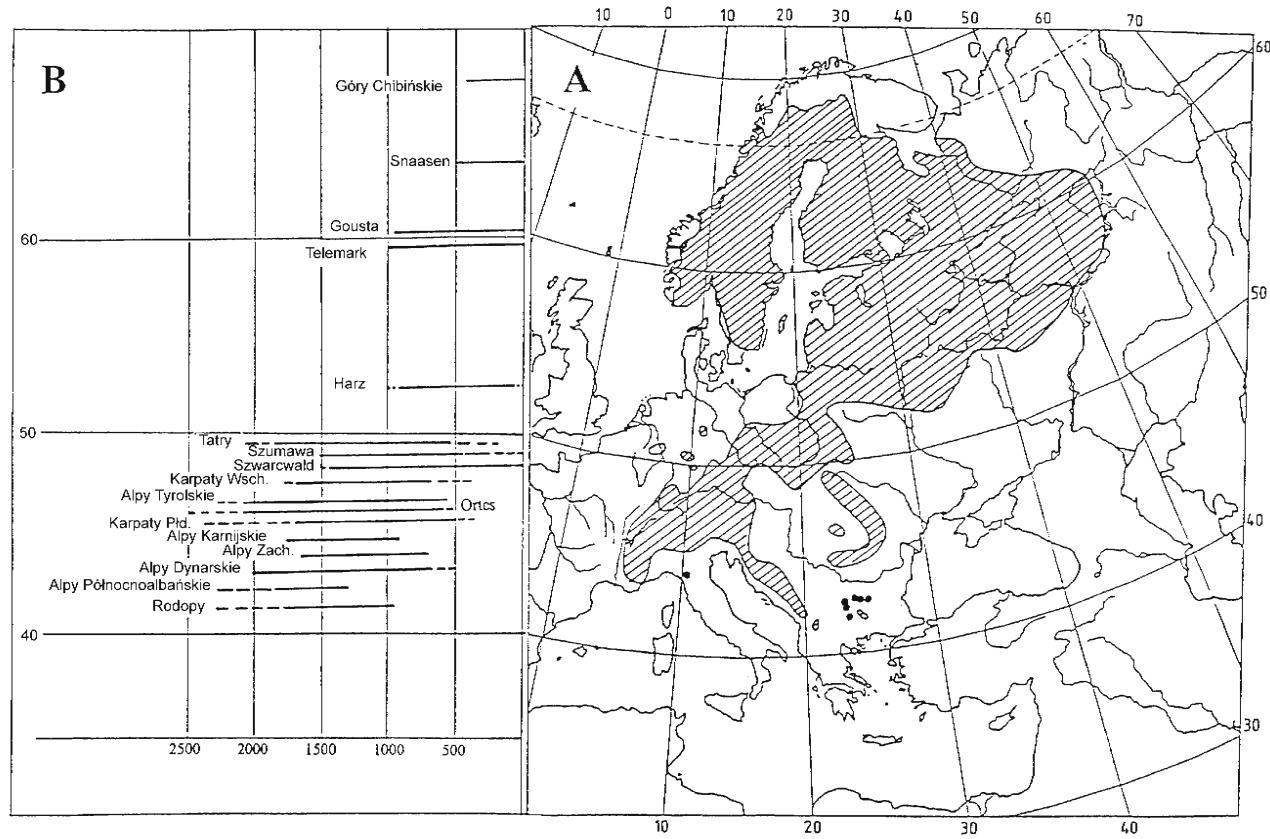


Figure 4.2. The geographic range of *Picea abies*: A) latitudinal distribution; B) altitudinal range (after BORATYŃSKA 1998)

Table 2. Altitudinal distribution of *Picea abies* in particular regions of Europe

Country	Region	Latitude N	Occurrence of <i>Picea abies</i>				References
			lower limit		upper limit		
			scattered (m)	in closed stands (m)	in closed stands (m)	scattered (m)	
Finland	Menesjoki	68°33'			400		SCHMIDT-VOGT 1977
Sweden	Torne	68°00'			350		HULTÉN 1971
	Lule	67°50'			450		HULTÉN 1971
	Jamtland	63°30'			650		HULTÉN 1971
Norway	Svanvik	69°27'			40		SCHMIDT-VOGT 1977
	Snaasen	64°00'			540		SCHMIDT-VOGT 1977
	Eidsfjell	61°30'			680		SCHMIDT-VOGT 1977
	Tron	60°40'			1250		HULTÉN 1971
	Bydgin	61°20'			1160		HULTÉN 1971
	Gousta	60°00'			940		SCHMIDT-VOGT 1977
	Telemark	59°50'			1000		SCHMIDT-VOGT 1977
Poland	Karkonosze Mts	50°50'	500–600	1100	1300 (1390)	1550	BORATYŃSKI 1991
	Tatry Mts	49°10'	700	1200	1650	1700	PAWŁOWSKI 1956
Slovak Republic	Tatry Mts	49°10'	700	1200	1700	2075	MYCZKOWSKI <i>et al.</i> 1975
	Nizhne Tatry Mts	48°55'			1527		BLATTNÝ and ŠTASTNÝ 1959
Czech Republik	Karkonosze Mts	50°40'			1380	1550	SKALICKÁ and SKALICKÝ 1988
Ukraine	Chornokhora Mts	48°20'	550	1500	1650	1800	ŠRODOŇ 1947; CHOPIK 1976
Romania	Bihor Mts	46°30'	400	770	1700	1860	SAVULESCU 1952; BELDIE 1967, 1972

Table 2. *cont.*

	Bucegi Mts	45°00'		900	1800	2380	SAVULESCU 1952; BELDIE 1967, 1972
Bulgaria	Rila Mts., Pirin Mts	42°00'	950	1200	1700	2200	STOJANOV 1963;
Greece	Rhodope Mts	41°40'		1400	1900		BORATYŃSKI <i>et al.</i> 1992
Bosnia and Herzegovina	Dynarian Alps	43°00'–44°00'	500–700	800	2000	2200	SVOBODA 1953; SCHMIDT-VOGT 1977
Albania	Mountains of N Albania	42°00'		1700	1800	2100–2200	SCHMIDT-VOGT 1977;
Italy	Alps	46°30'	300	1450	1750		FENAROLI and GAMBI 1971
	Alta Anauria (Trentino)	46°00'	1020	1180	1780		LONGO 1972
	Alpi Carniche	46°50'		950	1700		PIGNATTI and POLDINI 1969; FERLUGA and POLDINI 1978
Austria	North Tirol	47°10'	460–500	700	1800	2800	POLATSCHEK 1997
	East Tirol	47°00'	680–720	850	1750	2550	POLATSCHEK 1997; PEER 1981
	Voralberg	47°00'	399	700	1780	2538	POLATSCHEK 1997
Switzerland	Graubünden	46°00'–47°00'		600	1900	2270	BRAUN-BLANQUET and RÜBEL 1932
	N Ketten, Luftfenchtigkeit	47°00'	800	1200	2000	2400	HESS <i>et al.</i> 1967
Germany	Bavarian Alps	47°00'		400	1735	1910	KÖSTLER and MAYER 1970
	Schwarzwald	49°00'	650	800	1500		SCHMIDT-VOGT 1977
	Harz	52°00'	150	350	900	1000	DENGLER 1913; SCHROEDER 1973
France	Jura	47°00'	800	1000	1400	1600	DÉBAZAC 1977;
	Alps	45°00'	300	600	1800	2000	SCHMIDT-VOGT 1977

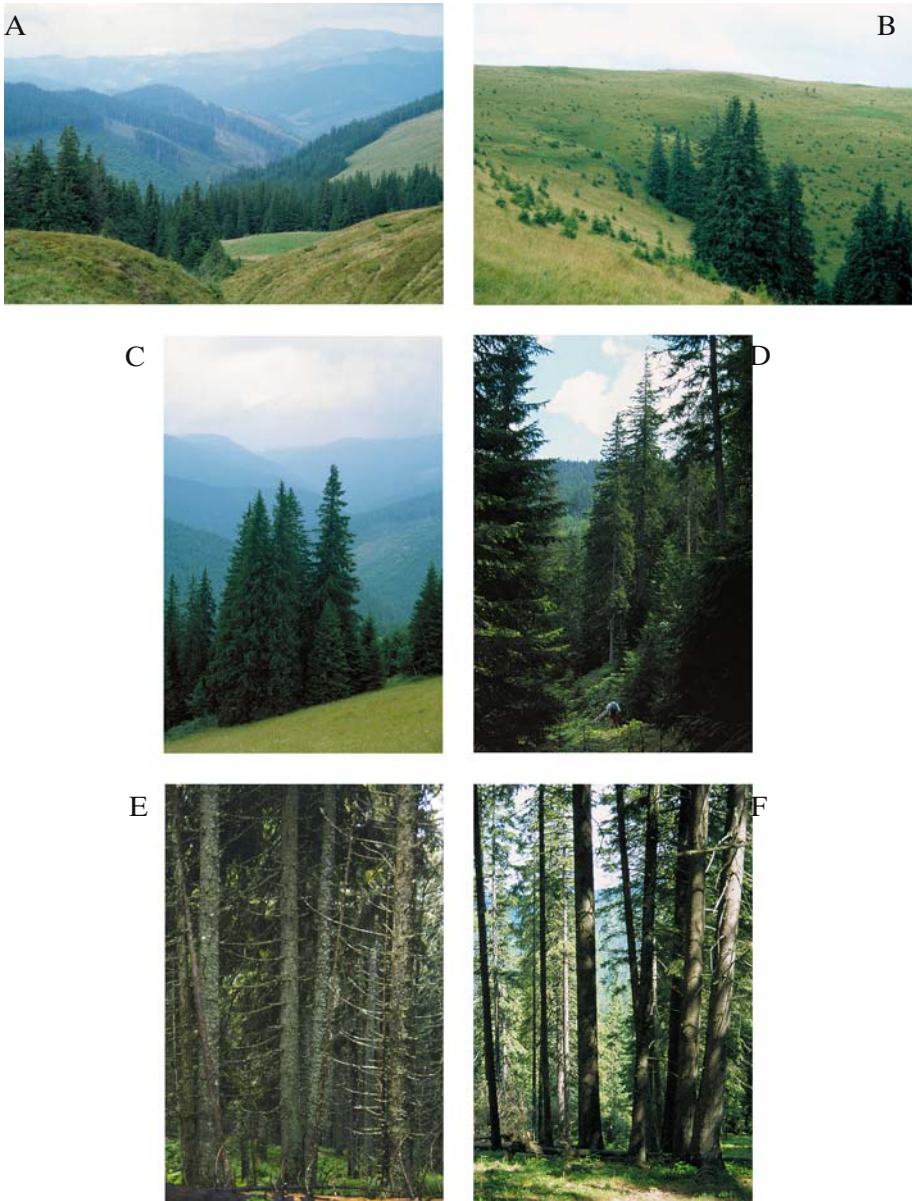


*Figure 4.3. Norway spruce trees and forests in the eastern Carpathians
(photo A. BORATYŃSKI)*

Upper montane forests/mountain pastures zone in the Hrynyavska Polonina (A, B) and Gorgany (C) mountains, Poland; Spruce colonize abandoned pastures (B); D–F, monotypic spruce forests in the Gorgany mountains at elevations of 1100–1300 m

A



B



*Figure 4.4. Upper forest tree line in the Karkonosze mountains (Sudety Mts.)
(photo A. BORATYŃSKI)*

A – forest tree line on the northern slopes of Czarny Grzbiet; B – influence of temperature inversion on the patterning of the upper forest tree limits on the slopes of the Łomniczka glacial cirque

A



B



C



D



E



Figure 4.5. Norway spruce at the climatic mountain tree line in the Karkonosze (Sudety Mts.) (photo A. BORATYŃSKI)

A – degeneration of an old stand with regeneration; B–C – bio-groups of spruces at the forest tree line; D – dead and dying spruce at the forest tree line; E – an individual spruce at the forest tree line with typical crown damage



Figure 4.6. Spruce above the upper forest line in the Karkonosze mountains (Sudety Mts.) (photo A. BORATYŃSKI)

A–C – about 100 m above the tree line; D–F – about 200–300 m above the tree line

Carpathian range it may occur on both upland and lowland sites. Both portions of the species range are connected, mainly in Poland, but also partly in Byelorussia (Fig. 4.2).

Altitudinal range

At its northern arctic range limit, *P. abies* may be found at altitudes as low as sea level. Overall, the upper altitudinal limit of the species is inversely correlated with latitude (PEARSON'S correlation coefficient $r = -0.95$, Fig. 4.2). The species attains an altitude of about 400 m in northern Finland and in the Khibiny Mts on the Kola Peninsula at a latitude of 67°50'N. The altitudinal limit increases to 940 m in southern Norway at latitude of about 60° and to 1000 m at 59°50'N (SCHMIDT-VOGT 1977). The altitudinal range of the *Picea abies* subsp. *abies* in central Europe is linked to local climate conditions and physiography. The species forms a tree line (Figs 4.4 and 4.5) only in the highest mountain ranges (Table 3). The occurrence of high altitude stands is modified by local conditions, including slope, aspect, and parent material. The highest stands in the Central-European mountain ranges occur in the most extensive mountain ranges and west-facing slopes (ZIENTARSKI 1985).

Table 3. Norway spruce stands in the countries of Europe

Country (year)	Area hectares	Total forest area %	Literature
Bulgaria (2000)	155,700	4.7	GAGOV 2000
Czech Republic (2000)		55.0	VANČURA and MALA 2000
Finland (1986–98)		25.1	SEVOLA 1999
France (1997)*	1,345,000	9.9	ANONIM 1999
Germany (2000)		33.0	KLEINSCHMIT 2000
Hungary (1983)	15,200	1.0	Timber Bulletin for Europe, 35, 7
Netherlands (1981)	17,138	8.0	Timber Bulletin for Europe, 33, 10
Poland (1978)	610,000	7.2	Timber Bulletin for Europe, 31, 3, 2
Poland (1997)	513,000	5.8	ANONIM 2001
Slovak Republic (1997)		27.2	NOVOTNY and FILLO 1997
Sweden (1979)		48.0	Timber Bulletin for Europe, 31, 5, 3
Switzerland (1979)		20.0	Timber Bulletin for Europe, 32, 3, 4
Russia (2000)		12.0	EFIMOV <i>et al.</i> 2000

* together with *Abies alba*

Picea abies reaches its upper altitudinal limits about 200–300 m above the forest tree line. It occurs as isolated individuals or in groups in more or less deformed form (see Chapter 11) in shrub communities of *Pinus mugo*, *Alnus*

viridis, *Salix silesiaca*, *Sorbus aucuparia*, etc. (Fig. 4.6). It grows also in the alpine meadow communities as polycormic individuals 1–2 m tall.

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5. THE CENTRAL EUROPEAN DISJUNCTIONS IN THE RANGE OF NORWAY SPRUCE

ADAM BORATYŃSKI

5.1. THE SPRUCELESS BELT IN CENTRAL EUROPE

The determination of the geographic range of *Picea abies* in central Europe and the origin of a spruceless belt between the mountains of central Europe and northeastern Europe has served as an intriguing puzzle for a number of investigators. Additionally, a natural disjunction in the species range in the western Carpathians has been discussed previously. The problems concerning both disjunctions have been summarized by ŚRODOŃ (1967a, b) and the seminal study of SCHMIDT-VOGT (1977). The aim of the present work is to summarize the prior findings and include literature evidence from paleobotany, biogeography, as well as genetic and morphological evidence to understand the present geographic distribution of Norway spruce in central Europe.

5.1.1. *The history of the spruceless belt*

RIVOLI (1884) first described the geographic range of Norway spruce in central Europe. STRZELECKI (1894) produced a precise distribution of the spruce forests in the western and eastern Carpathians. By contrast, earlier published reports were largely superficial and incomplete. For example, a number of reports describe the presence or absence of spruce forests in particular parts of the Polish kingdom (KLUK 1808; SZUBERT 1930; WAGA 1848). The oldest range maps of Norway spruce in central Europe depict the Carpathian forests (HERBICH 1860; BRODOWICZ 1888).

The range of Norway spruce in the Russian empire, including Polish lands under occupation, was drawn by KÖPPEN (1889), but was very schematic and incomplete. The first complete range map of Norway spruce in central Europe was prepared by RACIBORSKI (1912), and was probably based on the earlier published data of RIVOLI (1884) and STRZELECKI (1894). This map was later modified and supplemented by SZAFAER (1916), RACIBORSKI and SZAFAER (1919), and KULCZYŃSKI and WIERDAK (1928). All these maps fail to delin-

create a spruceless belt between the Carpathians and the northern, boreal part of the species contemporary range (Fig. 5.1).

Following World War I, a map of *Picea abies* distribution in the Polish Kingdom compiled by LASPEYRES was published (PAX 1918). Areas lacking spruce forests on the Masovian Lowland between the central European montane and northeastern European lowland portions of the species range were shown for the first time. Three years later RIVOLI (1921) depicted the distribution of Norway spruce stands in central and northern Europe and distinguished four range limits as follows: 1) the northern, polar limit; 2) the southern boundary of the northern, lowland portion of the species range; 3) the lower limit of the central European mountain ranges; and 4) the upper altitudinal limit in the central European mountain ranges.

The mapped locations of the range limits (after RIVOLI 1921) were dependent upon climate and largely correlated with the isotherms of the summer months and modified based on regional site conditions. In furthering RIVOLI'S work, SZAFER (1921) examined the biogeography of Norway spruce in central Europe (mainly contemporary Poland) using the concept of latitudinal limits to the spruce range known from Scandinavian literature sources. He also depicted the distribution of Norway spruce in central Europe in which the "spruceless belt" was fully shown for the first time (Fig. 5.1).

SZAFER'S map (1921) was subsequently edited numerous times with only minor corrections (e.g. SZAFER 1935, 1937, 1959, 1972; JEDLIŃSKI 1928; OBIŃSKI 1947; STECKI and KOŚCIELNY 1955; WŁOCZEWSKI 1968), despite evidence that the spruceless belt, in fact, contained numerous dispersed and isolated spruce stands. Thus, the depiction of a Norway spruce range with a spruceless belt in central Europe on the Masovian and Podlasiian Lowlands and in Polessia and Volhynia is largely based on duplication of SZAFER'S map, despite contrary evidence (ŚRODOŃ 1967a, b). The contemporary distribution of stands of *Picea abies* of natural origin in Poland and Ukraine (BORATYŃSKA *et al.* 1980; MELNYK 1993, see also Chapter 4) clearly reveals that the area considered to be free of spruce is, in fact, covered with dispersed spruce stands.

5.1.2. The disjunction

The factors that determine the range limits of tree species are autogenic and anthropogenic in origin. The autogenic factors underpinning tree species distribution, especially in central Europe, are linked to the ecological characteristics of the species, its migration history in the Holocene, and the geographic distribution of potential habitats. Human activities have played an important role in the vegetation history in central Europe. Evidence of human activities extends to the prehistoric era in the Masovian-Podlasiian Lowland, Polessia, and Volhynia regions (HENSEL 1980, BRODA 1998).

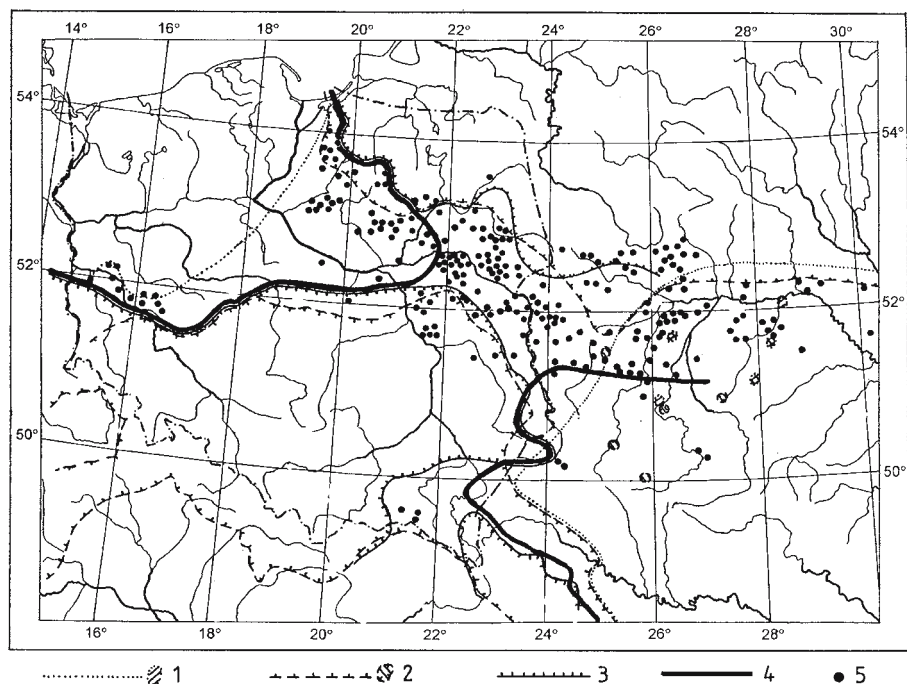


Figure 5.1. Geographic range limits of the Norway spruce in central Europe after various authors (BORATYŃSKI 1998)

1 – after RACIBORSKI (1912) and RACIBORSKI and SZAFER (1919); 2 – after SZAFER (1921); 3 – after SZAFER (1959, 1972); 4 – after ŚRODOŃ (1967b); 5 – the island localities after JEDLIŃSKI (1926, 1927), WIERDAK (1927a, b), PACZOSKI (1930), GROß (1934), TYMRĄKIEWICZ (1935), SOKOŁOWSKI (1968c, 1972, 1974a), SLOBODYAN (1962), GOLUBETS (1972), KONDRATYUK (1968), KOZLOVSKAYA and PARFENOV (1972) and MELNYK (1993)

5.1.2.1. Characteristics of the spruceless belt

On the basis of the site requirements of *Picea abies* and the distribution of the potential habits in the spruceless belt, it appears that a lack of suitable sites does not limit the occurrence of the species there. The ecological properties and site requirements of Norway spruce (see Chapter 11) enables the species to grow and even prosper in the area, but only on the most mesic and productive sites (JEDLIŃSKI 1922, 1926, 1927, 1928; PACZOSKI 1925, 1930). Rich and sufficiently mesic forest sites are present in the Masovian-Podlassian Lowland, Polessia, and Volhynia. However, these sites cover rather small areas, particularly in Masovia and Podlissia (SOKOŁOWSKI 1968c; MATUSZKIEWICZ *et al.* 1995).

5.1.2.2. *Holocene migration history*

The migration routes of *Picea abies* during the Holocene in central Europe have been described previously (e.g. SZAFER 1931, 1935; ŚRODOŃ 1967b, 1977; HUNTLEY and BIRKS 1984; HUNTLEY 1988, GIESECKE and BENNETT 2004, see Chapter 1). The southern limit of the species on the Scandinavian Peninsula and also on the central European lowlands is thought to represent an ongoing migration (SZAFER 1931, 1935; SCHMIDT-VOGT 1977). SZAFER'S view was that the northern, boreal range and southwestern, Carpathian range were joined during the Holocene climatic optimum about 4000–5000 years before present (BP) in Podlussia and Masovia (SZAFER 1931). However, the pollen diagrams later did not appear to support this hypothesis (SZAFER 1935), nor did the palynological investigations of the peat bogs of the spruceless belt (LUBLINERÓWNA 1934). Contemporary pollen maps also show a low proportion of Norway spruce pollen grains throughout the spruceless belt region (RALSKA-JASIEWICZOWA 1983; HUNTLEY and BIRKS 1983). However, this evidence does not preclude the occurrence of dispersed stands of the species. For example, pollen diagrams of the contemporary layers of the peat bogs ("0 BP", see Fig. 5.2) contain a rather small fraction of spruce pollen grains when compared with the distribution of the natural and planted stands of the species in Poland (Fig. 5.3). Thus, even a low frequency (below 2%) of spruce pollen grains does not rule out the occurrence of the species, as noted by ŚRODOŃ (1967b, 1977). ŚRODOŃ (1967b, 1977) suggests that the boreal and southern ranges of Norway spruce met in the spruceless belt during the Atlantic period of the Holocene. This idea is supported by the observation of spruce pollen grain frequencies of about 2% in the isopollen maps of 6000, 5000, and particularly of 4000 BP (Fig. 5.2).

5.1.2.3. *Intraspecific variability*

The Norway spruce in central Europe originated from at least three Pleistocene refugia (SZAFER 1931, 1935; ŚRODOŃ 1967b, STASZKIEWICZ 1966, 1967, 1976; RALSKA-JASIEWICZOWA 1983; HUNTLEY and BIRKS 1983). Consequently, it may be supposed that populations from the boreal part of the species range differ from those originating in the southern portion in terms of growth, morphology, and phenology. The biometric traits of cones, seeds, and pollen grains of Norway spruce populations from various parts of the species range have been compared. PACZOSKI'S (1925) work was the first of such studies and described significant differences between cones of populations of Norway spruce from the Białowieża Primeval Forest in northeastern Poland and the Tatra Mts in southern Poland (Table 1). Another interesting early study compared of 119 samples of seeds from foresters' seed collections in Poland (TYSZKIEWICZ 1934b) and demonstrated large differences between northeastern and southern seed sources.

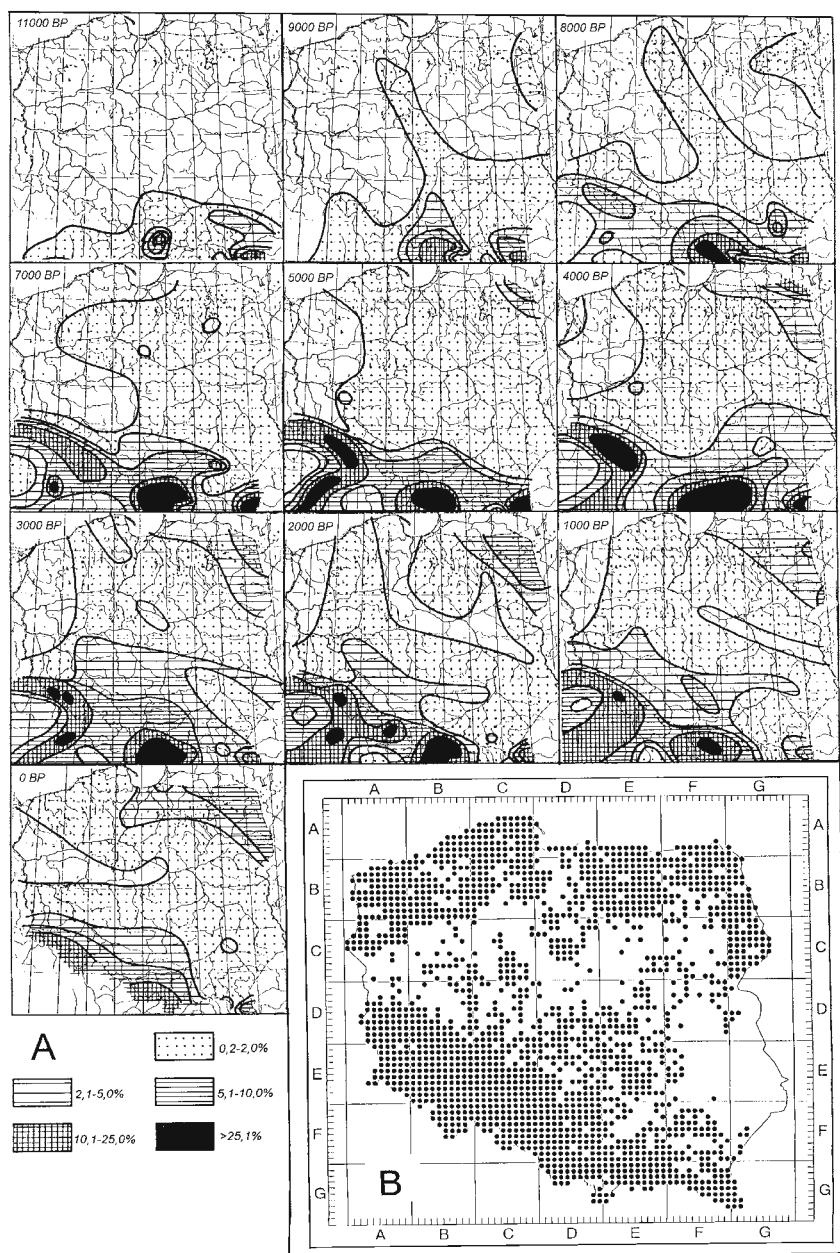


Figure 5.2. Range expansion of Norway spruce throughout the Holocene in central Europe

A – isopollen maps compiled from RALSKA-JASIEWICZOWA (1983) and RYBNÍČKOVÁ and RYBNÍČEK (1988), modified; B – distribution of the species in Poland (ZAJĄC and ZAJĄC 2001)

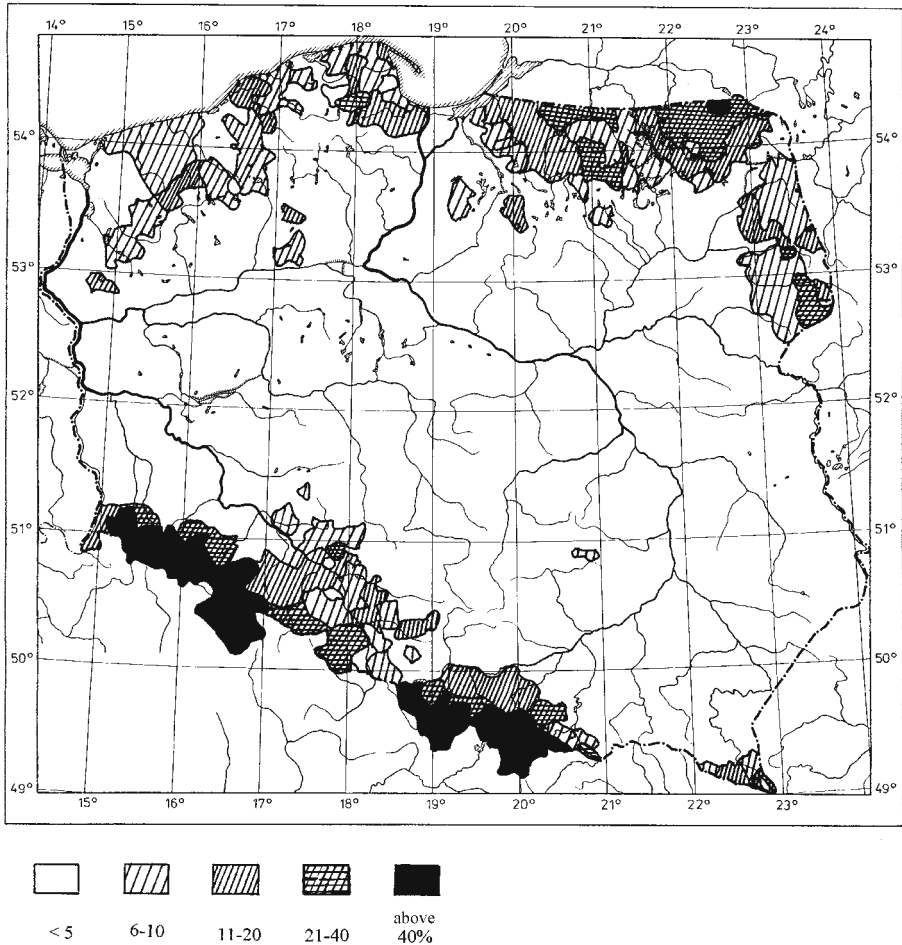


Figure 5.3. The role of Norway spruce in the forests of Poland (after BORATYŃSKI 1998)

Participation of the area covered with the Norway spruce stands in the forest area of Polish State Forests (after ŻYBURA'S data)

Most studies of geographic variation confirm differences between north-eastern and southwestern, mountain population groups, yet the differences are not always significant (Table 1). Evidence from isoenzyme studies suggests that more or less sustained gene flow has occurred between the northeastern and southwestern, mountain populations of the species in Poland (LEWANDOWSKI *et al.* 1997; LEWANDOWSKI and BURCZYK 2002). The mountain populations of the eastern and western Carpathians differ from each other. However, the pattern of variation indicates that gene flow has occurred among most of the studied populations. The genetic evidence supports the observed

Table 1. Studies of population and range-wide trait variation of *Picea abies* in central Europe

Trait	Number of samples	Remarks and results	Source of data
Seed	119 from Poland	Seed collected by foresters in managed stands, probably not always of natural origin. Lack of seeds from stands of spruceless belt. The differences between northeastern (boreal) and southern (mountain) populations are described.	TYSZKIEWICZ 1934b
Pollen	15 from Europe	The author interprets the results based on an a priori assumption of existence of a spruceless belt (for an alternative view, see ŚRODOŃ 1967a, b). Lack of samples from the spruceless belt. The results confirm differences between boreal and mountain populations.	DYAKOWSKA 1964
Cones	2	Samples from Białowieża and Tatra Mts are compared. Spruce from Białowieża originates from western (central) Europe and not from the eastern portion of the species contemporary range.	PACZOSKI 1925
	2	Samples from Białowieża and Czarnohora Mts (eastern Carpathians) are compared. The spruce from Białowieża resembles provenances from the north and northeast.	KORZENIEWSKI 1953
	16	The spruceless belt does not form a distinct limit between the northern and Carpathian populations, but differences exist between populations from western and eastern Carpathians.	STASZKIEWICZ 1966, 1967, 1976
		The subfossil and contemporary cones from the western Carpathians do not manifest differ.	KETNER 1966
		The frequencies of the form <i>europaea</i> and <i>acuminata</i> indicate that the poleisian populations are of Carpathian origin.	JURKEVICH and PARFENOV 1967
	26	The samples from central Poland are of intermediate character between those from the northeast and from the Carpathians.	CHYLARECKI and GIERTYCH 1969

Table 1. cont.

Growth and phenological traits	26	Great differentiation in examined traits confirms the permanent diffusion of northeastern populations through mountain populations and vice-versa. The eastern and western Carpathian populations are also similar.	GIERTYCH 1973, 1976b
Cones of trees from provenance trials	20	Populations from northeastern and central European mountains differ. The provenances from intermediate locations have cones similar to those from the northeast or from the mountains.	BARZDAJN 1996
Growth and phenology	20	The provenances from central Poland are intermediate between northeastern and montane provenances or are similar to Carpathian sources.	BARZDAJN 1997
Genetic variation (isoenzymes)		Small differences between northeastern and central European montane populations indicate gene flow.	LEWANDOWSKI <i>et al.</i> 1997
		Extensive gene flow and historical events have erased strong differences between central European and northeastern populations; actual differentiation depends more on the geographic distance than on provenance.	LEWANDOWSKI and BURCZYK 2002

intermediate characteristics of Norway spruce populations from central Poland (CHYLARECKI and GIERTYCH 1969; GIERTYCH 1973, 1976; BARZDAJN 1996, 1997). Following the last glaciation, *Picea abies* from the Carpathians likely migrated first to the north (Fig. 5.2), followed by a migration from eastern Europe to the southwest. The traces of that first migration from the Carpathians northward are manifested in the Polessian populations, located north of the spruceless belt and exhibiting a high frequency of the cone trait var. *acuminata*, characteristic of populations of the eastern Carpathians, whereas the var. *europaea*, characteristic for the boreal part of the species range, occurs frequently in northern Byelorussia (JURKIEWICZ and PARFIE-NOW 1966; JURKEVICH and PARFENOV 1967). The similarity of cone traits among the Bialovezhan populations and the eastern Carpathian populations can also be explained on this basis (BARZDAJN 1996, 1997).

5.1.2.4. Human impacts on the contemporary distribution of Norway spruce in the “spruceless belt”

Human activities in the early historical period could have contributed to moderate range expansion of some tree species, including Norway spruce

(ŚRODOŃ 1967b, 1977). However, extensive colonization and intensification of agriculture, resulting in deforestation, began in central Europe about 2000 years ago. Land use change likely fragmented and eliminated Norway spruce stands, especially in areas where it occurred naturally at low frequencies (JEDLIŃSKI 1922, 1926, 1927, 1928; ŚRODOŃ 1967b; BRODA 1998).

Deforestation connected with human settlement has had the greatest impact on the contemporary range of Norway spruce. The permanent colonization of the Masovian and Podlассian regions began as early as 2000 years ago (HENSEL 1980). During this time agriculture expanded gradually at the expense of forests as human populations increased. Although the above-mentioned regions of central Europe have been densely populated since the Middle Ages, large contiguous forests still cover the region. Further colonization in the 14th and 15th centuries resulted in deforestation and fragmentation of the largest forest complexes (HENSEL 1980). The most fertile forestlands were converted to agriculture during that period (BRODA 1998). Consequently, the gradual reduction of *Picea abies* stands in the "spruceless belt" was largely the result of land use conversion from forest to agriculture, owing to the fact that the species occurred on the most productive and mesic sites (see Chapter 11).

Another cycle of intensive deforestation took place in the 18th and 19th centuries (ROMANOWSKA 1934; CZERWIŃSKI 1974). These regions were deforested much more in the 19th and the first decades of 20th centuries than at present. Today forests in the region are largely restricted to the most dry and sandy soils, which are less desirable for agriculture. The contemporary forest composition in the region is 40–50% planted Scots pine stands established about 70–80 years ago on abandoned agricultural lands (JAKUBOWSKA-GABARA 1985; BRODA 1998). In this region the occurrence of large forest stands is rare. However, it is worth noting that Norway spruce occurs in most large forest stands (JEDLIŃSKI 1922; TYMRKIEWICZ 1935; SLOBODYAN 1962; SOKOŁOWSKI 1968c, 1972, 1974a; CZERWIŃSKI 1974; MELNYK 1993).

The presence of Norway spruce in this region was commonly associated with timber stands during the first decades of 20th century. Spruce stands were reported to occur only in administrative districts where forest cover exceeded 20% of the land area, whereas outside of the spruceless belt, the occurrence of the species was independent of the forest cover percentage (JEDLIŃSKI 1922). This relationship likely arises from an increase in suitable sites for Norway spruce outside the Masovian and Podlассian Lowlands.

Habitat loss and contemporary forestry practices are other key factors that limit the occurrence of *Picea abies* in the Masovian and Podlассian Lowlands. For example, wetland drainage and the lowering of the water table have altered the hydrology in many areas (JEDLIŃSKI 1927). Silvicultural practices, including clear-cutting that results in the removal and loss of Norway spruce seed trees, likely reduces natural regeneration of the species (see Chapter 13). Forestry practices in the region prefer the establishment of Scots pine plantations at the expense of Norway spruce and other forest trees. It should be

noted that outside this region, the contemporary geographic area and coverage of *Picea abies* has increased largely as a result of it being a common species in plantation forestry for timber production in central Europe for the last 200 years (BORATYŃSKA *et al.* 1980; ŻYBURA 1990; SCHMIDT-VOGT 1991; MELNYK 1993).

5.2. THE CARPATHIAN DISJUNCTION

Norway spruce is naturally absent in the lower Beskid Mts (Beskid Niski), the lowest range of the western Carpathians and in the Pogórze Dynowskie and Pogórze Rzeszowskie regions in Poland for a distance of about 60 km. The lack of Norway spruce in these regions was described in the latter half of the 19th century (RIVOLI 1884; BRODOWICZ 1888; REHMAN 1895). This disjunction was depicted cartographically by WIERDAK (1927b) and subsequently adopted on the map of Norway spruce distribution in central Europe (KULCZYŃSKI and WIERDAK 1928; SZAFER 1937). The lack of the spruce in the lower Beskids was explained by a lack of suitable climatic conditions. The hot and dry southerly winds were considered the main factor (RIVOLI 1884; REHMAN 1895). The occurrence of natural Norway spruce stands in the Bieszczady Mts on aspects and topographic positions shielded from the southerly winds appears to confirm this notion (ZARZYCKI 1963).

A natural origin of the Carpathian disjunction of Norway spruce has been supported by the observations of greatly reduced frequencies of pollen found in the peat bogs from the region (RALSKA-JASIEWICZOWA 1983; RYBNÍČKOVÁ and RYBNÍČEK 1988; see also Fig. 5.2), as well as in the variation of contemporary and sub-fossil cones of regional Norway spruce populations (MEZERA 1939; HOLUBČIK 1969b; STASZKIEWICZ 1966, 1967, 1976). Nevertheless, it should be mentioned, that in the early Holocene the populations of the western and eastern Carpathians were in contact with each other. The high frequency of the cone variety *acuminata* that is characteristic of the eastern Carpathians in the Tatras (western Carpathians) appears to support this opinion (MEZERA 1939; STASZKIEWICZ 1976). Recent palynological studies also concur (ŚRODOŃ 1990).

The contemporary distribution of *Picea abies* indicates an absence of the species in the lowest parts of the western Carpathians and associated submontane regions. These regions were covered with forests with a high abundance of Norway spruce in the Holocene about 5000 years ago. Subsequently, this forest type was largely replaced by broad-leaved forests (ŚRODOŃ 1990). In the higher mountain ranges, Norway spruce has colonized the upper elevations and forms the contemporary high-elevation forest type present in this region. The shortage of this habitat in the lower portions of the western Carpathians is likely one reason that *P. abies* survived there only in sparse populations on the northern slopes, along riparian zones, and on landslides. Many

remnant stands were eliminated by human activities in historical times (ŚRODOŃ 1990).

5.3. CONCLUSIONS

1. The northeastern and southwestern ranges of Norway spruce once overlapped on the Masovian, Podlассian, and Polessian Lowlands during the middle Holocene. Populations originating from the Carpathian refugium first migrated to Volhynia and southern Polessia and then to the Masovian and Podlассian Lowlands.
2. Norway spruce populations from the east migrated to central Europe later during the middle of the Holocene and subsequently spread to the southwest. Signs of this migration are represented in the intermediate morphological and phenological traits of populations in the regions north of the Carpathians and south of the Białowieża Primeval Forest in northeastern Poland. The spruceless belt was originally covered with forests that included Norway spruce.
3. The reduction Norway spruce presence and abundance in the lowland areas between the Carpathians and the northern contiguous portion of the species range is likely the result of human activities, mainly the deforestations beginning in the Middle Ages, the drainage of numerous wetlands, and silvicultural practices over the last two centuries.
4. The Carpathian disjunction in the geographic range of Norway spruce range is the result of the comparatively lower altitudes of that montane region. *Picea abies* was present in this region about 5000 years ago. Broad-leaved forests subsequently replaced Norway spruce stands and its present-day occurrences are restricted to small isolated stands on cooler, wetter sites. Logging eliminated many other remnant stands.

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6. ANATOMY, EMBRYOLOGY, AND KARYOLOGY

Bud structure and shoot development

ALINA HEJNOWICZ

6.1. PRIMARY GROWTH

The description of bud development presented here is based primarily on the findings of HEJNOWICZ and OBARSKA (1995) and related studies. The embryonic shoots of vegetative and reproductive buds are visibly easy to differentiate in winter. With the aid of a microscope, it is possible to differentiate between bud types some months earlier. For example, in Poland the differentiation of the bud type takes place sometime in June (unpublished data; Fig. 6.1).

The embryonic shoot in the vegetative winter bud, encased by bud scales, possesses all of the next year's needle primordia, but not the lateral bud primordia. At the basal portion of the embryonic shoot in the cortex and pith there is a nodal diaphragm, termed a crown (Fig. 6.2). It is comprised of thick-walled parenchyma cells with irregularly thickened, but not lignified walls. A ring of vascular bundles interrupts the crown. In late autumn a gap arises below the crown due to the autolysis of pith cells (Fig. 6.2). Young needles or needle primordia in vegetative embryonic shoots are spirally arranged on the shoot axis in a specific pattern (phyllotaxis). Occasionally the phyllotaxis may change during shoot ontogeny, whereas the position of the primary vascular system is more stable. This suggests that the vascular system has a role in the positioning of successively initiated leaf primordia on the apex (ZAGÓRSKA-MAREK 1995). In the winter bud, below the base of the embryonic shoot, the bud scales are joined together at the base forming the receptacle.

The organization of the shoot apical meristem in spruce is typical for many *Coniferopsida*. At the apex there are a fixed number of apical initials, below which the central mother zone is located. Further below there is a pith-rib meristem zone, which produces pith cells. The peripheral meristem zone occurs on the flanks of the apical meristem and produces the scale and needle primordia (Fig. 6.1). The zonation of the apical meristem and the number of

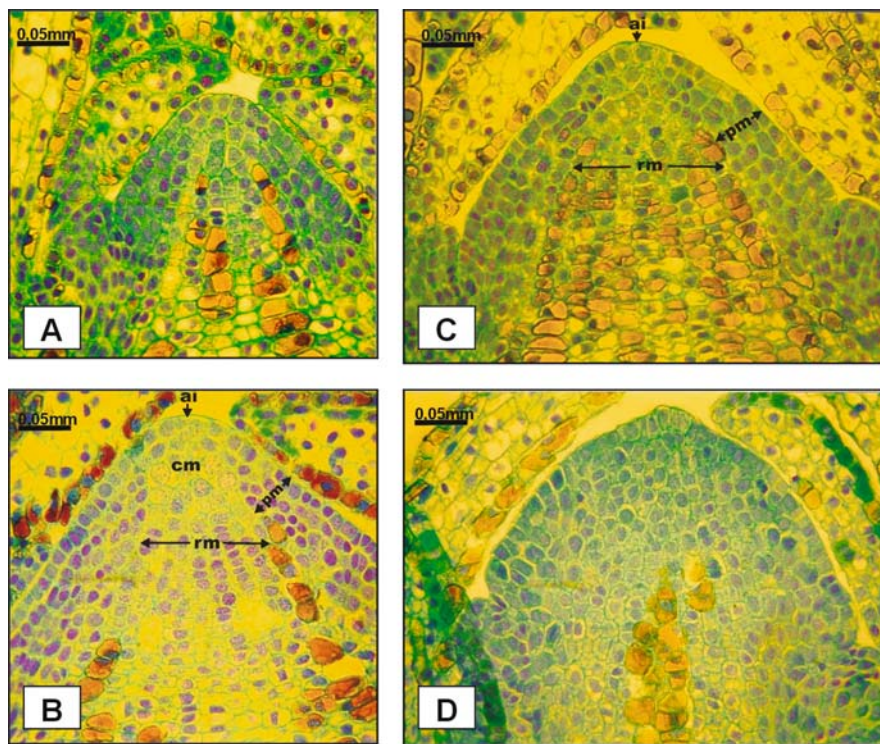


Figure 6.1. Shoot apex in longitudinal section. Feulgen reaction with fast green. Tannin cells are orange (photo A. HEJNOWICZ)

A -shoot apical meristem of the vegetative bud during the initiation of the bud scales for the following year's bud; early June; B – apical meristem of the male bud during the initiation of the first microsporophylls; early June. Beneath the apical initials (ai), central mother cells are visible (cm). Tannin cells are less numerous than in photo A; pm – peripheral meristem zone, rm – pith-rib meristem; C – apical meristem of the vegetative bud during the initiation of the needle primordia; mid-July; many tannin cells are visible in the apex; D – apical meristem of the male bud during microsporophyll initiation; mid-July; there are a few tannin cells in the apex.

cell layers in the different zones changes during shoot development. The number of vertical files of cells in the pith meristem also depends on stem vigor. For example, the width of the pith meristem decreases during shoot growth and with increasing branch order. The organization of the meristem tissues in the spruce shoot apex typical for a mature plant is achieved in seedlings as young as 30-days old (GREGORY and ROMBERGER 1972).

Lateral bud primordia arise in the axils of the elongating needles in late April, just when the apical meristem of the mother shoot has initiated bud scales for the following year's bud (HEJNOWICZ and OBARSKA 1995). Bud scale initiation lasts for about 2 months during the spring. Afterwards in late

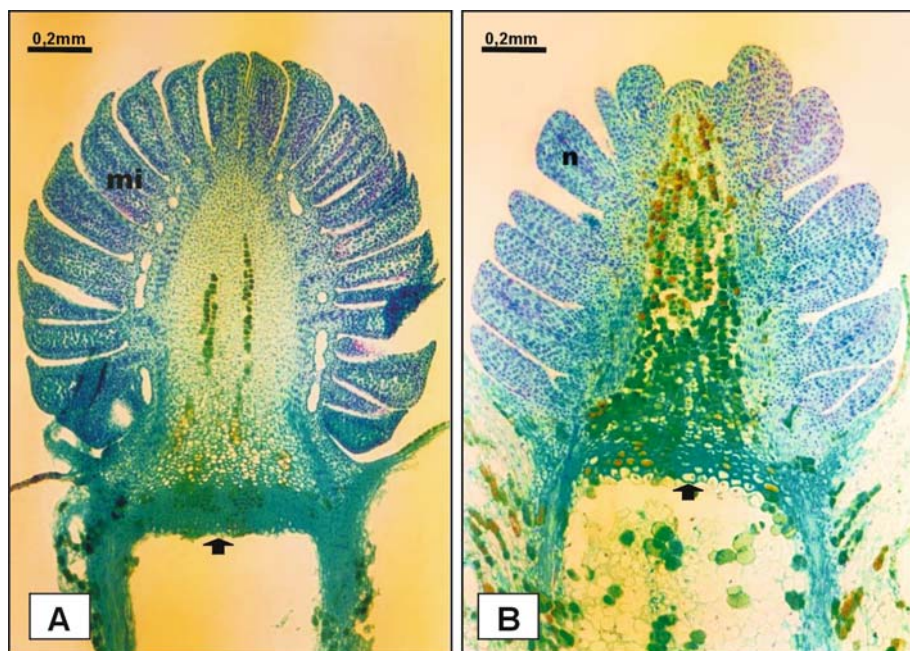


Fig. 6.2. Embryonic shoot of the winter bud in median longitudinal section; Feulgen reaction with fast green. Tannin cells in the pith are stained yellow or green. Arrows indicate the nodal diaphragm (crown). (photo A. HEJNOWICZ)

A – male embryonic shoot; mi – microsporophyll; B – vegetative embryonic shoot; n – needle

June or early July, needle primordia are formed in the vegetative bud. This process terminates in early September.

As early as June, the two types of embryonic shoot can be distinguished. The main difference between them is in the abundance of tannin cells in the young pith (Figure 6.1A, B). This difference is magnified during the next period of bud growth (Fig. 6.1C, D). In male reproductive buds, the number of tannin cells is much lower than in the vegetative buds (Figs 6.2, 6.3 and 6.4). The abundance of tannin cells in an embryonic shoot makes it possible to determine the bud type before the leaf primordia (needles or microsporophylls) become discernible.

One of the signs of the onset of bud activity is the accumulation of starch. In spruce, starch accumulation precedes the resumption of mitotic activity by about a month (GUZICKA 2001). In a winter bud, starch is undetectable with cytochemical methods under a light microscope (HEJNOWICZ and OBARSKA 1995). Nevertheless, under a transmission electron microscope, small starch grains were observed in some cells of the embryonic shoot of buds collected in January (GUZICKA and WOŹNY 2003).

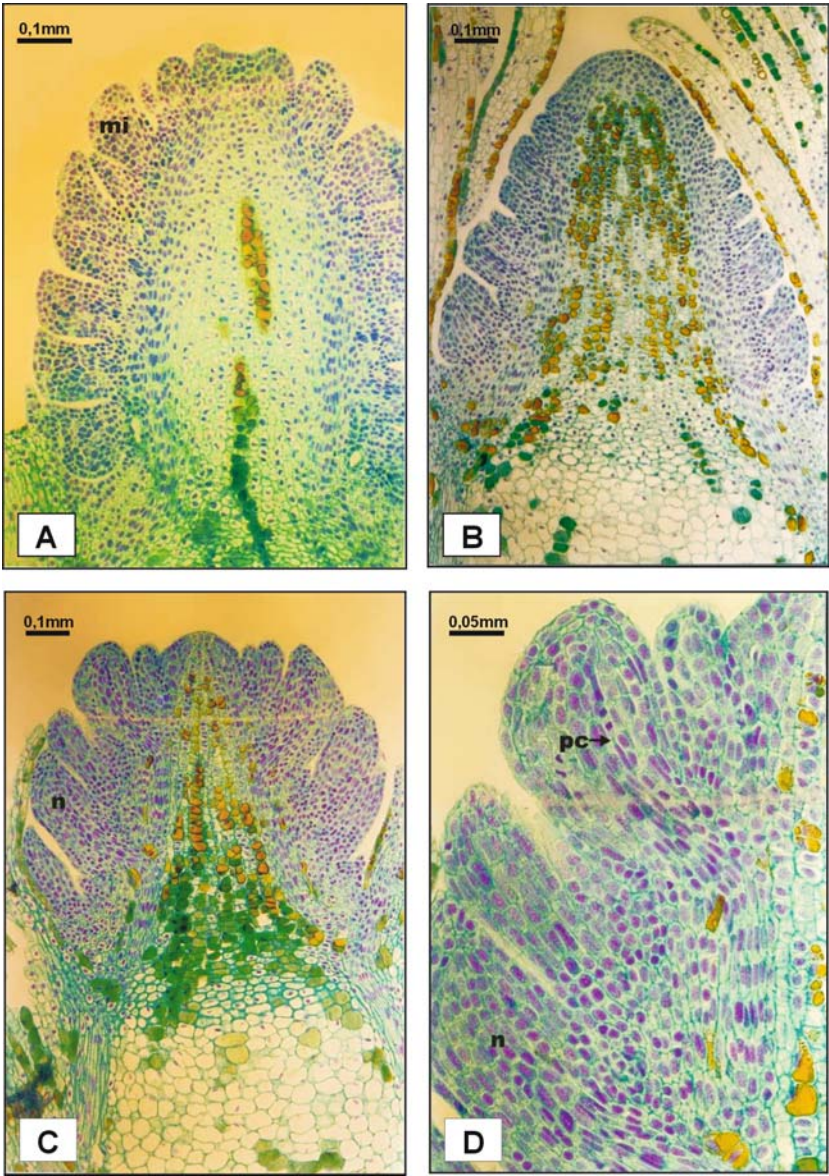


Figure 6.3. Embryonic shoot in longitudinal section; Feulgen reaction with fast green (photo A. HEJNOWICZ)

A – male embryonic shoot in mid-August; mi – microsporophyll; there are some tannin cells in the pith; B – vegetative embryonic shoot in mid-August; many tannin cells in the pith; C – vegetative embryonic shoot; late September; n – young needle; D – an enlarged part of C; pc – procambial strands; n – young needle

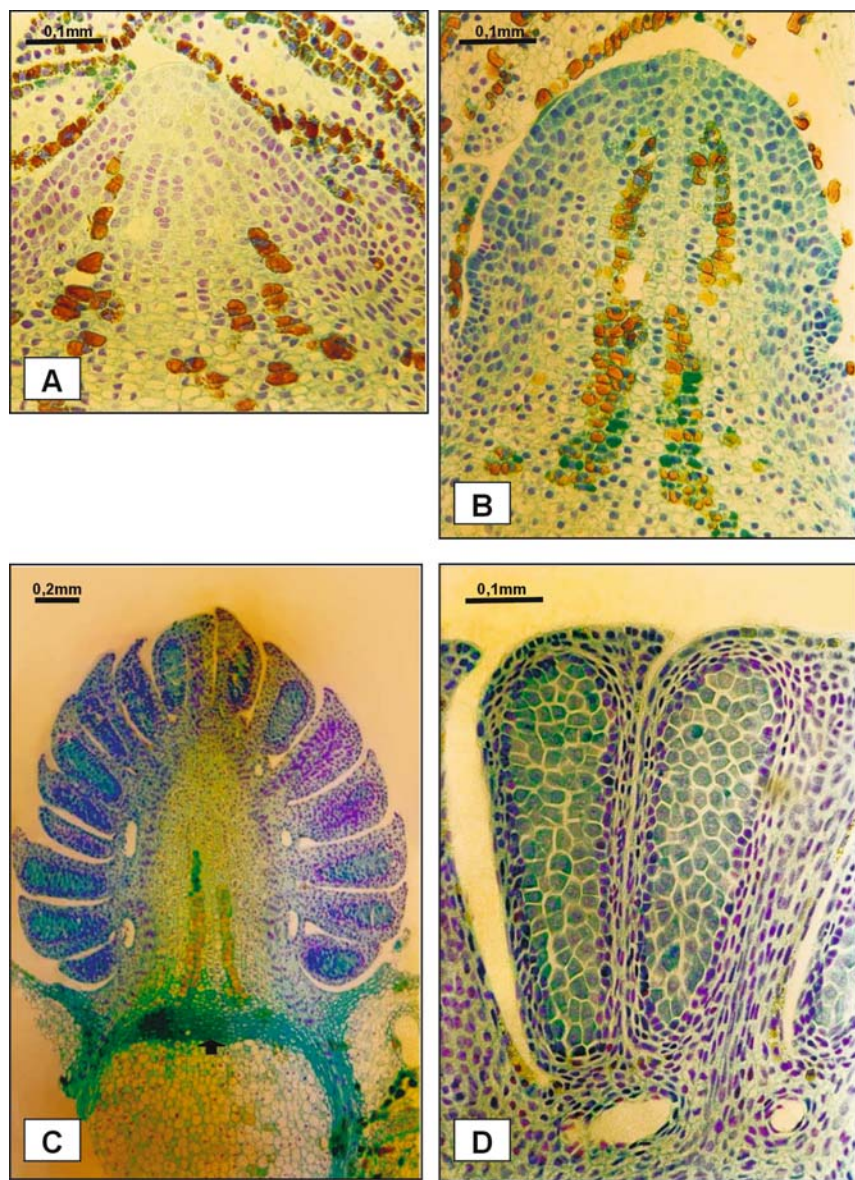


Figure 6.4. Development of the embryonic shoot of the male bud
(photo A. HEJNOWICZ)

A – early June; B – mid-July; C – late September (arrow – crown); D – microsporophylls with sporogenic tissue; mid-November

Before bud burst, the length of the embryonic shoot increases twofold due to internode elongation. About a month earlier, mitotic activity starts in different parts of the embryonic shoot (HEJNOWICZ and OBARSKA 1995). The first cells to divide are those of the scale and needle primordia, as well as the peripheral meristem of the apex. Eventually, the cells of the apical zone divide distally. The resumption of bud development depends primarily on air temperature. Temperature influences the time interval between the first mitoses in the embryonic shoot and bud burst. The time interval is the shortest when air temperature rises quickly. Typically, the first mitoses occur 3 to 4 weeks before bud burst (HEJNOWICZ and OBARSKA 1995). Shoot elongation begins already in the closed bud. Shoot elongation lasts for about 6 weeks in the lower portions of the tree crown. It appears that rainfall has no influence on the period of shoot elongation, but influences the elongation rate and the final shoot length (HEJNOWICZ and OBARSKA 1995).

6.2. SECONDARY GROWTH

6.2.1. *Vascular cambium*

In spruce the resting cambial zone is comprised of four to eight layers of radially arranged cells. In the cambial zone there is a single layer of initial cells, several layers of xylem mother cells located internally to the initials, and phloem mother cells located externally. Some of the mother cells remain as meristems, while the initials produce new mother cells. Sometimes in undifferentiated xylem and phloem, files of cells, two or four cells surrounded by a common primary cell wall can be seen (SANIO'S fourth).

The cambial initials, whose derivatives produce the axial system, are called fusiform initials. In winter they have a folded cell membrane (plasmalemma), large elongated nuclei, numerous small vacuoles, plastids, amyloplasts, and small amounts of endoplasmic reticulum (TIMELL 1980). The ray initials are rich in lipid bodies. When the spring growth starts, the small vacuoles join into one large vacuole. Simultaneously, golgi bodies (which were invisible in the resting cambium) appear together with multi-vesiculate structures that participate in cell wall formation (TIMELL 1973).

The resumption of cambial activity in the spring depends on air temperature. Initially it also influences mitotic activity and the size of the cambial derivatives. Water is the main factor affecting cambial activity during the next phase of shoot growth. Water deficit can be compensated by enhanced mineral nutrition (DÜNISH and BAUCH 1994). Cambial activation in central-European climatic conditions takes place in April. It may be delayed due to low temperatures in March and April. In years with high March and April temperatures, 10% of the xylem growth ring may arise in April, whereas growth may be

delayed by a month during a cold spring (WENK and FIEDLER cit. SCHMIDT-VOGT 1986).

Three periods of seasonal cambium activity may be distinguished in spruce (GREGORY 1971): the starting phase when the meristematic mother cells initiated in the previous year divide; the main phase during which 80% of the growth ring arises; and the last phase when the rate of cell division decreases. The cessation of cell division takes place in September. As with cambium activation in spring, the growth cessation depends on climatic conditions, mainly temperature.

Cambial activity in *Picea abies* begins beneath the emerging new shoots and proceeds basipetally, toward the trunk and root. Cell divisions begin about 2 weeks before bud break, followed by cell divisions in the trunk a few days later (at a height of 1.3 m) and about a month later in roots (LADEFOGED 1958). The stimulus inducing cambial activity is hormonal. The direction in which the cambial cell divisions proceed coincides with the direction of the displacement of the hormonal stimulus. Factors other than temperature, such as photoperiod, light, and environment influence the rate of mitotic activity of cambium cells. Consequently, these environmental factors determine the width of the annual growth ring (among others see: ŻELAWSKI and WODZICKI 1960, WODZICKI and WITKOWSKA 1961, ESCHRICH and BLECHSCHMIDT-SCHNEIDER 1992, DÜNISCH and BAUCH 1994).

The circumference of cambial cylinder increases as the core of the secondary xylem becomes thicker. Both multiplicative (BANNAN 1963) and anticlinal-pseudotransversal divisions of the cambial initials contribute to circumference growth. Each of the new cells elongates by apical intrusive growth. As a result, the new sister cells come to lie side by side in a tangential plane. The sister cells are shorter than the mother cell. As the anticlinal-pseudotransversal divisions commonly occur at the end of the growth period, their derivatives (xylem and phloem) near the boundary of the annual growth ring are the shortest (see "Secondary xylem")

6.2.2. Bark

The thickness of Norway spruce bark is small in comparison with other *Coniferopsida*, attaining 10–12 % of the trunk diameter on average. Bark is comprised of tissues external to the cambium: the secondary and primary phloem, cortex, periderm, and rhytidome. The latter is comprised of tissue layers isolated by the periderm. Rhytidome constitutes the outer bark in older stems and roots.

The secondary phloem occupies 50–85% of the total bark width. Growth rings of the secondary phloem are typically 0.2–0.3 mm wide. In trees from nutrient poor sites, the phloem growth rings are two-fold narrower than in trees from optimal sites (KARTUSCH *et al.* 1991). Within the youngest phloem, the borders between growth rings are distinct (Fig. 6.5A). Within the oldest phloem, the ring boundaries are less distinct. Nevertheless, the borders can be

estimated based on the shape of the sieve cells. The sieve cells differentiating at the beginning of the growing season are square in cross section, whereas at the end of the growth period they appear flattened in a tangential plane.

A growth ring of secondary phloem is comprised of 10–12 layers of sieve cells and a single layer of parenchyma cells (Fig. 6.5). In narrow rings the number of layers is reduced. From 60–90% of the secondary phloem is comprised of sieve cells, parenchyma cells, and rays. Fibers are absent. In older phloem some parenchyma cells become sclereids. There are also numerous crystals of calcium oxalate. Sieve cells are about 2.8 mm long and 0.02 mm wide. The radial walls of sieve cells possess sieve-fields. Their pores remain open for about two years (HOLDHEIDE 1951). As a rule, sieve cells in spruce function only for one season and a short part of the next one (HUBER cit. ESAU 1969). The sieve cells are crushed in old phloem.

Phloem parenchyma forms discontinuous strands in the middle of the growth ring. The length of parenchyma cells is about 75 μm and their width is initially smaller than that of sieve cells. Later the parenchyma cells increase in

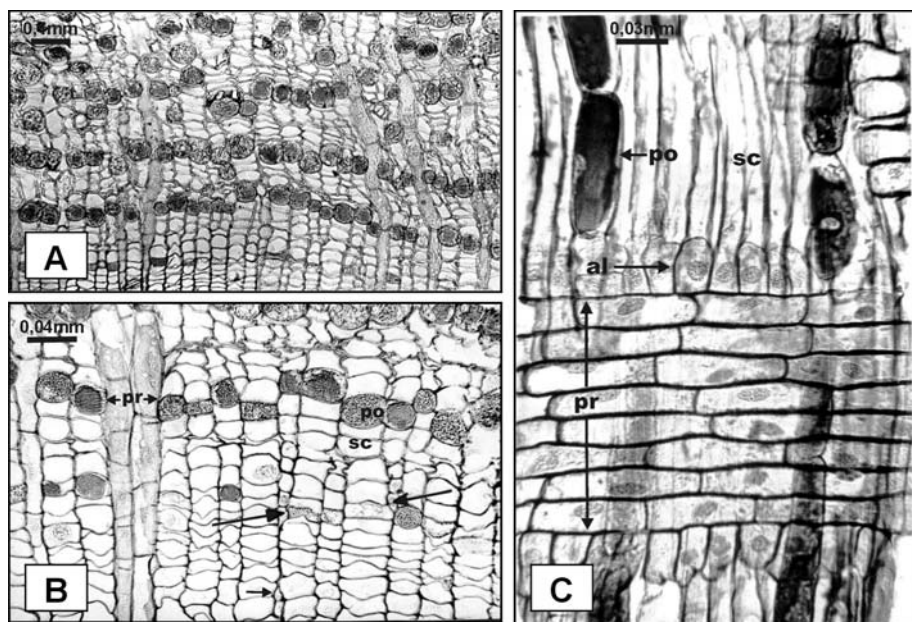


Figure 6.5. Living bark (photo A. HEJNOWICZ)

A – secondary phloem in cross section; B – cambium and secondary phloem in cross section; arrows – eliminated files of cambium cells; sc – sieve cells, pr – ray, po – phloem parenchyma cells; C – secondary phloem in radial section; al – albuminous cells of the ray, pr – ray parenchyma cells, po – phloem parenchyma cell

width. Some of the parenchyma cells become sclereids. Their walls become thick and lignified, but owing to the presence of pits, these walls maintain contacts between adjacent cells. Sclereids are numerous in the phloem of trees from poorer sites (KARTUSCH *et al.* 1991).

Phloem rays are arranged in a single series and contain parenchyma and albuminous cells at their margins (Fig. 6.5C). Albuminous cells lack starch, whereas parenchyma cells are very rich in starch. Albuminous cells are functionally associated with the sieve cells. Thus, they resemble the companion cells of angiosperms, but do not originate from the same precursor cells as the sieve tube members (SRIVASTAVA 1963, TIMELL 1973). In spruce, in addition to the uniseriate rays, there are also multiseriate ones with horizontal resin ducts. In phloem ray cells there are numerous calcium oxalate crystals, depending upon the content of available calcium in the soil (KARTUSCH *et al.* 1991).

The periderm includes the cork cambium (i.e. phellogen) that produces the periderm, composed of phellem formed on the outer side by the phellogen, and phelloderm (living parenchyma cells) formed on the inside of the phellogen layer. In spruce the first phellogen arises in the cortex and functions only for one season. Subsequent phellogen cells arise in the deeper layers of secondary phloem. The periderm is layered and comprised of sclerified, spongy, and phlobaphene cork layers. Four or more layers of sclerified cork cells alternate with those of the other cork layers and indicate seasonal growth increments. Phelloderm is comprised of two to three layers of parenchyma cells. As a tree grows, the number of cork cells decreases. In roots the spongy and sclerified phellem of the periderm are each comprised of one layer of cells. Old phellogen layers are eventually cut off to form the outer bark scales or plates. Each scale is comprised of periderm and secondary phloem cut off by phellogen. Scales on the stem surface are typically small and are sloughed off. In roots they are much larger and remain intact.

In the periderm there are isolated regions distinguished from the phellem by the presence of intercellular spaces, called lenticels. These structures permit the entry of air through the periderm. The phellogen of a lenticel is continuous with that of the periderm. The outer loose tissue formed by the lenticular phellogen defines the border of the lenticel. Like the phellem, it is comprised of layers of stained, spongy, and phlobaphene cells (WUTZ 1955).

In *Picea abies*, bark thickness and microscopic structure depend to a high degree on light environment. Trees from shaded sites have bark two- to three-fold thinner than individuals growing in high-light sites. Differences in microscopic structure are also quantitative. The secondary phloem in shade-grown trees is up to two-fold narrower than in high-light trees. The length and width of sieve cells are greater in high-light than shaded trees. High-light grown trees have six times more sclerenchyma cells in the bark of stems than in shaded trees (EREMIN 1982).

6.2.3. Secondary xylem

Secondary xylem of *Picea abies* is macroscopically homogenous. The border between sapwood and heartwood is not sharp, both types of wood are histologically identical. Annual growth rings are distinct (Fig. 6.6). The width of the growth rings varies along a radius from the pith outward. Ring widths are greatest for a relatively short period (until about the 20th growth ring, depending on the distance from the tree base), after which annual growth increments decline slowly. Environmental factors have a profound effect on the growth rate and ring widths in mature wood. Each growth ring can be divided into early and late wood (Fig. 6.6A, B, D). Late wood occupies from 2 to 30% of the total growth ring thickness (HEJNOWICZ 1969). In trees from poor habitats, the late wood constitutes a greater proportion than in trees growing in favorable conditions.

Up to 90% of the wood structure is comprised of tracheids. These are narrow, elongated cells 2–5 mm long on average and 0.01–0.06 mm wide. The mean radial diameter of an early wood tracheid (0.026–0.058 mm) is twice greater than in late wood (0.01–0.025 mm) (HEJNOWICZ 1969). Growth rate and tracheid length are related. The longest tracheids are found in growth rings 1–2 mm thick. The usual inverse relationship between ring thickness and tracheid length tends to be reversed in very narrow rings. Finally, the dependence of cell length on growth rate (in terms of ring thickness) is also related to the frequency of pseudo-transverse divisions of cambial cells. Within a growth ring, the mean tracheid length is the greatest in the transition zone from early to late wood, and the smallest near the growth ring border (BANNAN 1963).

The tracheid wall is built of a compound middle lamella and the secondary walls frequently comprised of three major layers: S1, S2, S3. The thickest is the S2 layer, which occupies 80% of the entire width of the secondary wall. The separation of the secondary wall into three layers is the result of the different orientations of microfibrils (constituents of the cell wall consisting of cellulose molecules). There exists a positive correlation between cell wall thickness and several environmental factors, such as day length, light intensity, and temperature. For example, in tracheids formed at 7°C, cell walls are twice thicker than those formed at 23°C (RICHARDSON 1964).

In the walls of the tracheids there are the bordered pits typical for *Coniferopsida* (Fig. 6.7). The pit diameter is 0.011–0.022 mm. Two opposing pits are called a pit-pair. Each pit has a pit cavity. The secondary wall may overarch the pit cavity forming a border. The pit cavity is enclosed by the border and opens into the cell lumen. A thickened membrane is present in the middle of the pit. This thickening forms the torus. Pits are located mainly on the radial walls of early wood and are abundant on the overlapping ends of tracheids (Fig. 6.7B). Tangential tracheid walls may bear pits in the late wood. In spruce some wide early-formed tracheids may have two rows of pits. The mean number of pits per tracheid ranges from 70–210.

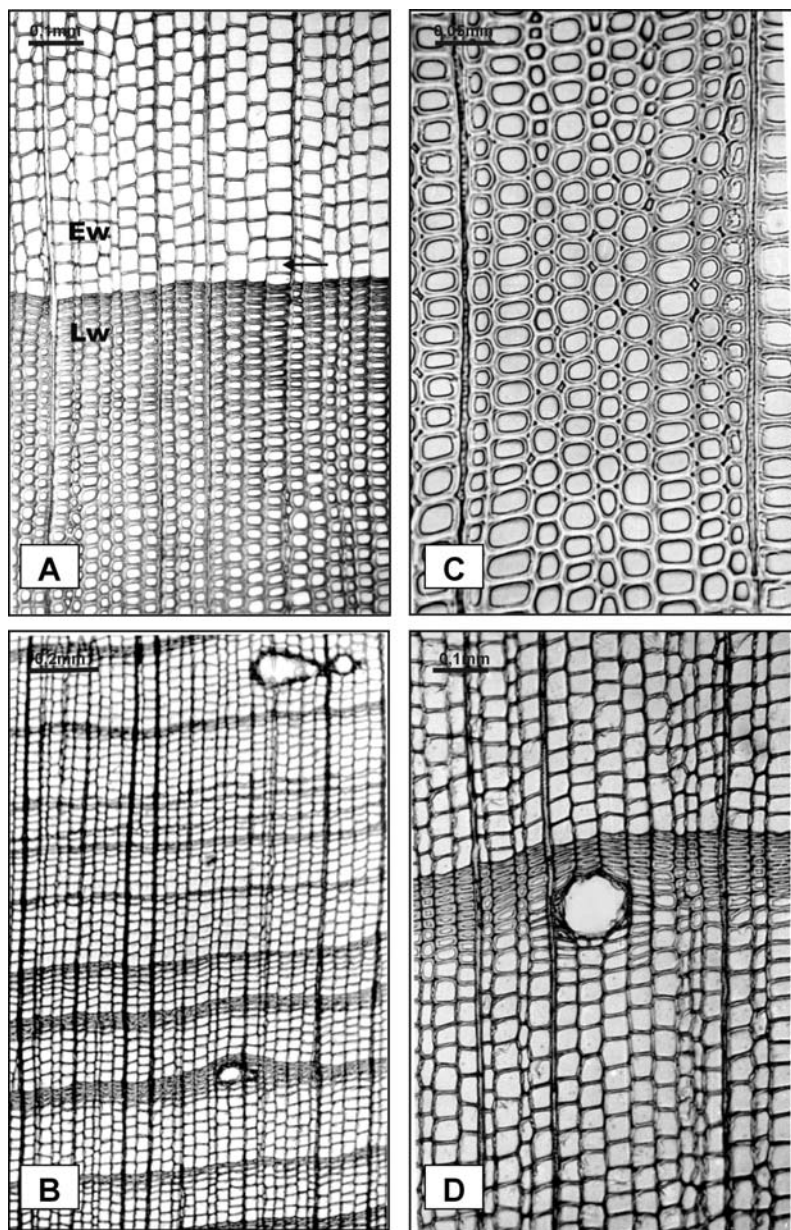


Figure 6.6. Stem wood in cross section (photo A. HEJNOWICZ)

A – parts of the two adjacent growth rings; Ew – early wood, Lw – late wood; arrow – trabecula;
 B – stem wood from the peripheral part of an old tree; C – reaction (compression) wood; D –
 axial resin duct with thick-wall epithelial cells; late wood

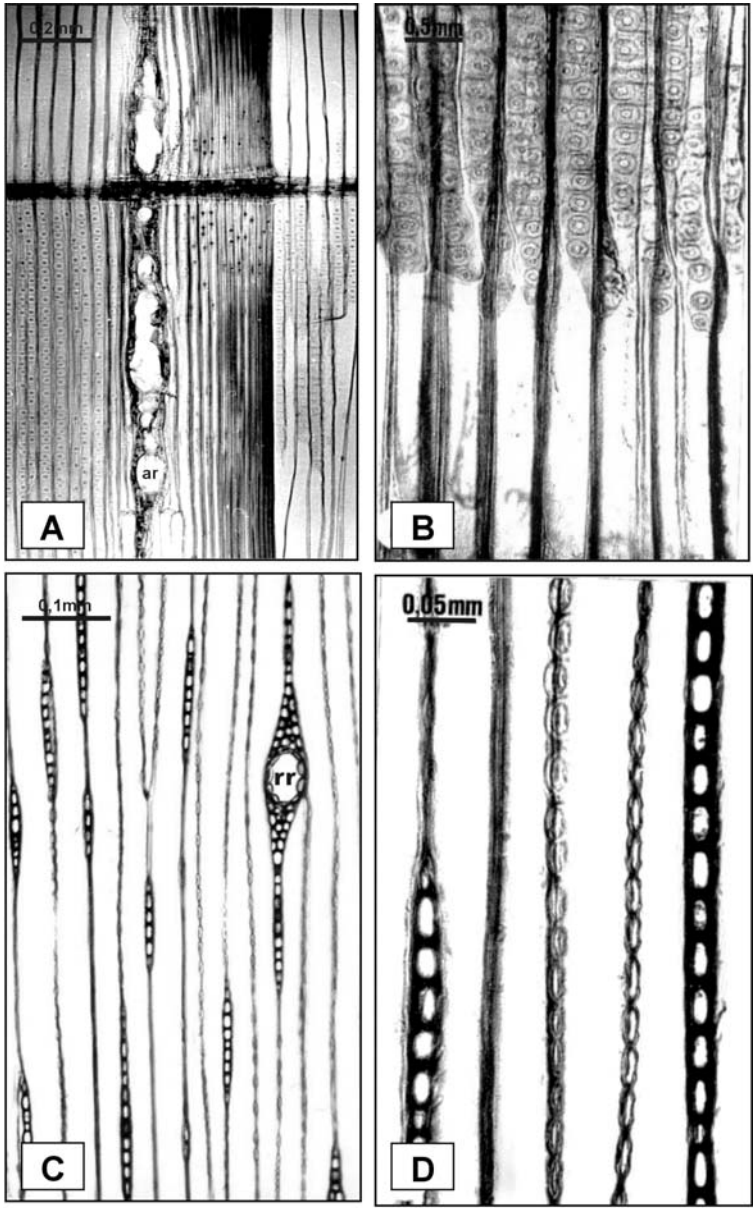


Figure 6.7. Stem wood in longitudinal radial (A and B) and tangential (C and D) section (photo A. HEJNOWICZ)

A – axial resin duct (ar) in late wood; B – bordered pits in tracheid walls; C – wood rays; rr – horizontal resin duct; D – bordered pit (bp) in radial tracheid wall

It has long been known that spruce wood exhibits excellent resonating properties, particularly in slowly growing trees. Therefore, spruce is frequently used in the construction of musical instruments. When selecting spruce wood for its resonating properties, it is of the utmost importance that it possesses a regular, even structure. The growth rings should be of the same width, with a smaller proportion of late wood and larger diameter bordered pits in the early wood tracheids and rays in comparison to nonresonant wood (KOCZWAŃSKA 1970). For this purpose the wood must be floated in water for a long period of time. Presumably, bacteria damage the pit membranes in the tracheids during floating so that the tori do not occlude the pits any longer. However, in examined samples of spruce wood from old Italian violins dating from the 16th to 18th centuries, the pit membranes remained intact (BARLOW and WOODHOUSE 1990).

Spruce wood possesses trabecula, rod like parts of the cell wall extending radially across the lumen of axial tracheids (Fig. 6.6A). They are more numerous in tracheids of trees growing under unfavorable conditions and often arise near injured tissues (GROSSER 1986). Spruce wood rays are heterogenic and uniseriate (Fig. 6.7A). Some of them include horizontal resin ducts, which usually occur near the center of the fusiform ray (Fig. 6.7C). There are 30–50 rays per 1mm^2 of a tangential section. The rays are numerous near the pith. They are comprised of two kinds of cells: parenchyma cells and ray tracheids, which are located usually on the ray margins. The rays are about 0.1–0.2 mm in height and are comprised of 6–12 cells.

In radial longitudinal section, the characteristic arrangement of pits can be observed in a cross-field over the radial wall. Cross-field is the portion of a radial section bounded by the upper and lower horizontal walls of a ray parenchyma cell, and the wall of an axial tracheid. The pitting at the cross-fields is used for the identification of conifer wood types. In spruce the pitting is of the piceoid type, but some other kinds of pitting (cupressoid, taxodioid) can also occur in the first several growth rings (HEJNOWICZ 1969).

Resin ducts in *Picea abies* wood run axially between the axial tracheids, and radially in the fusiform rays. The axial ducts occur mainly in the transitional region of the growth ring (Figs 6.6B, D and 6.7A). Resin ducts in *Picea abies* are schizogenous in origin, meaning they are formed from the splitting of adjacent cells. They are lined with 7–12 resin-producing epithelial cells. There are two kinds of these cells: thin- and thick-walled. Thin-walled cells have no secondary walls. Simple pits are present in the anticlinal walls between the thick-walled cells and absent in tangential walls facing the canal lumen (TAKAHARA *et al.* 1983). In spruce heartwood, the thin-walled epithelial cells grow into intercellular resin duct lumens, forming the thylosoids. Resin ducts can also develop in response to injury, occurring as very large cysts or pitch pockets formed in the same manner as the resin ducts.

The type of reaction wood in spruce is compression wood. The stimulus of gravity and the distribution of endogenous growth hormones are important

factors in initiating the development of reaction wood. Compression wood in gymnosperms is formed in regions of high auxin concentration. Tracheids in compression wood are shorter than those in normal wood. Their cell walls are thicker, much more lignified, and appear rounded in transverse sections. The inner (S3) layer of the secondary wall is absent and the S1 layer is more loosely attached to the primary wall and the S2 secondary wall layer. The microfibril angle in the S2 layer is much greater ($30\text{--}50^\circ$) than in tracheids of normal wood ($10\text{--}30^\circ$).

6.3. ROOT STRUCTURE AND DEVELOPMENT

The spruce root tip has a single group of initials arranged in a transverse tier (Fig. 6.8). Consequently, the vascular cylinder, cortex, and root cap have common initials (the open type of apical organization). The root cap is a structure protecting the apex and assisting the growing root in soil penetration. It is comprised of vertical cell files building the columella with transversally dividing cells. The columella produces derivatives for lateral portions of the root cap. While new cells are produced, the cells on periphery of the root cap are sloughed off.

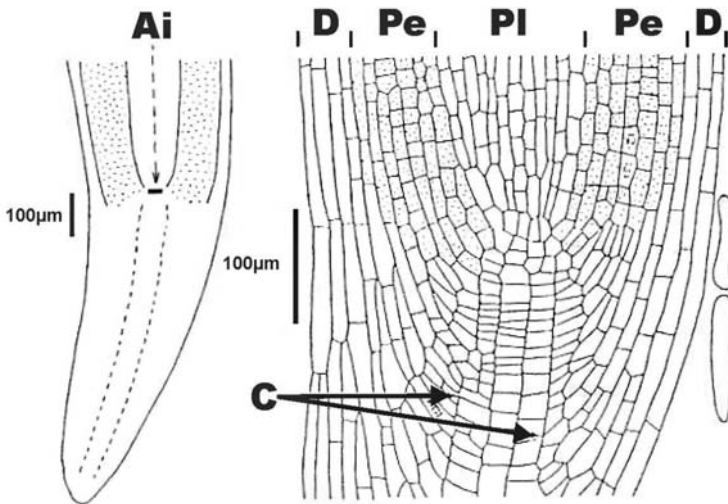


Figure 6.8. The median longitudinal section of the root tip of spruce (ESAU 1977)

Ai – apical meristem center; D – dermatocalyptrogen; C – columella; Pe – periblem (the future root cortex); Pl – plerome (the future central vascular cylinder)

The root of Norway spruce is diarchic, possessing two primary vascular strands comprised of proto- and metaxylem, which alternate with the two proto- and metaphloem strands. The vascular cylinder occupies the center of the root. The external layers of vascular cylinder are called the pericycle. The innermost layer of the cortex differentiates into the endodermis. Casparian strips are present in the radial and transverse anticlinal walls of the endodermal cells (JORUS 1987). These band-like structures develop within the primary walls and contain suberin and lignins. The casparian strips establish the barrier to apoplastic movement of solutes into the vascular cylinder. Endodermal cells differentiate a short distance from the apical center. Metakutis, a protective layer of suberized cells typical for other woody plants that covers the apical meristem is absent in spruce roots (PLAUT 1910).

The secondary structure of spruce roots differs from the stem. The periderm is constructed of only two or three layers of cells with thick, lignified walls. The arrangement of the cells in the secondary phloem is not as regular as in the stem. Sclereids are absent, but gelatinous fibers, which are absent in stem, are present in roots (CUTLER *et al.* 1987). In woody roots the growth rings are narrower and the transition from early to late wood is less distinct than in the stem. Axial and ray resin ducts are similar to those of stem wood.

6.4. LEAF STRUCTURE

Needles persist on *Picea abies* shoots for 5–7 years. The shape of the needle in cross-section is diagnostic for the genus *Picea* (NESTEROVICH *et al.* 1986). The shape of needle in cross-section varies along the length of the needle. It is rhomboid in the middle, somewhat flattened near the base, and almost square near the needle apex. The needle is single veined and has a distinctly differentiated endodermis. A thick-walled epidermis with a heavy cuticle and stomata covers the needle (Fig. 6.9). Stomata occur in longitudinal rows on all four sides of the needle in three to four rows on the upper side and one or two on the lower side. The stomata of *P. abies* are deeply sunken and appear as though suspended from the subsidiary cells, which overarch them (Fig. 6.9). There are 40–50 stomata per mm² of needle surface (COLLEAU 1968, ČIŽKOVÁ 1988).

Sclerified hypodermis occurs beneath the epidermis except under the rows of stomata. Mesophyll lies between hypodermis and endodermis and occupies 92% of the cross-sectional area. The vascular cylinder occupies 6.7% of the needle cross-section. In spruce the vascular cylinder is four times smaller in diameter than in pine (ČIŽKOVÁ 1988), and is much larger in trees from higher than lower elevations (DRAXLER and RUPPERT 1989). Two collateral bundles are located at the center of the vascular cylinder. The xylem is on the adaxial side (toward the shoot axis), and phloem on the abaxial side. Vascular bundles are comprised of proto- and meta-phloem cells and proto- and metaxylem elements. Protophloem cells are crushed very early in needle ontogeny.

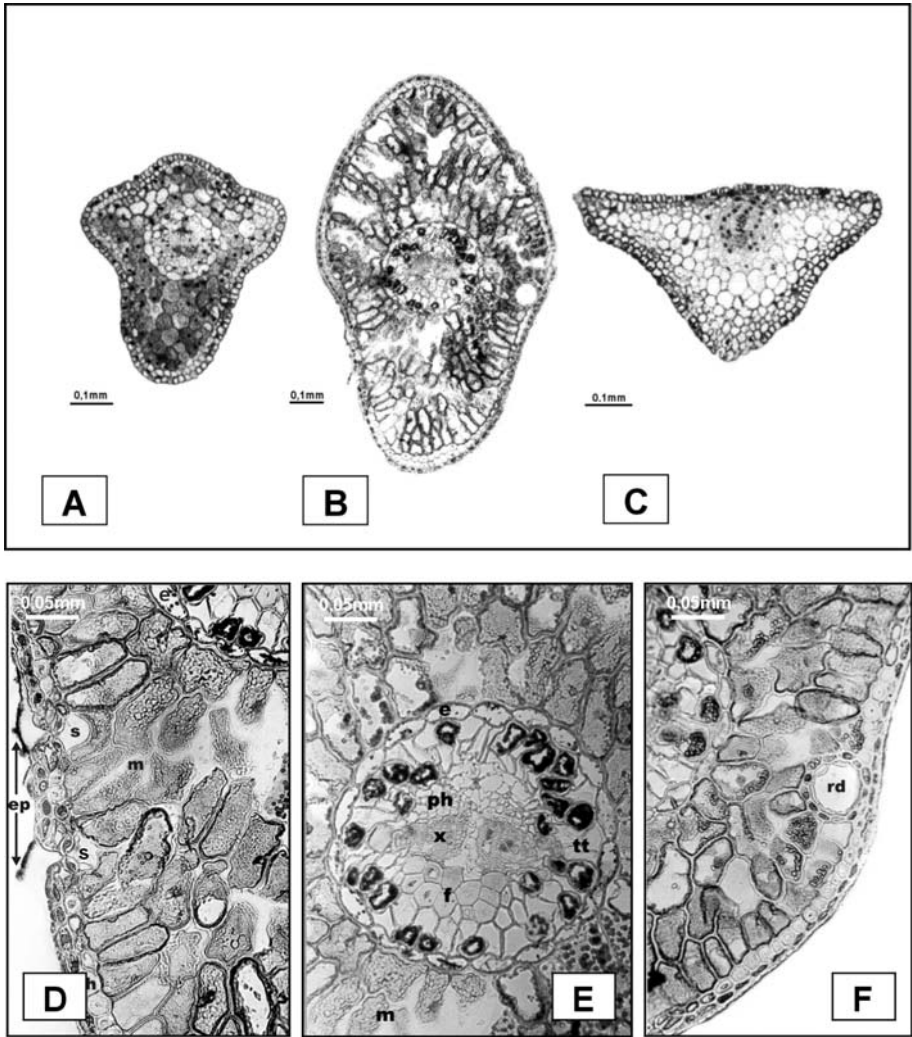


Figure 6.9. Spruce needle in cross section (photo A. HEJNOWICZ)

A – young needle; early May; B – two-year-old needle; C – bud scale; early May; D – marginal part of the needle: ep – epicuticular waxes, s – stomata, e – endodermis, h – hypodermis, m – mesophyll; E – central part of a two-year-old needle: e – endodermis, f – fibers, x – xylem, ph – phloem, m – mesophyll, tt – transfusion tissue; F – marginal part of the needle: rd – resin duct

Epidermal cells are flat (Fig. 6.9D, F) and about $7\text{ }\mu\text{m}$ thick. The outer tangential wall is thicker than the inner wall. It is covered with a thick layer of cuticle and epicuticular waxes (Fig. 6.9). The thickness of an epidermal cell is about $9\text{ }\mu\text{m}$. There are five phases of epidermal cell wall differentiation: protodermal; steady; unsteady; lignification; and secondary modification (e.g. accumulation of polyphenols). The last phase occurs in the second to fifth year of needle growth (TENBERGE 1992). Hypodermal cells are $0.021\text{ mm} \times 0.018\text{ mm}$ in cross-section. During needle maturation their walls became thicker and more lignified.

Mesophyll, the photosynthetic parenchyma, consists of cells with vertical ridges protruding into the cell lumen. The ridges develop as invaginations of the primary cell wall. Resin ducts are sparse and lie mainly under the hypoderm as elongated cysts, 2 mm long. They are lined with 5–7 epithelial cells and surrounded by a sheath of 8–10 thick-walled cells (Fig. 6.9F). The endodermis is a single-cell thick layer of parenchyma lacking chloroplasts (Fig. 6.9E). The number of cells comprising the endodermis in *Picea* species is relatively constant and is regarded as a diagnostic feature within the genus (MARCO 1939).

6.5. REPRODUCTIVE CYCLE

Most of the information on the reproductive cycle presented in this chapter is based on the following sources: MIYAKE (1903); HÅKÅNSSON (1956); SARVAS (1968); MIKKOLA (1969); ANDERSSON *et al.* (1969); CHRISTIANSEN (1972); JONSSON (1973); ANDERSSON (1980); MOSHKOVICH (1992) and OWENS *et al.* (2001). Contrary to the other *Picea* species, the development of reproductive organs of Norway spruce is only sparsely illustrated. However, it seems that there are no fundamental differences in the reproductive cycle between Norway spruce and other spruce species and a number of other species of the *Pinaceae* family.

6.5.1. *Microsporogenesis and microgametogenesis*

The determination of the male bud takes place in late spring or early summer. In mid July, the first microsporophyll primordia become visible in the embryonic shoot (Fig. 6.1D). During the following months, two microsporangia with well-defined sporogenic tissue develop inside a microsporophyll. The microsporangial initials are hypodermal in origin. The inner layer of microsporangium develops into the tapetum. At this stage the male buds enter into the winter dormancy period. During the next spring, the sporogenous cells divide and microsporocytes develop (i.e. microspore mother cells). The common wall of the microsporocytes is lysed. The nuclei of the tapetum cells divide but cytokinesis is absent and mature tapetum cells are predominately binucleate.

In central Europe, meiotic divisions of the microsporocytes take place in late April and last only for a few days. The air temperature has a significant influence on meiosis. At -2°C some irregularities have been observed, whereas at -10°C all the dividing microspore mother cells die (ANDERSSON 1980). Each functional microsporocyte gives rise to four haploid microspores, which are enclosed within the wall of the microsporocyte for some time. When the microspores enlarge, the wall disintegrates and connections between the microspores disappear. Two bladders or wings are formed on each spore due to the separation of the outer and inner layers of the microspore wall.

Before the pollen is shed, a mitotic division of the microspore gives rise to a two-celled gametophyte comprised of the central and the prothallial cell. The division of the central cell in turn, gives rise to a second prothallial and to an anteridial cell. The latter divides forming a generative cell and tube cell. Both prothallial cells soon become flattened and die. This is usually the stage in which pollen grains are released into the air.

The diameter of the mature pollen grain in spruce is $70\text{--}90\text{ }\mu\text{m}$. Pollen grains are two-fold larger than in *Pinus* species and have smaller air-filled wings. Consequently, they are not dispersed as far as pine pollen grains. There are numerous amyloplasts in the cytoplasm of the mature pollen grains. The generative cell of the germinating pollen grain divides, giving rise to the spermatogenic and stalk cells. CHRISTIANSEN (1972) did not observe the stalk and tube cells in microgametophytes of *Picea*. On the contrary, HÅKÅNSSON (1956) has noticed both these cells in *Picea* pollen tubes.

6.5.2. Megasporogenesis and megagametogenesis

Female buds like the male buds are initiated the growing season prior to the year in which flowering occurs. In Poland, the differentiation of female buds usually takes place in June. In July the first scale primordia arise on the shoot apical meristem. A month later the first primordia of ovuliferous scales (seed scales) are initiated in the axils of some scale primordia. A bract subtends each ovuliferous scale. The bracts are much shorter than the associated ovuliferous scales. Up to 10% of the cone scales are sterile. The sterile scales are mainly formed near the end of the growing season and at the beginning of the next one.

Each ovuliferous scale bears a pair of ovules, attached at the base of its adaxial surface. The ovule consists of the nucellus, i.e. the central body of vegetative cells, which later encloses the sporogenous cells, and a single integument (ovules are unitegmic). The ovule is inverted and a conspicuous micropyle points inward toward the cone axis. The sporogenic tissue differentiates in early spring (in March) from the subepidermal initial cell at the apex of the nucellus. The megaspore mother cells (megasporocytes) and the nucellar cap, located above them, are formed in sporogenic tissue. The nucellus enlarges and the megasporocyte yields a tetrad of haploid

megaspores. Three of them soon degenerate and the fourth, the chalazal megaspore, functions as a mother cell of the megagametophyte. During the free nuclear period of growth, the mitotic divisions of the megagametophyte nuclei are not followed by cytokinesis. When cell walls are finally formed, the coenocytic megagametophyte is converted into cells. The free nuclear period lasts for several weeks. The female gametophyte is completely cellular 10–14 days after pollination. Earlier, the free end of nucellus becomes slightly concave and the pollen grains are deposited into the shallow cavity.

On the micropylar pole of the megagametophyte, one or several superficial cells divide periclinally and differentiate into two cells: a small outer primary neck cell; and a larger inner central cell. By means of two successive anticlinal divisions and two periclinal divisions of these four cells, an eight-celled neck is formed. The neck cells are arranged in two or sometimes four tiers. The central cell is the archegonial mother cell.

The number of archegonia produced by a single gametophyte varies considerably. There are from one to seven (mean 2.8–3.4) archegonia present in a single ovule (SARVAS 1968). Half of the 300 ovules studied by MIYAKE (1903) had four archegonia, 25% of them had three; 20% had five; and in individual ovules there were two, three or seven archegonia. In mid May each of the archegonium mother cells enlarges and their nuclei divide, giving rise to a small ventral canal cell. The nucleus of the egg cell is about 0.1 mm in diameter. The nucleus moves to a central position in the egg. When mature, the egg is jacketed by a distinct layer of cells with numerous proteinaceous bodies in the cytoplasm.

6.5.3. Pollination and fertilization

In the climatic conditions in Poland, pollen shedding takes place in late April or early May. At this time the axis of the young megasporangiate cone elongates and the ovuliferous scales separate. Pollen grains transported by the wind enter the space between the scales and adhere to the pollination drops, which are exudates of the open ends of the inverted ovules (RUNIONS *et al.* 1995). Pollen grains in the liquid fill the micropylar canal of the ovule, which is enclosed by the edges of the integument. After pollination the ovuliferous scales are drawn together and remain tightly pressed. A few days after the pollen grains entered the pollen chamber, the growth of pollen tube begins. When the pollen tube approaches half the distance to the egg cell, the spermatogenous cell of the male gametophyte divides to form two male gametes of unequal size. The tube cell, stalk cell, and male gametes move toward the tip of the pollen tube.

Pollen tube growth is dependent upon air temperature, usually quantified by a degree-day index, the sum of the mean daily temperature above a base temperature of 5°C. In Finland, pollen tube growth starts at 220 degree-days (SARVAS 1968). Four to five weeks after pollination, the pollen tube penetrates the nucellus. Since several pollen grains may have reached the apex of

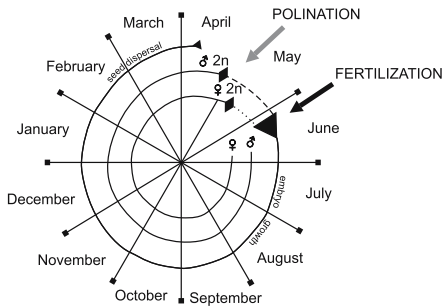


Figure 6.10. Reproductive cycle in the climate conditions of Poland

the nucellus, a corresponding number of tubes may be formed. However, typically only one tube reaches the female gametophyte. The tip of a pollen tube forces itself between the neck-cells and then ruptures, discharging the two male gametes, the tube nucleus, and stalk cell into the cytoplasm of the egg cell. Usually the smaller male gamete, tube nucleus, and stalk cell degenerate. Initially, the nuclei of the male and female gametes are separated by their nuclear envelopes. Following syngamy, the nucleus of the fertilized egg contains one paternal and one maternal hap-

loid complement of chromosomes. These two sets of chromosomes soon become arranged along the equatorial region of a separate or common spindle, but with several poles. In the late metaphase a single spindle is observed. The interval between pollination and fertilization is about 30 days. The complete reproductive cycle of *Picea* extends over a two-year period (Fig. 6.10).

6.5.4. Embryogeny

The division of the zygote nucleus yields two nuclei, each of which promptly divides forming four free nuclei in middle of the egg cytoplasm. Soon afterward, the nuclei move to the lower end of the archegonium, where a third division occurs accompanied by cell wall formation (Fig. 6.11). The first wall formed is transverse to the proembryo axis. The eight nuclei lie in two tiers. The proembryo consists of a lower tier of four cells with walls, and an upper tier, devoid of walls adjacent to the egg cytoplasm. The lower tier is the primary embryonic tier. It gives rise to the three tiers, namely, the primary and secondary suspensor tiers, and embryonic tier. Divisions of the embryonic tier are simultaneous with the elongation of the secondary (proper) suspensor, developing into the embryonal tubes (Fig. 6.12). Synchronization of these processes is a characteristic feature for *Picea* and not for *Abies*. Proembryo development is complete about 40 days after pollination.

During the early stage of primary suspensor elongation, the apical tier of the embryonic cells gives rise to several additional cell tiers (E_1 , E_2 , etc., Fig. 6.12.), owing to a series of transverse divisions. These cells elongate and serve to push the growing embryo farther into the corrosion cavity of the gametophyte. The embryo system is supplied food materials stored in the female gametophyte cells, which are digested. The female gametophyte being a nutritive haploid tissue is sometimes incorrectly called endosperm.

Six or seven weeks after pollination, the embryo is spherical in shape, and two weeks later the cotyledon primordia are already visible. In mid August the embryo is fully developed. During embryo growth, the integument differentiates into a seed coat. Simple polyembryony can occur in spruce; however, two embryos are rarely observed in ripe seeds. Simple polyembryony refers to the phenomenon in which each of the fertilized eggs of a single gametophyte produces separate heterozygotic embryos. Cleavage polyembryony, typical for pines, does not occur in spruce.

6.6. KARYOTYPE

The number of chromosomes (x) for *Picea abies* is 12. Tetraploids and mixoploids occur very rarely in nature. Artificial triploids and aneuploids were obtained after treating the seeds with colchicine (ILLIES 1951/52) or X rays (BEVILACQUA and VIDAKOVIĆ 1963, ŠIMAK *et al.* 1968). The relative length of the metaphase chromosome, which is used for idiogram (karyogram) construction, is 70–130 (BIAŁOBOK and BARTKOWIAK 1967, TERASMAA 1971, 1972). The longest one is almost twice as long as the shortest. The ten pairs of homologous chromosomes are metacentric. The relative length of the chromosome arms is 1.0–1.7. Two other chromosomes (numbers 9 and 12) are submetacentric. Their centromeres lie near the end of one of the arms. The relative length of the arms is 1.8–2.1. A secondary contraction, the cleaving of small fragments of chromosomes (satellite or trabant), occurs in five chromosomes: numbers 2, 3, 5, 6, and 10 (Fig. 6.13).

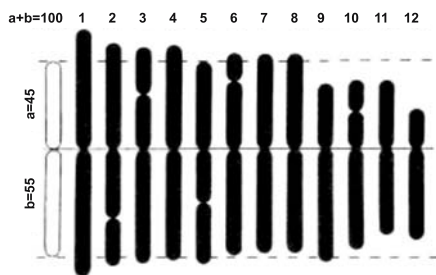


Figure 6.13. Karyogram of *Picea abies* (TERASMAA 1971)

chromosome numbers from the longest to shortest one; a–b – relative lengths of the chromosome arms

Other researchers claim that the number of satellite chromosomes in *P. abies* is much fewer, and that some of the “satellites” may be artifacts arising during the cytological tissue preparation (BIAŁOBOK and BARTKOWIAK 1967, GABRILAVICHYUS 1972). It seems that some of the satellites may have gone unnoticed owing to the treatment of the studied material with colchicine, which causes the chromosome to contract for easier counting, and that some secondary contractions on slides were not visible. This is confirmed by the fact that in interphase nuclei, the number of nucleoli is always ten or fewer (TERASMAA 1972). Chromosomes with satellites participate in nucleoli restitution.

7. GROWTH AND NUTRITION

STANISŁAWA PUKACKA

7.1. HORMONAL REGULATION OF GROWTH AND DEVELOPMENT

Plant growth and development are regulated by phytohormones or growth regulators, low-molecular weight compounds present in cells in relatively low concentrations, acting in tissues remote from the place of their synthesis. Plant hormones may be divided into five basic groups: auxins, gibberellins, cytokinins, abscisic acid, and ethylene. Recently, polyamines and brassinosteroids have also been recognized as growth regulators. Of the many studies of plant hormones, studies of forest trees and particularly the conifers, constitute only a small fraction of the published works. With regard to papers dealing with coniferous trees, most of the studies on hormonal regulation of growth and development have been conducted on Scots pine (*Pinus sylvestris*). This review examines the role of plant hormones in regulating growth and development of Norway spruce [*Picea abies* (L.) KARST.] and evaluates the current state of research in this field.

7.1.1. The occurrence of phytohormones and their role in growth and development

7.1.1.1. Auxins

Auxins belong to the best-known group of growth regulators. Auxins are natural and synthetic substances that stimulate the elongation of shoots and coleoptiles. Indole-3-acetic acid (IAA) is the most important naturally occurring auxin in higher plants. In coniferous trees, IAA is responsible for many developmental processes, including shoot elongation, cambial activity, xylogenesis, and response to photoperiod. It is synthesized in the needles and buds and then transported to other organs. Auxin movement proceeds on the principle of a slow polar transport and fast, nonpolar transport through the phloem. There are no data in the literature on auxin transport in Norway spruce.

WODZICKI and WODZICKI (1981) suggest that the wave theory of basipetal auxin transport from the top to the base occurs in spruce as it does in pine. Indole-3-acetic acid occurs in plant tissues in both free and bound states. STEEN (1972) observed IAA in *Picea abies* buds and seedlings using bioassays. In the last few years, improved techniques, such as high-performance liquid chromatography (HPLC), mass spectrometry, and immunological tests have been used to determine the IAA content in plant tissues.

Bioassays were also used by IVONIS *et al.* (1983), who studied the annual dynamics of the growth regulator in needles of one- and two-year-old trees of Norway spruce. In that study, high levels of auxins were present during the period of bud dormancy. FACKLER *et al.* (1986b), using immunological assays to determine IAA distribution in the needles of Norway spruce, found that IAA levels depended on position in the tree crown, age, and season. These authors reported that free auxin concentration in the needles was higher in a shaded crown position than in full sun. The highest auxin content in the young needles of the crown apical zone was recorded in May and decreased to a minimum in July before increasing again in October. Seasonal differences in IAA content in the needles of the lower whorls were much less pronounced. Free IAA constituted 93% of the total IAA content in the buds, whereas bound IAA was predominant in the needles. In summary, the authors found that on the basis of the absolute contents of free and bound auxins in spruce needles, no conclusions can be drawn in relation to the potential growth abilities of tree organs. PSOTA *et al.* (1992) examined IAA content in the needles of 10- and 240-year-old trees of *Picea abies* throughout the year. They found that auxin content declined from October to November, after which it increased and achieved its maximum in July. IAA content in the needles of an old tree was significantly lower than that of a 10-year-old tree, whereas changes in its level in the annual cycle were significantly smaller.

DUNBERG (1976) found a marked increase in auxin content in spruce shoots from May to July, indicating a role of IAA in shoot elongation. SANDBERG and ERNSTEN (1987) examined free and bound IAA contents in the seeds of *P. abies* before and during germination, using combined methods of HPLC and gas chromatography coupled with mass spectrometry. The content of bound auxin in seeds was several times higher than that of free auxins. During seed germination, bound auxin gradually decreased to a stable minimum, whereas the content of free auxin continually increased until the fifth day of germination, after which it also decreased to the initial level. The authors assumed that the increase in free IAA content resulted from the hydrolysis of conjugates of IAA, and not from *de novo* synthesis. A preliminary treatment of spruce seed with auxin had no influence on germination (SANDBERG 1988).

Exogenously applied auxins promote rooting. POPIVSHCHII and SHAPKIN (1986) found that soaking spruce seedlings in IAA and NAA (naphthale-

neacetic acid) enhanced growth, increasing height, diameter, and biomass of needles, shoots, and roots for two years following treatment. MAUER and PALATKOVA (1989) as well as SEABY and SELBY (1990) found increased growth of lateral roots in *Picea abies* seedlings following treatment with natural auxins and NAA.

Changes in auxin levels may occur in plants in response to environmental stress. For example, WESSLER and WILD (1993) tracked the IAA content in needles of *Picea abies* in declining stands on industrial sites in Germany. The auxin level in the needles of visibly injured trees was significantly lower than that of healthy trees.

7.1.1.2. Gibberellins

Gibberellins (GA) constitute a large class of compounds (about 80 have been described to date) with a characteristic, basic terpenoid structure. Not all of them are biologically active and not all of them occur in higher plants. KATO *et al.* (1962) first detected gibberellins in conifers in the cones of *Juniperus chinensis*. DUNBERG (1973) first investigated gibberellin-like substances in the shoots of *Picea abies*, finding that these substances as well as auxins both influence shoot elongation (DUNBERG 1974). Gibberellins are synthesized in leaves. They occur in both free and bound states in cells. Their prime role consists of regulating plant height growth, shoot elongation, and the transition of the plant from the vegetative to the reproductive stage and associated processes, including the induction of flowering and regulation of seed germination. In the case of Norway spruce, the majority of studies have concerned the role of gibberellins in flowering.

7.1.1.3. Cytokinins

Cytokinins occur in young, actively dividing meristemic cells of shoots and roots. They are synthesized in roots and are transported to other plant organs through the xylem along with water and solutes. The best-known cytokinins are zeatin and 2-isopentenyladenine, which are known to also occur in coniferous trees. Cytokinins participate in the regulation of many plant processes, such as cell division, shoot and root morphogenesis as well as organ senescence. ROGOZIŃSKA (1967) first noted the presence of cytokinins in Scots pine. SEBANEK *et al.* (1991) examined cytokinin content in the needles of 10- and 240-year-old individuals of Norway spruce. They found no differences in cytokinin content between young and old trees, but noted two characteristic annual minima in November and March. BOLLMARK *et al.* (1995) found that zeatin riboside (ZR) was the most abundant cytokinin in Norway spruce buds and that also isopentenyladenosine (iPA) was present in all samples. The level of zeatin-type cytokinins was correlated with bud size. CHEN *et al.* (1996) followed the levels of endogenous ZR and iPA in the terminal buds, whorl buds,

and lower lateral buds in shoots of the uppermost whorl of 15- to 20-year-old trees of Norway spruce from June to September. Bud growth was greatest during August and September and was correlated with ZR levels, indicating the importance of cytokinin for bud development. Differences in ZR levels among bud types also suggested that this hormone may control the form of individual branches in the tree.

SCHWARTZENBERG and HAHN (1991) found a high content of free and bound cytokinins in the needles of declining *Picea abies* trees growing on a site contaminated with industrial pollutants. Cytokinin content was correlated with the degree of the needle injury. KRAIGHER and HANKE (1996) determined the level of isopentenyladenine- types of cytokinins in needles of Norway spruce seedlings growing on soil substrates from polluted and unpolluted forest research plots. They found higher levels of cytokinins in seedlings grown on polluted soils.

In some conifers, e.g. Douglas fir (*Pseudotsuga menziesii*), cytokinin is involved in the induction of flowering (IMBAULT *et al.* 1988). Cytokinins can be used exogenously to rejuvenate plant organs as has been shown in Norway spruce (BOURIQUET *et al.* 1985; MATSCHKE *et al.* 1991).

7.1.1.4. Absciscic acid

Absciscic acid (ABA) belongs to a group of growth inhibitors commonly occurring in plants. It is synthesized in all plant cells having plastids. Its content in tissues can be successfully determined by gas chromatography, liquid chromatography, and immunological assays. ABA plays a major role in regulating bud and seed dormancy, water relations, as well as in the processes of plant acclimation and response to stress factors.

There are several reports concerning a regulatory role of ABA in Norway spruce. HEIDE (1986) injected ABA to the apical buds of *Picea abies* seedlings and caused a transient inhibition of shoot elongation. She did not confirm a decisive role of ABA in inducing bud dormancy. QAMARUDIN *et al.* (1993) determined the ABA content in seedlings of two *Picea abies* populations from Sweden and Romania in a study of bud dormancy and frost tolerance. They found no correlation between ABA content and bud dormancy, or frost hardness of these two populations of spruce. FACKLER *et al.* (1986a) found an increased ABA content in the needles of five-year-old spruce trees exposed to ozone. YANG *et al.* (1993) revealed the influence of ABA on the synthesis of the ethylene precursor, amino-cyclopropane-carboxylate (ACC), in needles of Norway spruce injured by industrial pollution. In that study, ABA restricted ethylene synthesis and thereby assisted in needle response to environmental stress.

There are no separate reports in the literature on the role of absciscic acid in regulating water relations and drought resistance of Norway spruce. However, a number of studies have involved *Picea mariana*, *P. glauca*, *P. sitchensis*, and

other spruce species. The role of ABA in plant drought resistance consists of the regulation of stomatal conductance and in maintaining a suitable osmotic potential as well as inducing gene expression and synthesis of specific proteins that protect cells from dehydration injury. Generally, plants exposed to drought stress accumulate ABA in their cells. However, a higher concentration of abscisic acid does not always ensure a higher drought tolerance. ROBERTS and DUMBROFF (1986) found that ABA content in seedlings of *P. mariana* and *P. glauca* exposed to a drought stress initially increased, but declined with a large increase in water stress. Increasing ABA content was correlated with declining transpiration rates. After re-hydration of the seedlings, ABA levels returned to their initial values and transpiration increased. SILIM *et al.* (1993) using the retardant-mefluidide, which caused an increase in the dehydration tolerance of *P. glauca* seedlings, found that it induces an increase in ABA content in the needles, a decrease of stomatal conductance, and the resultant maintenance of a high osmotic potential in shoots. TAN and BLAKE (1993) also revealed ABA accumulation in *P. mariana* seedlings exposed to drought stress, but they found no correlation between the amount of ABA and the degree of resistance to dehydration among progenies. TAN and BLAKE (1993) observed that ABA accumulation in the needles of *P. mariana* exposed to drought was concomitant with an increase in electrolyte leakage from the cells, which according to them, was a result of the interaction between abscisic acid and membrane lipids, leading to changes in membrane permeability. ABA alone applied exogenously had a similar effect. The same phenomenon occurred in the needles of *Pinus banksiana* and in the leaves of *Eucalyptus grandis*. JACKSON *et al.* (1995) compared the dehydration stress tolerance of 3-year-old individuals of *Picea sitchensis* and *Pinus sylvestris*. In both species the concentration of ABA in cells increased 11-fold as the water deficit increased. However, *Pinus sylvestris* displayed a higher tolerance to drought than spruce. In spruce, the response of stomatal cells to an increased level of abscisic acid was delayed, and consequently, the osmotic potential declined during dehydration.

7.1.1.5. Ethylene

Ethylene also belongs to the group of growth inhibitors. It is the only hormone in a gaseous form. It is synthesized in the majority of plant organs. It is detected and measured using gas chromatography. Ethylene regulates fruit ripening, leaf and flower senescence, leaf and fruit drop, seedling growth, seed and bud dormancy, and participates in root and flower induction. The mechanism of its action is not fully understood. Environmental conditions and other hormones, such as auxin, promote ethylene biosynthesis.

EKLUND (1993) suggested that the maintenance of a low ethylene content in shoots is important for the process of wood formation. Later studies (EKLUND and TILTU 1999; EKLUND *et al.* 2003) indicated a positive relation-

ship between spiral grain angle in the last growth ring and ethylene concentration in stems of *Picea abies*. The authors confirmed that ethylene affects wood formation quantitatively, as measured by increased compression wood and an increase in left-handed spiral grain angle. INGEMARSSON (1995) found that ethylene stimulates lignification and cell wall formation in *P. abies* seedlings. BOLLMARK and ELIASSON (1990a) examined the participation of ethylene in root induction in excised 4-week-old spruce seedlings. They found a stimulating effect of ethylene on root formation along with a simultaneous degradation of cytokinins.

EKLUND *et al.* (1992) investigated the influence of drought stress on ethylene production in spruce and found no correlation between ethylene production and drought stress. In contrast, DRIESCHE and LANGEBARTELS (1994) observed an increase in ethylene synthesis and its precursor, ACC (1-amino-cyclopropane-carboxylate), in 4-year-old spruce trees subjected to drought and ozone stresses separately. However, in the combined ozone and drought treatment the synthesis of ethylene and ACC was reduced and was associated with reduced injury. The authors suggest that in young spruce trees exposed to ozone, drought stress has less of an effect on tissue injury, and consequently ethylene production is also decreased. An increase in ethylene synthesis and ACC was also observed in spruce needles following treatment with acid mist (CHEN and WELLBURN 1989). A simultaneous application of other growth regulators, such as IAA, ABA, kinetin, and gibberellic acid, had no effect on ethylene production. WILKSCH *et al.* (1998) studied the emission of ethylene and its ACC and MACC (malonyl-amino-cyclopropane-carboxylate) precursors in Norway spruce growing on contaminated and uncontaminated sites in Germany. The emission of ethylene and its precursors was considerably higher in injured trees.

7.1.1.6. Polyamines

In the recent years, a considerable number of studies have examined the role of polyamines in plant growth and development (SLOCUM *et al.* 1984; BAGNI and BIONDI 1987; GALSTON and KAUR-SAWHNEY 1987). KONIGSHOFER (1989, 1991) found seasonal changes in polyamine content in juvenile and mature trees of Norway spruce that were dependent upon age. In contrast to juvenile organs, shoots of mature spruce individuals grown from seed, grafted trees, as well as buds prior to sprouting, are characterized by a pronounced increase of putrescine content at the time of intensive shoot sprouting. A transient increase in polyamine content in juvenile shoots was observed prior to shoot sprouting. Polyamine content varied annually from peak concentrations in the newly formed needles to lowest concentrations during the period of shoot sprouting (May-July). Similar changes were observed in juvenile as well as in mature spruce individuals, indicative of polyamine involvement in the regulation of shoot elongation. The occurrence of abundant levels of putrescine in

the shoots in the cambial region during its intensive activity suggests that polyamines in Norway spruce may also be involved in diameter growth.

Polyamines occur also in seeds of Norway spruce. SANTANEN and SIMOLA (1999) observed that putrescine levels were approximately ten times higher in the embryo than in megagametophyte tissues, whereas spermidine and spermine levels were nearly identical in both tissues. The authors suggest that polyamines may play a role in the accumulation of seed storage proteins and in the maturation of *P. abies* seeds.

TENTER and WILD (1991) showed that the putrescine content in needles of injured and declining spruce trees was several-times higher in comparison to healthy trees. In that study, the marked differences in the content of putrescine and the ratio of putrescine to spermidine may serve as indicators of the general condition of trees growing in areas subjected to industrial pollutants. SANDERMAN *et al.* (1989) and DOHMEN *et al.* (1990) observed putrescine accumulation in spruce needles in response to ozone stress, suggesting a role of polyamines as factors stabilizing membranes under oxidative stress conditions. LANCHERT and WILD (1995) found a negative correlation between the potassium ion content and putrescine content in needles of Norway spruce. Stress-induced membrane injury is often manifested by increased electrolyte leakage, followed by a decline in potassium content in cells. A strong negative correlation of putrescine with K ions in Norway spruce trees was also observed by KAUNISTO and SARJALA (1997) and suggested that putrescine concentration can be used for describing symptoms of potassium demand in spruce trees of various sizes and varying nutritional status.

7.1.2. Hormone participation in the regulation of flowering

Flowering is one indication of the transition of a plant from its juvenile stage to physiological maturity. PHARIS *et al.* (after JACKSON and SWEET 1972) suggested that the juvenile period in coniferous trees encompasses the time period when the appropriate hormones have not achieved a sufficient concentration to induce flowering. Further investigations demonstrated a key role of gibberellins in flowering in terms of both absolute level and composition. The influence of gibberellins on the induction of flowering depends on their molecular structure, specifically on the number and location of the double bonds and hydroxyl groups. Gibberellins differ in terms of their effects on plant proteins, such as enzymes, transporter proteins, or receptors.

In Norway spruce, ODEN *et al.* (1982, 1987) identified the following gibberellins: GA₁, GA₃, GA₄, and GA₉. DUNBERG (1974) isolated six gibberellins from spruce shoots and found that a high content of endogenous gibberellin-like compounds during the initiation of flower buds ensures abundant flowering. IVONIS *et al.* (1981) and IVONIS (1988) also found a correlation between gibberellin content in spruce needles and the initiation of flower buds.

CHALUPKA *et al.* (1982) found that covering shoot apices of spruce with polyethylene resulted in an increased production of male flowers and a simultaneous increase in content of a less-polar gibberellin in shoots. ODEN *et al.* (1994) determined the content of the endogenous gibberellins GA₁, GA₃, GA₄, and GA₉ in elongating shoots of Norway spruce grafts during the period of flower bud differentiation in response to two treatments: cool and wet vs. hot and dry. The cool and wet treatment exhibited decreased numbers of flower buds, whereas the hot and dry treatment stimulated flowering. They also found that gibberellin GA₉ was the dominant GA and that the content of all gibberellins increased during the period of shoot elongation and declined when shoot elongation ceased. The ratio of GA₉ to GA₁ was 12.5 in the cool and wet treatment and 36.6 in the hot and dry treatment, suggesting that this ratio may serve as an index of reproductive buds.

In many studies, exogenously applied gibberellins have been used to induce flowering with the aim of understanding of the role of gibberellins in the flowering process. BLEYMÜLLER (1976, 1978) sprayed spruce shoots with GA₃ solution, which stimulated the differentiation of female flowers. DUNBERG (1980) applied several gibberellins as well as NAA to induce the production of seed and pollen cones. He obtained the best results with a direct shoot injection with a GA_{4/7} mixture, followed by an additional application of GA₉. The same mixture of the less-polar GA_{4/7} gibberellins appeared to be the most effective in inducing flowering in spruce in the experiment of SCHACHLER and MATSCHKE (1991). In contrast, JOHNSEN *et al.* (1994b) concluded that the regulation of flowering and the sex determination process is also possible under strictly controlled external temperature conditions. A single application of gibberellin GA_{4/7} to a Norway spruce stem cross section during the late stage of shoot elongation in the experiment of FOGAL *et al.* (1996) resulted in a noticeable increase in the number of female strobili and a reduction in the number of vegetative buds.

Exogenously applied gibberellin GA_{4/7} is also known to stimulate flowering in other spruce species, such as *Picea mariana* (HO 1991), *Picea glauca* (MARQUARD and HANOVER 1984; ROSS 1988), and *Picea engelmanni* (ROSS 1990). However, the effect of GA_{4/7} on the sex of the set flowers differs among studies. HO (1991) and MARQUARD and HANOVER (1984) obtained an increase in male flowers, whereas CECICH (1985) and ROSS (1988, 1990) found increases in the abundance of both male and female flowers. Degree-day accumulation during the period of shoot elongation in *Picea glauca* modified the production of pollen cones (ROSS 1991). ROSS (1990) was able to stimulate male and female flower set in *Picea mariana* using a GA_{4/7} mixture and NAA. SMITH and GREENWOOD (1995) also succeeded in stimulating seed and pollen cone production in *P. mariana* as a result of shoot injection with a GA_{4/7} mixture and a simultaneous root pruning. The effect of gibberellins and root pruning decreased after the application of cytokinin. The authors concluded that a

decrease in cytokinin content in developing buds as a result of root pruning may enhance flowering.

ODEN *et al.* (1995) investigated gibberellin transport and metabolism during bud differentiation in *Picea abies*, using deuterium- and tritium-labeled gibberellin GA₄ injected into the xylem below an elongating shoot and needles. This study revealed that gibberellins were transported first to the needles and then back to the stem and lateral buds. In other experiments, a mixture of deuterium-labeled GA₉ and tritium-labeled GA₄ were injected into elongating shoots of one abundantly flowering family and one sparsely flowering family and grown either under hot and dry conditions and under cool and wet conditions conducive for flowering. In all treatments, gibberellin GA₉ was transformed into GA₅₁, GA₄, GA₃₄, and GA₁; whereas gibberellin GA₄ was transformed into GA₃₄, GA₁, and GA₈. In cold-treated clones the main metabolite of GA₉ was GA₅₁. In clones treated with heat, more GA₉ was transformed into GA₄. The main metabolite of GA₄ was GA₃₄. The authors suggest that active forms of gibberellins involved in bud differentiation are regulated in specific shoot regions and that their metabolism is influenced by different environmental factors, such as root activity, water potential, and temperature. These findings concur with those of earlier experiments of MORITZ and ODEN (1990) on the metabolism of deuterium- and tritium-labeled gibberellin GA₉ in the shoots of Norway spruce during bud differentiation.

7.1.3. Application of growth regulators in somatic embryogenesis

In recent years, there has been an increased interest in the relatively new method of plant propagation through somatic embryogenesis. This method is particularly useful in coniferous trees, where other methods of vegetative propagation are somewhat less successful. Norway spruce is easily cultured *in vitro* and there are comparatively many reports on obtaining somatic embryos of different spruce species. Somatic embryos of spruce are obtained through multiplication of cotyledon, seed, and entire zygotic embryo tissues on appropriate media. Growth regulators are of primary importance in generating somatic embryos. In the first stage, the applied medium contains auxins and cytokinins. The most frequently used auxins are: NAA (ARNOLD and HAKMAN 1988; JAIN *et al.* 1988; AFELE *et al.* 1992; CHALUPA 1987), 2,4 D (2,4-dichlorophenoxyacetic acid) (BELLAROSA *et al.* 1992; SUSS *et al.* 1990) as well as IBA (indole-3-butyric acid) (ROBERTS *et al.* 1990; CHALUPA 1987). Benzyladenine (BA) is the most frequently used cytokinin, though SUSS *et al.* (1990) also used kinetin. BELLAROSA *et al.* (1992) obtained a high yield of somatic embryos of Norway spruce on a medium with both 2,4 D and BA.

Abscisic acid plays an important role in the process of somatic embryo production at the final stage of culture to obtain fully viable embryos (ATTREE *et al.* 1990). BOZHOKOV *et al.* (1992) found that ABA applied simultaneously with

BA improves the quality of somatic embryos of Norway spruce. Absciscic acid promotes the maturation of somatic embryos, which consists of the synthesis of certain storage proteins (HAKMAN *et al.* 1990; ROBERTS *et al.* 1990). Only after an adequate period of growth in the presence of ABA are somatic embryos capable of generating an entire plant on a medium lacking the hormone. Absciscic acid is a factor governing the expression of genes responsible for the synthesis of storage proteins (ROBERTS *et al.* 1990; HAKMAN 1993; FLINN *et al.* 1993). In addition, an appropriately selected ABA concentration and an osmotic agents, such as mannitol or polyethylene glycol (PEG), together increase the resistance of the embryo to dehydration (ROBERTS 1991; ATTREE *et al.* 1991, 1994; STASOLLA *et al.* 2002). Then, the so-called “artificial seeds” can be prepared for germination. According to LEAL *et al.* (1995), somatic embryos of coniferous trees may be useful models in studies of gene expression.

VAGNER *et al.* (1998) studied the content of endogenous growth regulators during the development and maturation of somatic embryos of Norway spruce. They found that the level of endogenous ABA depends to a large extent on its prior concentration in a given medium. After removal of ABA from the medium, ABA levels in embryos are maintained for some time. The IAA content decreases during the development of somatic embryos and increases again in the period of late maturation. Cytokinins (isopentenyladenine, isopentenyladenosine, zeatin and zeatin riboside) behave similarly. Embryogenic tissue produces 40 times less ethylene than non-embryogenic tissue. FIND (1997) also showed that endogenous ABA levels in somatic spruce embryos were dependent upon on the exogenous concentration of ABA and on the osmotic potential of the medium. A decrease in osmotic potential of the medium caused a decrease in ABA concentration and an increase in embryo germination.

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7.2. MINERAL NUTRITION

7.2.1. *Methods in evaluating mineral requirements*

The nutritional status of trees is most frequently assessed on the basis of the elemental analysis of leaves (MATERNA 1960; KRAL 1963; FIEDLER *et al.* 1965; LAVRICHENKO 1968; TAMM 1968; ZECH 1968; SWAN 1972; LINDER 1995 and others). In spruce, needles sampled for this purpose should be collected be-

tween mid-August and mid-September (TOUZET *et al.* 1970), preferably from the same sector of the tree crown (JUNG and RIEHLE 1966), and separately for each needle age class cohort or from the youngest age class (LINDER 1995). Roots, wood, or bark are also sampled for chemical analyses (INGESTAD 1959; OVINGTON 1959; FORNES *et al.* 1970; FEGER *et al.* 1991) as well as whole plants, especially small seedlings (KRAL 1961; FÖBER and GIERTYCH 1968, 1970a; FÖBER 1974).

The nutrient requirements of trees may also be based on soil analyses. EVERS (1967a, b, 1972) suggests that soil nutrient status depends on the ratios among elements in the soil. FIEDLER and NEBE (1963) as well as HUNGER and FIEDLER (1965) observed a negative correlation between tree height and the C:N ratio in the humus horizon. Nevertheless, HORN *et al.* (1987) found that needle analysis frequently provides more information on the nutritional status of trees than does routine soil analyses.

Employing multiple methods at the same time should increase the accuracy of the assessment of the nutritional needs of trees. These methods include visual evaluation of plants, chemical analysis of the soil, needles, and whole seedlings, as well as growth (HUNGER and NEBE 1964; LEAF 1970; WITT 1987). Other reported methods for evaluating the response of spruce trees to fertilization include: needle color assessment on the youngest shoots (LUUKKANEN *et al.* 1971), measurement of organic acid concentrations in needles (CLEMENT 1977), chlorophyll fluorescence (BAILLON *et al.* 1988), and the measurement of electrical resistance in the cambium zone (HÜTTL *et al.* 1990).

7.2.2. Symptoms of deficiency and toxicity

7.2.2.1. Deficiency symptoms

Spruce seedlings growing under conditions of nitrogen deficiency exhibit poor development and slower growth (FÖBER and GIERTYCH 1968; SWAN 1972; FIEDLER *et al.* 1973). The young needles, especially the tips appear light yellow (INGESTAD 1959). Mature needles may appear small and yellowish-green in color (BAULE and FRICKER 1973; FIEDLER *et al.* 1973). Chlorosis arising from nitrogen deficiency is typically observed throughout the tree crown in all needle age classes and often appears evenly distributed over the entire forest stand (HARTMANN *et al.* 1988). The shoots are short and poorly branched. Summer shoots do not develop and the growth period is often shortened (BAULE and FRICKER 1973; FIEDLER *et al.* 1973). Root growth is comparatively more vigorous; however, the roots may grow long and thin (INGESTAD 1959; BAULE and FRICKER 1973). Clear symptoms of nitrogen deficiency are observed when its concentration on a needle dry mass basis falls below 1% (FIEDLER *et al.* 1973; HARTMANN *et al.* 1988).

Young needles of seedlings growing under conditions of phosphorus deficiency are short and yellow, especially at tips (INGESTAD 1959). Old needles are dark green, often with a purplish hue. In older trees, needles are grey or bluish-grey, and later they turn purple, purplish-brown, or even red (BAULE and FRICKER 1973). Older needles change color more quickly and to a greater degree than younger needles. Later on they slowly senesce but are not shed, thus contrasting with the remaining younger, healthy needles (BAULE and FRICKER 1973). The roots of spruce seedlings lacking phosphorus are long and thin (INGESTAD 1959). Symptoms of phosphorus deficiency are observed when concentrations on a needle dry mass basis are below 0.08–0.1% (SWAN 1972; HARTMANN *et al.* 1988).

In coniferous trees, potassium deficiency results in an initial yellowish-green and later yellow discoloration of needle tips (BAULE and FRICKER 1973). When the deficiency is severe, the needle tips turn reddish-brown, brown, or purplish-brown, and eventually senesce. Young needles are especially discolored, although their bases often remain green, and the transition between colors is gradual (INGESTAD 1959; MAYER-KRAPOLL 1964). According to ZECH (1968), there are two types of symptoms of potassium deficiency. When P supply is sufficient and K is lacking, mainly the young needles in the outer parts of the tree crown turn yellow or red at their tips, while older needles in the inner parts of the crown remain green. If both P and K are deficient, older needles are discolored first, and appear yellow at the tips or greyish with green spots. Discoloration is most severe in autumn and winter, and occasionally early spring (MAYER-KRAPOLL 1964; ZECH 1968; BAULE and FRICKER 1973). The symptoms are often exacerbated by high light intensities (ZECH 1968). Tree growth slows (ZECH 1968; FORNES *et al.* 1970; BAULE and FRICKER 1973) and roots appear short, thin, and poorly branched (INGESTAD 1959). Lignification of young shoots is often incomplete, so the tree is prone to frost damage, drought, and pathogens (BAULE and FRICKER 1973). Symptoms of potassium deficiency are observed when its concentration on a needle mass basis is below ca 0.4% (HARTMANN *et al.* 1988).

A lack of magnesium causes yellowing of needles (LIU and TRÜBY 1989; ROBERTS *et al.* 1989; FINK 1991; SCHAAF and ZECH 1993) and symptoms occur at concentrations below ca 0.03% needle dry mass (HARTMANN *et al.* 1988) and below 2 $\mu\text{eq/g}$ of soil (LIU and TRÜBY 1989). The needle tips turn yellow, while their bases remain green (INGESTAD 1959; BAULE and FRICKER 1973) and the transition between colors is sharp (MAYER-KRAPOLL 1964). Chlorosis progresses from older to younger needles (HARTMANN *et al.* 1988). Needle discoloration is the most conspicuous in autumn. When magnesium deficiency is severe, the needle tips first turn orange-yellow, then brown, and finally they senesce (BAULE and FRICKER 1973). In seedlings, roots are often poorly branched (INGESTAD 1959). The changes in spruce needle morphology that result from shortages of potassium and especially magnesium are due to the

modification of chloroplast structure, partial accumulation of starch in mesophyll cells, premature necroses, and sunken tracheids in vascular bundles (FINK 1991).

Calcium deficiency is rarely observed in conifers, even if its uptake is limited by soil acidification. In hydroponics, the visual symptoms of calcium deficiency include browning of twig tips, followed by their senescence (BAULE and FRICKER 1973). In spruce seedlings, INGESTAD (1959) observed yellowing of young needles, whereas all needles had yellow or brown tips and postponed development of apical buds. Root growth was also poor; they were short and densely branched. Calcium deficiency reduces plant height, but the response of Norway spruce is less than that of other coniferous trees.

In case of iron deficit in Norway spruce, young needles are completely yellow, while older needles are light green or green (ZECH 1968). In INGESTAD'S (1959) experiments, spruce seedlings grown in hydroponic cultures lacking iron had light-yellow young needles, thick and long roots, and a lack of bud development.

Symptoms of manganese deficiency are observed when its concentration in needles is below 20 ppm (ZECH 1968; FIEDLER *et al.* 1973; HARTMANN *et al.* 1988). Developing needles turn yellow. The discoloration is most apparent in autumn and winter in lower and inner portions of the tree crown.

When the copper concentration in spruce needles is below 2–3 ppm, the tips of apical shoots die in autumn and winter (MATERNA 1962; FIEDLER *et al.* 1973). Likewise, the critical level of boron in current-year needles appears to be ca 3 ppm (BRÆKKE 1979, 1983). Drought reduces the uptake of boron. Symptoms of boron deficiency include shoot death and disruption of apical dominance. Sensitivity in terms of visible injury varies among populations.

7.2.2.2. Toxicity symptoms

Excessive rates of nitrogen fertilization often accelerate tree height growth, but trees may exhibit poor root growth and limited mycorrhizal development (FIEDLER *et al.* 1973). Lignification may be compromised to the extent that the trees become prone to frost damage. Particularly harmful is the excessive nitrogen fertilization of planted seedlings in competition with weeds. In contrast, high phosphorus availability may result in a slight decrease in seedling growth, but no other unfavourable symptoms are observed (FIEDLER *et al.* 1973).

ZECH (1968, 1970) describes the chloroses observed on spruce trees grown on calcareous soils. On young spruce trees, current-year needles are whitish-yellow, especially at tips. According to ZECH, this discoloration is often due to a deficiency of iron in needles and reduction in manganese. In other cases, young needles started to turn yellow in July and the discoloration proceeded from the lowermost to the uppermost branches. Such symptoms are usually observed in young forest stands or in older trees and are probably caused by shortages of physiologically active iron.

An excess of trace elements may also be a stress factor for plants. In a polluted environment, the dominant factors in acid soils are toxic concentrations of polyvalent cations and low concentrations of nutrients. High aluminium levels in hydroponic cultures of spruce seedlings, ranging from 350 to 1200 $\mu\text{mol AlCl}_3/\text{l}$ of medium, greatly limit root growth (GODBOLD *et al.* 1988). The treatment of five-year-old spruce seedlings with aluminium under acid stress, causes swelling of root tips and increases their fragility (VOGELEI and ROTHE 1988). Under conditions of poor mineral nutrition, an excess of aluminium or manganese in hydroponic cultures of spruce seedlings causes a so-called golden chlorosis of needle tips, as in the case of magnesium deficiency (HECHT-BUCHHOLZ *et al.* 1987).

GLATZEL (1985) reports negative effects of lead, zinc, copper, and nickel, reflected in slower tree growth and a reduction in needle and root length, when the total concentration of those elements was higher than 2 g/1 kg humus. In laboratory experiments, heavy metal compounds limited the germination and growth of spruce seedlings, causing chloroses and necroses, and consequently the death of whole seedlings at high concentrations (FOBER 1978, 1979). High levels of the heavy metals lead, cadmium, arsenic, zinc, and copper in the substrate injured the roots of spruce seedlings (GODBOLD *et al.* 1985a, b; ZÖTTL 1990).

In the case of heavy pollution with SO_2 , needles on the youngest shoots turn yellow-brown or red-brown from the tip towards the base of the needle (HARTMANN *et al.* 1988). Necrotic spots or bands occur in the central part of the needle. Other pollutant effects such as chloride toxicity may appear on spruce trees growing along roadways. Visible symptoms occur when the concentration of chloride in needles reaches 0.25–0.35% on a dry mass basis (HARTMANN *et al.* 1988). In early stages, pale greenish-yellow areas without well-defined borders can be seen on younger needles, and less intensively on older needles. As a result of the long-term effects of chloride, needles of the previous-year's shoots appear dark copper-brown in the spring, and are shed in early summer. Buds are also dead, or if they develop, the new shoots have needles of only one or two age classes. In addition, ozone pollution may cause a chlorotic mottle in needles of spruce trees, appearing as well-defined pale yellow to yellow-brown spots (HARTMANN *et al.* 1988). Visible injury arising as symptoms of a disease are often the result of a complex of factors. It is important to make detailed observations of early stages, which tend to be more diagnostic and easier to distinguish.

7.2.3. Uptake of mineral elements

The uptake of individual elements and their concentration in plants depends mainly on their concentration in the substrate, and generally increases with increasing concentration in the culture medium. Nitrogen is taken up as ammo-

nium and nitrate ions. Norway spruce seedlings prefer nitrate, which is accumulated more readily and in larger amounts (GEORGE *et al.* 1999). In hydroponic cultures, Norway spruce seedlings grow best on a medium where the NO_3/NH_4 ratio is 55/45, and a total N concentration of 3.7 mmol/l (SANCHEZ *et al.* 2000). Likewise, field experiments indicate that fertilization has a significant positive effect on the uptake and concentration of individual elements in plants (BRÆKKE 1979, 1983; MATZNER 1985; MURACH and SCHÜNEMANN 1985; NILSSON and WIKLUND 1992; DREYER *et al.* 1994; NILSSON *et al.* 1995; MOILANEN *et al.* 1996; INGERSLEV and HALLBACKEN 1999).

Interactions among individual nutrients can be observed. A higher nitrogen supply reduces the concentrations of phosphorus and potassium in needles of 3-year-old spruce seedlings, clearly increasing the N/P and N/K ratios (SEITH *et al.* 1996). Potted spruce seedlings treated with ammonium sulphate have lower concentrations of magnesium in needles and higher concentrations of aluminium and iron (WILSON and SKEFFINGTON 1994). Application of nitrate significantly reduces plant phosphorus concentration. In spruce stands growing on the dry bogs of northern Finland, nitrogen fertilization decreased the concentrations of calcium, zinc, and boron in needles (MOILANEN *et al.* 1996). Application of nitrogen and phosphorus in a young spruce stand resulted in a sharp reduction in boron concentration, which is most often explained as a dilution effect (ARONSSON 1983; NILSSON *et al.* 1995). Intensive potassium fertilization of Norway spruce plantations increases nitrogen and magnesium uptake (FORNES *et al.* 1970). GLATZEL (1970) reports a significant reduction in calcium content in needles of 2-year-old spruce seedlings treated with potassium or with nitrogen, phosphorus, and potassium simultaneously.

Application of magnesium fertilizers may result in a critical dilution of potassium in needles of spruce seedlings (JANDL 1996). Liming with magnesium limestone increased the concentration of magnesium and calcium in needles of 15–25-year-old spruce trees in the western part of the Czech Republic (MATERNA 1989), but significantly decreased concentrations of potassium, calcium, manganese, and aluminium in 10-year-old trees in the Vosges Mts in France (DREYER *et al.* 1994). MATZNER (1985) and MURACH and SCHÜNEMANN (1985) observed increased uptake of magnesium following liming of a 100-year-old spruce stand. However, intensive liming caused a reduction in the boron content of needles of the youngest four age classes. If liming is accompanied by boron fertilization, then the manganese content of needles may decline (LEHTO and MÄLKÖNEN 1994). In another study, a greater supply of boron resulted in increased rates of magnesium uptake from the soil (BRÆKKE 1979).

In hydroponic cultures, ions are taken up from the medium very quickly. One-year-old spruce seedlings, treated with labelled phosphorus absorbed a large amount of this element within a 24-h period, and over the next six days their phosphorus content increased only by 30% (FOBER and GIERTYCH

1970b). Following maximum absorption of potassium and sodium by pine and spruce seedlings, these elements were exuded by the roots (GLADUNOV 1966). Drought reduces the uptake of nutrients (BECKER and LÉVY 1983; BRÆKKE 1983; HUNGER and MARSCHNER 1987; GRABAROVA and MARTINKOVA 2001). The availability and uptake of elements is also very strongly affected by soil pH (LEHTO and MÄLKÖNEN 1994), especially the pH of the rhizosphere, and by the surface area of roots (MARSCHNER *et al.* 1991).

In general, fertilization with an element, especially on poor sites, causes an increase in its concentration in plants. If the nutrient had earlier limited plant growth, then the increase in biomass caused by fertilization results in a decrease in concentrations of other elements because of a dilution effect. Application of an element, especially in amounts exceeding growth requirements, may enhance the uptake of other elements. There are antagonisms between some elements, so the presence of certain ions in the substrate may limit the uptake of others. Calcium is mainly stored in older organs, whereas phosphorus and potassium are transported to developing organs. The uptake of nutrients by plants is affected by various factors including light intensity, the concentration and form of nutrients in the substrate, soil water relations, the physico-chemical properties of the substrate, and the developmental stage of the plant.

7.2.4. Concentration of elements in organs

The concentrations of elements in leaves reflect the nutrient status of the individual plant and may provide valuable information on potential deficiencies before visual symptoms are observed. Foliar concentrations also form the basis for fertilizer recommendations. In addition, high concentrations of some elements may serve as indicators of industrial pollution in the environment. Thus, it is important to assess range of nutrient concentrations in needles, characteristic of various levels of mineral nutrition, ranging from severe deficiency to luxury consumption, or toxicity. Numerous publications report the values of individual elements in various organs of seedlings and older trees (e.g. FOBER and GIERTYCH 1971; FOBER 1977; ABRAZHKO 1985; OGNER and BJØR 1988; STIENEN and BAUCH 1988; FINÉR 1989; FEGER *et al.* 1991; RANGER *et al.* 1992; NILSSON and WIKLUND 1994; BORATYŃSKI and BUGAŁA 1998). Table 1 shows concentrations of various elements measured in trees of various ages. Within the ranges of deficient concentrations of individual elements in needles, a significant growth response to fertilization is expected if other factors do not limit plant growth. Within the optimum ranges, and especially within ranges of luxury consumption, fertilization is generally ineffective. In addition, the proportional relationships between individual nutrients are important for proper nutrition. In one-year-old needles of optimally growing spruce trees, the N:P:K ratio was 67:8:25, but with increasing tree age, the

Table 1. Ranges of element contents in one-year-old needles of Norway spruce (% or ppm on a dry mass basis)

<i>Severe deficiency</i>	<i>Intermediate deficiency</i>	<i>Suboptimal range</i>	<i>Optimum range</i>	<i>Luxurious content</i>	<i>Reported by</i>	<i>Tree age</i>
Nitrogen %						
			2.40–2.42	3.40	INGESTAD 1979	6 weeks
<1.00	1.00–1.30	1.30–1.80	1.80–3.00	>3.00	SWAN 1972	6 months
			1.81–2.20		RIKALA 1979	Seedlings
0.8–1.3	1.0–1.6	1.08–2.4	1.7–2.4		CAPE <i>et al.</i> 1990	
			1.4–2.0		FIEDLER and KATZSCHNER 1990	10 yr
			1.4–1.7		BERGMANN 1983	Mature
	1.2–1.3		1.3–1.5		ZÖTTL 1990	Mature
Phosphorous %						
			0.37–0.40	0.44	INGESTAD 1979	6 weeks
<0.10	0.10–0.15	0.15–0.20	0.20–0.40	>0.40	SWAN 1972	6 months
		0.05–0.11	0.10–0.30		MÜLLER 1988	1 yr
			0.27–0.28		RIKALA 1979	Seedlings
			0.12–0.25		FIEDLER and KATZSCHNER 1990	10 yr
			0.12–0.20		BERGMANN 1983	Mature
	0.11–0.12		0.12–0.15		ZÖTTL 1990	Mature

Potassium %						
<0.20	0.20–0.30	0.30–0.45	1.05–1.17	1.23	INGESTAD 1979	6 weeks
			0.45–0.80	>0.80	SWAN 1972	6 months
	0.30		0.76–0.82		RIKALA 1979	Seedlings
			0.70–1.10		MÜLLER 1988	1 yr
0.64–1.05				FIEDLER et al. 1973	Young	
0.14–0.4	0.2–0.7	0.4–1.21	0.7–1.23		CAPE <i>et al.</i> 1990	Mature
	0.4–0.45		0.45–0.60		ZÖTTL 1990	Mature
			0.5–1.0		BERGMANN 1983	Mature
Magnesium %						
<0.05	0.05–0.10	0.10–0.12	0.09–0.10	0.12	INGESTAD 1979	6 weeks
			0.12–0.35	>0.35	SWAN 1972	6 months
	0.02–0.07		0.09–0.16		MÜLLER 1988	1 yr
			0.16–0.19		RIKALA 1979	Seedlings
0.13–0.15				FIEDLER <i>et al.</i> 1973	Young	
0.02–0.05	0.03–0.07	0.05–0.31	0.07–0.14		CAPE <i>et al.</i> 1990	Mature
	0.06–0.08		0.08–0.10		ZÖTTL 1990	Mature
			0.1–0.2		BERGMANN 1983	Mature
Calcium %						
			0.08–0.10	>0.10	INGESTAD 1979	6 weeks

<0.05	0.05–0.10	0.10–0.12	0.12–0.85	>0.85	SWAN 1972	6 months
	0.02		0.09–0.16		MÜLLER 1988	1 yr
			0.44–0.67		FIEDLER <i>et al.</i> 1973	Young
			0.20–0.65		FIEDLER and KATZSCHNER 1990	10 yr
	0.1–0.2		0.2–0.3		ZÖTTL 1990	Mature
			0.4–0.7		BERGMANN 1983	Mature
Sulphur %						
			0.082		BRÆKKE 1979	13–19 yr
			0.07–0.13		CAPE <i>et al.</i> 1990	30 yr
			0.12–0.21		CAPE <i>et al.</i> 1990	
Boron ppm						
1.5–4			16.5–22.5		RIKALA 1979	Seedlings
			8–16		BRÆKKE 1979	13–19 yr
	3		20–25	50	BRÆKKE 1983	21 yr
			10–30		BERGMANN 1983	Mature
Molybdenum ppm						
			0.04–0.20		BERGMANN 1983	Mature
Copper ppm						
			7.4–8.0		RIKALA 1979	Seedlings
			3.3		BRÆKKE 1979	13–19 yr

2	2–12	ZÖTTL 1990	Mature
	5–12	BERGMANN 1983	Mature
13	Manganese ppm		
	625–725	RIKALA 1979	Seedlings
	200–5000	FIEDLER and KATZSCHNER 1990	10 yr
	50–500	BERGMANN 1983	Mature
	Zinc ppm		
	28–36	FIEDLER et al. 1990	2 yr
	31.6	BRÆKKE 1979	13–19 yr
	15–25	ZÖTTL 1990	Mature
	13–50	BERGMANN 1983	Mature
	Iron ppm		
	30–300	FIEDLER and KATZSCHNER 1990	10 yr
	41	BRÆKKE 1979	13–19 yr
	Aluminium ppm		
	72–300	NEBE 1991	
	Strontium ppm		
	20–32	PARIBOK <i>et al.</i> 1989	
	Rubidium ppm		
	5–16	PARIBOK <i>et al.</i> 1989	

nitrogen level may increase and the phosphorus level may decrease (FIEDLER and HÖHNE 1987).

Nutrient levels in plant organs depend on many factors, including seasonal variation (WYTTEBACH and TOBLER 1988). Seasonal dynamics of spruce needle growth and nitrogen accumulation is more clearly reflected in the absolute nitrogen content of individual needles than in nitrogen concentration. Within the first 6 weeks of needle development, a rapid increase in the absolute nitrogen content is observed, while nitrogen concentration decreases. In summer the dry mass of individual needles and the absolute nitrogen content are increasing continuously, reaching maximum values in autumn, while nitrogen concentration remains constant (BAUER *et al.* 1997). Concentrations of elements may change in successive years. In 1-year-old needles of 25-year-old Norway spruce trees, maximum differences in concentrations among seven successive years (1987–1993) approached 60% for potassium and manganese, 40–50% for calcium, magnesium, and sulphur, 35% for phosphorus, and 9% for nitrogen (LINDER 1995). Nutrient concentrations in needles may be affected by the accumulation of starch in spring and the subsequent decrease in starch concentration. According to LINDER (1995), the starch concentration in Norway spruce needles varies during the growing season from 0 to 30% of dry mass.

Concentrations of nutrients in needles are not the same in all parts of the tree crown. One-year-old needles have higher concentrations of nitrogen, phosphorus, potassium, magnesium, and lower concentrations of calcium, manganese or sulphur, compared to older needles (HÖHNE 1963; FOBER 1976; NEBE 1991; RANGER *et al.* 1992; RACHWALD 1996; DOHRENBUSCH and JAEHNE 1998; HAHN and MARSCHNER 1998; INGERSLEV 1999; ROBERTZ and LINDER 1999). In late June in the current-year needles of older Norway spruce trees, concentrations of nitrogen, phosphorus, and potassium are higher in inner and lower portions of the crown, whereas calcium levels increase towards the top and outer crown positions (FOBER 1976).

In addition to environmental factors, the concentration and content of elements in various organs and tissues is affected by genetic factors. There is a great potential for intraspecific selection within Norway spruce (provenances, families, clones) with respect to nutrient metabolism and use (FOBER and GIERTYCH 1971; KLEINSCHMIT 1982; FOBER 1986; SCHMIDT-VOGT 1991; SABOR *et al.* 1994).

7.2.5. Nutrition and growth

7.2.5.1. Nitrogen

Nitrogen has the largest impact on tree growth, and nitrogen fertilization usually increases the size and dry mass of the plant. Positive results of nitrogen application are readily observed in experiments with young Norway spruce seedlings (INGESTAD 1959; FOBER and GIERTYCH 1968; SWAN 1972). A

greater nitrogen supply enhances shoot growth often at the expense of root growth, resulting in a declining ratio of root to shoot dry mass (CLEMENSSON-LINDELL and ASP 1995; SEITH *et al.* 1996; HATTENSCHWILER and KORNER 1998; GEORGE *et al.* 1999).

Positive effects of nitrogen fertilization may be observed both in nurseries and in young and old forest stands. In the literature, there are many examples of increased tree height (GUSSONE and ZÖTTL 1975; KUKKOLA 1978; ORLOV *et al.* 1987; NILSSON and WIKLUND 1992; BERDEN *et al.* 1997), basal area (FIEDLER *et al.* 1977; KREUTZER 1981; MEAD and TAMM 1988, NILSSON and WIKLUND 1992), and volume (BAULE and FRICKER 1973; FIEDLER *et al.* 1973; NEBE 1974; FIEDLER *et al.* 1977; SARAMAKI and VALTANEN 1981; WESTMAN *et al.* 1985; HOLSTENER-JØRGENSEN and HOLMSGÅRD 1993). In an experiment conducted by MEAD and TAMM (1988), a significant increase in basal area was associated with a higher tree taper following nitrogen treatment. According to NEBE (1970), among 64 selected experiments concerned with nitrogen fertilization of spruce stands, 40 gave positive results. On the basis of numerous experiments carried out in Germany and Scandinavia, he calculated that the mean increase in volume per hectare after application of 100 kg N/ha amounted to 1–3 m³ per year. Under favourable climatic conditions, the influence of fertilization may approach 20 m³ (FIEDLER *et al.* 1973).

7.2.5.2. Phosphorus

The response of spruce seedlings to phosphorus fertilization is reflected in increased height and dry mass (INGESTAD 1959; SWAN 1972). Fertilization with superphosphate is highly effective in forest nurseries (BAULE and FRICKER 1973). There are also examples of a positive influence of phosphorus fertilization in spruce stands. In an experiment conducted in the state forests of Baden-Württemberg, stem volume was 14% higher in a fertilized plot than in the control. In the United Kingdom, on more fertile peaty soils and on strongly podzolized soils of moors, new shoots of spruce trees were 50% longer in the first few years after fertilization. Phosphorus treatment provides positive results if the soil contains sufficient amounts of other nutrients (BAULE and FRICKER 1973). Long-term intensive fertilization of a spruce stand in central Sweden with ammonium nitrate and superphosphate resulted in a three-fold increase in stem volume in comparison with the control (ERIKSSON *et al.* 1996).

7.2.5.5. Potassium

FORNES *et al.* (1970) report that in a 19-year-old spruce plantation, spruce trees fertilized with potassium were on average 19.2% taller than in the control. Similarly, potassium treatment had a significant impact on the growth rate of 4-year-old spruce seedlings planted in a sandy soil (HOLSTENER-JØRGENSEN and GREEN 1971; TAMM 1968; NEBE 1974; MELZER 1980).

Optimum potassium supply enhanced root growth and reduced the symptoms of stress in spruce trees exposed to environmental pollution with nitrogen (SETZER and MOHR 1998). Stem volume also increases in response to potassium fertilization (TAMM 1968; NEBE 1974; MELZER 1980). Potassium plays an important role in multi-component fertilizers with nitrogen, phosphorus and sometimes other elements, which significantly improves tree growth (MANGALIS 1969; GLATZEL 1971; HOLSTENER-JØRGENSEN and GREEN 1971; GUSSONE and ZÖTTL 1975; PURO 1977; HAVERAAEN 1978; NYS 1981; SHEEDY 1982; HUNGER 1985; STURE 1986; SARNACKI 1988; HÖGBERG *et al.* 1992; NILSSON and WIKLUND 1992; HOLSTENER-JØRGENSEN and HOLMSGAAARD 1993; SUNDSTRÖM 1998; INGERSLEV and HALLBACKEN 1999).

7.2.5.3. *Calcium*

MAYER-KRAPOLL (1968) found that in response to liming, the rate of tree height growth increased by 26%. EVERS (1963) recorded a substantial improvement in the growth rate of slow-growing spruce trees after application of calcium sulfate. In a seedling pot experiment with peat, calcium treatment improved seedling growth, although in some treatment combinations calcium reduced the positive effect of other fertilizers (HAVERAAEN 1978). KRAMER and ULRICH (1985) observed increased biomass production by 3-year-old spruce seedlings after application of 4 t or 6 t CaO/ha. In a spruce stand over 30-years-old in Limousin, France, liming resulted in a significant increase in stem diameter and basal area (NYS 1981).

A positive effect of calcium on plant growth is sometimes observed only upon combining fertilizers with nitrogen (HOLSTENER-JØRGENSEN and BRYNDUM 1970, NYS 1981), phosphorus (MELZER and LUCKE 1984; HUNGER 1986), magnesium (BOSCH *et al.* 1986), or other nutrients (MAYER-KRAPOLL 1968; BUSHS *et al.* 1970; HAUSSE 1971; NYS 1981; HUNGER 1985, 1986; HOLSTENER-JØRGENSEN and HOLMSGAAARD 1993). It must be noted that liming often improves soil properties, enhances the positive effect of other fertilizers, and reduces injury from environmental pollution (FEHLEN and PICARD 1994). Nevertheless, in the literature there are many examples of no effects or even negative effects of calcium on spruce growth, both in seedlings and in young or old forest stands.

7.2.5.4. *Magnesium*

There are some reports of a positive effect of magnesium on spruce seedlings (INGESTAD 1963; JANDL 1996) and forest stands (BAULE and FRICKER 1973). Magnesium may be effective in multi-component fertilizers (KOMLENOVIČ *et al.* 1969; GUSSONE and ZÖTTL 1975; BOSCH *et al.* 1986). Magnesium treatment or its presence in multi-component fertilizers improves the health of weakened forest stands exposed to environmental pollution, especially to acid rain. It slows down the decline of trees and improves their nutritional status. More-

over, magnesium may have positive impacts on soil properties by increasing the buffering capacity and consequently improving nutrient supply (HEINS-DORF *et al.* 1988, 1990; KATZENSTEINER *et al.* 1992; SCHAAF and ZECH 1993).

7.2.5.5. *Micronutrients*

In forestry research, fertilizers with micronutrients are rarely applied, although these elements are essential for the balanced nutrition of trees. BRÆKKE (1979, 1983) observed a positive effect of borax treatment on the growth of spruce stands on peatlands in Norway. An application of 0.12 kg B/ha in combination with P and K fertilization increased the rate of tree height growth by 18–49% compared to an unfertilized control.

7.2.6. *Conclusions*

Mineral fertilization enhances net photosynthetic carbon gain in spruce (SOIKKELI and KARENLAMPI 1984a, b; MAREK and LOMSKÝ 1987; HAAG *et al.* 1992; NILSEN 1995), and thus tree growth and development. Moreover, various nutrients have strong indirect effects on root system development, especially on the growth of fine roots (ROST-SIEBERT 1983; ABRASHKO 1985; MURACH and SCHÜNEMANN 1985; ASP *et al.* 1988; VOGELI and ROTHE 1988). The nutritional requirements of individual elements are closely related to plant developmental processes and phenology throughout the growing season, such as tree crown growth in spring, trunk growth in summer, root growth in autumn, and dormancy in winter (SATO and MUTO 1953).

INGESTAD (1979) determined the optimum concentrations of nutrients in culture media for Norway spruce seedlings. He reports that the mass proportions of nutrients should be: 100 N, 50 K, 16 P, 5 Ca, and 5 Mg, and the absolute N content for maximum growth rate of seedlings should be between 60–80 mg/l of medium. The preferred form of nitrogen is ammonium or a mixture of ammonium and nitrate, as it reduces the risk of negative effects of other cations. EVERS (1967c) reports that in spruce stands with optimum growth, the C/N ratio in the surface layer of the soil is 20.3, while C/P, C/K, and C/Ca ratios are respectively 112, 92, and 54. Obviously, there is a wide range of tolerance, so maximum values are: 24–26 for C/N, 350–450 for C/P, and 400–500 for C/K (EVERS 1967b, c).

In addition to nutrient ratios, the pH of the culture medium or the soil solution is important for Norway spruce growth. Optimum values vary from 4.5 to 5.0 (INGESTAD 1967), although sufficient growth is possible even at pH ranging from 3.6 to 4.2 (FIEDLER 1975). In an experiment described by SCHÖNNAM-GRUBER (1958), two-year-old spruce seedlings in hydroponic culture absorbed the largest amounts of mineral salts at a pH of 5.5.

It is noteworthy that interactions between genotype and mineral nutrition are observed for many traits of spruce trees, reflected in differing responses of

provenances, breeding lines, or clones to nutritional conditions. In one-year-old spruce seedlings, the interaction between phosphorus concentration in culture media and breeding lines within provenances was significant for major traits of growth and development (FOBER 1990). Similar findings, although for fewer traits, were obtained with varying nitrogen and calcium nutrition (FOBER 2004). The significance of the genotype-environment interaction component of variance indicates that possibilities exist for the selection of genotypes suitable for specific site conditions, as well as for genotypes that remain stable over many nutrient levels. Preferred genotypes could include those that efficiently absorb nutrients from the soil or have low nutrient requirements.

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8. REPRODUCTION

WŁADYSŁAW CHAŁUPKA

8. 1. REPRODUCTIVE DEVELOPMENT

8.1.1. *Juvenile phase and first flowering*

Initiation of the first reproductive organs (also termed strobili or flowers) is commonly considered the end of the juvenile phase and the onset of reproductive maturity in forest trees (WAREING 1959; GIERTYCH 1976c; POETHIG 1990). The evidence to date suggests that this phase change is correlated with some minimum number of growth cycles and/or minimum tree height or size (see CHAŁUPKA and CECICH 1997). Consequently, DORMLING *et al.* (1968) proposed two ways of shortening the juvenile phase in *Picea abies* under controlled conditions: (1) if the deciding factor is the number of completed growth cycles, it would be possible to accelerate a phase change by shortening the individual growth cycles; (2) if the deciding factor is determined by tree size, then an accelerated change in phase could be achieved by artificial stimulation of growth in phytotron conditions.

Under natural conditions, the average length of the juvenile phase in *Picea abies* is 20–25 years (WAREING 1959); however, first flowering in this species may be observed as early as 9–10 years (WINIARSKI 1886; STARCHENKO 1964; CHAŁUPKA 1972; SZYDLARSKI 1980). More abundant flowering coupled with a substantial production of mature seeds typically occurs much later. PANOV (1950) reported seed setting by *P. abies* trees in Bosnia at 25 years in open-grown trees, 25–30 years in trees along stand edges and greater than 35 years in trees of the stand interior. In Poland, individual open-grown trees mature at the age of 30–40 years, whereas individuals tend to mature at 60–70 years when grown in forest stands (TOMANEK 1966). Cone and seed production increases with tree age, attaining its maximum at 110–120 years in the Białowieża Primeval Forest (CHAŁUPKA 1972). After a period of maximum production, cone and seed production diminishes with tree age (HAGNER 1955; USKOV 1962).

8.1.2. *Distribution of strobili*

8.1.2.1. *Position in a tree crown*

On open-grown trees of *Picea abies*, the female strobili cover the outer portions of the crown, frequently extending to the lowest branches, especially in a year of abundant flowering (KOZUBOV 1974). However, most of the female strobili cover the upper and southern part of the crown (HAGNER 1955) and it is assumed that this is related to a higher insolation and temperature of the buds (PUKACKI 1980). Male strobili are typically found mostly in the lower half of the crown (LONGMAN 1989). The crowns of Norway spruce trees growing in a dense stand differ in terms of strobili distribution. One can recognize three zones: an apical zone, in which about 60% of the female strobili and 43% of the male strobili are distributed, a middle zone with 31% of the female and 39% of the male strobili, and the lower zone with 9% of the female and 18% of the male strobili (ELIASON and CARLSON 1968).

8.1.2.2. *Position on a branch*

According to TIREN (1935), male strobili can develop from apical buds, lateral buds, buds between whorls, and from buds subtending the branches, whereas female flowers as a rule develop from apical buds only. It appears that there is a sex gradient with an increasing proportion of female strobili in the lower shoot orders and an increasing proportion of males in the higher shoot orders (MININA 1960). DÉBAZAC (1965) associates the sex differentiation of shoots with the vigor of the apical meristem, and classifies Norway spruce shoots from the point of view of their function and degree of sexual specialization, distinguishing juvenile vegetative shoots, shoots with female strobili, and shoots with male strobili.

8.1.3. *Reproductive cycle*

8.1.3.1. *Initiation and differentiation of reproductive buds*

Norway spruce, as other *Pinaceae*, is a monoecious species and its strobili are initiated on current shoots a year before flowering (LONGMAN 1989). Flower bud initials are laid down towards the end of the height growth period. In Byelorussia, flower buds of *Picea abies* are formed in late July (JURKEVICH and GOLOD 1966), whereas in Bulgaria flower buds are formed in late May through the end of June (PLOSHCHAKOVA-BALEVSKA 1970).

The factors governing vegetative and reproductive bud differentiation are not well understood and remain an intriguing problem. According to DÉBAZAC (1965) the timing of bud differentiation is strictly related to the rate of mitotic activity of the apical meristem. VARNELL and ROMBERGER (1967) believe that bud function in Norway spruce is determined after their initiation.

At the time of flushing, the apical meristems are indistinguishable. In June, the male strobili primordia are first differentiated taking on a hemispherical shape. At that time both the female strobili and the primordia of vegetative buds take on a parabolic shape and remain similar until July, when the first ovuliferous scale primordia are initiated. The differentiation of reproductive buds in *Picea abies* seems to be closely related to the metabolism of endogenous gibberellins, and the ratio between GA₉ and GA₁ concentrations in the shoots may be used as a specific indicator of reproductive potential of the buds (MORITZ and ODÉN 1990; ODÉN *et al.* 1994).

Thus, depending on latitude, flower buds are microscopically distinguishable at the end of July and in August (TIREN 1935; KOZUBOV *et al.* 1981). Presumably at that time, the normal course of flower bud development can be disturbed, resulting in a number of abnormalities in strobili formation, e.g. female cones proliferated with shoots (JONEBORG 1945), or split cones (LEANDERSON 1970; KOZIOŁ and KRUPSKI 1994). Flower buds differentiated in the summer continue their development in the fall until the end of October, and undergo only quantitative changes during the winter by increasing in size (PLOSHCHAKOVA-BALEVSKA 1970).

8.1.3.2. Pollination and fertilization

Meiosis in the micro and megaspore mother cells precedes spring bud burst and elongation, representing the first stage of flowering (JURKEVICH and GOLOD 1966). The timing and rate of these events in different years are related to the air temperature, often quantified by a relatively consistent annual heat sums or degree-days (SARVAS 1972).

A few days after the buds open, female strobili enter a phase of receptivity. In Norway spruce, metandry is observed and receptivity is generally attained prior to pollen shedding on the same tree (ANDERSSON 1965; SARVAS 1968; ERIKSSON *et al.* 1973). Pollination takes place in Poland between late April and early May (TYSZKIEWICZ 1949), and in Byelorussia during the first half of May (JURKEVICH and GOLOD 1966). In Finland, flowering begins at the end of May, and pollen shedding lasts about two weeks (SARVAS 1957; 1968; NIKKANEN 2001). Latitude and elevation have a significant effect on the phenology of Norway spruce flowering. On the basis of several studies conducted by Russian authors, JURKEVICH and GOLOD (1966) claim that with a shift from south to north, the delay in the time of anthesis is on average two days per degree of latitude. In Romania at an elevation of 500–600 m Norway spruce begins to flower in early May, and above 1000 m in late May and early June (TOMESCU *et al.* 1967), whereas in Bulgaria flowering begins five weeks later at an elevation of 2100 m than at an elevation of 1000 m (VELKOV *et al.* 1967).

The diurnal and seasonal course of pollen shed is closely associated with temperature and relative humidity. During the day, pollen flight is maximal

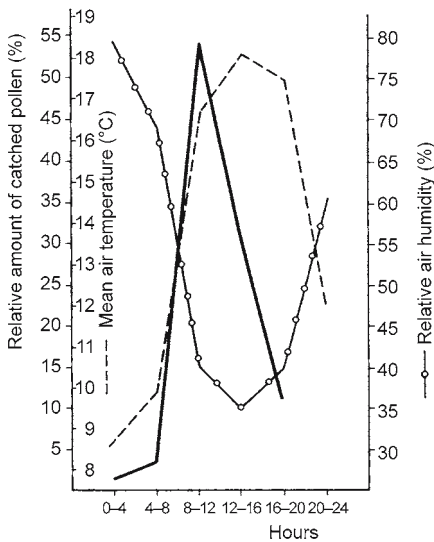


Figure 8.1. Diurnal course of pollination of Norway spruce in Finland (according to SARVAS 1955)

between 8 AM and noon, followed by a decline during the afternoon and a complete cessation at night (Fig. 8.1). Strong winds may hasten pollen shed and rains can stop it for some time (SARVAS 1955). The total production of pollen in mature Norway spruce stands varies among years. During a year of abundant flowering, pollen deposition may reach 120–160 kilograms of pollen per hectare (SARVAS 1968).

Pollen grains are transported by the wind to the female strobili and deposited at the bottom of ovuliferous scales. The receptive period of female strobili lasts 9–16 days as was observed by Prof. RISTO SARVAS (NIKKANEN 2001). The number of grains received by a single ovule can exceed 100, but only a few of them are transferred through the micropylar

canal to the pollen chamber, which is able to hold 5.1 pollen grains on average. Pollen transfer with the aid of the so-called pollination drop takes place during the night and can be disturbed by night frosts. Yet, pollen grain germination in a pollen chamber frequently exceeds 90% in southern Finland (SARVAS 1968). Immediately after reaching the chamber, the pollen grains germinate, the pollen tubes penetrate the nucellus, and finally fertilization occurs 3–4 weeks later (MIYAKE 1903; HÅKANSSON 1956; CHRISTIANSEN 1972; KOZUBOV 1974).

8.1.3.3. Seed maturation and fall

After fertilization, embryo development continues during the summer months. At the end of August, the embryo is fully differentiated with cotyledons, plumule, primary roots, and provascular bundles in the hypocotyl. Seeds attain full maturation at the end of September in Sweden, and in October in Poland and Byelorussia (HÅKANSSON 1956; TYSZKIEWICZ 1949; JURKEVICH and GOLOD 1966). Although some seeds are released from the cones already in September (SOKOŁOWSKI 1921; OPSAHL 1951), most seeds fall in late winter, when the moisture content of the cones is reduced to 18% (MESSER 1956).

The quality of Norway spruce seeds is dependent on many factors. The proportion of full seeds in the total crop and their weight vary with crown position and are higher in the lower than upper crown. Higher percentages of full seeds

are also observed in southern than northern crown positions (MESSER 1956). The frequency of full seeds is also evidently dependent on the abundance of pollen shed. During a poor flowering year, the percentage of full seeds is considerably lower (SARVAS 1968).

8.1.4. Flowering in seed orchards

The first male and/or female strobili appear on *Picea abies* grafts at the age 3 to 5 years (DORMLING 1970; KOZUBOV *et al.* 1981; MELCHIOR 1987; EFIMOV 1993). However, abundant flowering in seed orchards (more than 20 cones per graft) can be expected 12 – 20 years after grafting (NILSSON and WIMAN 1967; ERIKSSON *et al.* 1973, CHALUPKA 1988). It is possible to accelerate flowering by several years through grafting scions on the top of stocks about 0.5 m in height (DIETRICHSON and TUTTUREN 1978).

In general, the numbers of female and male flowers are well correlated, but in some years female flowering is much poorer than male flowering (ERIKSSON *et al.* 1973; SKRØPPA and TUTTUREN 1985; CHALUPKA 1988; NIKKANEN and RUOTSALAINEN 2000). Abundant female flowering is not always well correlated with cone crop, as crop production is strongly affected by the abortion of strobili and cones owing to injury caused by late frosts at the time of receptivity (ERIKSSON *et al.* 1973). The percentage of aborted cones ranges from 1 or 2 to over 12 percent and is similar in both greenhouse and outdoor *Picea abies* seed orchards (JOHNSEN *et al.* 1994a).

Flowering and seed production in *Picea abies* seed orchards is strongly affected by inter- and intra-clonal variation (NILSSON and WIMAN 1967; ERIKSSON *et al.* 1973; WERNER 1980; SKRØPPA and TUTTUREN 1985; CHALUPKA 1988, CHALUPKA and ROŻKOWSKI 1995; NIKKANEN and RUOTSALAINEN 2000). Distinct variation in the flowering periodicity and abundance among grafts of the same clone could be associated with topophysis (DORMLING 1970; SARVAS 1970), height (REMRÖD 1972; ERIKSSON *et al.* 1973), and/or stock origin (MELCHIOR 1987).

Long-term studies of flowering on *Picea abies* seed orchards indicate marked periodicity of cone crops similar to that observed in mature stands (WERNER 1980; DIETRICHSON 1989; NIKKANEN and RUOTSALAINEN 2000). The periodicity of *Picea abies* clones flowering in the same seed orchard can also be influenced by their geographic origin. Northern clones moved to southern latitudes produce cones and seeds more frequently and in larger amounts than in their place of origin (SKRØPPA and TUTTUREN 1985; MELCHIOR 1987; CHALUPKA 1988; EFIMOV 1993; CHALUPKA and ROŻKOWSKI 1995). At first this finding seemed to support the idea of an accelerated and increased production of *Picea abies* seeds by moving clones from a cold to warmer climate, i.e. from north to south as well as from high to lower elevations, or growing them in greenhouses under a temperature regime higher than ambient. How-

ever, it was observed that such treatments cause unexpected aftereffects. The altered environment in which sexual reproduction occurs causes increased abortion at early stages of embryogenesis and significantly affects many qualitative traits of *Picea abies* seedlings derived from seeds developed in this manner (SKRØPPA and JOHNSEN 2000; OWENS *et al.* 2001; SAXE *et al.* 2001).

8.1.5. *Natural protection against selfing*

Norway spruce is partly able to protect itself against selfing. Metandry is the first barrier to self-pollination, but its effectiveness is diminished because of prolonged female strobili receptivity, which overlaps with pollen shed on the same tree. However, metandry is assisted by a limited capacity of the pollen chamber. Generally only the first pollen grains contacting the surface of nucellus have an opportunity to achieve fertilization. Thus, the limited capacity of the pollen chamber acts to prefer early pollinators, resulting in important genetic consequences (SARVAS 1968). Another barrier against selfing is embryo abortion caused by lethal genes during the different phases of proembryo development (from syngamy to the second mitosis). This results in the rejection of most self-fertilized embryos (KOSKI 1971). These natural protection mechanisms against selfing could be very ineffective in a year of insufficient pollen shed. The probability of self-pollination in such years is very high, and the genetic quality of the seed diminishes. Consequently, Norway spruce seeds should be collected only in years of abundant cone crops (SARVAS 1968).

8.1.6. *Periodicity of flowering and seed crops*

Some self-regulation of the periodicity of flowering and seed crops exists in Norway spruce stands. Abundant flowering will substantially reduce the number of vegetative buds in the crown. In addition, cones that are formed during the same growing season as the seeds utilize a considerable amount of assimilated carbon. Consequently, this diminishes the number of new shoots and buds in the year after flowering and markedly reduces the possibility of new strobili initiation (TIREN 1935, GORCHAKOVSKI 1958; ZYKOV 1967; CHAŁUPKA *et al.* 1975b). In general, abundant cone crops in Norway spruce are not observed in two consecutive years even though the environmental conditions are suitable for flower induction (CHAŁUPKA and GIERTYCH 1973; INNES 1994; KANTOROWICZ 2000).

The gap between two consecutive abundant crop years varies depending on geographic location. In Byelorussia, as well as in the northeastern part of European Russia, large crops occur every 3–5 years (USKOV 1962; MOLCHANOV 1967). On average, seed crop frequency in Poland is comparable to that of Sweden and Finland, where abundant seed crops occur every 11–12 years or 12–13 years, respectively (SARVAS 1957, 1968; HAGNER 1965; CHAŁUPKA and

GIERTYCH 1973; KANTOROWICZ 2000). Good seed crops are most frequent in the central regions of the geographic range of Norway spruce, and their frequency declines as one moves towards the limits of the range (DOLGOSHOV 1958; CHAŁUPKA and GIERTYCH 1973).

8.1.7. Factors affecting cone and seed production

8.1.7.1. Soil fertility, stand characteristics, and individual variation

MOLCHANOV (1950) reports that seed crops in *Picea abies* differ depending on the forest site type with the highest crops observed on the richest sites. However, this relationship is apparent only in years of a poor cone crop, whereas in good seed years, Norway spruce stands yield seeds in quantities unrelated to site index (BARABIN 1969).

The growth characteristics of trees and their crown position within the stand also play a role in flowering and seed production. The number of male and female strobili increases substantially with an increase in the average dominant height of a *Picea abies* stand (SARVAS 1968; CHAŁUPKA *et al.* 1975a). The mean crop on trees of *Picea abies* in the 1st and 2nd KRAFT class was much higher than on trees from the lower classes, and trees from these two upper classes produced 86% of the total cone crop in the stand (MESSER 1956). A similar positive correlation exists between tree diameter at breast height and cone crop (HAGNER 1958; USKOV 1962; ELIASON and CARLSON 1968; CHAŁUPKA *et al.* 1975a).

8.1.7.2. Climatic factors

The influence of climatic factors on reproductive development must be divided into two separate periods: (1) before strobili initiation, and (2) during flower and cone development. The period through strobili initiation appears more sensitive to the influence of weather than the second period. Many authors attach considerable importance to air temperature, particularly at the time of strobili initiation, e.g. a year before flowering. It has been observed in many studies, that the mean daily temperature in late June and early July or in July is significantly correlated with the cone crop abundance the following year (TIREN 1935; EKLUND 1957; BRØNDBO 1970; CHAŁUPKA 1975a; LINDGREN *et al.* 1977; ILSTEDT and ERIKSSON 1982).

An important climatic factor operating together with temperature is insolation which is also well correlated with flowering abundance. Abundant cone crops in *Picea abies* were observed when the mean hours of sunshine in the previous June attained a minimum 9 hours per day (ZVIEDRE 1970; CHAŁUPKA 1975a). Similarly, low precipitation during the summer affects the initiation of flower buds and results in a good cone crop the following year (TIREN 1935; TYSZKIEWICZ 1949), whereas excessive precipitation has an opposite ef-

fect (BRØNDBO 1970; BASTIDE, Ia and VREDENBURCH, van 1970). Based on the information reviewed above, it is possible to predict good seed years in advance with some degree of reliability (LEIKOLA *et al.* 1982; PUKKALA 1987a).

8.1.8. Artificial stimulation of flowering

8.1.8.1. Wound treatments

Among a number of methods, strangulation enhanced male strobili initiation on mature *Picea abies* seed-trees 2–3 years after treatment (STEFANSSON 1948), whereas ringing significantly stimulated female strobili initiation in 13-years-old Norway spruce trees (CHALUPKA 1997). Top and branch pruning as well as root pruning did not influence flowering (KOZUBOV *et al.* 1981) and severe pruning resulted in a large reduction of cone production in a seed orchard (NILSSON and WIMAN 1967; SAMUELSON 1979).

8.1.8.2. Mineral fertilizers

Using different fertilizers to stimulate cone and seed production in *Picea abies* trees can be effective when nutrients are carefully chosen for the local soil conditions (MÄLKÖNEN 1971). Cone production has been significantly increased in *Picea abies* stands when nitrogen, phosphorus, and potassium were applied to the soil a year prior to flowering (SKOKLEFALD 1970; MÄLKÖNEN 1971; ENESCU *et al.* 1973; CHALUPKA 1976). In a series of foliar nutrition experiments, VOGL (1960) noted a significant relationship between an increased accumulation of phosphorus in the buds of *Picea abies* and the floral induction process.

8.1.8.3. Modification of climatic factors

Covering *Picea abies* grafts with polyethylene in late June and early July significantly enhanced male (BRØNDBO 1969; CHALUPKA and GIERTYCH 1977; CHALUPKA 1981) and female flowering next year (REMRÖD 1972). However, covering individual trees with polyethylene or growing them in polyethylene greenhouses may modify many microclimatic conditions and it is difficult to decide which factor is the most important one. The intensity of sunlight transmitted by polyethylene declines by 25% when the cover is dry, and by 60% when the cover is covered with moisture. However, in both cases the transmission of far-red light (above 670 nm) increases and the temperature under the cover is elevated by several degrees (PUKACKI 1981; CHALUPKA 1985).

Even if temperature is a major factor influencing the process of flower primordia initiation in covered spruce grafts (TOMPSETT and FLETCHER 1977, 1979; OLSEN 1978), light still remains a primary factor and can directly affects the process of flower induction. This supposition has been confirmed by detailed studies of light transmission through the bud scales of forest trees using

fiber optics (CHALUPKA and GIERTYCH 1979; PUKACKI and CHALUPKA 1982; PUKACKI and GIERTYCH 1982). Inserting optic fibers into the buds bypassed the protective role of bud scales and enhanced the transmission of full, direct sunlight inside the bud, stimulating the initiation of female strobili in mature *Picea abies* trees (KOSIŃSKI and GIERTYCH 1982).

8.1.8.4. Growth regulators

Unsuccessful trials with growth retardants first indicated a possible role of plant hormones in flower induction in *Picea abies* (DUNBERG 1974). In later experiments, a significant interaction between CCC (chlorine chloride) and GA₃ (gibberellic acid) in the stimulation of female and male flowering was achieved in *P. abies* grafts (BLEYMÜLLER 1976; CHALUPKA 1979). In addition, GA₃ applied alone a year before flowering stimulated both the number of flowering grafts and mean number of strobili per graft (CHALUPKA 1981).

The results of several studies on the metabolism of endogenous gibberellins indicated their likely involvement in floral induction in *P. abies* (DUNBERG 1979; CHALUPKA *et al.* 1982; DUNBERG *et al.* 1983). A more pronounced stimulation of *P. abies* flowering was obtained when less polar gibberellins were applied at the time of flower induction. Supplying a GA_{4/7} mixture by spraying or by stem injection significantly increased the number of flowers initiated on *P. abies* grafts (DUNBERG 1980; SCHACHLER and MATSCHKE 1991; JOHNSEN *et al.* 1994b; HÖGBERG and ERIKSSON 1994), whereas for *P. abies* seedlings a carry-over effect was observed in the second year following GA_{4/7} treatment (BONNET-MASIMBERT 1987, 1989; CHALUPKA 1997). The effect of the GA_{4/7} mixture was enhanced by the addition of GA₉ (DUNBERG 1980), when combined with higher temperatures in a greenhouse (LUUKANEN 1979, JOHNSEN *et al.* 1994b) and ringing (BONNET-MASIMBERT 1987, 1989; SCHACHLER and MATSCHKE 1991). A stimulation effect of hormonal treatments on the flowering of *P. abies* grafts was also observed in the case of kinetin and maleic acid hydrazide (BLEYMÜLLER 1978; RONIS 1983) and no interaction was observed between the effects of GA_{4/7} and root pruning (HÖGBERG and ERIKSSON 1994) or NAA (naphthyl acetic acid) treatment (DUNBERG 1980).

8.1.9. Cone and seed crop in relation to vegetative growth

Flowering, cone development, and seed maturation in *Picea abies* take place in one growing season. Consequently, it is essential to examine both flowering and seed crop production jointly when evaluating their effects on growth. By contrast, the joint effect on growth is both larger and easier to estimate than in the case of *Pinus sylvestris*, where flowering, cone development, and seed maturation extend over two growing seasons and may result in overlap with seed yield of other years (FOBER 1976).

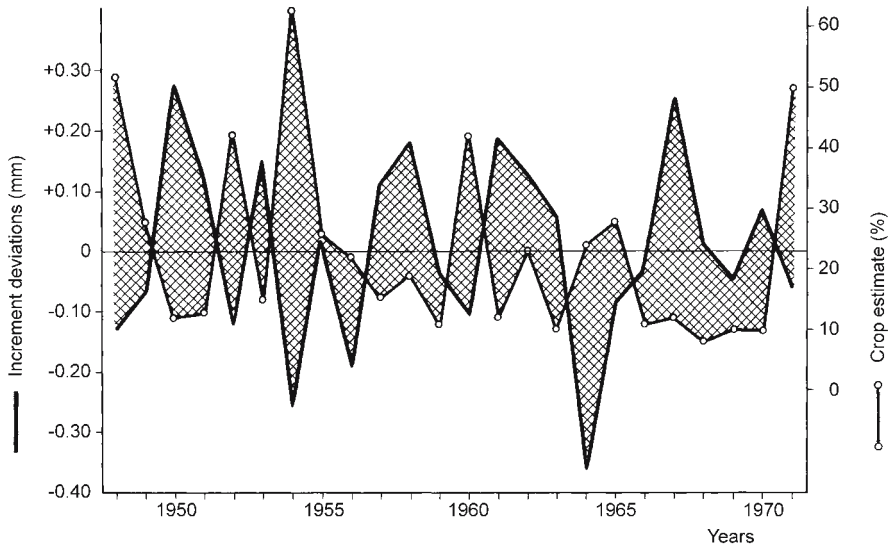


Figure 8.2. A comparison of cone crop data and growth increment deviations from the fitted line (according to CHAŁUPKA 1975a)

A significant negative correlation between cone crop and radial growth increment is readily observable (Fig. 8.2). The width of the annual ring in the years of abundant cone and seed crop production in *Picea abies* may be reduced by 18–42% compared with the growth increment of non-flowering years, and a growth reduction is also detectable in the year following seed fall (MIKOLA 1950; DANILOV 1953; EKLUND 1954; HOLMSGAARD 1955; JONSSON 1969; BUYAK 1975). In years of an abundant cone crop, the percentage of *P. abies* late wood as well as the specific gravity of wood declines (CHAŁUPKA *et al.* 1977; PUKKALA 1987b). Estimates in a mature stand of *P. abies* revealed that the production of 1 kg of dry mass of reproductive structures (cones, seeds, and male flower residues) is associated with a loss of about 3 kg of wood dry mass (CHAŁUPKA *et al.* 1975b).

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8.2. VEGETATIVE PROPAGATION

8.2.1. Grafting

Grafting of forest tree species began in Sweden by ANDERSON in 1906 (WERNER 1979). Grafting is used for the propagation of ornamental varieties and the establishment of seed orchards. A key advantage of grafting compared to other methods of asexual reproduction is the absence of an age barrier in the ortet, permitting the propagation of very old trees. Spruce can be grafted either in the field or in a greenhouse. Grafting in a greenhouse requires planting rootstocks in pots. The most common rootstocks are 3 or 4-year-old *Picea abies*. For production of large quantities of vigorous shoots for grafting, SYRACH-LARSEN (1956) recommends grafting permanent rootstocks with a diameter of 5–10 cm at the grafting union. In such situations, the rapid growth of grafted shoots will enable further collection of material for grafting after one 1 or 2 years. Grafting 6- or 7-year-old permanent rootstocks at a height of 0.5 m and cutting the rootstock above the grafting union guarantees rapid growth and a regular form of the graft (NAESS-SCHMIT and SØEGAARD 1960, after WERNER 1979).

The best scions are obtained from the tops of vigorous one-year-old shoots from the upper or outer parts of the crown (GIERTYCH and PRZYBYLSKI 1965; HRYNKIEWICZ-SUDNIK *et al.* 1991). Grafts developed from scions obtained from the upper tree crowns flower more frequently and more abundantly compared to grafts developed from the lower crowns, an important trait for seed orchard grafts (DORMLING 1970, 1976). While it is possible to graft twigs (ŚLASKI and SĘKOWSKI 1988), older scions are more difficult to establish. Scions that exhibit discolored needles or necrotic apices are rarely successful grafts, likely a result of poor cell division.

The most appropriate times of the year for grafting Norway spruce is February-March in greenhouses (KRÜSSMANN 1964) and May in the field (SYRACH-LARSEN 1956; GIERTYCH and PRZYBYLSKI 1965) or in August-September in field or greenhouses (KRÜSSMANN 1964; GIERTYCH and PRZYBYLSKI 1965). Rootstocks may be grafted near the root collar at a height of 5–10 cm or in the middle of the shoot apex (HRYNKIEWICZ-SUDNIK *et al.* 1991). Grafting last-year's shoots produces better results in comparison to three-year old shoots (MEHNE 1990). Old and thick rootstocks can be grafted at a height of 1.3 m (SYRACH-LARSEN 1956). The success of grafting depends on accurate technique and sterile conditions. In the *Pinaceae*, resins may prevent proper bonding between the graft and rootstock. This necessitates grafting at low temperatures and frequent washing.

8.2.2. Grafting methods

The majority of grafting methods of Norway spruce place scions on the side of the rootstock. GIERTYCH and PRZYBYLSKI (1965) demonstrated a higher effectiveness of lateral grafting compared to scion grafting into a cleft in the shoot apex. Whenever rootstocks are thick, SYRACH-LARSEN (1956) recommends cutting the rootstock, especially when using the method in which the scion is placed beneath the bark within two parallel incisions.

Lateral grafting is carried out using the side-grafting method (DORMLING 1963). A firm union between the scion and the rootstock prevents tissue isolation by resin flow, and is often strengthened with polyethylene straps, rubber bands (BÄRTELS 1982), or cotton strings (HRYNKIEWICZ-SUDNIK *et al.* 1991). In addition, PROKAZIN'S method (1962) also known as the "cambium to cambium" or "pith to cambium" method is also effective. In this procedure, a cut is made to expose the cambium on the rootstock and the scion is cut on one side at an angle or along the pith. The advantage of this method is that the two parts fuse properly even in the case of less accurate work. When grafting weak scions, scions may be cut on two sides forming a wedge (both cuts must have a common longitudinal edge) and inserted into a notch cut into the rootstock.

To date, bud grafting of coniferous species has not been practiced widely. SEVEROVA (1951) described a method of grafting *P. abies* rootstocks with *P. pungens* scion resting buds. Norway spruce trees can also be grafted using the chip-budding method (KOHNET 1991). Micro-budding is another form of bud grafting in which buds are collected from ortets or from *in vitro* meristematic cultures on rootstocks from several-week old seedling cultures *in vitro* or *ex vitro*. The objective of this kind of propagation is the rejuvenation of ortet tissue, but this is not always achieved (EWALD *et al.* 1991).

The fusing of *Picea abies* grafts typically begins with cell divisions of the rootstock cambium on the fourth day after grafting. The functional merger of phloem and xylem tissues occurs in the 5th–8th week (MEHNE 1990). Physiological indicators of the fusion process include the water potential and water content of the scion tissues (BEASON and PROEBSTING 1988). It is possible to accelerate the growth of grafted plants in controlled-environment chambers (NIENSTAEDT 1959).

In contrast to forestry, the nursery practice does not recommend outdoor spruce grafting (TERPIŃSKI 1984; ŚLASKI and SĘKOWSKI 1988; HRYNKIEWICZ-SUDNIK *et al.* 1991), since graft success is often highly weather dependent. In forest nurseries, rootstocks are typically planted at 50 × 25 cm spacing and grafted after attaining a diameter of 6–8 mm. In the case of spring grafting, shoots soon begin to develop from buds of the established scions. Apical portions of the stock may then be removed the following year. In the case of summer grafting, the formation of grafted plants may be terminated in spring of the following year.

8.2.3. Layering

Norway spruce will naturally layer and the resulting shoots can be used for propagation (RUBTSOV 1952). However, this technique is not widely used because it is difficult and the success rates are rather low. Aerial layers are recommended for propagating valuable or endangered ortets. The rooting medium is peat moss (*Sphagnum* sp.) saturated with water, which is used to wrap the base of the layered shoot. To prevent drying, the peat moss is covered tightly with plastic wrap and with aluminium foil to protect against overheating. Placing several incisions in the shoot and treating with auxins will stimulate rooting. Layering is recommended for *P. abies* and *P. pungens* in April before bud burst. The shoots should be cut in a 2–3 mm ring and treated with a growth stimulator containing up to 0.5% IBA.

8.2.4. Rooted cuttings

It is difficult to establish the origin of this method of propagation. KLEINSCHMIT *et al.* (1973) quote PFIFFERLING'S reports (1830) about successful rooting of *Picea abies* cuttings. KURDIANI (1908) propagated 11 species of trees in a hotbed and obtained 84% rooting effectiveness for *P. abies*. Therefore, this tree species is not particularly difficult to propagate (KOBENDZA 1922). Today the propagation technique by cuttings is used in tree breeding and commercial production of selected planting material and ornamental plants as well as in the protection of genetic resources *in situ*.

Norway spruce cuttings are rooted with needles and should be exposed to light throughout the rooting period. Cuttings are placed directly into the substrate to a depth of about 2 cm. Appropriate controlled-environment facilities that provide heating and watering are helpful (LEPISTÖ 1974). KLEINSCHMIT *et al.* (1973) recommended setting the rooted cuttings in April and May, when air temperatures range from 5 to 30°C, whereas LEPISTÖ (1974) recommended temperatures of 20–25°C during the day and 10–15°C at night. DORMLING *et al.* (1977) and DORMLING and KELLERSTAM (1981) applied air temperatures of 17 to 18°C and lighting of 7–8 klx intensity for 18 h a day. Substrate heating is only recommended when rooting is conducted in winter (DEUBER and FARRAR 1940; LEPISTÖ 1974), whereas in spring and summer it is likely detrimental (KLEINSCHMIT 1972a, b). Shading, ventilation, and water are essential during summer when overheating may occur (RADOSTA 1987; VOLNÁ *et al.* 1990) and it becomes important to prevent drying (HARTIG 1986). High humidity encourages the development of fungal diseases, in particular, grey mold (*Botrytis cinerea*); however, fungal diseases can be prevented by appropriate ventilation or use of fungicides such as captan and benomyl (KLEINSCHMIT *et al.* 1973; WÜHLISCH 1984).

Standard substrates used for seedling rooting are blended mixtures of sand and fine peat most commonly at a 1:1 ratio. When automatic sprinkling is unavailable, the proportion of fine peat in the mixture is often increased. Perlite and vermiculite are frequent supplements (HRYNKIEWICZ-SUDNIK *et al.* 1991). *P. abies* cuttings are sensitive to rooting in different substrates (KLEINSCHMIT *et al.* 1973). Presumably, rooting conditions can influence the effectiveness of the various substrates. KLEINSCHMIT *et al.* (1973) recommended the exclusive use of pure gravel with a grain diameter ranging from 3–7 mm. Alternatively, LEPISTÖ (1974) advises the application of peat moss or a mixture of peat moss and garden peat. BENTZER (1985) considers a mixture of peat and perlite a useful potting medium for rooting. ŠKOLEK (1987) recommends an all-purpose substrate made up of a mixture of gravel and perlite (1:1). VOLNÁ *et al.* (1990) recorded the best results in pure sand. Other authors recommend a 1:1 mixture of peat and vermiculite (ARMSON *et al.* 1980). Other media include the use of a mixture of sand and humus from forest stands (PELKONEN 1981), compost (KLEINSCHMIT 1972a), bark compost and sand (KOŠULIČ 1984), blocks of mineral wool (JOHNSEN *et al.* 1985) as well as other mixtures. Substrate reaction (pH) has no clear effect on rooting (LARSEN 1946; KLEINSCHMIT *et al.* 1973).

8.2.5. Stimulators

Growth stimulators commonly include the auxins IAA, IBA, NAA as well as their salts. The effect of auxins can be enhanced by rooting co-factors (LIPECKI and DENNIS 1970) or by a rhizocaline complex (MICHNIEWICZ 1969). Sometimes they are added to commercial preparations together with fungicides (most often Captan and Benomyl). The three most common methods of treating the base of the cuttings with stimulators are: 1) soaking in water-based solutions (0.01 – 0.1%) for 8 to 48 hours; 2) soaking in alcohol-based solutions (0.1 – 2%) for several seconds (quick dip method); and 3) dusting with talc powder containing from 0.1 to 2% auxins often mixed with co-factors and fungicides. Root stimulating activity has also been shown for secretions of mycorrhizal fungi, e.g. *Laccaria laccata* (SCOP. ex FR.) BK. et BR (CHMELIKOVÁ and CUDLIN 1990).

Growth stimulators generally must not come into contact with needles, as they may be toxic at the above-mentioned concentrations. The preparations should be selected to suit individual seedling types. Stimulators usually increase the proportion of successfully rooted cuttings and nearly always improve the quality of the root system. LARSEN (1946) claims that the positive impact of IAA is evident only in optimal outdoor conditions. Despite the frequent application of auxins in the propagation of *P. abies*, there are few direct comparative studies. DEUBER and FARRAR (1940) observed only a negative effect of auxin IBA on rooting. PAULE and ŠKOLEK (1983) rooted cuttings

from 1- and 2-year-old spruce trees using powdered forms of IAA (0.5% and 1%), IBA (0.5% and 1%) as well as the AS-1 preparation and observed either no effect or reduced rooting. In contrast, MEDEDOVIĆ (1987), using 0.125% IAA, reported increased rooting of shoots of 4-year-old ortets from 80 to 96% and from 10 to 60% in 12-year old trees. IAA potash salt (IAK) at 0.25% concentration improved rooting in shoots from 12–16-year-old trees from about 40 to 90%. JOHNSEN (1986) observed interactions between the action of auxin and the type of cuttings. KLEINSCHMIT *et al.* (1973) recommend the application of 0.1% IAK preparations. The use of auxin preparations for rooting is banned in Sweden (BENTZER 1985) and discouraged by LEPISTÖ (1974). Despite this, the above-mentioned authors report a very high success of rooting of *P. abies* shoots on a commercial production scale. Therefore, it is very likely unnecessary to treat *P. abies* cuttings with an exogenous auxin.

8.2.6. Age of maternal plants (cyclophysis)

With increasing age of the ortet, the capability of cuttings to develop roots decreases; they tend to develop poorer root systems and maintain plagiotropic and slow growth longer after rooting (ROULUND 1975, 1979; KLEINSCHMIT 1972a, b, 1992; JESTÆDT 1980; SCHACHLER and MATSCHKE 1984; WÜHLISCH 1984; MEDEDOVIĆ 1987). Commercial propagation requires cuttings not older than 4 years and developed either from seeds or vegetatively. In this case, rooting success may approach 100%. Progenies of plus trees are frequently selected for cuttings (KLEINSCHMIT *et al.* 1973; KLEINSCHMIT 1974; LEPISTÖ 1974; BENTZER 1985; JOHNSEN 1985, 1986; WERNER and PETTERSSON 1981; VOLNÁ *et al.* 1990). DEUBER and FARRAR (1940), EWALD and SCHACHLER (1990), and JANSON (1990) report the rooting of cuttings from mature trees. However, progeny derived from older ortets require more time to attain proper form and growth characteristics (BENTZER 1988; DEKKER-ROBERTSON and KLEINSCHMIT 1991; KLEINSCHMIT 1992).

One of the ways to overcome age effects (cyclophysis) is to use serial propagation. Rejuvenation is achieved by grafting (FRÖHLICH 1961) or micro-grafting (EWALD and SCHACHLER 1990; EWALD *et al.* 1991). However, EWALD *et al.* (1991) failed rejuvenate *P. abies* micro-grafts, but did in the case of *Larix europaea*. DORMLING and KELLERSTAM (1981) recommend rejuvenation of maternal plants using a system of treatments comprised of controlled-environments, cutting, and grafting. Treatment of ortets with cytokinins contributes to partial rejuvenation of *P. abies* clones, recognized by reduced flowering and an increased rooting capability (BOURIQUET *et al.* 1985; MATSCHKE *et al.* 1991). O-vaniline applied externally was effective in shoot rejuvenation (EWALD and SCHACHLER 1990). Serial propagation of young ortets used in tree breeding and clonal forestry prevents clone-aging effects (CLAIR *et al.* 1985; DEKKER-ROBERTSON and KLEINSCHMIT 1991).

8.2.7. *Timing of shoot collection and planting cuttings*

There is a strong effect of the time of year on the rooting ability of cut shoots. The optimal time is when shoot growth has fully ceased (GIROUARD 1975). DEUBER and FARRAR (1940) found minimal rooting (18%) of plants harvested in October and maximal rooting (64%) of plants harvested in December. For ornamental plants, the recommend period for shoot harvesting and planting ranges from June to August (KRÜSSMANN 1964; BÄRTELS 1982; ŚLASKI and SĘKOWSKI 1988; OSIECKA 1989; HRYNKIEWICZ-SUDNIK *et al.* 1991). In clonal nurseries of *P. abies*, a variety of combinations of harvesting and planting are possible in practice. The combinations include: shoot collection in November and rooting in winter or the following spring (LEPISTÖ 1974), shoot harvesting in January and rooting in May or shoot collection in late February or March (or up to May) followed by direct rooting (KLEINSCHMIT *et al.* 1973; BENTZER 1985). It is not recommended to harvest the shoots in spring, since the shoots may exhibit winter frost damage (FREIJ 1986). Ideally, shoots should be harvested in the autumn when winter dormant. Rooting carried out from August until the middle of September gives very good results (FREIJ 1986). Spring rooting of shoots harvested in autumn requires cold storage in plastic bags at temperatures ranging from 4 to -5°C among various studies (KLEINSCHMIT *et al.* 1973; LEPISTÖ 1974; FREIJ 1986; BEHRENS 1987; WERNER and PETTERSSON 1981). Short-term storage of cuttings wrapped in peat moss can be accomplished in galvanized boxes in an unheated basement or shaded place outdoors (KLEINSCHMIT *et al.* 1973; JESTAEDT and RAPP 1977). Cultivation of maternal plants under growth chamber conditions and rooting them in air-conditioned glasshouses may permit propagation in 5–6 week rooting intervals and rapid regeneration of selected clones (JOHNSEN 1985).

8.2.8. *Collection of shoots in the crown*

The crown position from which shoots are harvested can affect rooting and subsequent growth. Position effects can be greater in older ortets (KLEINSCHMIT *et al.* 1973; GIROUARD 1974). Lateral shoots of 2- or 3-month-old cuttings root earlier in comparison with axial and dominant shoots, but develop fewer first-order roots (JOHNSEN 1986). VOLNÁ and RADOSTA (1985) recorded better rooting of cuttings derived from the tops of axial shoots (in the second-year ortets) than from cuttings obtained from the base of axial shoots and sylleptic shoots. In studies carried out by ROULUND (1975), the rooting capability of *P. abies* shoots usually decreased with tree height. HAUCK (1987), in experiments rooting shoots from grafts of plus trees, found slightly better rooting in second order than first order shoots, although overall rooting was poor. HAUCK and VOLNÁ (1990) showed that rooting capability of different shoots

of one ortet could range from 0% to 96%. Shoots from the highest and lowest crown positions did not set roots. Differences in rooting capabilities of shoots from 4-year-old ortets are of no practical significance (BENTZER 1988). The causes of reduced rooting capacity of shoots derived from upper parts of the crown include cell specialization and a high level of biosynthesis of cytokinins, which are strong inhibitors of root development (BOLLMARK and ELIASSEN 1990b).

8.2.9. Cutting size

VOLNÁ and RADOSTA (1985, 1987) failed to find an influence of the size of the cuttings (including the growth of shoots from the previous year) on the extent of rooting. However, cutting size exerts some influence on the quality of rooting and the final planting material. Larger cuttings develop larger root systems and exhibit greater growth after rooting. However, HAUCK (1987) noted that large-diameter cuttings did not set roots, thin cuttings died rapidly, and medium-diameter cuttings rooted the best. Cuttings of two- and three-year-old shoots with short annual growth increments died after two months. Nevertheless, in propagating ornamental varieties, cuttings of two-year-old wood are sometimes used, especially in the case of dwarf varieties (OSIECKA 1989). The need to regenerate selected ortets quickly may necessitate the use of shoot fragments to produce cuttings (HAYMÖLLER 1981). It is essential that the basal portion of the shoots have at least four side buds (KLEINSCHMIT *et al.* 1973).

8.2.10. Population and individual variation

In large-scale propagation of selected clones, it was found that clones differ, sometimes widely, in their rooting capabilities (KLEINSCHMIT *et al.* 1973; TOMKOVÁ *et al.* 1987; CHLEPKO and TOMKOVÁ 1990; JANSON 1990) and development of root systems (TOMKOVÁ *et al.* 1987; CHLEPKO and TOMKOVÁ 1990). JOHNSON (1986) observed significant variation and complex interactions of the mean number of roots between families, types of cuttings, and auxin treatment, which made the assessment of genetic factors difficult. SKRØPPA and DIETRICHSON (1986a) determined variance components for individual sources of variation in two groups of controlled crosses as follows: paternal variances of 15% and 1%; 14% and 13% for families (within paternal lines); 12% and 36% for clones within families; and 59% and 50% for environmental variance components. Hence, genetic factors comprised 41% and 50% of the total variance. Rooting repeatability amounted to 0.30 and 0.59 for clones within families and 0.89 and 0.85 in the case of family means. The heritability of rooting in cuttings ranged from 0.38 to 0.75, as determined by MERGEN (1960, after GIERTYCH 1977).

8.2.11. Growth after outplanting

Growth depends on genetic potential, ortet developmental stage, quality of the root system, and vigor (FOSTER *et al.* 1987). Cuttings with terminal buds develop plants with a reduced height increment, fewer forks, and a higher proportion of plagiotropic trees in comparison with cuttings developed from basal shoots lacking terminal buds (HAVMÖLLER 1981). The fewest number of plagiotropic plants is derived from shoots obtained from the highest whorl (BENTZER 1988). Trees of vegetative origin derived from young ortets initially grow faster than cuttings (KLEINSCHMIT and SCHMIDT 1977; HARTIG 1986, ŽĎÁRSKÁ 1988; KLÍMA 1990; GEMMEL *et al.* 1991). KLEINSCHMIT (1974) suggests outplanting propagated material on plantations as long as the ortet age does not exceed 20 years, even though ROULUND (1974) reported reduced growth of trees derived from 9-year-old ortets compared to plants of seed origin. With increasing age, the growth of trees of vegetative origin catches up with that of trees of seed origin, if genetic variability is disregarded (ROULUND 1974; KLEINSCHMIT and SCHMIDT 1977; HARTIG 1986, ŽĎÁRSKÁ 1988). The basic features of root systems of vegetatively propagated trees remain unchanged for at least 25 years after planting (KLÍMA 1990; MAUER and PÁLATKOVÁ 1994). Long-term observations of *Picea abies* trees of vegetative origin reveal that morphological differences, in relation to plants of seed origin, remain for decades, but that such trees are of full value and can be used in plantation forestry.

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9. GENETICS

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9.1. PROVENANCE VARIATION AND INHERITANCE

9.1.1. Introduction

Provenance experiments are used to identify natural genetic variation. Provenance experiments consist of samples of various populations grown in a common environment. The oldest designed provenance experiment with Norway spruce dates from 1938. At that time the International Union of Forest Research Organizations (IUFRO) organized a series of trials in several countries, using seed collected from 36 sources in various parts of the species range. In 1939 another series was started with 14 seed sources; however, this series included only a small number of co-operators, owing to the onset of World War II. In 1964 IUFRO began the next series of experiments, collecting seed from 1100 origins, representing the entire geographic range of the species. In 1972 a series of trials was established in several countries with seeds originating from Polish seed stands and later obtained IUFRO status. All remaining trials with Norway spruce scattered throughout Europe were organized on a national basis, even though some of them also included several foreign provenances.

For the 1938 trial, Poland supplied seed from six stands (Białowieża, Istebna, Radom, Stołpce, Wilno, and Dolina). The latter three occur today beyond the eastern border of Poland, whereas the provenance known in the literature as Pforten, is from a place that is now in Poland (Brody Forest District on the Nysa river). The seeds were sown in nurseries and several trials were established in Poland. The trials in Adrychów and Rycerka lost their documentation during the war. In 1941 a site was established in the Lubień Forest District; however, owing to considerable early mortality, it was unwittingly supplemented with spruce of unknown origin, rendering the site unsuitable for scientific use. The Germans also established a trial in what is now the Lubliniec Forest District (sub-district Dobrodzień). However, this trial later proved impossible to find due to lack of documentation. It contained the full set of provenances and was supervised from Eberswalde in Germany. However, at

present there are no known records of it in their archives. Poland did not participate in the 1939 trial. It included a provenance under the number 10, named "Poland", but its actual origin is unknown.

For the 1964 trial, Poland supplied seed from 91 stands. Seedlings for the entire experimental series were grown in the Pein and Pein commercial nursery near Hamburg, Germany. The seedlings were delivered to 20 co-operators in 1968, including professor STANISŁAW BAŁUT from the Kraków Agricultural Academy. He established his trial in the Krynica Experimental Forest District, including the full set of 1100 provenances. For the 1972 trial, all 20 seed stands originated in Poland. Five trials were established in Poland in Knyszyn, Kórnik, Siemianice, Niepołomice, and Głuchów (MATRAS 1993).

Apart from the international trials, several national trials were also established. In Poland the Warsaw Agricultural Academy has explored this topic since 1958 and the Institute of Dendrology of the Polish Academy of Sciences since 1964 (GIERTYCH 1970). Some older German trials are also of interest to Polish scientists in light of the fact that they include provenances from western and northern regions of Poland, namely Borki (Borken), Stronie Śląskie (Seitenberg), Piechowice (Petersdorf), and Brody (Pforsten). Overall, Polish participation in provenance experiments on Norway spruce is no less intensive than that of western European countries and there are a sufficient number of publications to attempt a synthesis of the results obtained to date.

9.1.2. *Trait differentiation*

9.1.2.1. *Growth traits*

It is a common opinion that the greatest wood volume, tree height and diameter, as well as the best height and girth increments are attained by Norway spruce from the so called "northeastern group" (from NE Poland, Lithuania, Latvia, Estonia, northern Belarus, and western Russia) and from the Carpathians, from the Bihar Mts in Romania to the Beskid Śląski in the west. Also the German provenance Westerhof is often mentioned as growing well. It is used in Germany as a standard for comparisons. Bohemian, southern Scandinavian, and central German provenances grow more slowly. Poorer still are provenances from the Alps, central and northern Scandinavia, northern and southern Russia and from the Balkans. As a rule, provenances from higher elevations have poorer growth than provenances from lower ones. The published results of Norway spruce provenance trials include the following: ALEKSANDROV 1985, 1993; ANONIM 1981; BALDWIN 1967; BALDWIN *et al.* 1973; BAŁUT and SABOR 1993; BERAN 1993; BOUVAREL and LEMOINE 1957; CORRIVEAU *et al.* 1989; DANUSEVICIUS 1993; DIETRICHSON 1963, 1967a, 1979; EDWARDS 1955; ERICKSSON *et al.* 1975; FOTTLAND and SKRØPPA 1989; FOWLER 1979; FRÖHLICH 1966; GÄRTNER 1975, 1980; GATHY 1960a, 1960b; GIERTYCH 1976a, 1979, 1984; GØHRN 1966; GÜNZL 1969, 1979ab; HAGMAN 1971, 1979;

HEIKINHEIMO 1956/58; HÉOIS and VAN DE SYPE 1991; HOLST 1963; HOLUBČÍK 1984; JANSON 1968; KIELLANDER 1970a; KING and RUDOLF 1969; KÖNIG 1981; KORABLEV *et al.* 1975; KRUTZSCH 1973, 1974, 1975; KNUDSEN 1956; KUPCHINSKIY *et al.* 1980; LACAZE 1969a, 1970; LANGLET 1960, 1963, 1964; LINES 1973ab, 1974, 1979; MAGNESEN 1972; NANSON 1964, 1981; NATSVLISHVILI 1981; PALTSEV 1980; PAVES 1982; PERSSON and PERSSON 1992; PRESCHER 1982; RAU 1983; RED'KO and DURSIN 1982; ROHMEDEER and BEUSCHEL 1970; ROLLER 1971; ROSTOVTSEV 1967; ROSTOVTSEV and KURAKIN 1981; RUBNER 1957; RUDOLF and SLABAUGH 1958; SCHMIDT-VOGT and KOCIĘCKI 1985; SLABAUGH and RUDOLF 1957; SZÖNYI and UJVÁRI 1975; TEICH and MORGENSTERN 1969; TROEGER 1958; UJVÁRI 1986; UJVÁRI and UJVÁRI 1979; VANČURA and VINŠ 1983; VENN 1964; VINCENT and FLEK 1953; VINCENT and VINCENT 1964; VINŠ 1963, 1967, 1976; VINŠ and VANČURA 1977, 1979; VISHNYAKOV 1969; WEISGERBER 1979; WEISGERBER *et al.* 1977, 1984, 1985; WEISS 1981; WEISS and HOFFMANN 1968, 1969; WERNER 1976; ŽDÁRSKÁ 1968, 1973, 1980.

A typical pattern of growth differentiation among Norway spruce provenances is shown in the findings of the many IUFRO 1938 trials, in which units of standard deviation of the average wood volume among the numerous trials are plotted onto a map of Europe (Fig. 9.1).

From this general picture of volume production there are several notable deviations, depending on the location of the experimental area. When the experimental areas are close to one another, e.g. for three German trials of the 1964/68 IUFRO study, the agreement of the results is very good (the rank correlations are high) (KÖNIG 1976). With increasing stand age, however, the correlations weaken (GIERTYCH 1989; PLIURA and GABRILAVICIUS 1993) and the differences among provenances also diminish (RONE 1984). In comparing experiment locations that are distant from each other or on different site types, the growth results can differ. A comparison of 20 Polish Norway spruce populations in a 5-year-old trial in Knyszyn (Poland) has shown that trees from NE Poland were tallest, whereas in France those from the Beskid Wysoki (Carpathians) were tallest (LACAZE and KOCIĘCKI 1979). In the vicinity of Arkhangelsk, Finnish and northern Russian provenances grow better than those from southern Russia (VOÍCHAL 1968; DURSIN 1976). In Karelia, the superiority of southern populations disappears after age 10, since in these extreme climatic conditions local races prove to be better adapted (SHCHERBAKOVA 1989). In Scandinavia the Carpathian provenances lose their growth superiority with time and the trees are susceptible to vertical frost cracks, whereas at age 23 populations from the vicinity of the Lithuania-Poland-Byelorussia region continue to grow quite well (PERSSON and PERSSON 1992). In the far north or at high elevations, local Scandinavian races or those from southern Finland and Sweden do better than populations of continental origin (DIETRICHSON 1963; LANGLET 1960; PERSSON and PERSSON 1992). In

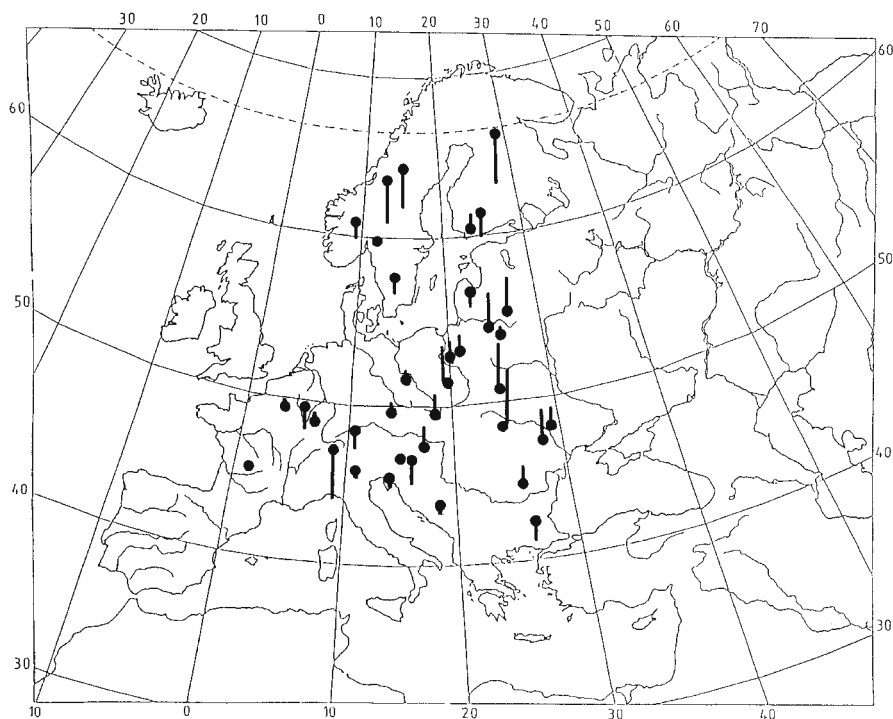


Figure 9.1. Wood volume of *Picea abies* (L.) KARST. derived from various IUFRO 1938 trials and expressed in units of standard deviation from the location mean and plotted onto a map of Europe. Histograms pointing upwards indicate by how much a provenance exceeds the location mean and histograms pointing down indicate by how much it is below the mean. Deviations in the range -0.1 to $+0.1$ are within the diameter of the black dot. Based on the last report from this trial (GIERTYCH 1984).

the Czech Republic and Hungary, Norway spruce from the Beskid Wysoki and other localities in the eastern Carpathians grow better than populations from the NE provenance group (KRUTZSCH 1973; VINCENT and FLEK 1953; VINŠ 1963, 1967; ŽDÁRSKÁ 1973), probably because of the lower incidence of late frosts in this region. In Germany (Hesse) out of the 20 Polish populations only two grew less than the Westerhof standard (ANONYM 1981). On the German plots, and particularly in the Alps, high mortality and poor growth increments at age 25 were noted for populations from NE Poland, while provenances from Oberpfaltz, Bavaria, Thuringia, and Bohemia grew well (RAU 1993). In Slovakia, the Romanian provenance grew much less than all local provenances, of which the most promising were those from central Slovakia (PAULE 1980). Of the local provenances in Bulgaria (Rila Mts) only Terekliitsa (1450 m elevation from the Rhodopy Mts) attained a medium growth ranking, while all the other Bulgarian populations exhibited poorer growth (ALEKSANDROV 1985, 1993).

In contrast, in Romania the best growing provenances after 23 years were those from Norway, Italy, lower Silesia, and southern Bohemia and the poorest from Istebna and the Poland-Lithuania-Byelorussia region (LĂZĂRESCU and CARNIȚCHI 1963); After 35 years the best were French, Finnish, and local provenances (LĂZĂRESCU and BENEĂ 1973). However, this finding completely differs from those obtained in all other trials. On the Altai, in SE Khazakhstan, a population from St. Petersburg grew better than those from more central parts of European Russia (VISHNYAKOV 1969).

Crown width is a trait that is quite independent of the other growth traits. Norway spruce provenances of alpine origin have wide crowns, Scandinavian provenances have narrow crowns, and central European provenances exhibit crowns of intermediate width (ANTOINE 1974). In general, the results of provenance experiments are affected not only by the location (genotype-environment interaction) but also by their age (GIERTYCH 1998) and the type of silvicultural treatment (e.g. thinnings) (GIERTYCH 1996).

9.1.2.2. Phenological traits

9.1.2.2.1. Spring flushing (bud burst)

It is generally claimed that the ranking of provenances in the timing of spring bud burst is always the same, regardless of the location of an experiment. The first to open buds are the Scandinavian and Karelian provenances, and the more northern their origin, the earlier they begin to flush. Next are the Alpine provenances, followed by German, Bohemian, Sudetan and western Carpathian provenances (of the latter the Istebna provenance is the last to flush). Later still are the provenances from the southern Carpathian Mts, Serbia, Bulgarian, Lithuanian-Byelorussia, central Russia, and NE Poland. Provenances closer to the Baltic flush somewhat earlier than the more continental sources. Among the more eastern populations, e.g. from the Urals, again an earlier flushing is observed (BAŁUT and SABOR 1993; BEUKER 1994a; BOUVAREL and LEMOINE 1957; DIETRICHSON 1979; EDWARDS 1955; GÄRTNER 1980; GATHY 1960a, b; GIERTYCH 1972; GØHRN 1966; GÜNZL 1979b; HÉOIS and VAN DE SYPE 1991; HOLUBČÍK 1973; KIELLANDER 1966, 1970b; KIELLANDER and NILSSON 1967; KRUTZSCH 1973, 1975; LACAZE 1968, 1969a, 1970; LANGLET 1960, 1963, 1964; LINES 1960, 1973a,b, 1974; MAMAEV *et al.* 1982; NANSON 1964, 1981; PAL'TSEV 1980; PRESCHER 1982; RED'KO and DURSIN 1982; SABOR 1984; SCHÖNBACH 1957; SKRØPPA and MAGNUSSEN 1993; TROEGER 1958; TYSKIEWICZ 1968; VANČURA and VINŠ 1983; VINŠ and VANČURA 1977, 1979; WEISGERBER *et al.* 1977; WEISS and HOFFMANN 1969; ŽĎÁRSKÁ 1968, 1973). Each Norway spruce population requires a genetically determined "heat sum" (degree days) in the spring to initiate bud burst (LINDGREN and ERIKSSON 1976). Altitudinal distribution does not appear to play an important role in the determination of this trait (DIETRICHSON 1969a, b; LACAZE 1969a). LANGLET (1963) and ŽĎÁRSKÁ (1973) suggest that Nor-

way spruce from higher elevations flush earlier, whereas HOLZER (1963) and VINCENT and VINCENT (1964) conclude the opposite.

LANGLET (1960, 1963) believes that the annual onset of vegetative growth is decided entirely by thermal factors, and not by photoperiod; however, it is difficult to establish a correlation between timing of bud break among provenances in a common environment and any single climatic factor of the region of origin. This may possibly be the result of longer-term climatic changes or from the migration history of the species (GIERTYCH 1972). Prior to the spring flush, an increase in respiration intensity is observed (SÆTERSDAL 1956) as well as an increase in sensitivity to frost damage (DAY and PEACE 1946). These phenomena occur in the same rank order among the individual provenances as is later observed for bud flushing.

9.1.2.2.2. *Lamma's growth*

As a rule, western and southern provenances have a reduced tendency for a second growth flush in the summer (Lamma's growth) than do eastern or Scandinavian provenances (KIELLANDER 1970b; LACAZE 1969a). Studies conducted in Kórnik, Poland have shown that the Polish provenances most ready to resume summer growth are those from central Poland, from the Beskid Wysoki and Gorce Mts. Other montane provenances exhibit Lamma's growth less frequently than lowland populations (BEDA 1988; HOLZER 1993; LACAZE and ARBEZ 1971; SCHMIDT-VOGT 1964; WÜHLISCH and MUHS 1987). Within populations, families demonstrate greater differentiation in the occurrence of this trait than among populations (NANSON 1971). HOLZER (1967b) believes that the tendency for Lamma's growth is correlated with early flushing in the spring, when injury from late frosts is common. This correlation may only hold within a given location, particularly in comparisons of populations along mountain slopes or among families within populations. In contrast, the provenances from NE Poland and adjacent regions of Russia, Lithuania and Byelorussia flush very late, but have a greater tendency for summer growth than those from southern or western Europe which flush earlier.

9.1.2.2.3. *Bud set*

In view of the difficulty of determining the actual time of terminal budset in the summer and autumn, this trait has been much less frequently reported than spring flushing. There is little doubt that northern, northeastern, and eastern provenances terminate shoot growth earlier and the Carpathian and Alpine provenances much later. Norway spruce from higher elevations become dormant earlier than those from lower elevations (HOLUBČÍK 1973; HOLZER 1993; GENYS 1969; MAGNESEN 1972; MAMAEV *et al.* 1982; MODRZYŃSKI 1988b; ROBAK and MAGNESEN 1970; SKRØPPA and MAGNUSSEN 1993). Phytotron studies show that southern and lowland populations of Norway spruce require a longer night to set bud; whereas northern and high-elevation populations require shorter night lengths (DORMLING 1976; HOLZER 1978; MAGNESEN 1977). Upon transfer northward, southern

populations terminate growth later than the local sources, owing to a longer night length requirement and greater sensitivity to morning and evening twilight (DORMLING 1977, 1979). It is often suggested that good growth is determined less by an earlier onset of growth in the spring than by a later growth cessation in the fall (BOUVAREL 1961; GENYS 1969; KIELLANDER 1970a, b; LANGLET 1963; MAGNESEN 1971; MAMAEV *et al.* 1982; SKRØPPA and MAGNUSSEN 1993). However, not all provenances respond in this manner (KIELLANDER 1970a, b). The location of the experiment is also important. For example, Norway spruce from NE Poland and adjacent regions, which set bud relatively early, exhibit superior growth in Sweden compared to a Bohemian provenance, which sets bud much later. In contrast, the Bohemian provenance grows much better in Hungary, probably because it better utilizes the longer growing season, which would not be possible in Sweden owing to the early frosts (KRUTZSCH 1973).

Spring flushing is not correlated with the timing of growth termination among provenances (KIELLANDER and NILSSON 1967). It is suggested that for some provenances, bud set is determined by the shortening photoperiod (HOLZER 1978; LANGLET 1963; MAGNESEN 1969; ROBAK 1962b). Undoubtedly, the northern provenances are more sensitive to photoperiodic changes (MAGNESEN 1972). However, air temperature also plays a role here, at least in the development of the winter bud and cold acclimation (MAGNESEN 1969).

9.1.2.2.4. *Radial growth cessation*

DIETRICHSON (1963) developed a method to determine the timing of radial growth cessation based on the correlation between growth increment cessation and the proportion of unligified wood in the annual growth ring. This permits a relative determination of the time of growth cessation from anatomical analyses of stem cross sections. Lignification occurs earlier in Norway spruce from more northern and northeastern regions than populations from western European or Alpine regions (DIETRICHSON 1963, 1964; WORRALL 1975), as does bud set. However, in eastern Carpathian provenances, lignification is comparatively intermediate (DIETRICHSON 1969a), as trees of these populations terminate apical growth later (MAGNESEN 1972). The timing of wood lignification does not correlate with altitude of origin (DIETRICHSON 1969a) or with volume increment (the best growing Norway spruce have a median timing of lignification). Shoots of trees that flush early in the spring become lignified late in the autumn, most likely without any clear dependence on photoperiod (DIETRICHSON 1963).

9.1.2.3. *Resistance to various factors*

9.1.2.3.1. *Late frosts*

As a rule, late flushing provenances are more resistant to late spring frosts (BALUT and SABOR 1993; DAY and PACE 1946; DIETRICHSON 1969a; GÜNZL 1979b; HOLZER 1967b, 1969a, 1993; KIELLANDER 1970b; KIELLANDER and

NILSSON 1967; KRUTZSCH 1973; LACAZE 1969a; LANGLET 1963; PRESCHER 1982; SABOR 1989; ŠINDELÁŘ 1984; SLABAUGH and RUDOLF 1957; STERN 1966; WEISGERBER *et al.* 1977; WERNER 1976), although there is evidence to the contrary (EDWARDS 1955; TYSKIEWICZ 1968; RED'KO and DURSIN 1982). As was shown in Sweden (HANNERZ 1994), it is possible to determine the risk of late frost injury at a given planting site and Norway spruce population based on the degree-day requirement for flushing and the probability of frost in the two weeks following the accumulation of the required degree-day value (summation of daily temperature values above a 5°C base).

9.1.2.3.2. *Early frosts*

Early frosts primarily injure Alpine provenances that have a high incidence of Lamma's growth (DIETRICHSON 1963; KIELLANDER 1970b). In general, these provenances also terminate height growth late in the growing season. Early bud set is associated with an earlier resistance to winter injury (HOLZER *et al.* 1991). Injuries arising from early frosts restrict shoot growth in the following year (DIETRICHSON 1967a), but resistance to the autumn frosts is only occasionally correlated with poor growth (DIETRICHSON 1979; KIELLANDER 1970b). In general, frosts in late spring cause more damage than early autumn frosts. Resistance to these two climatic factors is not correlated (KIELLANDER and NILSSON 1967).

In Finland, northern populations attain winter acclimation of both buds and needles earlier than more southern populations, but populations do not differ in cold tolerance in winter or in the timing of de-hardening in the spring (BEUKER 1996). In Sweden, Scandinavian populations and those from the Poland-Lithuania-Byelorussia region were most resistant to early frosts (PERSSON and PERSSON 1992). MAGNESEN (1996) suggests that thermal conditions determine winter acclimation, but only after photoperiod has induced bud set. Consequently, southern populations growing in Norway may lack an appropriate time interval for winter acclimation (ROBAK 1962b). Crosses of central European and Scandinavian provenances combine good growth and resistance to late and early frosts (NILSSON 1958).

9.1.2.3.3. *Winter temperature*

Scandinavian populations and those from northern and northwestern Russia are most resistant to winter temperatures, whereas the most sensitive populations originate from Romania, Ukraine, and western Europe (DURSIN 1976; HOLST 1963; ROSTOVTSEV 1967; SCHEUMANN and HOFFMANN 1967; SKRØPPA and DIETRICHSON 1986b; SLABAUGH and RUDOLF 1957). Data on the cold resistance of Norway spruce from central and western Europe are inconclusive. High mountain populations are probably more resistant; however, there are also some very resistant lowland populations (e.g. Brody from the Lusitan Nysa river). Resistance to winter temperatures and early autumn frosts are independent traits (SÆTERSDAL 1963). It is difficult to differentiate injuries arising from these two causes, which may explain some of the inconsistencies

reported in the literature. As a rule, Norway spruce survives severe winter temperatures, regardless of origin, only after the trees have entered winter dormancy (HOLZER 1969b). However, fast-growing trees, particularly those from the Carpathians, may exhibit vertical cracks following sudden drops in temperature (SKRØPPA and DIETRICHSON 1986b). More recently, it is believed that these cracks arise in the autumn during the formation of late wood (PERSSON and PERSSON 1992; PERSSON 1994). Injuries caused by winter freezing often reappear in consecutive years within the same provenances and on the same trees (DIETRICHSON 1986). Populations from the upper tree limit in the mountains are more resistant to injury related to low temperatures (HOLZER 1993).

9.1.2.3.4 *Snow*

Snow damage is a separate problem, often unrelated to cold injury. In general, only central European and western Carpathian provenances are resistant (BALDWIN *et al.* 1973; BRAUN *et al.* 1983; ROHMEDE and BEUSCHEL 1970; VENN 1964; WEISS and HOFFMANN 1968, 1969). In Belgium, Romanian populations of Norway spruce were also resistant (NANSON 1981). In contrast, eastern and northern races of Norway spruce are highly susceptible to snow damage, primarily wet and heavy snow that promotes breakage when enveloping the twigs.

It is well known that spruce morphology differs along altitudinal gradients in mountainous regions. The flat-branched type of crown in populations originating from high elevations favors the shedding of excess snow and is considered a genetic adaptation (HOLZER 1993); however, there is no clear correlation between altitude and resistance to snow damage among provenances. Yet, it is commonly recommended not to transfer fast-growing races to higher elevations, since the most frequent cause of observed snow damage is the lack of snow-damage resistance in introduced populations (SCHMIDT-VOGT 1972).

9.1.2.3.5 *Summer drought*

Tolerance to summer drought has been observed in populations from Poland and Slovenia, whereas German populations were intermediate and Alpine and northern provenances were least tolerant (SLABAUGH and RUDOLF 1957; FRÖHLICH 1960; HOLST 1963). In Norway, late summer drought is thought to result in numerous vertical cracks, particularly in fast-growing continental provenances maintained in open stands and growing on good soils, but having uneven annual increments (DIETRICHSON *et al.* 1985). In the mid-Volga region in years of average precipitation, the better growing Norway spruce populations are from western, north-western, and central parts of the former USSR; whereas in dry years, local populations grew better, particularly those originating beyond the Urals (i.e. *Picea obovata*) (KAMALTIKOV and LIBRECHT 1984). A summer drought resulted in a uniform reduction in annual increment among all Polish provenances of Norway spruce (URBAŃSKI 1987; BURCZYK and GIERTYCH 1991). Late summer drought causes vertical cracks

in trees exhibiting high radial growth rates and low wood specific gravity. In Scandinavia, this tendency excludes the use of some of the fastest growing populations of spruce, e.g. from Istebna in Poland (PERSSON 1994).

9.1.2.3.6 *Winter drought*

Winter drought can be a serious problem, although not when accompanied by freezing temperatures that prevent water transport (HOLZER 1969b). In contrast, when transpiration occurs while the soil and roots are frozen, the resultant drying is more tolerated by German than Norwegian provenances (SÆTERSDAL 1963). GÜNZL (1979b) notes that the most susceptible provenances are those that have been transferred the farthest from their elevation of origin. Following winter injury to the cambium, continental populations more frequently show top drying than Scandinavian provenances (DIETRICHSON 1967a). When cut for Christmas trees, Norway spruce of Polish origin lose their needles more quickly than provenances from Austria (THOR 1976).

9.1.2.3.7. *Shade*

Populations also differ in resistance to shading. Progeny of a population that developed under a canopy grew better in shaded conditions and more poorly in full sunshine than did progeny of a population that developed in an open environment (DUTKIEWICZ 1979).

9.1.2.3.8. *Mammal damage*

Mammals differentially browse Norway spruce trees of various seed origins. In Canada, the red squirrel caused much more injury among Norway spruce trees of German origin than of any other provenance (VIIDIK 1973). In Finland and Norway, voles (*Microtus agrestis* L.) damage trees of Continental provenances much more than local sources (HAGMAN 1973; EIKELAND and BLINGSMO 1991). In Belgium, bark damage by deer is most severe on trees that grow best, e.g. of the Istebna provenance in Poland, although those from the southern Carpathians are less damaged (NANSON 1981).

9.1.2.3.9. *Insects*

Variation in resistance to insect injury has been evaluated in a number of provenance trials. Spruce sawfly (*Pristiphora abietina* Hart.) outbreaks were observed in trials in Austria and France. In France, the earlier flushing spruces were more resistant to this pest (BOUVAREL and LEMOINE 1957), whereas in Austria both the earliest and the latest flushing populations avoided attack. However, in consecutive years there was better agreement between individual trees than between provenances, suggesting a genetic correlation irrespective of the phenological concurrence of the insect and the spruce (HOLZER and SCHULTZE 1988). There is an individual and a population differentiation in resistance to spruce gall-lice (*Sacchiphantes viridis* RATZ.) (FRIEND and WILFORD 1933). According to BALDWIN *et al.* (1973), southern races from the Balkans and from the Alps are more resistant, although NANSON (1971) found no geographic relationships and considerable within population variation. On the other hand, BALUT and SABOR (1984, 1993) found a strong geographic dif-

ferentiation of this trait among the 1100 populations tested in Krynica, Poland. Northern, north-western, and extreme southern (also Alpine) populations are very resistant, while the remaining populations (including the majority of Alpine ones) are very sensitive. In Hungary, JEREB (1977) obtained contrasting results. The Hungarian (eastern Alps) sources were more resistant than the Swedish populations. Similarly, near St. Petersburg, the most susceptible populations were the western ones (from the Baltic countries, from Tarnopol (western Ukraine) and from Pskov, and the most resistant were the local populations (RED'KO and DURSIN 1982). In the Czech Republic, population differences were not observed (ŠINDELÁŘ 1984). In North America, the white pine weevil (*Pissodes strobi* HART.) frequently feeds on Norway spruce trees. Scandinavian and Latvian populations are resistant, as well as western Carpathian and several Alpine sources. The Balkan sources are highly susceptible as well as those from north-eastern Poland and Lithuania (SLABAUGH and RUDOLF 1957; HOLST 1963; BALDWIN *et al.* 1973).

9.1.2.3.10. *Fungi*

Resistance to fungal diseases is less well documented. Differential resistance of provenances to the root rot fungus (*Heterobasidion annosum* (FR.) BREF. after artificial inoculation has not been observed (TRESCHOW 1958); however, in a plantation trial in Bulgaria, local provenances were less affected than northern sources (ALEKSANDROV 1985). A search for genetic resistance of spruce to this fungus is still of interest (DIMITRI and FRÖHLICH 1971). The honey fungus (*Armillaria mellea* (VAHL.: FR.) KUMMER) frequently attacks spruce stumps. In Kórnik, Poland, we have not found any provenance differentiation in this respect on stumps following a thinning conducted in the trial area a few years earlier. Norway spruce provenances differ in the degree to which they establish mycorrhizal associations with various strains of fungi (GÖBL and HOLZER 1976).

9.1.2.3.11. *SO₂ and other pollutants*

There is some degree of differentiation in resistance to SO₂. Norway spruce from the mountains and from northern Europe demonstrated a greater resistance to the effects of this gaseous pollutant than do lowland and southern provenances (TZSCHACKSCH and WEISS 1972). The most resistant were populations from the Bohemian-Moravian uplands, from the Harz, Karkonosze, and the Erz Mts (VANČURA 1993). There is also some provenance variation in resistance to soil pollution with heavy metals (Cu(NO₃)₂, ZnCl₂, PbCl₂, CuSO₄), but there are no geographic patterns and no provenance x type of pollution interactions (FOBER 1979). In contrast, provenances differed in response to treatment with SO₂, Al, and SO₂ + Al and the effects depended on the type of factor used (GEBUREK and SCHOLZ 1992).

Radiation resistance differs among seeds of various Bulgarian populations (LD-50, from 500 to 100 kilorads). The most resistant seed lots were from the Rhodope Mts, and the most susceptible were those from the Ossogovo Mts

(ALEKSANDROV 1976). Seeds from mountain regions more readily exhibit chromosomal injury; however, in a seed germination test they tolerated radiation treatment more than lowland sources (GANCHEV and CVETKOVA 1977).

9.1.2.4 Wood quality traits

High stem quality is typically associated with rapid growth, thus provenances recommended because of their growth characteristics usually have stems of higher quality (NIȚU *et al.* 1984). However, as a rule, no significant differences are reported between provenances in stem straightness (WEISGERBER *et al.* 1985). Stem pruning is generally very poor in Alpine and Black Forest Norway spruce; however, stem pruning increases towards the northeast through the Harz and Sudety Mts to the Baltic regions (FRÖHLICH 1966). Alpine populations grown in Belgium tend to form forks, and Romania sources form bayonets (dry tops with a side shoot becoming dominant) (NANSON 1964). In Sweden, double leaders and their resultant dead knots occur least commonly in Norway spruce from the Poland-Lithuania-Byelorussia region and most commonly in Alpine and southern populations, whereas the Scandinavian populations are intermediate in this trait (PERSSON and PERSSON 1992). In Norway, local populations have fewer stem defects than continental sources (EIKELAND and BLINGSMO 1991).

In France, considerable differences were observed in the specific gravity of wood among Norway spruce populations of various geographic origins (PARROT 1960; LACAZE and POLGE 1970; SARTER 1986). Wood specific gravity was negatively correlated with the time of spring flushing and positively correlated with Lamma's growth frequency. Baltic provenances have exceptionally low wood specific gravity (LACAZE and POLGE 1970; NANSON *et al.* 1975). In France, Carpathian populations (e.g. Istebna, Orawa) grow well, but their wood properties are not very good. In contrast, populations from north-eastern Poland and from Brda in the Czech Republic combine good growth with good wood quality, and are ranked higher in this respect compared to the French populations (SARTER 1986). Spruce provenances from Germany have a greater wood specific gravity than the earlier flushing spruce from Norway, owing to a greater proportion of late wood. Consequently, more wood pulp is obtained from a given volume of wood, making these trees more valuable for the paper industry, even though the quality of cellulose obtained from wood of Norwegian provenances of spruce is higher (KLEM 1957). NANSON *et al.* (1975) claim that in Belgium there is no differentiation in bark thickness or in the proportion of late wood. In Bulgaria, local populations have comparatively better wood traits (ALEKSANDROV 1985). Other authors such as KNUDSEN (1956), STAIRS and ADAPA (1969) found no provenance variation in wood specific gravity, even after considering the effect of faster radial growth increment, which always reduces wood density (STAIRS and ADAPA 1969; BLOUIN *et al.* 1994). Intra-population variation in wood specific gravity is considerable

both on an individual basis and for half-sib progenies (KNUDSEN 1956; MERGEN *et al.* 1964; NILSSON 1963b; WORRALL 1975; BLOUIN *et al.* 1994), though not always so (RONE 1970). The correlation of this trait with the time of spring flushing is positive in the USA and Germany, where late-flushing individuals have denser wood since they have proportionally more late wood (LANGNER and STERN 1964; MERGEN *et al.* 1964), and negative in France where late-flushing trees have lighter wood (THIERCELIN 1970).

9.1.3. Correlations with geographic coordinates

9.1.3.1. Altitude

Trait correlations with elevation above sea level are most important. When planted in lowland common-garden plantations, Norway spruce provenances originating from higher elevations compared to lower elevation sources exhibit the following traits: reduced survival (VINŠ and VANČURA 1979), poorer growth (BARZDAJN 1982; GENYS 1969; HOLZER 1993; KONÔPKA and ŠIMAK 1990; KRAL 1961; LACAZE 1969a, b, 1970; MODRZYŃSKI 1993; NIȚU *et al.* 1984; SCHMIDT-VOGT 1972; VINCENT and VINCENT 1964), higher dry weight percentage in the seedlings (MAGNESEN 1972), higher gas exchange rates (OLESKYN *et al.* 1998), lower stem form factor (LINES 1979; BARZDAJN 1982), greater inter-population variability (FISCHER 1949), reduced tendency for Lamma's growth (BARZDAJN 1982; HOLZER 1993), earlier bud set in the autumn (BOSSEL 1983; GENYS 1969; HOLZER 1993; MAGNESEN 1972; MODRZYŃSKI 1988b; ROBAK and MAGNESEN 1970; SKRØPPA and MAGNUSSEN 1993), lower demand for a long night to induce winter buds (DORMLING 1973), greater resistance to early and late frosts (NIȚU 1979; NIȚU *et al.* 1984), more damage caused by wet snow (SCHMIDT-VOGT 1972), greater drought injury (FRÖHLICH 1960), lower sensitivity to SO₂ (TZSCHACKSCH and WEISS 1972), fewer cotyledons (HOLZER 1960), a lower concentration of chlorophyll and carotenoids (LINDER 1972), a lower capacity for anthocyanin production and therefore more green needles (HOFFMANN and SCHEUMANN 1967), a higher percentage of trees with bluish needles (LACAZE and ARBEZ 1971), a higher concentration of nitrogen, phosphorus, and calcium in needles (KRAL 1961; FÖBER and GIERTYCH 1971; OLEKSYN *et al.* 1997), and stems that less readily self-prune (FRÖHLICH 1960).

The reports are contradictory with regard to spring flushing. BOSSEL (1983) claims that in Switzerland, sources from higher elevations flush later, whereas BARZDAJN (1982) observed an opposite correlation among Polish populations. The established correlation of seedlings traits with the elevation of origin permits identification of the probable altitude of the stands from which an unknown seed lot may have originated (BARZDAJN and MODRZYŃSKI 1981). OLEKSYN *et al.* (1997) observed several interesting relationships. Seedlings of

populations from higher elevations, from 1000 to 1400 m, have a higher proportion of root dry mass as fraction of the total seedling dry mass (20–40%), while in populations originating from below 1000 m elevation, the root mass proportion is about 17% of plant dry mass.

9.1.3.2. *Longitude*

Provenance trials in the USA and the Czech Republic showed that tree height increased with an increase in eastern longitude of seed source origin (GENYS 1969; ŽĎÁRSKÁ 1968). However, for populations from the former USSR, PALTSEV (1989) has found near Moscow and SHUTYAEV (1995b) near Voronezh, that the western populations show the greatest growth, whereas those from the more north-eastern regions are poorer. With increasing longitude of origin, the mass of individual needles declines and their density on the shoot increases (ŽĎÁRSKÁ 1968). Resistance to late frosts increases with increasing longitude of origin, although among Austrian populations the trend is opposite (DIETRICHSON 1969a). CHZHAN SHI-TSYÚÍ (1969) and KURAKIN (1990) claim that the number of cotyledons increases with the longitude of origin, whereas POPOV (1982) and SHUTYAEV (1989) report an opposite trend. In general, the correlations with longitude depend very much on the composition of provenances tested and appear to be only of regional biological significance.

9.1.3.3. *Latitude*

Trait correlations with latitude of origin have been demonstrated in numerous provenance trials of Norway spruce. Many of these observations have restricted comparisons of Scandinavian with central European populations, often excluding eastern or southern populations. The following trait correlations have been reported with increasing latitude of origin: height increment declines (ŽĎÁRSKÁ 1968; NIȚU 1979), form factor increases (LINES 1979), the dry weight percentage in one-year-old seedlings increases (VENN 1964), number of cotyledons declines (SHUTYAEV 1989; KURAKIN 1990), the weight of needles, their length, and numbers on a shoot decline (BALDWIN 1967; ETVERK 1970; ŽĎÁRSKÁ 1968), the length of cones declines (BALDWIN 1967), spring flushing occurs earlier (GIERTYCH 1972; WORRALL and MERGEN 1967; WORRALL 1975; KRUTZSCH 1986), sensitivity to late frosts increases (DIETRICHSON 1969a; SKRØPPA *et al.* 1994), autumn bud set occurs earlier (GENYS 1969; MAGNESEN 1969; ROBAK and MAGNESEN 1970; WORRALL 1975), sensitivity to photoperiod increases (MAGNESEN 1972), a shorter night is needed for bud set (DORMLING 1973), sensitivity of seeds to germination temperature is lower (ŠIMAK and KAMRA 1970), sensitivity to winter desiccation increases (SÆTERSDAL 1963), and sensitivity to SO₂ increases (TZSCHACKSCH and WEISS 1972).

Among Swedish populations, a clinal differentiation is observed in the allelic composition of isozymes along a north-south axis (BERGMAN 1973). In

Finland, a similar gradient was observed for the degree of homozygosity for various enzyme systems (TIGERSTEDT 1974). In Scotland, LINES (1960, 1973b) observed a decrease in shoot pubescence from northern to southern sources. At the range limit of Norway spruce in far northern Scandinavia, trees have glabrous shoots (LINDQUIST 1948). On an experimental area in Voronezh, SHUTYAEV (1995a) observed glabrous shoots in trees of far northern populations, followed by strongly pubescent ones from the region between St. Petersburg and Viatka, and then decreasing pubescence with decreasing latitude of origin. BARZDAJN (1982) notes that in Poland there is a negative correlation between latitude and altitude, and as a consequence trait correlations are dependent on these two geographic parameters.

Data on growth traits of both northern and southern provenances lead to the conclusion that the best-growing provenances are those from central Europe (about 51°N), whereas growth declines in more southerly and more northerly sources (BALDWIN *et al.* 1973; UJVÁRI and UJVÁRI 1993; VINCENT and VINCENT 1964; VINŠ 1967; VINŠ and VANČURA 1979). There also exist latitudinal patterns of growth variation both north and south of central Europe. Likewise, the percent survival of trees also varies with latitude of origin in a similar manner (VINŠ and VANČURA 1979).

9.1.3.4. Length of the vegetative growth period

BOUVAREL (1961, 1962) notes that among French provenances of Norway spruce there exist correlations between the length of the vegetative growth period at the place of origin and the date of bud set, seedling height, and frequency of Lamma's shoots. NANSON (1974) reached similar conclusions for material from throughout Europe on a Belgian planting site. Except for Lamma's growth, which occurs in mid-summer, the above-mentioned trait correlations are associated with elevation of origin.

9.1.4. Genetic regionalization of spruce

From the provenance experiments discussed above, a distinct pattern develops from the natural division of the geographic range of Norway spruce into regions differentiated by heritable traits (Fig. 9.2). The boundaries between the regions are approximate and do not exclude the possibility of clinal variation crossing them. Short descriptions of the proposed regions are given below. The traits are discussed with reference to comparisons obtained from provenance experiments, and not from observations of the stands in situ. In general, there are no interactions between seed source origins and planting sites; therefore, the discussed differences are observed regardless of the location of the experiment.

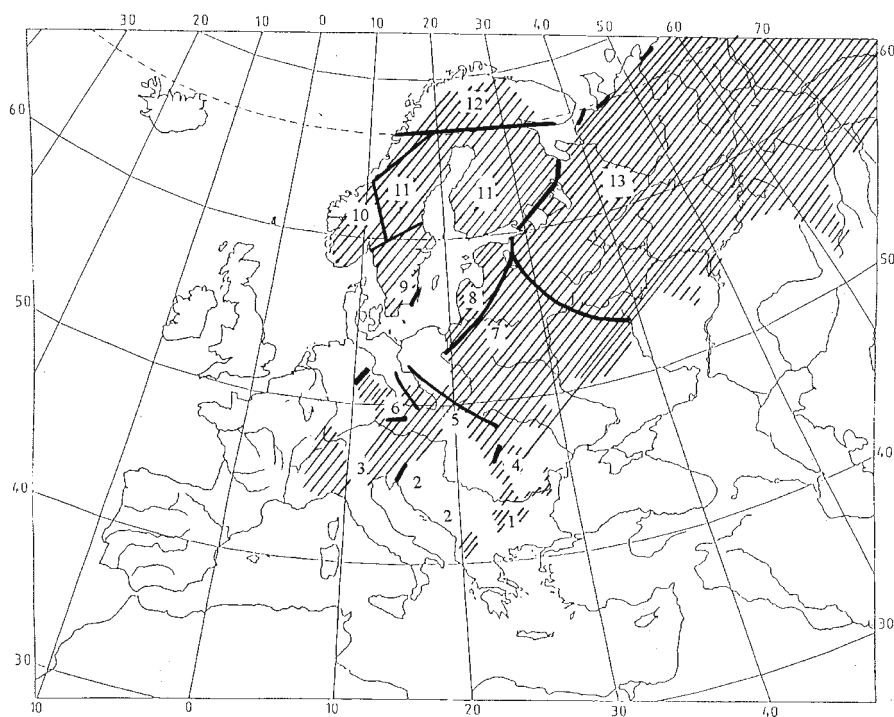


Figure 9.2. Distribution of *Picea abies* (L.) KARST. in Europe According to *Atlas Florae Europaeae*, simplified (JALAS and SUOMINEN 1973) with a division into 13 regions based on the findings of provenance trials.

1 – Bulgaria

This is an outlier population at the southern limit of the species range. Norway spruces from this region grow naturally at much higher elevations than elsewhere and generally grow poorly in lowland provenance trials. This population flushes very late in the spring, and thus it is resistant to late spring frosts, but is only moderately resistant to early autumn frosts and it is susceptible to attacks by the spruce sawfly (*Pristiphora abietina* HART.).

2 – East-Adriatic region

A population found in the Dinaric Alps links with the rest of the range only at the Italian-Slovenian border. It has poor to medium growth and flushes in the spring somewhat later than average. This population is resistant to both early autumn and late spring frosts. It has some resistance to the white pine weevil (*Pissodes strobi* HART.), but is susceptible to gall lice (*Adelges tardus* DREYF.) and the spruce sawfly (*Pristiphora abietina* HART.).

3 – Alps

This region covers the entire Alps and the Black Forest in Germany. Norway spruce populations from this region are highly variable, mainly because of the considerable altitudinal range. As a rule, trees from this region grow very slowly, though some provenances, e.g. Winterthur, Val di Fiemme or Lankowitz, have medium or even good growth in some trials. In the spring, these populations flush early and thus resistance to late frosts is below average. A strong tendency for Lamma's growth results in sensitivity to early autumn frosts. It is also sensitive to cold winter temperatures, particularly at more northerly locations with short photoperiods. These populations are resistant to the white pine weevil (*Pissodes strobi* HART.) and the spruce sawfly (*Pristiophora abietina* HART.), but they lack resistance to gall lice (*Adelges tardus* DREYF.). They have a tendency to produce forked stems.

4 – Eastern and Southern Carpathians

This region covers the entire eastern and southern Carpathians together with the Bihar and Gorgany Mts. Norway spruces from this region as a rule attain considerable heights and diameters. These populations flush late and thus are resistant to late spring frosts, but rather susceptible to early autumn frosts, low winter temperatures, and snow damage. These sources are also susceptible to the white pine weevil (*Pissodes strobi* HART.) and gall lice (*Adelges tardus* DREYF.) and have a tendency to form bayonets. In Romanian nurseries, Bihar provenances sometimes grow better than eastern Carpathian sources (LĂZĂRESCU 1966), and sometimes the opposite is true (ENESCU *et al.* 1979), whereas in the eastern Carpathians, the local provenances always grow best (GOLUBETS' and POLOVNIKOV 1973).

5 – Western Carpathians and the Sudetes

This region covers western Carpathians and Sudety Mts to the Elbe River, extending south to the Danube and in the north to Upper Silesia and the sub-Carpathian region. Norway spruce from this region grows very fast, particularly sources from the Beskid Śląski and Czech side of the mountains (ŠINDELÁŘ 1983). These populations exhibit an average date of flushing and a long height-growth period. They also grow Lamma's shoots and end vegetative growth later than other populations, and thus are moderately susceptible to late spring and early autumn frosts as well as cold winter temperatures. Seed sources in this region are resistant to drought, snow damage, and are highly resistant to the white pine weevil (*Pissodes strobi* HART.). Provenances originating from the Silesian Beskid (Beskid Śląski) are exceptional, particularly the Istebna provenance, which is characterized by rapid growth and late spring flushing, and thus has somewhat greater resistance to late spring frosts.

6 – Central Europe

This region covers Germany west of the Elbe and north of the Danube, but excluding the Black Forest, and including the Czech Republic south of the Elbe. Norway spruce populations from this region exhibit above average growth. These sources flush slightly later than average in the spring, and thus are quite resistant to late frosts. These sources demonstrate an above-average resistance to autumn frosts, cold winter temperatures, and an exceptional resistance to wet snow and ice damage. These populations have a low tendency to form stem forks. From this region, Norway spruce from the Bavarian Forest and from the Erz Mts exhibit slightly better than average growth and flush somewhat earlier.

7- The north-eastern region

This region covers Byelorussia, Lithuania, and Poland all the way to the Świętokrzyskie Mts and the Solska Forest, but it does not include the coastal regions of the Baltic. I do not draw the line along the Bug River as is often done but further south, just north of the Carpathian and Sudety Mts, since Norway spruce populations from central Poland appear to be more comparable to the north-eastern populations than to the montane sources (GIERTYCH 1973). Norway spruces from this region are characterized by much better than average growth, very late flushing, and early growth cessation. Thus, these sources are very resistant to late spring frosts and moderately resistant to early autumn frosts and low winter temperatures. However, these sources exhibit no resistance to damage by wet snow. Populations from this region are also susceptible to the white pine weevil (*Pissodes strobi* HART.).

8 – East-Baltic region

This is basically the same Norway spruce population region as the previous one (no. 7), but from more maritime regions. This area extends from the Bay of Gdańsk in Poland to Estonia, including all of Latvia. Norway spruce sources from this region are generally characterized by good growth, but exhibit earlier, nearly medium spring flushing and moderate resistance to the white pine weevil (*Pissodes strobi* HART.). These populations also have a somewhat greater tendency to form Lamma's shoots. In other traits, sources originating in this region are very similar to Norway spruce from region 7.

9- Southern Sweden

This region covers Sweden as far as 60° North latitude. Norway spruce sources from this region are characterized by a lower than average wood volume increment. There are somewhat better-growing races in the western portion of this region, but these are possibly sources introduced from central Europe (KRUTZSCH 1973). These populations also exhibit early spring flushing and early growth cessation in the autumn, thus they are susceptible to late spring

frosts, but resistant to early autumn frosts and to low winter temperatures. They are not resistant to snow damage. Among the Scandinavian Norway spruce sources, these are decidedly the best races of the species.

10 – Western Norway

This region covers Norway from the Swedish border to about 64° N latitude. Norway spruce populations from this region grow poorly and both flush and terminate growth very early. Thus, these sources are susceptible to late spring frosts, but resistant to early autumn frosts and cold winter temperatures. These populations are susceptible to snow damage and resistant to the white pine weevil (*Pissodes strobi* HART.). These populations have a tendency to form very shallow root systems (ŠIKA 1966).

11 – Central Scandinavia

This region extends from regions 9 and 10 to the Arctic Circle, and covers southern Finland and Russia to a line extending from Arkhangelsk to St. Petersburg. The traits characteristic of region 11 are: poor growth, early flushing, sensitivity to late spring frosts and snow damage, and resistance to early autumn frosts, low winter temperatures, and the white pine weevil (*Pissodes strobi* HART.). As a rule, Finnish Norway spruce sources grow better than Norwegian or Swedish populations from the same region.

12 – Northern Scandinavia

Norway spruce populations originating north of the Arctic Circle grow extremely poorly, flush very early, and end growth early. Only in northern Scandinavia, can these sources compete in growth with some southern races.

13 – The East-European Lowland

This is an extensive region. Populations originating here are no doubt differentiated, but have been little studied in provenance experiments. Interesting trait differentiation has been observed in a trial near Voronezh, which is shown in Fig. 9.3 (SHUTYAEV 1995b). In the east, Norway spruce populations of this region merge introgressively with populations of *Picea obovata* (CHZHAN SHI-TSYUÍ 1969). Sources from this region exhibit average growth. Sources from the southern portion exhibit somewhat better than average growth. These populations flush late and enter winter dormancy early, thus they are resistant to both late spring and early autumn frosts and to low winter temperatures. Overall, populations from the central-Russian part of this region are similar to those from region 7, with which they do not have a distinct boundary, and in the northern and eastern parts are similar to region 11.

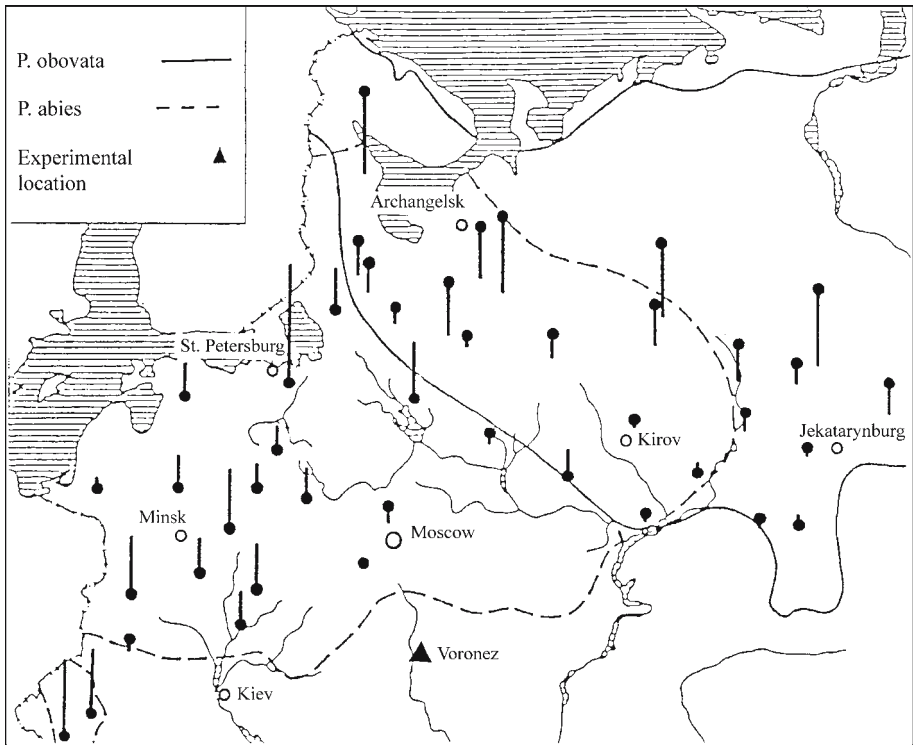


Figure 9.3. Wood volume of *Picea abies* (L.) KARST. obtained from a provenance trial in Voronezh, Russia, expressed according to the convention described in the legend of Fig. 9.1. (from the findings of SHUTYAEV 1995b)

9.1.5. Seed transfer

The main aim of provenance experiments is to determine seed transfer zones to increase wood production. Some authors have attempted to indicate conditions for successful transfers. It is generally considered safe to move seed to sites up to 200 m higher than the altitude of origin (BERGMAN 1965; KONÓPKA and ŠIMAK 1990; REMRÖD *et al.* 1972), or somewhat higher (STEFANSSON 1953; NIȚU 1979; NIȚU *et al.* 1984; PRAVDIN and ROSTOVTSEV 1979; ROSVALL and ERICSSON 1981), though this does not necessarily mean that growth and survival will be better than with local sources (KOWALSKI and WŁOCZEWSKI 1972a; PAULE 1986). At very high elevations, the elevational transfers should not exceed 50–100 m (GÜNZL 1979b). In regions prone to wet snow damage such transfers can be risky (SCHMIDT-VOGT 1972). Transfer of seed to lower elevations promotes seedling growth. Consequently, nurseries can be located at lower elevations (DAKEV 1969), but this does not provide better seedlings than from local seed (KOWALSKI and WŁOCZEWSKI 1972a). In Slovakia, it has been

found that regardless of the elevation from which seed sources originate, all grow best at an altitude of about 800–900 m (KONÔPKA and ŠIMAK 1990).

Northward seed transfer in Scandinavia by about 2.5° to 3°N latitude results in better growth than local sources (BERGMANN 1965; HEIKINHEIMO 1954; REMRÖD *et al.* 1972; PERSSON and PERSSON 1992; ROSVALL and ERICSSON 1981). In the far north or in high mountains on dry or poor sites, the permissible northward transfer is much less (REMRÖD 1972; ROSVALL and ERICSSON 1981). In Norway, the experience is that after many years the local races may in fact prove superior (DIETRICHSON 1961). When transferring seed to other places one has to be aware of the fact that the photoperiodic conditions change, which not every source will sustain without injuries (MAGNESEN 1972). However, Norway spruce populations from the Harz, Sudety, and Beskid Wysoki Mts are recommended for western Norway, and populations from northeastern Poland, Lithuania and Byelorussia are recommended for southern and eastern Norway (MAGNESEN 1972). In Iceland, only populations from northern Norway are capable of survival, attaining a height of less than 1 m at age 13 (BENEDIKZ 1974).

Long-term experience with continental races in Scandinavia indicates that populations from central Europe are most useful. German populations have been cultivated in Scandinavia for a long time and are better than local sources (KLEM 1956; KIELLANDER 1951; LANGLET 1964; MASCHNING and LANGNER 1971; ROBAK 1962a). However, results of provenance experiments ever more clearly indicate that seed sources best for Scandinavian conditions are populations from the north-eastern region (no. 7, Fig. 9.2) and from the Silesian Beskids, particularly from Istebna (region 5) and the eastern and southern Carpathians (region 4) (DIETRICHSON 1979; KIELLANDER 1966, 1970a, b; KRUTZSCH 1973, 1974; LANGLET 1960). Use of the Istebna (region 5) and Romanian (region 4) spruce population is recommended by almost all authors who have analysed the IUFRO trial of 1938 and later ones. In northern Scandinavia, recently doubts have arisen concerning the use of the Istebna Norway spruce source in view of the fact that vertical cracks appear on old trees (SKRØPPA and DIETRICHSON 1986; PERSSON and PERSSON 1992; PERSSON 1994). It is interesting that in Romania, there appears more benefit in transferring seed from the south northwards than from the north to the south (NIȚU 1979).

Within the territories of the former USSR, seed transfers were recommended from the south to north and not in the opposite direction (PRAVDIN and ROSTOVTSEV 1979, 1980). However, there are findings that support a different conclusion. In the Urals (Permskiĭ Leskhov) transfer of Norway spruce from the northern taiga to the southern one is useful; however, southward transfer of sources from Karelia (KORABLEV *et al.* 1975) is not recommended. In southwestern Siberia, it is also recommended to introduce sources from north-eastern Russia (DEMIDENKO *et al.* 1984). In Latvia, populations from

the vicinity of St. Petersburg are recommended, whereas the Carpathian sources praised in other areas appear unsuitable (RONE 1984). In Georgia, sources from region 7 (north-eastern) grew decidedly better than the more southern and local provenances, though these extensive transfers may eventually prove unjustified (NATSVLISHVILI 1981).

Transfer of seed sources from the west to the east provided good results in central European Russia (PRAVDIN and ROSTOVTSEV 1979, 1980; PALTSEV 1978, 1989), in the Urals (KORABLEV *et al.* 1975, 1976; KUPCHINSKIĭ *et al.* 1980; TISHECHKIN and KORABLEV 1980), in the Altai (VISHNYAKOV 1969) or Dzhungaria Ala-tau Mts (KOROBKO *et al.* 1983), and in south-western Siberia (DEMIDENKO *et al.* 1984). However, in other regions west to east transfers proved unfavorable (DANUSEVICIUS 1993). In southern Russia, near Voronez, 300 km south of the southern limit of the range of spruce, the best-growing sources were populations from the river Ob (probably *Picea obovata*), while western Carpathian, Karelian, and pre-Uralian populations grew poorly (VERESIN and IVANOV 1970). This unusual result is likely due to the vastly different growth conditions compared to those in which Norway spruce normally grows. In South Korea, an unusual result was also obtained. Fifty-year-old Norway spruce from Germany proved better than a local provenance of Japanese larch (*Larix kaempferi* SARG.), though this superiority declines further south among trials within the country (HWANG and HYUN 1979). In South Korea, 12 Romanian and 12 German Norway spruce populations were compared with the local Mandzhurian fir (*Abies holophylla* MAXIM.). The growth of the German sources surpassed the fir on all sites (on average by 27%) and the Romanian ones on six sites (on average by 4%). At an age of 8 years, the tallest were populations from the Palatinate and from the Black Forest (HAN *et al.* 1984). In another experiment, nine Romanian populations were compared with one each from Slovakia, France, Serbia, and Byelorussia. The latter two were decidedly poorer at age 9 and the French source was comparable with the poorer Romanian ones. The best sources were two Romanian provenances and one from Slovakia, from the eastern Carpathians (HAN *et al.* 1987).

Transfer of seed to the west, even to North America, as a rule provides good results. Norway spruce sources from region 7 and the late-flushing provenances from the Carpathians are recommended for forestry in France (LACAZE 1969a; HÉOIS 1992), Belgium (GATHY 1957; NANSON 1972), Holland (KRIEK 1975) and in the Great Lakes and the Gulf of St. Lawrence region in Canada (FOWLER 1979; HOLST 1963). In eastern Canada and in north-eastern USA, provenances from the Polish side of the Sudety and Carpathian Mts are recommended, but not sources from the Czech Republic, Slovakia, or Romania (FOWLER 1979). In Minnesota, sources from the European part of the former USSR (between 54° and 58°N latitude) proved better than those from northern Poland (Olsztyn region). They grew faster in height and were more resistant to spring frosts (VAN DEUSEN and NIENSTAEDT 1978). Further south

in Maryland, sources from the Harz Mts and from the vicinity of Boden Lake are recommended, but not those from the Baltic regions, from the Carpathians nor from Romania (GENYS 1979). In North Dakota, droughts that recur every few years eliminate all Norway spruce provenances (VAN DEUSEN and NIENSTAEDT 1978). Also on the central Russian plateau (Solekhnogorsk), Norway spruce from the east and northeast are recommended, but only for the production of Christmas trees (PALTSEV 1978). In central and northern Canada (Manitoba), the best-growing sources originated from Bashkiria and southwestern Siberia (KLEIN 1977). This is a transfer of almost half way around the globe. The growth of these provenances was comparable to that of second-generation Canadian populations (seed from an old plantation of Norway spruce in Chalk River, Ontario).

In some regions, introduction of provenances is not recommended at all, since in comparative plantations the local populations are clearly superior, e.g. in Latvia (GAILIS 1993). It is very difficult to perform an experiment in sufficiently uniform conditions so as to be able to definitively claim where the conditions are best for a given provenance. Some indication may come from the data of HEIKINHEIMO (1954) obtained from seedlings. For a given population, the highest seedling fresh weight was obtained from sites about 6°N of its place of seed origin (Fig. 9.4). Transfer further north reduces growth. In contrast, BEUKER (1994b) claims on the basis of an analysis of old experiments located in seven regions in Finland, that for a given provenance, transfer southwards increases its wood production.

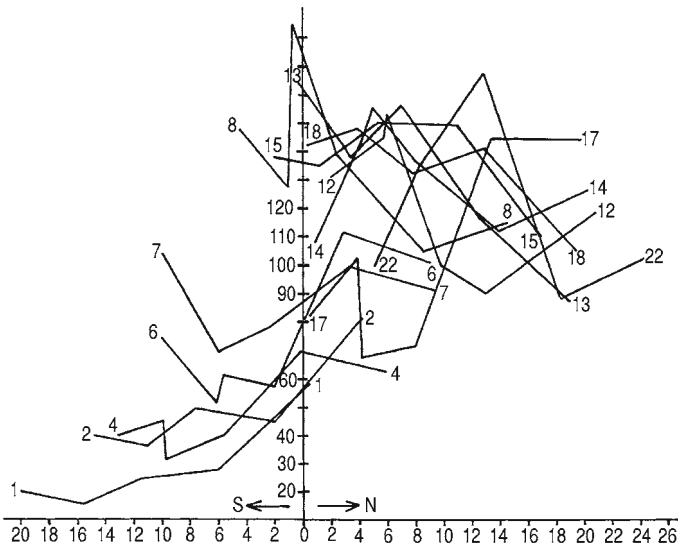


Figure 9.4. Fresh weight of spruce *Picea abies* (L.) KARST. seedlings growing at various distances north and south of the region of origin (derived from HEIKINHEIMO 1954)

9.1.6. Clonal variation

The phenomenon of poor flowering of Norway spruce in seed orchards over many years, as well as problems with pollen from beyond the plantation, have resulted in a growing interest in vegetative propagation of the species (NAPOLA 1993). Consequently, trials were begun to test clonal differences among trees with the aim of finding individuals suitable for plantation forestry (as with poplars). Clonal variation is considerable and is greater among clones than for progenies or provenances (VAN DE SYPE and ROMAN-AMAT 1989; ELERŠEK and JERMAN 1988; KLEINSCHMIT and SVOLBA 1991). In this manner, one can quickly obtain impressive selection effects. However, there are doubts as to whether this approach is justified.

For some traits, such as the timing of winter bud formation (HOLZER *et al.* 1991) or spring flushing, large differences are observed among clones, and full agreement between the ortet and the ramets. However, for growth traits such close agreement is more difficult to obtain (LECHNER *et al.* 1977). With increasing age, the clonal heritability of trees declines (VAN DE SYPE and ROMAN-AMAT 1989).

In Norway, the best individuals were chosen from among 8-year-old families representing the best provenances. After vegetative propagation, 20 clones that propagated most readily were selected (out of 336) and after several consecutive propagations (propagation cycles) no correlation was found between traits of ramets and ortets and between ramets of consecutive cycles. These observations included both growth and phenological traits (DIETRICHSON and KIERULF 1982). To minimize the role of "ease of propagation" on selection, propagations are currently made from increasingly younger ortets derived from seedlings or even embryos. However, early selection may have less relevance to selection of traits related to production. Fast-growing transplants may quickly outgrow herbaceous weed competition and grazing by mammals. These selections are readily used for afforestation and replanting because of lower costs for stand establishment. However, correlations with later growth should also be of interest. The overall aim of selection is typically not to facilitate plantation establishment, but to produce a high-yielding stand. Only older trees permit a complete evaluation of the utility of clonal material. There are examples of clones that grow fast when young but later decline in growth vigor. Likewise, there are other clones that begin growing more slowly, but later increase in growth rate and surpass those that were initially faster growing. Thus, one cannot bypass long-term testing in the field.

There are not many older clonal plantations of Norway spruce. On six sites in Germany, selection of the best clones at an age of 17 years assures genetic gains on the order of 9% for tree height, 24% for diameter, and 70% for volume of individual trees. Selection at the age of 4 years would be 40% less effective (KLEINSCHMIT and SVOLBA 1991). On these same experimental sites, clones that were taller in the nursery had greater mortality in the field, and

nursery selections based on height did not correlate with height in the field (ISIK *et al.* 1995). Clones may exhibit considerable phenotypic variation among planting sites (NAPOLA 1989). On older plantations in Sweden, clonal differences in resistance to vertical stem cracks have been observed (PERSSON 1994). Six years after planting (9 years after rooting), considerable clonal differences in wood density have been noted (CHANTRE and GOUMA 1994). On plantlets obtained by rooted cuttings of seedlings of controlled crosses, interesting data was obtained on the heredity of resistance to sudden changes in winter temperature. This resistance is correlated with the timing of spring flushing (DIETRICHSON 1993).

The vegetative propagation of spruces through embryogenesis is sometimes thought to assure genetic identity (MO *et al.* 1989). However, occasionally genetic changes do take place. The appearance of duplicate or additional chromosomes has been observed (FOURRE 1992; LELU 1988), which results in a completely different plant. Mutagenesis may also occur and these may be small changes that are neither noticed early enough nor prevented.

9.1.7. Progeny testing and heritability of traits

For a breeder it is very important to determine to what extent the progeny will inherit parental traits. To measure the degree of inheritance for a particular trait, the parameter of heritability (h^2) is used. Heritability is a measure of the genetic variability in relation to the total variability (phenotypic) including the variability caused by the environment. In other words, heritability is the difference between the progenies of selected and non-selected trees (genetic gain) in relation to the difference between the selected and non-selected parents (selection intensity). Information on this topic can be obtained from family comparisons or from correlations between the progeny and the parents. A different heritability is obtained for each trait and for each set of environmental conditions. Thus, published heritability values are not fully comparable; however, certain patterns do appear.

In general, correlations between the growth traits of parents and the traits of the progenies in controlled crosses are very weak (DANUSEVICIUS 1993). However, late flushing is correlated not only with resistance to late spring frosts, but also with resistance to sudden drops in winter temperature after a period of relatively mild weather (DIETRICHSON 1993). The controlled crossing of late flushing and late bud setting French sources with Swedish ones that are early in both these traits gave progeny of intermediate phenology (compared to open pollinated progeny of the parent trees). This would suggest additive inheritance (without domination of any particular form); however, considerable variation is observed in the progeny, which permits further selections in the second generation (ERIKSSON *et al.* 1978).

To improve growth traits, the artificial crossing of distant forms (outbreeding) gives good results. Thus trees of various provenances at an experimental site can be used for such work. Some progenies of Scandinavian and continental Norway spruce sources exceed by 17% the progenies of both parental forms growing in Scandinavia. These progenies are intermediate in phenological traits (NILSSON 1958, 1963a; NILSSON and ANDERSSON 1969, 1970). In order to stimulate heterosis through mating distant provenances, a seed orchard was established representing elite trees selected from the five best populations (out of 1100) having documented very good adaptability in many different environmental conditions (GIERTYCH 1993).

The greatest amount of data on inheritance of traits has been obtained from comparisons of half-sib progenies and provenance comparisons. In a Polish experiment with spruce from the Beskid Wysoki Mts (KRUPSKI *et al.* 1996), provenance heritability has high values for most traits in Kórnik (outside the native range of spruce), while in Nowy Targ, a site close to the original populations, only small heritabilities were observed. In contrast, family heritability was high both in Kórnik and in Nowy Targ. Single-tree heritability was low and similar at both locations. In practice this means that family selection is most effective, and provenance selection only on sites difficult for Norway spruce.

HOLUBČÍK (1972) suggests that in Norway spruce, heritability *sensu stricto* and heritability *sensu lato* (i.e. degree of additive inheritance and degree of total inheritance in relation to phenotypic variability) are very close to each other ($h^2_{ss} \sim h^2_{sl}$). This indicates that additive inheritance is the rule and the effect of genes with dominance plays a limited role in the inheritance of traits by Norway spruce. This is in disagreement with the observations of NILSSON and ANDERSON (1969) who indicate that the actual choice of a specific pair of parents (specific combining ability) is of greater importance. However, determination of the general combining ability from half-sib and from full-sib progenies gives similar results (NILSSON 1967).

The traits with the highest heritability are the time of spring flushing (LACAZE 1969b; LANGNER and STERN 1964; DIETRICHSON and KIERULF 1982; MERGEN 1960, NANSON 1971, 1981; VAN DE SYPE and ROMAN-AMAT 1989; HÉOIS *et al.* 1991) and resistance to late spring frosts (LANGNER and STERN 1964). Wood characteristics also have a high heritability, particularly wood specific gravity (KENNEDY 1966; KLEINSCHMIT and KNIGGE 1967; NANSON *et al.* 1975; NILSSON 1963b; RONE 1970; WORRALL 1975), percentage of late wood in an annual ring (KLEINSCHMIT and KNIGGE 1967; KENNEDY 1966; WORRALL 1975), and fiber length (NANSON *et al.* 1975). Qualitative traits such as stem straightness, basal sweep, branch thickness or tendency to form bayonets as a rule have a high heritability (KRUPSKI *et al.* 1996; NANSON 1971; KLEINSCHMIT and KNIGGE 1967). Other traits with a high heritability include resistance to snow damage (NANSON 1981), annual volume increment

(NANSON 1981) and the proportion of branches in the total weight of trees (KLEINSCHMIT and KNIGGE 1967).

Medium heritability values are typical for traits such as Lamma's growth (DIETRICHSON 1967b; LANGNER and STERN 1964; NANSON 1971), termination of height growth (WORRALL 1975), ease of rooting cuttings, the size of the root system obtained (MERGEN 1960), length of roots (NIȚU 1974), resistance to the gall lice (*Sacchiphantes viridis* RATZ.) (NANSON 1971), the length and persistence of needles (NANSON 1971), bark damage by animals (NANSON 1981), physical durability of wood (KENNEDY 1966), and fiber length (KENNEDY 1966; RONE 1970).

Growth traits demonstrate very different heritability values in various experiments, owing to the dependence of these traits on environmental conditions. Thus, the heritability of tree height is generally high and increases with increasing age (DIETRICHSON 1967b; DIETRICHSON and KIERULF 1982; HOLUBČÍK 1972; GIERTYCH 1969; KLEINSCHMIT and KNIGGE 1967; LANGNER and STERN 1964; NANSON 1971, 1981; NANSON *et al.* 1975; NILSSON 1963a; NIȚU 1974; ŠINDELÁŘ 1983; VAN DE SYPE and ROMAN-AMAT 1989; WORRALL 1975), but an opposite result was also reported (HÉOIS *et al.* 1991). Stem girth and radial growth increment exhibit a lower heritability than tree height and declines with age (HOLUBČÍK 1972; NANSON 1971, 1981; NANSON *et al.* 1975; NIȚU 1974; WORRALL 1975). Survival belongs to traits with medium heritability (HOLUBČÍK 1972; NANSON 1971, 1981; NANSON *et al.* 1975; NIȚU 1974; WORRALL 1975). Among traits with the lowest heritability, one should include the shape of buds (HOLUBČÍK 1972), onset of height growth (as distinct from spring flushing), the intensity of lateral shoot growth (WORRALL 1975; HOLUBČÍK 1972), resistance to low winter temperatures (DIETRICHSON 1993), and the branch angle (HÉOIS *et al.* 1991).

Seed orchards established from half-sib progenies of plus trees produce about a 15–17% increase in growth and a 12% delay in the time of spring flushing in the next generation, relative to populations raised from seed collected commercially from the same stands (TERRASSON 1992). Progenies of late-flushing individuals generally grow better than progenies of trees that flush early and terminate growth early (DIETRICHSON 1969b; ETVERK and HAINLA 1972). These differences decline with time (MOULALIS 1973). The progenies of trees with the var. *europaea* type of cones, or those intermediate between varieties *acuminata* and *europaea*, or *obovata* and *europaea* grow better than the progenies of trees with cones of var. *acuminata* or var. *obovata* (ETVERK and HAINLA 1972; ORLENKO and RUDENKOVA 1972). The progenies of plus trees grow better than the progenies of unselected trees (RUDEN 1963; TEICH 1972). However, DIETRICHSON (1967b) believes that provenance selection leads more quickly to an increase in volume production than does individual selection. In view of the high heritability of the timing of spring flush-

ing, selection with respect to this trait is very effective (LACAZE 1969b; LANGNER and STERN 1964; MOULALIS 1973; NANSON 1971).

Bark thickness is a heritable trait. Therefore, it is possible to select for this trait to obtain trees resistant to mechanical injuries caused during thinning (ROHMEDEK 1971). In contrast, bark flaking is a phenotypic trait that is dependent on the growth conditions (ROHMEDEK 1971). The trait of reduced branchiness ("snake spruce", f. *virgata*) in Norway spruce is dependent on several genes; thus considerable variation exists among these forms (HOLZER 1968).

9.1.8. Hybridization

Literature data on the artificial crossing of Norway spruce with other species are shown in Table 1. The group "successful, unchecked", includes crosses which produced seeds and seedlings, but for which the presence of intermediate forms has not been determined. The crosses *P. abies* × *mariana* and *P. abies* × *rubens* are doubtful (WRIGHT 1955, citing HEIMBURGER). These crosses are mentioned as unsuccessful in a later listing of RAUTER (1971) from the same experimental station where HEIMBURGER conducted his studies.

The easiest artificial cross is the cross between Norway spruce and *P. asperata*, particularly when *P. abies* is the paternal tree (ROULUND 1969). Another easy cross is possible with Siberian spruce, since there exists a large zone of intermediate forms with a clear introgression between the ranges of *P. abies* and *P. obovata* (CHZHAN SHI-TSYUÍ 1969; PRAVDIN 1972). However, there have been few attempts to obtain artificial crosses between these spruces. Crosses with the Serbian spruce (*P. omorica*) are also not difficult. Many attempts have been made to cross *P. abies* with *P. glauca* with little success. The latter species is resistant to the white pine weevil (*Pissodes strobi* HART.), an insect that causes much damage in plantations of Norway spruce in North America. HOLST (1955) suggested that resistance to this insect might be transferred from *P. glauca* to *P. abies* using *P. koyamai* or *P. sitchensis* as intermediates. However, this aim was not achieved. Crosses of *P. sitchensis* with *P. abies* are also difficult to obtain. There appears to be little future value of interspecific hybridization for breeding work.

The mating of various varieties of Norway spruce can be achieved without difficulty (POLANSKÝ and VACL 1933). Crosses made in southern Finland between distant populations of Norway spruce (inter-provenance crosses, Finnish × continental sources) produced progenies that demonstrated hybrid vigor with growth substantially higher than for open-pollinated progenies of the same maternal trees and for the local standards (NAPOLA 1989). However, such crosses may be of limited use owing to their poorer adaptation to climatic conditions (NAPOLA 1993). Crosses between neighboring trees in stands generally indicate that additive inheritance predominates. Dominance effects

Table 1. Interspecific hybrids of *Picea abies* (L.) KARST.

<i>Picea abies</i> as mother	<i>Picea abies</i> as father	Literature
<i>Successful, checked</i>		
	<i>P. mariana</i>	JEFFERS 1971
<i>P. asperata</i>	<i>P. asperata</i> , <i>P. omorica</i>	ROULUND 1969
<i>P. koyamai</i> , <i>P. asperata</i>	<i>P. aspera</i> , <i>P. montigena</i>	WRIGHT 1955
<i>P. orientalis</i>		
<i>P. mariana</i> , <i>P. rubens</i>		HEIMBURGER (ex WRIGHT 1955)
	<i>P. pungens</i>	ZABOLOTNOVA 1972
	<i>P. sitchensis</i>	LANGNER (ex WRIGHT 1955)
<i>P. koyamai</i> , <i>P. sitchensis</i>	<i>P. glauca</i>	ANONIM 1971
<i>P. (mariana x rubens)</i>		
<i>P. obovata</i> , <i>P. sitchensis</i>		JOHNSON 1939
<i>P. asperata</i>	<i>P. asperata</i>	VIDAKOVIĆ 1982
<i>P. asperata</i> , <i>P. glauca</i>	<i>P. glauca</i> , <i>P. omorica</i>	KOBLIHA 1993
<i>P. omorica</i>	<i>P. pungens</i>	
<i>P. sitchensis</i> , <i>P. glauca</i>		HOFFMANN 1985
<i>P. omorica</i>		
<i>Successful, unchecked</i>		
<i>P. montigena</i>	<i>P. glauca</i> , <i>P. engelmannii</i>	WRIGHT 1955
<i>P. maximowiczii</i>	<i>P. retroflexa</i> , <i>P. omorica</i>	
<i>P. asperata</i>	<i>P. asperata</i> , <i>P. glauca</i>	JEFFERS 1971
<i>P. likiangensis</i>	<i>P. orientalis</i> , <i>P. omorica</i>	
<i>P. asperata</i> , <i>P. koyamai</i>		MIKKOLA 1969, 1970
<i>P. obovata</i>		
	<i>P. glauca</i>	RAUTER 1971
<i>P. orientalis</i>		NEFES (WRIGHT 1955)
	<i>P. rubra</i>	JOHNSON 1939
<i>Unsuccessful</i>		
	<i>P. sitchensis</i>	FAULKNER <i>et al.</i> 1970
<i>P. glauca</i> , <i>P. orientalis</i>		JEFFERS 1971
<i>P. omorica</i>		
<i>P. glauca</i>		KLAHN and WHEELER 1961
<i>P. glauca</i> , <i>P. mariana</i>	<i>P. (sitichensis x glauca)</i>	RAUTER 1971
<i>P. rubens</i>		
<i>P. omorica</i> , <i>P. sitchensis</i>	<i>P. sitchensis</i> , <i>P. jezoensis</i>	ROULUND 1969
<i>P. jezoensis</i>		

<i>P. glauca</i> , <i>P. retroflexa</i>	<i>P. mariana</i> , <i>P. maximowiczii</i>	WRIGHT 1955
<i>P. glauca</i>	<i>P. glauca</i> , <i>P. mariana</i> , <i>P. rubens</i>	HEIMBURGER (ex WRIGHT 1955)
<i>P. glauca</i>	<i>P. glauca</i> , <i>P. orientalis</i>	NEFES (WRIGHT 1955)
<i>P. glauca</i> , <i>P. mariana</i>	<i>P. glauca</i> , <i>P. mariana</i>	MIKKOLA 1969
<i>P. jezoensis</i> , <i>P. omorica</i>	<i>P. sitchensis</i> , <i>P. jezoensis</i>	
	<i>P. engelmannii</i>	WRIGHT 1962
<i>P. pungens</i>	<i>P. rubens</i>	KOBLIHA 1993

(non-additive) and maternal effects (cytoplasmic inheritance) disappear after the nursery stage (SKRØPPA 1993).

9.1.9. Self-fertilization

Controlled self-pollination of Norway spruce produces viable seed of the same weight and size as is obtained after cross pollination. However, there are fewer seeds per cone (DIECKERT 1964) and the percentage of full seeds is much lower, and the growth of seedlings (KLAHN and WHEELER 1961; DIECKERT 1964; ANDERSON *et al.* 1974) and older trees originating from self-fertilization is much slower (LANGLET 1940; ERIKSSON *et al.* 1973; SKRØPPA 1993). The degree of self-sterility in trees from the same stand differs substantially, which indicates that genetic load (content of lethal and sub-lethal genes) is highly variable (SKRØPPA 1993). KOSKI (1970) estimates on the basis of studies with radioactively labelled pollen, that in natural conditions about 7% of a tree's own pollen falls on its female flowers, though on the windward side this may reach as much as 24%. By use of marker genes, self-pollination was estimated at 3–10% in Norway spruce (WALLES 1967; KOSKI 1970). However, there is little homozygosity in isolated populations, such as the population on the Åland Islands (TIGERSTEDT 1974). Growth reduction caused by inbreeding is more evident in poor than good growth conditions (ANDERSSON *et al.* 1974; ERIKSSON and LINDGREN 1975).

9.1.10. Genetic principles demonstrated in Norway spruce

Like other forest tree species, the open-pollinated progeny of plus trees of Norway spruce do not differ as much in growth compared to the progeny of randomly selected trees (NAPOLA 1993). In provenance experiments, changes in the ranking of populations often occur with increasing age. Treating the latest measurements as the most reliable, one can demonstrate the unreliability of juvenile evaluations, particularly for family comparisons from close neighborhoods (MIKKOLA 1989). KÖNIG (1989) believes that only at an age of 7–10 years one gets an evaluation of tree height and stem diameter that can be useful for se-

lection purposes, since earlier ones correlate poorly with growth dimensions at an age of 21 years. On the other hand, quite unexpectedly, the correlation of tree size with the initial seed mass improves with increasing age (GIERTYCH 1989). It is difficult to explain and utilize this information in practice.

In Finland, an older provenance experiment was compared with a younger one (BEUKER 1994a). A greater phenological agreement with the local climate was observed in the older than younger trial, which would suggest an increasing adaptation to the local climate through thinning and mortality (artificial and natural selection). On the other hand, the adaptation attained in the nursery may affect provenance comparisons at least to the pole stage, as was shown in a 20-year-old German experiment with 15 provenances raised in three nurseries at three different elevations (MELZER and KARGE 1991). Comparison of progenies of selected seed stands in Denmark has shown that stands selected earlier produced poorer-growing progeny than those originating from later selections (MADSEN 1989). This would indicate that the ability to select improved with time.

Quite unexpectedly, the existence of non-MENDELIAN inheritance was demonstrated in Norway spruce. Seeds collected from trees growing in a milder climate (in seed orchards located at lower elevations or at warmer southern locations than the origin of the clones; in warmer years; in greenhouse conditions, etc.) even after controlled crosses, produced progeny that were to some degree adapted to the place where the seeds developed, and not to the conditions from which the parents originated. A comparison of nine pairs of parents in controlled crosses of the same clones made in southern and in northern Norway has shown that in eight of them there was a greater resistance to autumn frosts when they were formed in the north than when they were formed in the south (SKRØPPA and JOHNSEN 1990). In Finland, 11 pairs of full-sibs were obtained in the north and south of the country, and the progeny were subjected to artificial frosts in a phytotron. Progenies obtained in the north were more resistant (SKRØPPA *et al.* 1994). Similar results are obtained when making the crosses at various elevations (SKRØPPA *et al.* 1994). This may be an effect of the environment (also of the root stock) on individual adaptation during the embryonal stage of tree development. In addition, gametic or embryonal selection is also possible, that is the maternal environment may have an effect on the genetic quality of the progeny that develops there (JOHNSEN 1988).

Another non-MENDELIAN effect that has been demonstrated in Norway spruce is the occurrence of a morphological trait, out-turned cone scales (f. *deflexa*), that is always inherited, but only from the mother (i.e. via the cytoplasm). This trait was found in all the progeny of a single tree on several planting sites far removed from each other (GIERTYCH 1992).

Having a marker gene, e.g. an albino, it is possible to confirm MENDELIAN principles of inheritance in Norway spruce. Trees having the recessive albino

gene following artificial self-pollination will produce normal green seedlings, seedlings which are initially yellow-green and later becoming green in color (f. *aurea*), and albino forms which survive as long as the food reserves from the seed are available (f. *xantha*) at ratio of 1:2:1 (WALLES 1967; ANDERSSON *et al.* 1974). On the other hand, when such a tree is pollinated with pollen from a normal tree (a backcross), only green and yellowish (f. *aurea*) forms are obtained at a ratio of 1:1 (LANGNER 1953). Seed obtained from open pollination of such trees produces about 4% albino seedlings, indicating that at most 16% of the progeny arise from self-pollination (WALLES 1967). Today, various molecular genetic markers (isozymes, DNA fragments, terpenes) are used to confirm MENDELIAN inheritance. This is a topic of a separate chapter (9.2).

9.1.11. Cytogenetics and mutagenesis

Norway spruce has an $n=12$ haploid number of chromosomes (BIAŁOBOK and BARTKOWIAK 1967; KIELLANDER 1950; SANTAMOUR 1960; SAX and SAX 1933; TERASMA 1971). Nine chromosomes possess a metacentric centromere (ratio of arms length 1.0–1.7) and three chromosomes possess a sub-metacentric one (ratio of arms length 1.7–3.0) (BIAŁOBOK and BARTKOWIAK 1967; TERASMA 1971). Chromosome no. 3 has a secondary constriction (BIAŁOBOK and BARTKOWIAK 1967). Some of the other chromosomes also exhibit secondary constrictions occasionally, but these are not always visible and sometimes occur on one homologue only (TERASMA 1971). Chromosome no. 1 has the greatest variation in length depending on the population (BIAŁOBOK and BARTKOWIAK 1967; TERASMA 1971). Chromosome no. 1 is particularly long in the population of Norway spruce from Istebna, Poland (BIAŁOBOK and BARTKOWIAK 1967). Changes in the length of chromosomes and other aberrations can be obtained by irradiating with gamma rays (BEVILACQUA and VIDACOVIĆ 1963) and by applying a high temperature (ERIKSSON *et al.* 1970). Applying colchicine to seeds led to the formation of tetraploid plants (KIELLANDER 1950) or tissues, morphologically differing in the size of stomata (EIFLER 1955). Seedlings with abnormally small and thick stems have been found among the progeny of one tree. They had a varying number of chromosomes among cells (mixoploidy), which has also been found in many dwarf forms of Norway spruce (ILLIES 1958).

The occurrence of two or more embryos in one seed (polyembryony) occurs quite commonly in Norway spruce. Out of 220 seeds with double embryos selected via X-ray analysis, one seed had a diploid (normal) embryo and an abnormal one with a mosaic aneuploidy of 12–24 chromosomes per cell (ŠIMAK *et al.* 1968). ILLIES (1959) believes that this has nothing to do with polyembryony and that abnormal numbers of chromosomes occasionally occur. Triploids and mixoploids are generally weaker than the diploid forms and perish under natural conditions (KIELLANDER 1950).

Mutagenetic and cytogenetic studies have so far not yielded any benefits to breeding programs. Abnormal forms may at times be useful as ornamental plants, but the normal growth of trees appears to be attainable only by individuals possessing a normal diploid karyotype.

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LEON MEJNARTOWICZ AND ANDRZEJ LEWANDOWSKI

9.2. BIOCHEMICAL GENETICS

9.2.1. *Isoenzymes as genetic markers*

Despite its limitations, the electrophoretic separation of enzymes on various gels remains one of the most commonly used techniques in evolutionary and population genetics. The widespread use of isoenzymes as genetic markers resulted from the possibility of measuring variation at a level close to DNA by this easy, inexpensive, and rapid method that enabled simultaneous analyses. However, for individual isoenzymes to meet the criteria for a proper biochemical marker, information on the genetic basis of a given enzyme is required. Coniferous trees proved to be a particularly suitable research subject in this field, as their seeds contain the diploid tissue of the embryo and haploid tissue of the megagametophyte. In addition, the megagametophyte tissues from various seeds of an individual tree are good sources of information on the segregation of alleles during meiosis and on the frequency of recombination among the studied isoenzymatic loci. Research on megagametophytes of many species of coniferous trees indicates that the inheritance of many enzyme systems conforms to MENDEL'S laws. By determining the genotypes of the haploid megagametophytes, it is easy to identify the genotype of the maternal tree without laborious crossing (BARTELS 1971; BERGMANN 1971; PASTORINO and GREGORIUS 2002). Megagametophytic cells have the same genotype as the egg cell, as they are derived from the same haploid megaspore. Thus, a simultaneous analysis of the embryo and the megagametophyte originating within the same seed makes it possible to determine the pollen gamete pattern (MÜLLER 1977). The mode of inheritance of more than 20 enzymes has been studied in Norway spruce (BERGMANN 1974; LUNDKVIST 1979, POULSEN *et al.* 1983; ALTUKHOV *et al.* 1986; MUONA *et al.* 1987; LAGERCRANTZ *et al.* 1988; MORGANTE *et al.* 1989; GONCHARENKO *et al.* 1995).

9.2.2. Linkages among isoenzymatic loci

One of the first studies of the linkages among isoenzymatic loci in coniferous trees involved Norway spruce. LUNDKVIST (1974) reported that alleles in two loci encoding leucine aminopeptidase (Lap1 and Lap2) and the third locus of glutamate-oxaloacetate transaminase (Got3) segregate independently in this tree species. In later research, LUNDKVIST (1979), analyzing 11 isoenzymatic loci, found a linkage among three loci, Est1, Est2 and Aph1, and between Lap1 and Got3. POULSEN *et al.* (1983) confirmed the linkage between Lap1 and Got3, added 6-Pgd1 (6-phosphogluconate dehydrogenase) to that group, and described linkages between Mdh2 and Mdh3 (malate dehydrogenase) and between Got1 and Lap2.

The accumulation of data on recombination made it possible to prepare genetic maps and determine the distances between genes and their order. To date, several new linkage groups other than those mentioned above have been identified as follows: (1) Got1, Pgi2, Dia4, Adh; (2) Fle, Lap1, Me; (3) G6pd, Idh2, Gdh; (4) Pgm2, Mdh3; and (5) Fle2, Mdh2 (ALTUKHOV *et al.* 1986; MUONA *et al.* 1987; GEBURK and WUEHLISCH 1989; GONCHARENKO *et al.* 1994). Among these loci, the most strongly linked are two pairs of loci: Got1/Pgi2 and Gdh/Idh2, as the frequency of recombination between them amounted to 6.2% and 7.8%, respectively (MUONA *et al.* 1987; LEWANDOWSKI and MEJNARTOWICZ 1994). However, the lack of chromosomal markers has prevented the determination of the chromosomes on which the linkage groups are located.

The linkage groups identified in Norway spruce are very similar to those found in other *Picea* species and other conifers (CONKLE 1981; KING and DANCİK 1983; CHELIAK and PİTEL 1985; GONCHARENKO *et al.* 1994). This suggests that the genome of coniferous trees may be highly conserved and that no substantial chromosomal changes have taken place in the course of evolution at least within and between the genetic linkage groups analysed to date.

9.2.3. Isoenzymatic polymorphisms

Although electrophoretic methods enable the detection of only 25-30% of the total variation of the genome (LEWONTIN 1974), genetic variation in forest trees is very high (LEDIG 1986; MÜLLER-STARCK *et al.* 1992). The large amount of genetic variation in coniferous trees may not be too surprising owing to their population structure and life history characteristics (HAMRICK *et al.* 1979). Species with a large geographical range, long duration of generations, high fertility, high cross-fertilization and wind pollination, usually have a higher level of genetic variation (HAMRICK *et al.* 1979).

The most comprehensive study of the level and distribution of genetic variation in Norway spruce can be found in a study by LAGERCRANTZ and RYMAN

(1990). Those authors studied 22 isoenzymatic loci in 70 populations of spruce originating from throughout its natural geographic range. They found that 73% of the loci were polymorphic, the mean number of alleles per locus was 2.6, and the mean heterozygosity was 0.115. Other studies also confirm the high level of genetic variation in Norway spruce (GIANNINI *et al.* 1991; GÖMÖRY 1992; GONCHARENKO *et al.* 1995; MÜLLER-STARCK 1995; LEWANDOWSKI *et al.* 1997; MODRZYŃSKI and PRUS-GŁOWACKI 1998; GEBUREK 1998; KANNENBERG and GROSS 1999; SCHUBERT *et al.* 2001; LEWANDOWSKI and BURCZYK 2002). The level of genetic variation in Norway spruce is similar to that observed in other conifer tree species with a wide geographic range of distribution and for which a large number of isoenzymatic loci have been analysed (LEDIG 1986; MÜLLER-STARCK *et al.* 1992).

The distribution of genetic variation in spruce populations is consistent with patterns observed in most coniferous tree species (LOVELLES and HAMRICK 1984). As much as 95% of total variation of the species is observed within populations, whereas the remaining 5% of the variation occurs among populations (LAGERCRANTZ and RYMAN 1990). There are several factors that account for the low genetic variation among populations of most coniferous tree species, including spruce. It appears that the most important are: an extensive and continuous geographic range of distribution, a high population density, long-distance pollen dispersal, and predominant out-crossing (HAMRICK *et al.* 1979).

The low level of genetic variation in Norway spruce is reflected in low values of NEI's genetic distance (D) between populations. LAGERCRANTZ and RYMAN (1990) found that genetic distances between 70 populations never exceeded 0.04. The low level of genetic variation in Norway spruce is consistent with other studies throughout Europe (GIANNINI *et al.* 1991; GONCHARENKO *et al.* 1995; MÜLLER-STARCK 1995; GEBUREK 1999; FINKELDEY 1995; LEWANDOWSKI and BURCZYK 2002). Generally, in central European populations of Norway spruce, the level of isoenzymatic variation is lower, which may have arisen from a loss of genetic variation as a result of a radical decrease in population sizes in Carpathian refugia during the last glaciation (LAGERCRANTZ and RYMAN 1990). According to some authors, the present distribution of isoenzymatic variation of Norway spruce in Europe reflects events associated with dispersal of this species from refugia after the last glaciation (LAGERCRANTZ and RYMAN 1990; GIANNINI *et al.* 1991; MÜLLER-STARCK 1995; MODRZYŃSKI and PRUS-GŁOWACKI 1998; KANNENBERG and GROSS 1999).

Theoretical considerations suggest that the majority of molecular polymorphisms are selectively neutral and have variation patterns that are due only to mutation rate, genetic drift, and migration (LEWONTIN 1974; NEI 1975; AYALA 1976). However, BERGMANN (1978) found similar clinal variation patterns at the Aph-B (acid phosphatase) locus along different geographical

transects. He concluded that natural selection resulted in geographic variation at this locus and that one or several temperature variables function as a predominant selective agent.

At present, human activity may also significantly decrease the level of genetic variation in populations of forest trees. Comparing Norway spruce populations in Slovakia arising from natural regeneration with planted, artificial populations, GÖMÖRY (1992) found significantly lower levels of isoenzymatic variation in the artificial populations, which may have resulted from genetic drift caused by an insufficient number of maternal trees in afforestation.

9.2.4. Genetic structure and mating system

Studies of genetic structure are crucial for understanding the genetic processes taking place within populations. The mating system, which determines the methods of genetic information transfer from the parental generation to offspring, is an important factor conditioning the genetic structure of the population (STERN and ROCHE 1974; CLEGG 1980). Forest tree species vary considerably in modes of reproduction. Coniferous species are wind-pollinated with a high level of cross-fertilization. In addition, conifer pollen and seeds are adapted to dispersal by wind, even over large distances.

Norway spruce and Scots pine (*Pinus sylvestris*) were the first species for which the level of self-fertilization was assessed. On the basis of an analysis of alleles unique for a given population, MÜLLER (1977) and LUNDKVIST (1979) estimated the level of self-fertilization in seeds produced by individual trees. Populations from different regions had similar levels of self-fertilization. In a German population, the mean level of self-fertilization was 12%, ranging from 7% to 18% (MÜLLER 1977). In Sweden self-fertilization ranged from 0% to 26% for individual trees and averaged 11% (LUNDKVIST 1979).

Development of new statistical methods in the early 1980s enabled more refined analyses, making it possible to simultaneously analyse many loci and not necessarily unique alleles (SHAW *et al.* 1981; RITLAND and EL-KASSABY 1985). MUONA *et al.* (1990) compared the mating systems of two contrasting natural populations from Finland and the Slovakian Tatras. Those authors reported relatively low values of outcrossing ($t = 0.83$ and $t = 0.74$), representing self-fertilization of about 12 percent in the studied populations. Relatively high values of self-fertilization can be explained by a reduction in effective population size, owing to poor or irregular flowering or through collecting cones from the lower portions of the tree crown, which exhibit a greater frequency of self-pollination (SHEN *et al.* 1981, SHAW and ALLARD 1982). MORGANTE *et al.* (1991) reported much higher rates of outcrossing in Norway spruce in a study of two nearby populations that differed in stand density (25 trees/ha vs. 315 trees/ha), finding identical rates of outcrossing ($t = 0.96$). Increasing population density is typically associated with increasing outcrossing

rates in coniferous forest trees (FARRIS and MITTON 1984; KNOWLES *et al.* 1987; SHEA 1987). MORGANTE *et al.* (1991) suggests that the effect of population density on t values may exhibit a threshold response. On the other hand, lethal factors (KOSKI 1971) and polyembryony (SORENSEN 1982) can effectively eliminate the majority of embryos resulting from self-fertilization.

Inbreeding in populations of forest trees can cause an excess of homozygotes in the offspring (relative to the HARDY-WEINBERG equilibrium), reflected in a positive value of WRIGHT'S inbreeding coefficient (F). However, maternal trees usually exhibit negative F values. This is typical in both natural and artificial populations, e.g. in seed orchards. It seems that a negative F value for a population of maternal trees arises from natural selection, which favors heterozygotes and eliminates homozygotes (BROWN 1979; BUSH and SMOUSE 1992; YAZDANI *et al.* 1985).

The genetic quality of seeds collected in seed orchards is very important from the perspective of forest management. Research on mating systems conducted with the use of isoenzymatic loci indicates that a marked decrease in seed quality may arise from an increased frequency of self-fertilization, uneven contribution of clones to offspring production, or from fertilization with pollen from other populations (WHEELER and JECH 1992; PAKKANEN *et al.* 2000). When comparing two Norway spruce seed orchards in Sweden, PAULE *et al.* (1993) found genetic differences between the pollen pools contributing to seed formation. Although the level of self-fertilization was low (2% and 5% in the two populations), pollen originating outside the seed orchard substantially contributed to embryo formation. Although the seed orchards were relatively well isolated, non-local trees contributed as many as 10% to 17% of the paternal gametes. However, the actual level of contamination with alien pollen was likely much higher, since the methods enabled identification of only about 25% of the alien gametes. A Norway spruce seed orchard in southern Finland was analyzed in three different years in order to estimate pollen contamination rates. Allozyme-based paternity analysis revealed that the contamination rate was high at 69–71% and did not change among years (PAKKANEN *et al.* 2000). Such a high level of genetic contamination significantly decreases the breeding value of seeds produced in seed orchards.

Another issue related to seed orchards and small isolated populations is the uneven contribution of trees to seed production. This may be particularly important in seed orchards comprised of clones derived from various regions, as such clones can differ significantly in phenology. XIE and KNOWLES (1992) report that in a small, well-isolated plantation of Norway spruce in the USA, the majority of the studied trees were pollinated by a relatively small number of trees and the pollen parent contribution varied among maternal trees. FINKELDEY (1995) did not observe this phenomenon in large Norway spruce populations located within the natural range of this species in Germany. That author suggests that the high density of the populations, large amounts of pol-

len produced by most individuals, and the synchronization of pollen release and receptiveness of female cones, increase the efficiency of pollen flow, thus decreasing the possibility of uneven contributions of individual trees to the process of reproduction. The results of our studies also indicate that very efficient gene flow via pollen prevents genetic differentiation into subpopulations on a limited geographical scale.

The spatial distribution of genotypes was studied in naturally regenerated uneven-aged Norway spruce stands in Austria (GEBUREK 1998) and in the eastern Italian Alps by LEONARDI *et al.* (1996). In most cases the spatial distribution of genotypes was random. Extensive gene flow, due to long-distance dispersal of pollen and seeds, may account for the lack of observed spatial patterns. However, a few genotypes showed a significant clumped distribution over small spatial scales. It is suggested that selection processes driven by environmental variability might have caused significant clumping of these genotypes.

9.2.5. Genetic structure in polluted environments

Polluted environments may alter the genetic structure of Norway spruce populations (see reviews by GIANNINI 1990; MEJNARTOWICZ 1984; MEJNARTOWICZ and PALOWSKI 1989; MÜLLER-STARCK and SCHUBERT 2001). Environmental pollution acting through selection results in genetic impoverishment of populations. Pollution effects on the structure of forest tree populations was first documented in studies of an acid phosphatase (AcP) allozyme in a population of Scots pine. The number of AcP genes was lower in a subpopulation of resistant trees than in pollution-injured trees (MEJNARTOWICZ 1983). In Norway spruce needles the isoenzyme patterns of AcP and peroxidase (PD) reacted qualitatively and quantitatively to various stresses (HANTGE 1992). LONGAUER *et al.* (2001) and SCHROEDER and WOLF (1996) have found that injured trees of Norway spruce, European silver-fir (*Abies alba*), and European beech (*Fagus sylvatica*) exhibited higher levels of genetic diversity, consistent with earlier findings in Scots pine populations (MEJNARTOWICZ 1984).

Structural changes in the population may be caused by many factors, such as altered activity of enzymes or growth regulators under the influence of pollutants, or direct damage to DNA arising from plant exposure to ozone, sulphur dioxide, carbon dioxide, fluorides, radioactive irradiation, and other pollutants. An analysis of Norway spruce chromosomes in individuals exposed to ozone and carbon dioxide revealed numerous chromosome aberrations, bridges, increased viscosity, and other chromosomal abnormalities in trees growing in a polluted compared to control environment (MÜLLER *et al.* 1994, 1995; TAUSCH *et al.* 1994). Following the Chernobyl radioactive fallout, mutations in the activity of alcohol dehydrogenase, including an inactive form of

this enzyme (the so-called zero allele) and changes in electrophoretic mobility of glutamate dehydrogenase were observed in trees of nearby Norway spruce forests (GONCHARENKO *et al.* 1991).

The numerous isoenzymatic analyses of subpopulations of trees described as sensitive or relatively resistant to environmental pollution collectively fail to provide unambiguous evidence of changes in population structure, especially if the forest stand is exposed to low levels of chronic pollution (RADDI *et al.* 1994). Most studies confirm the existence of genetic differences between populations from polluted and control areas and between subpopulations of sensitive and resistant trees (BERGMANN and SCHOLZ 1987, 1989; BERGMANN and HOSIUS 1996; MEJNARTOWICZ 1983, 1986; MEJNARTOWICZ and PALOWSKI 1989). For example, pollution stress affects genes of the pentose phosphate pathway in Norway spruce. In comparison with maternal trees, the next generation sometimes has a higher frequency of heterozygotes in loci encoding some enzymes of that pathway, e.g. in locus G-6-PDH-A, under the influence of SO₂ and NO pollution (PRUS-GŁOWACKI and GODZIK 1995). At the same time, a higher ratio of homozygotes to heterozygotes was observed in offspring of Norway spruce trees from areas strongly polluted with heavy metals (BERGMANN and HOSIUS 1996). The greater genetic variation within groups of Norway spruce trees more tolerant to environmental pollution is thought to arise from selection favoring heterozygosity and from introgression (BERGMANN and SCHOLZ 1987).

The findings of isoenzymatic analyses obtained from a very large sample of over 1500 trees from 24 plots of Norway spruce in Germany support earlier hypotheses that the interactions of environmental and anthropogenic factors produces various responses, not always with the same trends in response. As did the first studies in this field, these findings also show there are significant differences between tolerant and sensitive trees with respect to genetic structure of subpopulations (LOCHELET 1994).

9.2.6. *Effects of forest management on genetic structure*

Forest management may exert a significant influence on the genetic structure of local populations. As early as 1978, HATTEMER (1978) noted that it is necessary to maintain genetic diversity in spruce stands, monitored with the use of isoenzymatic marker genes. In forest management it is often important to preserve the forest tree population adapted to local conditions. Isoenzyme studies of a large population of Norway spruce seedlings originating from the same seed pool but grown in three different nurseries, revealed significant differences in genetic structure (KONNERT 1994). These differences result either from natural selection of seedlings under different conditions, or – more likely – from the admixture of alien seed material.

Cultivation of Norway spruce in plantations also contributes to changes in population structure. In spruce plantations, disproportionate contributions of individual male clones to pollination and seed production are observed. According to XIE and KNOWLES (1992; 1994), over 50% of seeds resulted from fertilization with pollen of only 23% of male clones, and the level of self-fertilization was very high, approaching 9%. SKRØPPA and LINDGREN (1994) suggest that such large interclonal differences in paternity of Norway spruce attest to the existence of selection as early as the pollen stage. Those authors found altered segregation of paternal gametes in over 50% of the studied matings from pollen mixes, but not for maternal gametes, which may be due to post-zygotic viability selection, selective fertilization, or gametophytic incompatibility. GREGORIUS (1991) reports the theoretical considerations arising from preferences during fertilization in trees with the use of isoenzymatic marker genes as examples.

Genetic concerns have been raised regarding the vegetative propagation of Norway spruce by cuttings. Although a popular method, particularly in Scandinavia, it may lead to a higher level of inbreeding in the population. SKOV and WELLENDORF (1994) found that vegetative propagation did not decrease the genetic diversity of 10-year-old Norway spruce clones compared with the maternal population, but in two of 13 studied loci, they observed changes in allele frequency and an increase in the inbreeding coefficient from 0 in the maternal population to +0.21 among clones. Norway spruce stands created by planting or sowing have a lower heterozygosity than naturally regenerated stands, and are separated from natural populations by a large genetic distance (GÖMÖRY 1992). This may be one reason for their low resistance to fungal pathogens and insect pests and other abiotic factors. These findings attest to the importance of forest management practices aimed at natural regeneration of spruce stands.

9.2.7. Identification of populations by means of enzymatic methods

One of the first objectives of the application of isoenzymatic markers in forest tree genetics was an attempt to find characteristic genetic markers for different populations of Norway spruce (BERGMANN 1971). The genetic structure of populations of Norway spruce from some regions is characterized by the presence of rare alleles. For example, such alleles make it possible to distinguish Norway spruce trees from the Bavarian Forest and populations from some areas of north-eastern Poland, as well as to distinguish late bud-burst among spruce populations from the western and eastern Alps (GIANNINI *et al.* 1991; KONNERT and FRANKE 1991; ROTHE 1990). Some relict montane populations from the Bavarian Alps are characterized by the specific allele APH, which indicates that they are autochthonous (RUETZ and BERGMANN 1989). Isoenzymatic analysis of spruce stands in the Black Forest did not reveal signif-

icant differences in genetic distance between stands, irrespective of altitude and geographic distance between them. Thus, it can be concluded that most, if not all, spruce stands in this region – important with regard to the history of Norway spruce in central Europe – originate from the same center of natural distribution (KONNERT and FRANKE 1991).

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10. MYCORRHIZA

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10.1. THE MYCORRHIZAL STATUS OF NORWAY SPRUCE

10.1.1. Introduction

Plants come into contact with the soil environment through the rhizosphere, a complex interface between the root surface and soil. Specialized rhizosphere fungi colonize plant roots and form symbiotic structures termed 'mycorrhiza'. In the mycorrhizal symbiosis, the root and fungus together constitute a mutualism that controls the metabolism of both plant and fungus. There are different types of mycorrhiza, distinguished primarily by the morphology of the contact zone between the partners. The roots of many important forest trees such as spruce, pine, fir, and larch naturally form obligate fungal associations termed ectomycorrhiza (ECM). In this type of interaction, hyphae extending from a mycelial layer cover the surface of fine roots (called the mantle or sheath) and penetrate between root cells and form characteristic structures (called the HARTIG net) in the cortex. When not in contact with the mycelium, the root systems of many ectomycorrhizal tree species, but particularly those of pine and spruce, while functional, perform poorly in terms of total length growth, branching pattern, and ability to exploit the soil in which they develop. It is likely that these tree species co-evolved with their fungal partners and in so doing developed the strategy whereby carbon is allocated to fungal rather than root structures to facilitate nutrient absorption.

Norway spruce was among the first mycorrhizal plant species discovered by ALBERT BERNHARD FRANK, plant physiologist and forester, who embarked on his important research because the German State Forestry Department wished to find out whether the production of truffles could be increased. His paper in 1885 was the first general account of mycorrhiza. FRANK recognized that mycorrhizal colonization was widespread among several tree species, including Norway spruce. He also showed (1894) that the mycorrhizal symbiosis was beneficial for fungi and trees and increased the growth of the host plant. In the following years, the ectomycorrhizal relationship of Norway spruce was

the subject of detailed morphological and anatomical studies by STAHL (1900), YACHEVSKI (1933), and KELLEY (1950). Important studies on the ectomycorrhiza of Norway spruce were conducted by a group of Swedish researchers under the leadership of MELIN (MELIN 1922, 1923, 1924, 1925; LINDQUIST 1939; MODESS 1939, 1941; LIHNEL 1942; ROMELL 1938, 1939; BJÖRKMAN 1942, 1949, 1956). DOMINIK (1961) wrote the first comprehensive study of Norway spruce mycorrhiza.

10.1.2. Structure and development of Norway spruce ectomycorrhizal roots

The depth of the root system of Norway spruce is typically shallow, with several lateral roots and no taproot. On rocky sites, the roots may spread widely, twining over rocks. In bogs, Norway spruce tends to form plate-like roots (KÖSTLER *et al.* 1968). In Finland, a 140-year-old Norway spruce forest in a *Vaccinium-Myrtillus* vegetation type had a root zone extending only 30 cm into mineral soil (KUBIN 1977). SCHMID *et al.* (2000) studied the root distribution of Norway spruce in pure stands and in mixtures with European beech by means of the trench profile wall technique in two sites of contrasting bedrock types in Austria. In both sites, spruce roots were found at the maximum excavation depth of 1 m in the monospecific stands. The roots showed their maximum density in the humus and the top mineral soil layers. The root system of spruce was markedly shallower in the mixed than in the monospecific stands. This finding was even more pronounced in poorly aerated soils on Flysch-sediments than in well-aerated podzolic soils. Like all ectomycorrhizal trees, Norway spruce has a heterorhizic root system that is differentiated into long roots of potentially indefinite growth and short roots of restricted growth. Under natural conditions, short roots are converted into mycorrhizas by fungal colonization, whereas the long roots are not colonized or incompletely colonized, with the apex usually free of a fungal mycelium. Short roots, which fail to become colonized by a mycorrhizal fungus are aborted soon after emergence from the long root. As a result, virtually all of the short roots on the long roots of Norway spruce from natural forest stands are mycorrhizal (Fig. 10.1)

The mycorrhizal colonization of Norway spruce, as in other conifers, originates in the mycorrhizal infection zone (MIZ), i.e. a distinct section of a short root (MARKS and FOSTER 1973). Proximally, this zone is limited by the senescence of the cortical cells and competition with other fungi. The colonization process of short roots begins with the stimulation of the fungal growth in the presence of certain root metabolites. This effect is similar to MELIN'S (1963) M-factor effect and pertains only to ectomycorrhizal fungi. None of the common soil parasites and saprophytes, *Heterobasidium annosum*, *Trichoderma viride*, *Mycelium radialis atrovirens*, three *Penicilium* sp. and a *Mortierella* sp. showed any sign of growth stimulation on or around the roots in the *in vitro* experiments. The growth stimulation is discernible at distances of only a few mil-

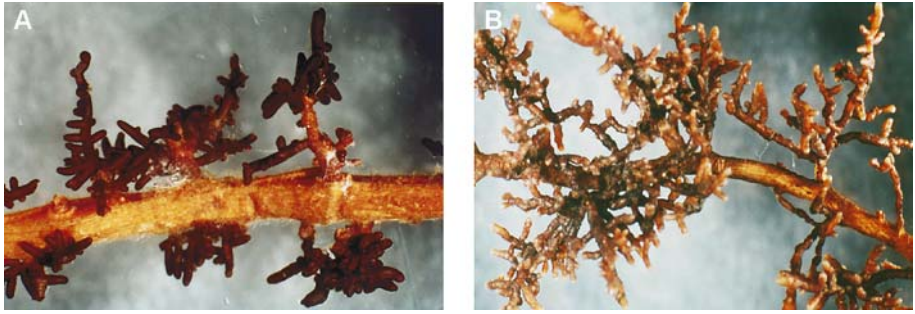


Figure 10.1. Mycorrhizas of an irregularly shaped pyramidal system of Norway spruce roots from a natural spruce forest (A) and forest nursery (B)
(Photo: B. KIELISZEWSKA-ROKICKA, M. RUDAWSKA)

limeters away from the root and is caused, in part, by factors other than the supply of photosynthetic carbohydrates. NYLUND and UNESTAM (1982) described the process of the establishment of the HARTIG net and the hyphal mantle during primary infection based on a model fungal species *Piloderma croceum* ERIKSS. et HJORTST. (= *Corticium bicolor* PECK), a common mycorrhizal symbiont of Norway spruce. The formation of a loose hyphal weft in the form of an envelope on the root is a prerequisite for fungal penetration of the host. According to NYLUND and UNESTAM (1982), the hyphal envelope is not identical to the normal mantle; it always consists of free, sparsely branched hyphae, which are never closely attached to the root surface. Single hyphae, originating from this envelope, then penetrate the short root surfaces with the exception of the apical meristem and differentiation zone. At the time of penetration, no morphological changes in the host tissue or cells are observed, as compared with uninfected portions of the root or non-inoculated roots. Single hyphae penetrate into the mature cortex of the root, evidently by mechanical action, first forming a compressed hypha, which is then “inflated”, possibly osmotically, so that the cortical walls separate along the middle lamellae. No signs of enzymatic degradation of host wall structures are discerned in the first steps of ectomycorrhiza formation. After an initial period of hyphal penetration, the morphology of the fungus gradually changes into a densely branched and labyrinth type of growth. This change, which always first occurs within the cortex and never on the root surface, gradually spreads and a regular, highly organized fungal structure of the HARTIG net begins to enclose all cortical cells in the colonization zone. No corresponding morphological response is noticed in the host, nor is any callose formed or are hypersensitivity reactions observed. Subsequently, a true mantle is formed consisting of an inner compact region and an outer more or less loose layer, depending on the fungal species forming the ectomycorrhiza (see Fig. 10.2, 10.3).

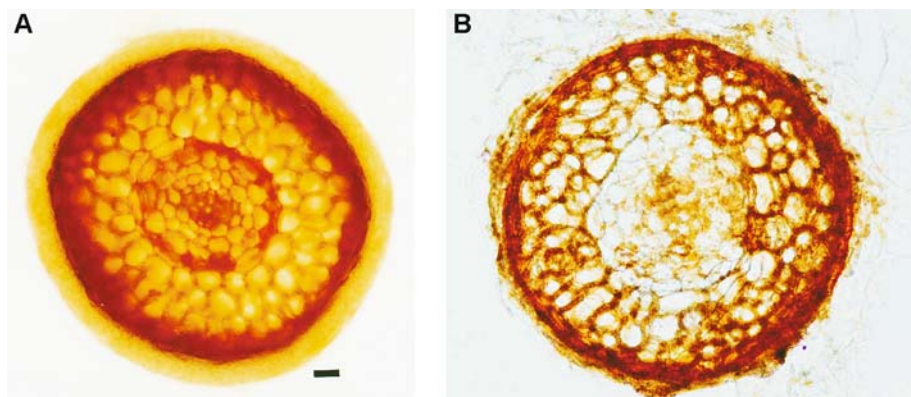


Figure 10.2. Cross section of mycorrhizal roots with two different kinds of mantle: A: smooth mantle, B: loose mantle (Photo: B. KIELISZEWSKA-ROKICKA)

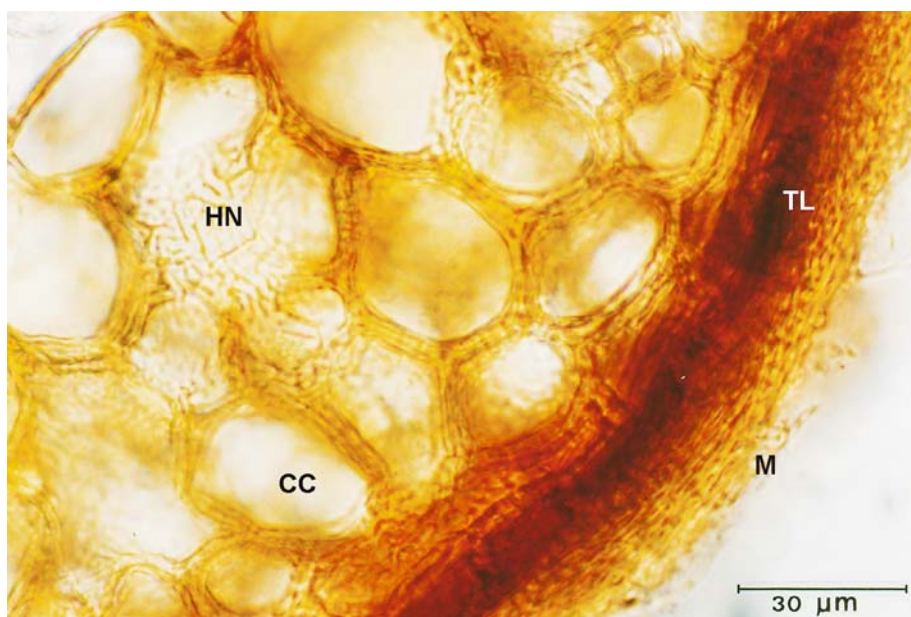


Figure 10.3. Cross section of Norway spruce mycorrhiza. Note: mantle (M), tannin layer (TL), and outer cortex cells (CC) with HARTIG net (HN) composed of a highly branched hyphal system growing transversally to the root axis in the direction of the endodermis (Photo: E. KURCZYNSKA)

The structure of the hyphal mantle in tangential, longitudinal sections has proved to be a valuable diagnostic feature for the determination of different mycorrhizal types. HAUG and OBERWINKLER (1987) distinguished two structur-

ally different types of plectenchymatous tissue in the mantle of *Picea abies* mycorrhizas. This tissue is comprised of more or less branched, interwoven, and partly blended individual hyphal elements. The "prosenchyma" represents a moderately compact tissue in which individual hyphal elements are clearly distinguishable along with large interhyphal spaces. A "synenchyma", called pseudoparenchyma by some authors, is a structure with few obvious interhyphal spaces and wide hyphae that are subdivided into short cells. The term "prosenchyma" and "synenchyma" represent the outermost points and there are many transitional and intermediate stages. Loose prosenchyma may be comprised of hyphae with distinct, large interhyphal spaces that may be filled with slimy matrix material. Large-diameter hyphae and oval to oblong-shaped hyphae are characteristic of compact prosenchyma. Subdivisions of "synenchyma" are based on the shape of the hyphal cells. In "irregular synenchyma", hyphal cells are oval or oblong and vary in size; in "puzzle synenchyma" the cells exhibit sinuate walls; and, in "polygon synenchyma" they are approximately isodiametric with fairly straight walls. HAUG and OBERWINKLER (1987) describe a total of 12 mantle types in Norway spruce mycorrhizas.

A layer of dead cells high in tannin content is typically found between the mantle and the cortex of many conifer ectomycorrhiza (Fig. 10.3). NYLUND (1981) found a tannin-cell layer in Norway spruce mycorrhiza and noted several common histochemical traits, such as the presence of both tannins and acid polysaccharides in dark-staining intracellular deposits and a lack of pits, indicating the absence of plasmodesmata joining the cortex at any stage of root development.

The most prominent feature of ectomycorrhizas is the HARTIG net (Fig. 10.3). There are differences in the Hartig net structure between the early colonization stages of mycorrhiza formation in previously uncolonized roots (NYLUND and UNESTAM 1982) and that of fully ensheathed mycorrhizas from the field (BLASIUS *et al* 1986). NYLUND and UNESTAM (1982) observed intercellular penetration by single hyphae orientated predominantly radially in relation to the root in early colonization. Subsequently, a change in the fungal morphology into labyrinthic tissue leading to HARTIG net formation takes place and forms the mantle. According to BLASIUS *et al.* (1986) in fully sheathed ectomycorrhizas, the development of the HARTIG net is initiated in the innermost layer of fully differentiated mantle and the penetration occurs in a broad lobed front by multiple hyphae, orientated transversally to the root axis.

The HARTIG net is formed by a highly branched, fingerlike or puzzle-like hyphal system (Fig. 10.2). The hyphae penetrate and grow mainly transverse to the root axis, resulting in typical indentation patterns on some tangential walls and a fountain-like separation of hyphae when growing from the radial to the tangential intercellular spaces. Septae formation within the branched hyphal system of the HARTIG net is rare. Structures, which, in sections, appear to be incomplete septae, are explained as the result of the branching pattern.

The HARTIG net connects the fungus and the root cortical cells and is important for nutrient transfer. The HARTIG net is organized to promote bi-directional transfer of ions and molecules and resembles transfer cell tissues, specialized structures, which in the plant kingdom have evolved to increase surface areas within cells of high metabolic activity and solute flux. KOTKE and OBERWINKLER (1986, 1987) described the Hartig net in mature mycorrhizas formed in vitro between *Amanita muscaria* and *Picea abies*. The tips of the fan-like branched hyphae contained dense cytoplasm with a large number of mitochondria and rough endoplasmic reticulum (rER) oriented in the direction of the hyphal growth, indicating active transfer of solutes between host and fungus. The lack of a septate structure of the hyphae results in the coenocytic, transfer cell-like structure of the HARTIG net.

Whereas the development and structure of the hyphal mantle and Hartig net are well documented in ultrastructure studies, less is known about the biochemistry of recognition and attachment in ectomycorrhiza. The effect of an auxin transport inhibitor (2,3,5-triiodobenzoic acid, TIBA) on aggregation and attachment processes during ectomycorrhiza formation between *Laccaria bicolor* S238N and *Picea abies* were investigated by RINCÓN *et al.* (2001). When the two species were growing separately, TIBA did not affect the cell wall polysaccharides or protein structures, which could play a role in the aggregation or attachment process. However, the presence of the host greatly increased the production of fungal polysaccharide fibrils, promoting hyphal aggregation and attachment to the roots. TIBA inhibited this host effect. Thus, the authors of that study hypothesized that TIBA, by preventing fungal indole-3-acetic acid (IAA) transport towards the root, inhibited the production or the efflux of host elicitors responsible for the increase of fungal polysaccharide fibril production.

Genetic markers for mycorrhiza development were identified by differential screening of a cDNA library obtained from fully developed *Picea abies*-*Amanita muscaria* mycorrhizas (NEHLS *et al.* 1999). Twenty-three cDNA clones were identified that showed altered gene expression during the ectomycorrhizal interaction. A detailed analysis was performed for two fungal cDNA clones, SC13 and SC25, exhibiting the most pronounced differences. SC13 encodes a protein of 184 amino acid residues that shows no homology with any sequence in databases. It was highly expressed in non-mycorrhizal hyphae, whereas its expression was decreased at least 50-fold in mycorrhizas and sporocarps. SC25 encodes a protein of 198 residues that shows weak sequence homology with extensin-like plant proteins. The expression of this gene was weak in non-mycorrhizal hyphae but about 30-fold higher in mycorrhizas and fruiting bodies. Because the expression of both developmentally regulated fungal genes was identical for mycorrhizas and fruiting bodies, a common mechanism for regulation of both developmental processes has been proposed.

10.1.3. Distribution of spruce mycorrhizas in the soil profile

In general, ectomycorrhizas are not uniformly distributed throughout the soil profile. More mycorrhizal root tips are observed in the upper humus layers than deeper in the soil profile. Apparently the conditions for mycorrhizal formation are more favorable in the humus than in the lower, mineral B-horizon. In the B-horizon, the proportion of mycorrhizas declines still further with increasing soil depth. Mycorrhizas were found to a depth of 1.25 m in *Picea abies* (SIREN and BERGMAN 1951), but were found up to 1.5 and 1.9 m in *Pinus sylvestris*, 2.6 m in *Fagus sylvatica*, and 3.0 m in *Quercus* sp. (WERLICH and LYR 1957; LOBANOW 1960). Several factors may be involved in the decrease of mycorrhizal abundance (percentage of root tips converted into mycorrhizas) with increasing soil depth. Oxygen content decreases and CO₂ concentration increases in deeper soil layers along with changes in microflora, the composition of organic soil components, or the nutrient status of soil and roots (MEYER 1973). HAUG *et al.* (1986) investigated Norway spruce mycorrhizas in a soil depth profile down to 1 m in 60 to 80-year-old stands in the Black Forest and near Tübingen, Germany. Up to eight different mycorrhizal morphotypes could be observed depending on depth (Fig. 10.4). Some of the morphotypes were present at all depths, whereas others were restricted to the upper layers. There were a greater variety of types in the upper 30 cm, with the number of types decreasing rapidly with increasing soil depth. However, living mycorrhizas could be found regularly at greater depths. Only black mycorrhizas of the *Cenococcum*-type could be found at depths below 1 m. FRANSSON *et al.* (2000) used a binomial model to test how different Norway spruce morphotypes are vertically distributed between the organic and mineral soil layers. The model showed that among the three most abundant morphotypes (*C. geophilum*, *Tylospora fibrilosa*, and *Piloderma* sp.) significantly more *C. geophilum* mycorrhizal root tips were associated with the organic layer than with the mineral layer. In contrast, significantly more *T. fibrilosa* mycorrhizal root tips were associated with the mineral layer than with the organic layer. In addition, all root tips colonized by *Lactarius* spp. were found in the mineral layer. *Piloderma* did not show any significant association with soil layer.

10.1.4. Above- and below-ground ectomycorrhizal community structure in a Norway spruce forest

The identification of the fungi involved in mycorrhizal symbiosis with Norway spruce is critical not only for understanding the diversity or dynamics of ectomycorrhizal populations but also for understanding the association of mycorrhizal types with certain habitats and their potential response to environmental factors. Until recently, descriptions of the species composition of ECM communities were almost exclusively based on sporocarp inventories,

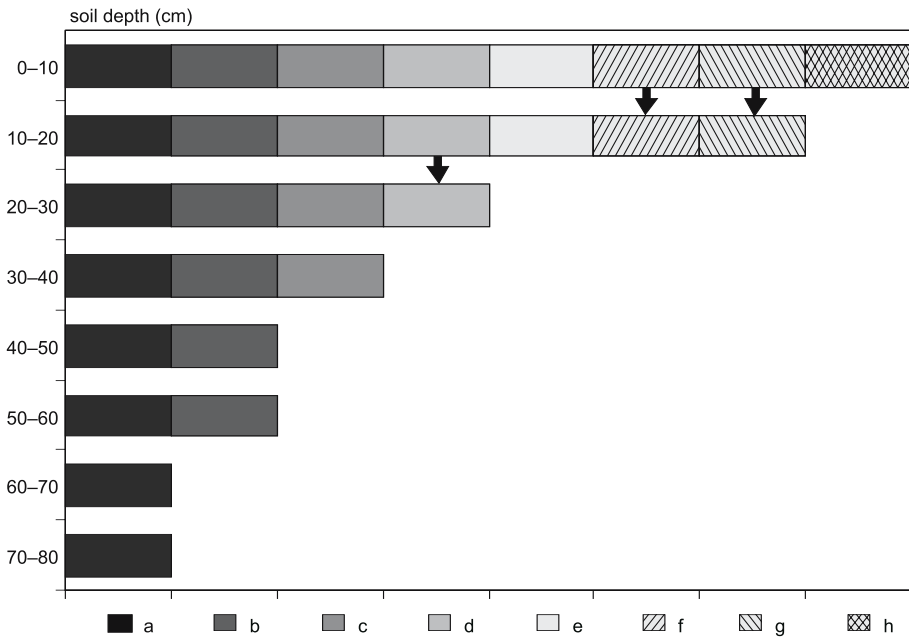


Figure 10.4. Distribution of Norway spruce mycorrhizal morphotypes in the soil profile; arrows indicate very low frequency of given morphotype: a – white-yellow; b – silvery; c – orange-yellow; d – dark brown; e – yellow-green; f – brown with a silvery layer; g – light brown; h – *Cenococcum* (after HAUG *et al.* 1986)

where it was assumed that sporocarp production reflects the relative abundance or importance of the species in the soil (VOGT *et al.* 1992). Although sporocarps indicate the presence of a species in the soil, their absence does not indicate the absence of a particular species (DAHLBERG *et al.* 1997). For example, important ECM species in the *Corticiaceae*, *Thelephoraceae*, and *Ascomycotina* all produce easily overlooked or hypogeous sporocarps or may not even produce sporocarps, i.e., *Cenococcum geophilum*. The results of recent studies in which mycobionts were identified using morphological or molecular methods have also indicated that sporocarp surveys do not accurately depict the structure of the ECM community present belowground (DANIELSON and PRUDEN 1989; TAYLOR and ALEXANDER 1990, 1991; MEHMANN *et al.* 1995; NYLUND *et al.* 1995; KÅREN and NYLUND 1996). As shown by DAHLBERG *et al.* (1997), at least half of the species of a belowground ectomycorrhizal community was comprised of species that did not produce conspicuous epigeous sporocarps.

There are few ectomycorrhizas that can be visually identified beyond all doubt by certain morphological features, such as the ectomycorrhizas of *Cenococcum geophilum*. For some species it is possible to determine an affilia-

tion with a particular genus, e.g. the ectomycorrhizas of the fungi in the genera *Tuber*, *Hebeloma*, *Laccaria*, or *Inocybe* (INGLEBY *et al.* 1990). Ectomycorrhizas of some *Lactarius* spp. can be recognized by their characteristic laticifers (AMIET and EGLI 1991).

Because positive identification of ectomycorrhizas is restricted to certain species, mycorrhiza scientists have resorted to an alternative classification into "mycorrhizal types" based on morphological features. Distinctive features for macroscopic classification are color, type of ramification and shape, structure of the mantle surface, and the presence and nature of hyphae and rhizomorphs. The color of mycorrhizas may differ greatly among fungal symbionts: black, black with yellow mycelia, dark brown to black, brown, purple or golden brown to dark brown, yellow to brown, brownish orange to yellow, olive-green to yellowish, light gray to yellowish, yellow-gray to rose-gray, gray to greenish gray, pinkish to reddish gray, gray to whitish, whitish to yellow-gray, gray to whitish (Fig. 10.5). With regard to the type of ramification, the mycorrhizal system of Norway spruce may be simple (not ramified), monopodially-pinnate, monopodially-pyramidal, and irregularly-pinnate (Fig. 10.5). The mantle surface may be smooth, smooth and silvery, smooth to reticulate, smooth to grainy, cottony, woolly, and short-spiny. On the basis of these and other macroscopic features, several ECM types can be distinguished on the roots of Norway spruce. EGLI *et al.* (1993) classified a total 22 mycorrhizal types for two Norway spruce stands in Switzerland. Microscopic investigation of mantle structures resulted in the identification of 7 additional types to give a total of 29.

The characterization and classification of ectomycorrhizas into "mycorrhizal types" based on morphological and anatomical features is sometimes problematic and unsatisfactory in many respects. Many macroscopic features, particularly color and ramification, are often inconsistent and influenced by aging and environmental factors (EGLI and KÄLIN 1991). The microscopic features of mycorrhizas, especially the mantle structure and its differentiation into distinctive layers, appear to be relatively stable and therefore better suited for distinguishing ECM types or species.

AGERER (1987–1995) in his *Colour Atlas of Ectomycorrhizae* used detailed descriptions of the anatomy of the mantle and HARTIG net in addition to tracing mycelial connections between ectomycorrhizas and sporophores to identify the mycorrhizas of Norway spruce. However, not all mycorrhizas were determined to the species level and several were named based on certain morphological characteristics, i.e.: *Piceirhiza bicolorata*, *P. oleiferans*, *P. chordata*, *P. conspicua* etc. The method of AGERER may provide robust identifications, but remains difficult to apply to species that neither form rhizomorphs nor conspicuous mycelium. In addition, the procedure is only applicable during the fruiting season of the fungi. Moreover, not all mycorrhizas exhibit species-specific diagnostic features. BRUNNER (1991) could not find any significant differences in morphology and anatomy between in vitro-synthesized ecto-



Figure. 10.5. Some distinctive mycorrhizal morphotypes from natural Norway spruce



forests (Photo: B. KIELISZEWSKA-ROKICKA, M. RUDAWSKA)

mycorrhizas of the species *Hebeloma crustuliniforme* and *H. cylindrosporum* on Norway spruce.

Morphotyping of mycorrhizas based on morphological and anatomical characterization of the ECM roots is but one approach to study the below-ground ECM composition. However, the resolution of such groupings is often low and highly dependent on the training and experience of the investigator. In many cases, too few distinct morphological characters are available, and these may change with ECM age; hence, an unambiguous species-specific identification of mycorrhizas is not possible. Molecular methods have provided excellent tools for studying the belowground community at the species level. The polymerase chain reaction-restriction fragment length polymorphism (PCR-RFLP) analysis of the internal transcribed spacer (ITS) region of the nuclear small rRNA gene has become a well-established method in this field (MEHMANN *et al.* 1995; GARDES and BRUNS 1996; JONSSON *et al.* 1999; TAYLOR and BRUNS 1999; PETER *et al.* 2001a,b). Such identifications are fully reproducible.

In the recent years the ectomycorrhizal community structure of Norway spruce has been studied in Slovenia (KRAIGHER 1999, TROŠT *et al.* 1999, VILHAR and KRAIGHER 1999), Switzerland (EGLI *et al.* 1993, MEHMANN *et al.* 1995, PETER *et al.* 2001a,b), Sweden (DALBERG *et al.* 1997, KÅREN and NYLUND 1996, ERLAND *et al.* 1999, MAHMOOD *et al.* 1999, FRANSSON *et al.* 2000, JONSSON *et al.* 2000) and Poland (KIELISZEWSKA-ROKICKA *et al.* 2003). Authors of these studies attempt to combine different methods of identification based both on aboveground sporocarp surveys as well as on belowground characterization by morphological and molecular approaches. The species richness of Norway spruce stands reported by different authors is quite variable.

KIELISZEWSKA-ROKICKA *et al.* (2003) studied ECM morphotypes in four mature forest stands of Norway spruce in different parts of Poland located in the Beskid Śląski Mts (Brenna, Salmopol), Roztocze upland (Zwierzyniec) and lowlands (Mirachowo). Three of the four sites were located within the natural geographic range of Norway spruce (Brenna, Salmopol, Zwierzyniec). The mycorrhizal colonization of fine roots of spruce at each of the study sites was nearly 100%. Thirty-nine mycorrhizal morphotypes were distinguished in total (15 to 28 per site). The highest diversity (28 morphotypes) was found in the upland forest stand located in the Roztocze National Park. For each of the forest stands, several site-specific mycorrhizal morphotypes were found. Over a period of seven years in a 40-year-old pure Norway spruce stand in Switzerland, MEHMANN *et al.* (1995) recorded fruiting bodies of 22 different fungal species. Eighteen ECM morphotypes were macroscopically classified and characterization by molecular tools resulted in a minimum of twenty-three RFLP-types. One of the most striking findings of this study is that only seven pattern-types could be linked to fungal species found as fruiting bodies in the

studied spruce stand, representing only one-third of all mapped fungal species. Different patterns of association between the morphotypes and fungal species were observed: (i) one morphotype represents one species, (ii) one morphotype represents several species, (iii) several morphotypes represent one species and (iv) a combination of (ii) and (iii).

In a 3-year sporocarp survey a total 128 species were observed at three separate sites dominated by Norway spruce in Switzerland (PETER *et al.* 2001b). The most abundant species were of the genera *Cortinarius* (*C. brunneus* as a species) and *Russula* (*R. ochroleuca* and *R. laricina*) in all three sites. Two hypogeous species were found by chance (i.e. *Chamonixia caespitosa* and *Elaphomyces granulatus*). Species that produce no or inconspicuous sporocarps were most abundant on the root system. Among them the corticiacean *Tylospora fibrilosa* was among the most abundant types, and at two sites accounted for 21–22% of all analyzed root tips. Likewise, *T. asterophora* comprised 13 % of all analyzed root tips. A striking difference was evident between the overall compositions of ECM species above- and below-ground. Using the PCR-method, only 22% (28 species) of the ECM species observed in sporocarp surveys were detected in mycorrhizas.

In addition to species composition, spatial structure is an important characteristic of mycorrhizal communities. In nature, species are often distributed neither uniformly nor randomly, but are aggregated in patches or distributed along gradients. Patchy distribution of ECM species and communities has been seen at different scales (e.g. microsite, stand, or landscape scale) in sporocarp inventories as well as in studies of ectomycorrhizas (DAHLBERG 1991, JONSSON *et al.* 2000).

10.1.5. Ectomycorrhizal fungi in Norway spruce forests

On a global scale over 5000 fungal species are presumed to form ectomycorrhizas with tree species (MOLINA *et al.* 1992). Norway spruce is one of the most important tree species in European boreal forests. One of the most widespread forest types consists of a Norway spruce overstory with an understory dominated by bilberry, *Vaccinium myrtillus*, and the ground vegetation, by the pleurocarpous feather mosses *Pleurozium schreberii* and *Hylocomium splendens* (SJÖRS 1965). In the boreal zone this forest type is among the most species rich in terms of ectomycorrhizal (ECM) fungi. In a recent compilation of habitat preferences based on the presence of sporocarps of the nearly 850 known ECM-forming macromycetes in Sweden, about 240 species were reported as being restricted to Norway spruce forests, while an additional 130 species were strongly associated with this habitat type (HALLINGBÄCK 1994). From 42 to 124 ECM species have been found in sporocarp surveys conducted in old, oligotrophic spruce forests in Fennoscandia (OHENOJA and KOISTONEN 1984; MEHUS 1986; DAHLBERG

1991; GULDEN *et al.* 1992; OHENOJA 1993; WIKLUND *et al.* 1995; BRANDRUD 1995). The number of reported species is strongly influenced by the prevailing weather as well as by the number of years covered by the study, the history of the studied forest, the design of the sporocarp survey, and the ability of the researcher to identify the sporocarps (ARNOLDS 1991). FRANSSON *et al.* (2000) in a 36-year-old stand of *Picea abies* reported that an average of 67% of the mycorrhizal fungal community consisted of root tips that were colonized by taxa producing resupinate fruiting bodies (e.g., *Amphinema*, *Piloderma*, and *Tylospora*) or by species that do not produce sporocarps (*Cenococcum*). Table 1 presents a compilation of literature findings reporting sporocarp surveys and the morphological, anatomical, and molecular identification of the fungal component of ectomycorrhizas. Changes in belowground ectomycorrhizal (ECM) community structure in response to elevated CO₂ and balanced nutrient addition were investigated in a 37-year-old *Picea abies* forest in Sweden (FRANSSON *et al.* 2001). The structure of the ECM fungal community was determined in 1997 and 2000 using a combination of morphotyping and molecular analyses. Significant effects on ECM community structure were found in response to elevated CO₂. Neither elevated CO₂ nor fertilizer application altered species richness; however, there was considerable variation among samples, which may have masked treatment effects on individual species. After 3 years, the effects of elevated CO₂ on community composition were of the same magnitude as those seen after 15 years of fertilizer application. These results show that increasing atmospheric CO₂ concentrations affect the community structure of root symbionts colonizing forest trees, potentially affecting the allocation and turnover of carbon and nutrients within forest ecosystems.

Table 1. Ectomycorrhizal fungal species that form symbiotic associations with Norway spruce (on the data by TRAPPE 1962; NYLUND and UNESTAM 1982; AGERER *et al.* 1996; AGERER 1987–1995; BRUNNER 1991; KRAIGHER *et al.* 1995; DAHLBERG *et al.* 1977; JONSSON *et al.* 2000; WIKLUND *et al.* 1995; REPÁČ 1996; KÅREN and NYLUND 1997; FRANSSON *et al.* 2000; PETER *et al.* 2001a, b)

Genus	Species
<i>Albatrellus</i>	<i>ovinus</i>
<i>Amanita</i>	<i>citrina</i> , <i>excelsa</i> , <i>fulva</i> , <i>gemmata</i> , <i>muscaria</i> , <i>pantherina</i> , <i>phalloides</i> , <i>porphyria</i> , <i>rubescens</i> , <i>spissa</i> , <i>submembranacea</i> , <i>vaginata</i>
<i>Amphinema</i>	<i>byssoides</i>
<i>Boletopsis</i>	<i>leucomelaena</i>
<i>Boletus</i>	<i>badius</i> , <i>edulis</i> , <i>rubellus</i>
<i>Calvatia</i>	<i>saccata</i>

<i>Cantharellus</i>	<i>cibarius, tubaeformis</i>
<i>Catathelasma</i>	<i>imperiale</i>
<i>Cenococcum</i>	<i>geophilum (=graniforme)</i>
<i>Chalciporus</i>	<i>piperatus</i>
<i>Chamonoxia</i>	<i>caespitosa*</i>
<i>Chroogomphus</i>	<i>helveticus ssp.tatrensis</i>
<i>Clavulina</i>	<i>cinerea, cristata, rugosa</i>
<i>Clitocybe</i>	<i>diatreta, rivulosa</i>
<i>Clitopilus</i>	<i>prunulus</i>
<i>Corticium</i>	<i>sulphureum</i>
<i>Cortinarius</i>	<i>acutus, albovariegatus, allutus, angelesianus, anomalus, anthracinus, argentatus, armeniacus, balteatus, betulinus, biformis, brunneus, callisteus, camphoratus, caninus, calochrous, cephalixum, collinitus, colus, croceus subsp. croceus, crystallinus, damascenus, decipiens, dilutus, elatior, elegantius, evernius, fasciatus, fulvoochrascens, fulvus, fuscomaculatus, gentilis, glaucopus, hercynicus, hoeftii, illuminus, incisus, infractus, junghuhnii, laniger, largus, limonius, malachius, multiformis, obtusus, olivaceofuscus, orellanoides, oricalceus, paleaceus, parvannulatus, percomis, purpurascens, rubicundulus, salor, sanguineus, saniosus, scaurus, scutulatus, sebaceus, semisanguineus, stillatitus, strobilaceus, subtortus, telamonia, tortotosus, traganusvariegatus, varicolor, varius, vibratilis</i>
<i>Dermocybe</i>	<i>cinnamomea, (=Cortinarius cinnamomeus)</i>
<i>Craterellus</i>	<i>cornucopioides</i>
<i>Elaphomyces</i>	<i>granulatus</i>
<i>Geastrum</i>	<i>coronatum, fimbriatum</i>
<i>Gomphidius</i>	<i>glutinosus, helveticus</i>
<i>Hebeloma</i>	<i>crustuliniforme, cylindrosporium, longicaudum</i>
<i>Helvella</i>	<i>infula</i>
<i>Hydnotria</i>	<i>cerebriformis*</i>
<i>Hydnum</i>	<i>repandum, rufescens</i>
<i>Hydnellum</i>	<i>peckii</i>
<i>Hygrophorus</i>	<i>agathosmus, camarophyllus, marzuolus, olivaceoalbus, piceae, pustulatus,</i>

<i>Inocybe</i>	<i>appendiculata, boltoni, eutheles, grammata, lacera, napipes, obscuroidia, sindonia, umbratica</i>
<i>Laccaria</i>	<i>laccata, montana</i>
<i>Lactarius</i>	<i>camphoratus, deliciosus, deterrimus, glyciosmus, helvus, lignyotus, necator, picinus, rufus, scrobiculatus, theiogalus</i>

<i>Leccinum</i>	<i>aurantiacum</i>
<i>Lepiota</i>	<i>rhacodes</i>
<i>Lepista</i>	<i>personata</i>
<i>Lycoperdon</i>	<i>gemmatum, pulcherrimum</i>
<i>Paxillus</i>	<i>involutus</i>
<i>Phallus</i>	<i>impudicus</i>
<i>Phellodon</i>	<i>niger</i>
<i>Phialocephala</i>	<i>fortini</i>
<i>Phlegmacium</i>	<i>aureopulverulentum, spectabile, subglaucopus</i>
<i>Piloderma</i>	<i>byssinum, croceum</i>
<i>Pisolithus</i>	<i>tinctorius</i>
<i>Polyporus</i>	<i>confluens, ovinus</i>
<i>Ramaria</i>	<i>aurea, largentii</i>
<i>Russula</i>	<i>acrifolia, azurea, betularum, consobrina, delica, decolorans, elephantina, emetica, integra, fragilis, furcata, fuscorubroides, laricina, nauseosa, nigricans, ochroleuca, olivacea, paludosa, puellaris, queletii, rhodopoda, rubra, sphagnophila, versicolor, vinosa, xerampelina</i>
<i>Sarcodon</i>	<i>imbricatum</i>
<i>Sarcosoma</i>	<i>globosum</i>
<i>Scleroderma</i>	<i>aurantium, verrucosum</i>
<i>Suillus</i>	<i>bovinus, flavidus, granulatus, luteus, piperatus</i>
<i>Thelephora</i>	<i>palmata, terrestris</i>
<i>Tylospora</i>	<i>fibrillosa</i>
<i>Tomentella</i>	<i>radiosa</i>
<i>Tricholoma</i>	<i>albobrunneum, aurantium, imbricatum, pessundatum, saponaceum, terreum, vaccinum</i>
<i>Tuber</i>	<i>puberulum</i>
<i>Tylopilus</i>	<i>felleus</i>
<i>Xerocomus</i>	<i>badius, subtomentosus</i>

* hypogeous species

10.1.6. Physiology

10.1.6.1. Uptake, translocation, and transfer of nutrients

Nutrient transport, namely absorption from the soil solution and transfer from fungus to plant, as well as carbon movement from plant to fungus are the key features of a mycorrhizal symbiosis. Several excellent reviews have examined the physiological functions of ectomycorrhizas (SMITH and READ 1997; HAMP *et al.* 1999; BUSCOT *et al.* 2000; CHALOT *et al.* 2002). Here, only certain aspects of plant-fungus interaction in ECM are described with a focus on *Picea abies* and its mycorrhizal symbionts.

Norway spruce is a dominant tree species in the boreal and temperate plant biomes and ECM fungi are adapted to mobilize the sparse and heterogeneous resources of phosphorus and especially nitrogen from the litter layer. This function is ensured by a high diversity of fungi able to form mycorrhizas with spruce (see Table 1). In forest soils, N is present either as NH_4^+ and/or NO_3^- and organic compounds such as amino acids, peptides, and proteins (CHALOT and BRUN 1998). Ectomycorrhizas very often form in soil layers where organic nitrogen compounds are present in large quantities, and there is increasing evidence that their success is dependent upon activities of their mycorrhizal fungi. Indeed, it is the fungal partner of the symbiosis that has the ability to degrade organic nitrogen and to take up and assimilate the products of hydrolytic degradation. Amino acid utilization by intact mycorrhizal systems of *Picea* is described by ALEXANDER (1983). Some mycorrhizal symbionts called 'protein fungi' (e.g. *Hebeloma crustuliniforme*) seem to be particularly efficient in degrading proteins (e.g. *Laccaria bicolor*, *L. proxima*) (FINLAY *et al.* 1992).

Inorganic nitrogen, which is usually less than 1% of the total nitrogen present in forest soils, is one of the major factors limiting tree growth in temperate forests (DICKSON 1989). Ammonium absorption is enhanced in intact spruce mycorrhizal root systems compared with non-mycorrhizal roots (RYGIEWICZ *et al.* 1984). Some mycorrhizal fungi (e.g. *Pisolithus tinctorius*) appear to be more effective in enhancing ammonium absorption by spruce seedlings than others (ELTROP and MARSHNER 1996). When supplied with NH_4 , NH_4/NO_3 or NO_3 , *Picea* grow best in NH_4 followed by NH_4/NO_3 and NO_3 (DICKSON 1989). Based on both ^{15}N labeling and mass balance calculations, hyphal ammonium acquisition in Norway spruce seedlings contributes up to 45% of total plant N uptake under N deficiency (JENTSCHKE *et al.* 2001b). In P deficient seedlings, the hyphal contribution to total plant N uptake amounted to 12%. The stimulation of nitrate absorption by mycorrhizal roots is more controversial. EK *et al.* (1994) studied the fate of ^{15}N from NO_3 and NH_4 fed to external mycelium in intact mycorrhizal systems. Glutamine has been identified as a major sink for absorbed N, with alanine, arginine, and aspartate-asparagine also important amino acids (BOTTON and CHALOT 1995).

The favorable effects of ECM fungi on plant nutrition have traditionally been attributed to the effect of the mycelium on uptake of dissolved nutrients from the soil solution (SMITH and READ 1997). This interconnected network of hyphae (or specialized aggregates, i.e. rhizomorphs) forms a supracellular compartment for the transport of nutrients from the site of nutrient capture to the sites of nutrient utilization and transfer. The contribution of extramatrical mycelium to N and P nutrition of mycorrhizal Norway spruce (*Picea abies*) was investigated by BRANDES *et al.* (1998). Seedlings either inoculated with *Paxillus involutus* or non-mycorrhizal were grown in a two-compartment sand culture system where hyphae were separated from roots by a 45 μm nylon net. The nutrient solution of the hyphal compartment contained both 1.8 mM NH_4^+ and 0.18 mM H_2PO_4^- or no N and P. The addition of N and P to the hyphal compartment markedly increased the dry weight, N and P concentration, and N and P content of mycorrhizal plants. Calculating uptake from the difference in input and output of nutrients in solution confirmed a hyphal contribution of 73% and 76% to total N and P uptake, respectively. Hyphal growth was increased at the site of nutrient solution input.

Although the total amount of P in the soil may be high, it is very immobile and generally unavailable for plant uptake because of its adsorption, precipitation, and conversion to recalcitrant organic forms. However, ECM fungi are thought to stimulate the uptake of P from poorly soluble sources in the soil. JENTCHKE *et al.* (2001a) demonstrated that *P. involutus* hyphae were able to take up and translocate significant amounts of P to their P-deficient spruce seedlings and stimulate seedling growth.

Although it is well known that ectomycorrhizas improve the mineral nutrition of forest trees, there has been little evidence that they mediate uptake of divalent cations such as Mg. Both non-mycorrhizal seedlings of Norway spruce and seedlings mycorrhizal with *Paxillus involutus* were grown in a sand culture system with two compartments separated by a 45- μm nylon mesh. Hyphae, but not roots, can penetrate this mesh. Labelling the compartment only accessible to hyphae with ^{25}Mg showed that hyphae of the ectomycorrhizal fungus *P. involutus* transported Mg to the host plant. No label was found in the non-mycorrhizal control plants. These data support the idea that ectomycorrhizas are also important for the Mg nutrition of forest trees (JENTSCHKE *et al.* 2000). The ectomycorrhizal mycelium may also play a role in K and Mg acquisition. JENTSCHKE *et al.* (2000; 2001a) have shown translocation of K and Mg through mycorrhizal hyphae and subsequent acquisition of these elements by mycorrhizal Norway spruce roots.

10.1.6.2. Carbon economy

The supply of carbohydrates to the fungus is pivotal for the functioning of ECM symbiosis. FRANK (1885) first suggested that ectomycorrhizal fungi depend upon trees for carbohydrates, which are transferred to fungi through net-

works of hyphae that encircle and penetrate receptive roots. Others later suggested that the attachment of hyphae to particular roots was a prerequisite for the fruiting of ectomycorrhizal fungi. ROMMELL (1938, 1939) showed that when sheet metal barriers severed the roots of around Norway spruce trees, no sporophores of mycorrhizal fungi appeared outside the trenched plots, a reasonable expectation if they depended upon the roots for carbon. The positive relationship between irradiance and carbohydrate concentration in the root system and the intensity of mycorrhiza development in *Picea* and *Pinus* shown by BJÖRKMAN'S (1942, 1949, 1956) experiments appear to be consistent with this prediction.

In general, the direction of carbon flow in trees is controlled by gradients between production (source organs such as needles) and consumption (sink organs such as roots, mycorrhizas) of photoassimilates. Carbon is directed to the most active sink area in a plant and the sink strength has been shown to control the rate of photoassimilate production. In mycorrhizal roots this regulatory mechanism is especially effective because the fungal partner constitutes a very strong sink. LOEWE *et al.* (2000) were able to show that mycorrhizae in Norway spruce direct assimilates toward the root, resulting in upregulation of net photosynthesis rates of the host. One of the key regulatory steps is probably that of sucrose synthesis in the leaf cytosol, mediated via fructose bis-phosphatase (FBPase) and sucrose phosphate synthase (SPS). FBPase activity is inhibited by the metabolite, fructose 2,6-bisphosphate (F26BP). For Norway spruce seedlings, it was shown that the amount of F26BP was greatly decreased in source needles of mycorrhizal plants compared to non-mycorrhizal controls (HAMPP *et al.* 1995; LOEWE *et al.* 2000). The properties of SPS also respond to mycorrhizal presence. The phosphorylation of SPS results in deactivation (i.e. lower sensitivity toward the activator, but increased sensitivity to the inhibitor). For Norway spruce seedlings, it was shown that the phosphorylation of SPS is lower in source needles of mycorrhizal than in non-mycorrhizal plants (increased activation of SPS in mycorrhizal plants) (LOEWE *et al.* 1996, 2000). The decreased levels of F26BP and increased activation of SPS indicate an increased capacity for sucrose formation as well as higher rates of photosynthesis in mycorrhizal plants. The driving force for sucrose allocation is assimilate consumption in the sinks, including mycorrhizas. Most ECM symbionts take up glucose and fructose, but do not transport sucrose. It is assumed that sucrose is delivered into the apoplast at the plant-fungus interface (HARTIG *net*) and hydrolyzed *via* the cell wall-bound invertase of their host (SALZER and HAGER 1991; NEHLS *et al.* 2001). SALZER and HAGER (1993) studied the regulation of cell wall-bound invertase in suspension-cultured cells of *Picea abies* roots. Two wall-bound isoforms of acid invertase were found, namely, a tight and an ionically bound form. The fructose concentration and the pH in the cell wall are important parameters regulating invertase activity. Both invertase isoforms were inhibited by fructose, and not by glucose

(SALZER and HAGER 1993). A notable property of the wall-bound invertases in Norway spruce cells is their narrow pH optimum at 4.5 with a significant decrease in activity between pH 4.5 and 6 (SCHAEFFER *et al.* 1995). The resulting hexoses are then taken up by fungal cells as well as by plant root cells (NEHLS *et al.* 2000). A prerequisite for the rapid uptake of monosaccharides is a membrane transport system. To date only one hexose transporter (AmMst1) has been identified from the ectomycorrhizal fungus *Amanita muscaria*, a common ECM symbiont of Norway spruce (NEHLS *et al.* 1998). The expression of this fungal monosaccharide transporter gene increases significantly in Norway spruce mycorrhizas. In contrast to the fungal partner, monosaccharide transport in Norway spruce root cells does not increase upon mycorrhizal development (NEHLS *et al.* 2000). The transcript level of the fungal monosaccharide transporter gene is much higher than that encoding the *P. abies* hexose transporter. Thus, the fungus represents the major carbohydrate sink in mycorrhizal fine roots. It can be assumed that the plant does not compete for hexose import at the plant-fungus interface, and that fungal activity determines the sink strength for carbohydrates in mycorrhizas (for reviews see also SMITH and READ 1997; HAMPP *et al.* 1999; CHALOT *et al.* 2002). Trehalose, a non-reducing disaccharide made up of glucose, was the principal sugar formed in excised mycorrhizas of Norway spruce trees (NIEDERER *et al.* 1989). Its content increased concurrently with the degree of fungal colonization, and decreased upon inorganic P fertilization and light deprivation, which also resulted in a decrease in mycorrhiza. Thus, trehalose can be considered a marker for the degree of mycorrhization of fine roots (similar to ergosterol or chitin). This sugar showed marked seasonal patterns, reaching its highest levels during the winter. Upon exposure of excised Norway spruce mycorrhizas to frost or desiccation, the content of trehalose roughly doubled. Therefore, NIEDERER *et al.* (1992) speculate that this sugar could play an important role as a mycorrhizal protectant against stress, particularly desiccation stress resulting from frost.

10.1.7. Ectomycorrhiza formation in response to nitrogen deposition

Increasing atmospheric deposition of inorganic nitrogen originating from industrial and agricultural N emissions has large impacts on mycorrhizal relationships in many regions. WALENDA and KOTTKE (1998) review the relationship between nitrogen deposition and ectomycorrhizas, including studies of Norway spruce seedlings and mature forest stands. Long-term N deposition studies indicate a prominent effect upon sporocarp formation. A rapid and marked decrease in the diversity and the production of ECM sporocarps of most species was observed in nitrogen-supplemented plots of a mature Norway spruce stand in Gårdsjön, Sweden (BRANDRUD 1995). Some species respond positively to increased N availability, whereas others decrease

in abundance and even disappear. Species of the genera *Cortinarius* and *Russula* exhibited declines in fruiting bodies, yield, and diversity (BRANDRUD 1995). In contrast, *Lactarius* species, especially *L. rufus* and *L. necator* as well as *Cantharellus tubaeformis* and *Paxillus involutus* exhibited increased fruiting-body formation after N fertilization (BRANDRUD 1995; BRANDRUD and TIMMERMAN 1998).

The question of whether the observed decrease in ectomycorrhizal sporocarps at higher N levels reflects a reduction of these fungal taxa in the soil can only be answered by investigating species diversity and abundance at the root level in terms of mycelial biomass and number of ectomycorrhizas. Several studies of N-deposition in Norway spruce stands include belowground measures of morphotypes, number of mycorrhizal root tips, or ergosterol content in fine roots (ALEXANDER and FAIRLEY 1983; BRANDRUD 1995; KÅREN and NYLUND 1997; NILSEN *et al.* 1998). Generally, only minor changes were observed belowground in response to N addition, whereas the aboveground sporocarp formation was negatively affected.

Although fertilization substantially decreased the diversity and the production of ECM sporocarps, no effects on mycorrhizal colonization, the total number of mycorrhizas, or frequencies of four common morphotypes were evident after five years in the experiment of BRANDRUD (1995). Following fertilization of a Norway spruce forest with ammonium sulphate in southern Sweden, nitrogen deposition primarily changed the species composition of the ECM fungi, whereas the number of species was less affected than that inferred from prior sporocarp inventories (KÅREN and NYLUND 1997). Unlike many prior studies, FRANSSON *et al.* (2000) conducted studies of chronic balanced additions of liquid fertilizer in combination with irrigation in a 36-year-old stand of *P. abies*. A clear shift in community structure was evident in response to fertilization, but fertilization had no effect on the total number of morphotypes or total number of root tips colonized by mycorrhizal fungi. Several morphotypes tended to increase in abundance with fertilizer treatment (e.g. *Cenococcum geophilum*, *Tylospora fibrillosa*, *Amphinema byssoides*).

Recent advances in PCR-RFLP identification of mycorrhizas have rapidly increased our knowledge of the effects of soil fertilization on the ectomycorrhizal community structure in Norway spruce forests (KÅREN and NYLUND 1997; JONSSON *et al.* 2000; PETER *et al.* 2001a). KÅREN and NYLUND (1997) classified mycorrhizas into morphotypes and studied them using the ITS-PCR-RFLP method in a simulated N deposition experiment. Morphotype analyses indicated possible shifts in species composition. Similarly PETER *et al.* (2001a) reported significant changes in belowground ectomycorrhizal composition following nitrogen addition for two years in a subalpine Norway spruce stand. JONSSON *et al.* (2000) found that nitrogen additions of 35 kg N ha⁻¹yr⁻¹ for six years in an oligotrophic *Picea abies* forest in Sweden did not affect the species richness or diversity of belowground ECM species. However,

species richness and diversity of sporocarps of ECM species were lower in the nitrogen-treated stand.

WIKLUND *et al.* (1995) tested the effect of increased and decreased water availability together with fertilization on basidiomata production in a 30-year-old Norway spruce stand in southwestern Sweden. Nitrogen addition had an obvious negative effect. In the fourth year of treatment, all mycorrhizal species ceased to produce basidiomata. Nitrogen-free fertilization resulted in reduced numbers and dry mass production of basidiomata by about 50% compared with the control. An increase in the number of basidiomata was observed as result of irrigation. However, no fructification occurred when nutrients were added together with the water. Artificial drought increased basidiomata number and biomass production. The production of *Cortinarius* species, *Lactarius theiogalus*, and *Russula emetica* increased as a result of irrigation, whereas a decrease was observed in *Boletus edulis* that instead was favored under the drought treatment. The effects of N addition and drought on ECM symbiosis of Norway spruce were also investigated in an outdoor lysimeter study (NILSEN *et al.* 1998). In that study, drought significantly decreased mycorrhizal colonization. Of all the ECM types, only the *Cenococcum geophilum* type showed a significant change in response to drought. N treatment alone did not affect either mycorrhizal colonization or mycorrhizal types. In general, it may be concluded that increased N deposition would result in decreased basidiomata production and number of mycorrhizal species and that an altered precipitation regime would change the species composition of mycorrhizal basidiomata in Norway spruce forests.

10.1.8. The protective role of mycorrhiza against pathogens

Ectomycorrhizal fungi may increase the disease resistance of their hosts through: 1) providing a barrier to pathogen penetration of root cells, 2) using root carbohydrate exudates, thereby reducing the chemical attraction of the root surfaces, 3) supporting the growth of antagonists in the rhizosphere, and 4) producing antimicrobial compounds (ZAK 1964). Through these mechanisms conifer seedlings are protected from root decay caused by several species of fungal pathogens: *Phytophthora*, *Pythium*, *Fusarium*, *Cylindrocarpon*, and *Cylindrocladium*. Several authors showed that mycorrhizal fungi protect Norway spruce seedlings against the root pathogens *Tricholoma saponaceum* and *Hebeloma crustuliniforme* and prevent infections of *Pythium* (PERRIN and GARBAYE 1983). SAMPANGI and PERRIN (1986) found that isolates of *Laccaria laccata* protected seedlings of Norway spruce from root rot caused by *Fusarium oxysporum*. When in contact with pathogenic fungi or bacteria, plants have the capability to respond with defense reactions, e.g. the formation of antimicrobial phytoalexins, the reinforcement of plant cell walls, and the induction of certain hydrolytic enzymes (BELL 1981). In both pathogenic and po-

tential symbiotic interactions, plant responses are probably triggered by elicitors, i.e. low molecular weight substances released by the plant or the microbe or both (DARVILL and ALBERSHEIM 1984), which bind to a receptor located in the plasma membrane of the plant cell. Intracellular signaling events following the binding of the elicitor to its receptor are poorly understood. One of the most peculiar effects observed during the early phase in plant-pathogen interactions is the transient formation of active oxygen by the plant (KEPPLER *et al.* 1989). SCHWACKE and HAGER (1992) showed that cell wall components from the ectomycorrhizal fungi *Amanita muscaria* and *Hebeloma crustuliniforme* and from the Norway spruce pathogen *Heterobasidion annosum* elicited a transient release of active oxygen species (mostly H_2O_2) in cultured Norway spruce cells. Interestingly, elicitors from mycorrhizal fungi had a lower H_2O_2 -inducing activity than equal amounts of cell wall preparations from the pathogen *H. annosum*. In symbiotic interactions such defense mechanisms have to be controlled and limited to allow the association of two different organisms.

The fine roots of tree species forming ectomycorrhizas contain constitutive soluble phenolics such as p-hydroxybenzoic acid glucoside, piceatannol and its glucoside, pinosylvin and its monomethyl ether, isorhapontin, picein, catechin, and cell wall-bound phenolics such as ferulic acid (MÜNZENBERGER *et al.* 1995). There is increasing evidence that phenolics are regulators in plant-fungi interactions, although their role in ectomycorrhiza is inconsistent. Some authors report an increase in phenolic material in mycorrhizas compared with uninfected roots and suggest that this is due to the influence of the fungal symbiont. However, others report no such differences (PICHÉ *et al.* 1981). These studies were based solely on anatomical and histochemical observations where only precipitated phenolics could be recorded. However, soluble, low-molecular-weight phenolics are thought to have a greater fungicidal activity than high-molecular-weight phenolic substances such as tannins. Non-mycorrhizal fine roots of Norway spruce contain higher concentrations of both soluble and cell wall-bound phenolics than mycorrhizas formed with *Laccaria amethystea* and *Lactarius deterrimus* (MÜNZENBERGER *et al.* 1990). Because most of the identified phenolic compounds exhibit strong anti-fungal activity against mycorrhizal fungi, MÜNZENBERGER *et al.* (1990) assume that a reduction in the concentrations of soluble and cell wall-bound phenolics is a prerequisite for mycorrhizal formation. These findings confirm that none of the mechanisms underlying pathogenic plant-fungi interactions are functioning in mature ectomycorrhizas.

10.1.9. Norway spruce mycorrhizas in forest nurseries and artificial mycorrhizal inoculation

Norway spruce is one of the most important tree species used in Europe for reforestation. The young seedlings are grown for three to four years in nurseries prior to planting. ECM fungal propagules in typical nursery soils are rather limited and sometimes nurseries are deficient in natural ectomycorrhizal fungi. Surveys conducted in several bare-root nurseries in Poland revealed a distinctive mycorrhizal structure in Norway spruce seedlings that differs significantly from that of mature trees. The extent of ECM colonization of individual seedlings ranged from 0–100% with an overall mean of 50%. A total of twelve ectomycorrhizal morphotypes were distinguished, with one to eight ECM types colonizing an individual spruce seedling (Fig. 10.6), depending on the seedling age, soil pH and fertility, and cultural conditions. By comparison, three ECM species were found on roots of *Picea abies* cuttings grown in a Bavarian nursery (WEISS and AGERER 1988).

In most bare-root nurseries, the procedures used to produce seedlings create environmental conditions that increase the level of root pathogens. As a result, the production of tree seedlings is often seriously affected by the proliferation of root pathogens (e.g. *Fusarium oxysporum*, *F. moniliforme*, *Pythium* spp.). Fungicides or fumigants are often used to reduce the populations of these microorganisms in the soil. Consequently, the natural mycorrhizal inoculum is drastically reduced or eliminated, resulting in a deficiency of mycorrhizas on seedling roots and reduced seedling development. Natural re-inoculation of seedlings grown in fumigated soil can occur from air-borne spores, but is often inconsistent. The use of introduced ectomycorrhizal fungi has been frequently suggested to ensure adequate ectomycorrhizas on tree seedlings grown in fumigated soils. As found by MARX *et al.* (1984), introduced ectomycorrhizal fungi can form mycorrhizas only after soil fumigation, because saprotrophic organisms and naturally-occurring ectomycorrhizal fungi may serve as antagonists to the introduced mycorrhizal fungi. Soil fumigation eliminated or reduced *Rhizoctonia solani*, *Pythium* sp., and probably *Fusarium oxysporum* propagules and improved Norway spruce seedling performance, particularly in the second year following treatment when height growth was improved by more than 50% (LE TACON *et al.* 1986). Nursery tests reveal that bare-root Norway spruce seedlings may be successfully inoculated under normal nursery conditions with the ectomycorrhizal fungus, *Hebeloma cylindrosporum*. Two years after inoculation, *H. cylindrosporum* increased Norway spruce growth by 40% in comparison with seedlings that were grown in fumigated soil and were mycorrhizal with the naturally occurring mycorrhizal fungus, *Thelephora terrestris*. Both fumigation and artificial inoculation increased Norway spruce seedling growth by 110%. *H. cylindrosporum* mycorrhizas persisted for two years and inhibited the recolonization of the roots by *T. terrestris*.

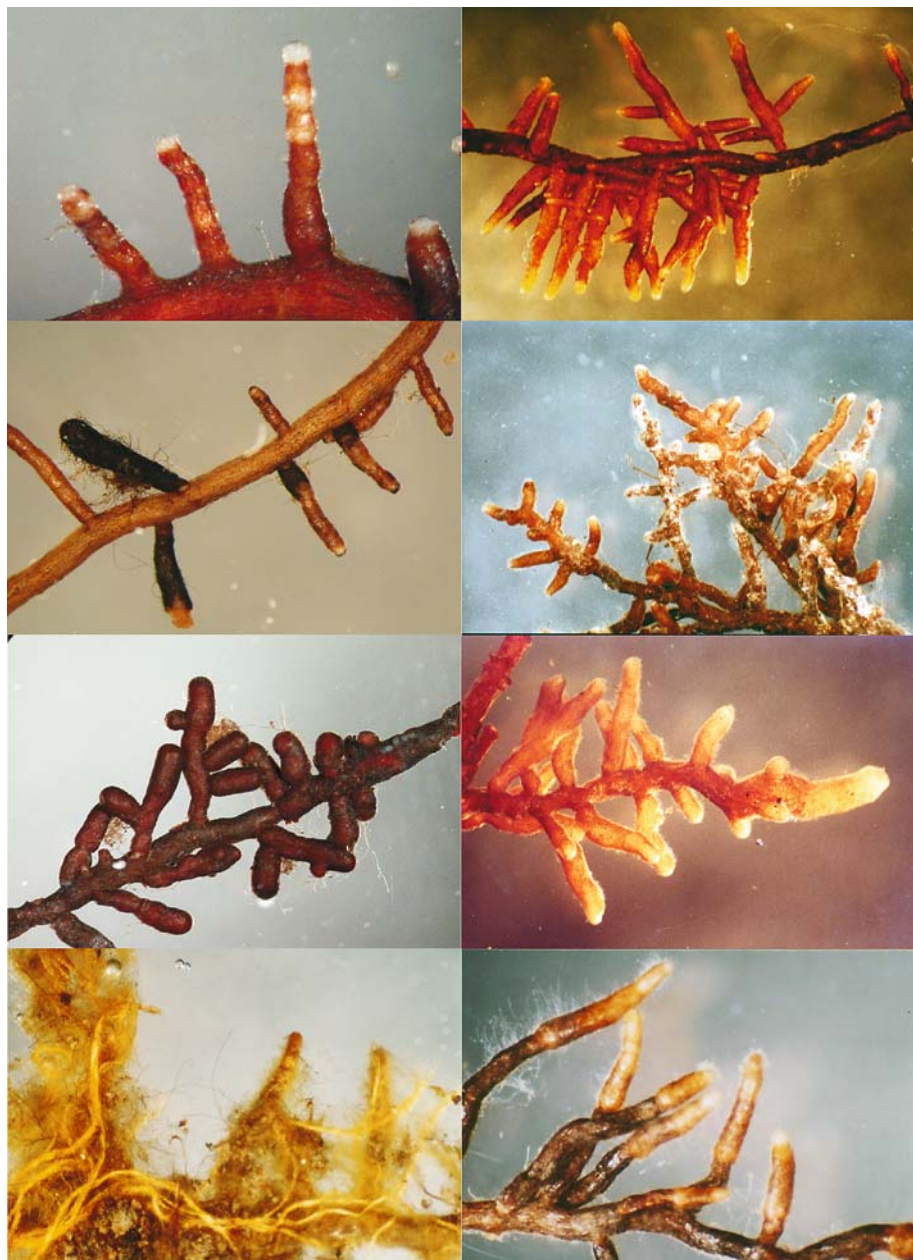


Figure 10.6. Characteristic mycorrhizal morphotypes of Norway spruce seedlings from forest tree nurseries (Photo: T. LESKI, M. RUDAWSKA)

As shown by LE TACON *et al.* (1986), Norway spruce seedling growth in the nursery can be stimulated by artificial inoculation with selected mycorrhizal fungi, even in soils of high fertility. Recently VODNIK and GOGALA (1997) and REPÁČ (1996) demonstrated that the mycorrhizal symbiosis of Norway spruce seedlings is enhanced by the application of fungal inoculum (forest litter, vegetative fungal inoculum) to the growth substrate at the time of sowing or planting. These findings should encourage researchers and foresters to further investigate the benefits of mycorrhizal inoculation of Norway spruce planting stock and the management of mycorrhizal associations in forest nurseries. Increased nutrient uptake is considered the most important symbiotic benefit for trees. However, in forest nurseries, biological control against soil-borne pathogens may be more important than the nutritional benefit of mycorrhizas. The greatest advantage of mycorrhizas for planting stock is probably the positive effect of fungi in the first and possibly second year after transplanting.

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10.2. ECTOMYCORRHIZAL SYMBIOSIS AND ENVIRONMENTAL STRESSES

The development, maintenance, and function of ectomycorrhizas are regulated, at least in part, by the availability of carbohydrates. The cyclic development and senescence of ectomycorrhizas are correlated with shoot growth rhythms that regulate the translocation of carbohydrates from shoots to roots (PANKOW *et al.* 1989). Mycorrhizal communities are affected by environmental stresses. Generally, stress is defined as an environmental factor that elicits potentially injurious chemical or physical changes in an organism (LEVITT 1980), regardless of whether the change is beneficial or detrimental to the organism (ANDERSEN and RYGIEWICZ 1991). In the case of mycorrhiza, any factor that can alter carbohydrate allocation to roots has the potential to influence the symbiosis (NYLUND 1988).

10.2.1. Vitality of mycorrhizas – criteria

The vitality of ectomycorrhizas of trees depends on natural factors such as soil properties (e.g. texture, chemical composition, moisture, availability of min-

eral nutrients), climate, and on the fungal species and strain (KOTTKE *et al.* 1993). The longevity of ectomycorrhizas of boreal and temperate forests is generally several months (HARLEY and SMITH 1983); however, environmental stresses may accelerate the aging and turnover rate of the mycorrhizal fine roots (e.g. KOTTKE *et al.* 1993). Although turgor has been a traditional criterion of mycorrhizal vitality, detached and dead ectomycorrhizas have been shown to remain turgid even after 8 months (FERRIER and ALEXANDER 1985). Anatomical and physiological criteria may provide reliable information on the vitality of ectomycorrhizas. In this regard, vital stains such as fluorescein diacetate (FDA) may be useful. FDA is a fluorogenic substrate, which is taken up by diffusion through intact membranes and is non-fluorescent until it is hydrolyzed by esterases to form fluorescein. Fluorescein accumulates in intact, living cells causing both fungal and root cells to fluoresce (e.g. SÖDERSTRÖM 1977; RITTER *et al.* 1989). Aging of Norway spruce mycorrhizas starts at the external surface of the fungal mantle and proceeds towards the stele of the mycorrhizal root tip (KOTTKE *et al.* 1993). The fungal mantle peels off and gradually disappears. The mantle-free mycorrhizas may still possess a living, functional Hartig net (AL ABRAS *et al.* 1988). Such mycorrhizas have been observed in mature forest stands (MEYER 1973), forest nurseries (AL ABRAS *et al.* 1988), and in laboratory cultures (EL FARES 1974). The mantle-free mycorrhizas appear dark brown in color, because the external cortical cells produce phenolic compounds that protect against pathogenic microorganisms (AL ABRAS *et al.* 1988).

The physiological criteria of mycorrhizal vitality include respiratory activity (AL ABRAS *et al.* 1988), ATP-ase activity in the HARTIG net (LEI and DEXHEIMER 1988), the concentration of ATP (PANKOW *et al.* 1989), and the concentrations of substances specific for the mycobiont, such as trehalose (NIEDERER *et al.* 1988) or ergosterol (SALMANOWICZ and NYLUND 1988). The most suitable chemical measure of the amount of living fungal biomass in mycorrhizal root tips or the biomass of the extramatrical mycelium in the soil is the quantification of ergosterol, the principal sterol of membranes of living fungal cells of many *Basidiomycotina* and *Ascomycotina* (LÖSEL 1988; WEETE 1989). The level of ergosterol in biological material is positively correlated with the concentration of ATP and is a reliable indicator of the biomass of living fungal membranes of a metabolically active mycelium (RUZICKA *et al.* 2000).

10.2.2. Influence of natural stresses

10.2.2.1. Water stress

Water availability is often the main factor limiting plant growth. Even in temperate, relatively wet regions, summertime water deficits can reduce plant bio-

mass accumulation. Water stress may influence the growth of root systems and their ectomycorrhizas.

It appears that moderate drought stimulates mycorrhiza formation and maintenance; but at low soil water potentials, the mycorrhizal fine roots may die. Due to the fact that ectomycorrhizas develop on the first-order fine roots of Norway spruce, a high branching density of the very finest roots promotes the formation of the mycorrhizal symbiosis. Naturally-occurring water stress in summer resulted in decreased numbers of mycorrhizas in the humus layer (0–5 cm) in a mature Norway spruce stand when compared to a similar, regularly watered stand (FEIL *et al.* 1988). However, the branching density of the fine roots increased in the drought treatment, and after rewetting, the number of mycorrhizas increased rapidly on the non-irrigated plot. Similar results were observed in a water-stress experiment with pot-cultures (FEIL *et al.* 1988).

A low water potential in the root environment reduces ion uptake and transport to the shoot, decreases carbon assimilation rate via stomatal closure, reduces the allocation of carbohydrates from shoot to root, and has a negative effect on mycorrhizal colonization. Drought reduced mycorrhizal colonization in a Norway spruce stand (WIKLUND *et al.* 1995). Similarly, in an outdoor pot study with 6-year-old cuttings of Norway spruce, drought (below -1.5 MPa) significantly decreased mycorrhizal colonization and altered the mycorrhizal morphotypes (NILSEN *et al.* 1998). Field observations and experimental data indicated that the black mycorrhizas, developed by the fungus *Cenococcum geophilum*, were less sensitive to water stress than other ectomycorrhizal fungi (MEYER 1987b; LO BUGLIO 1999).

Trees have developed a number of defense mechanisms that regulate water flux during drought, including stomatal closure, osmotic regulation, reduced leaf growth, defoliation, and xylem embolism. One whole-plant mechanism is the accelerated growth and turnover of ectomycorrhizal fine roots. Since ectomycorrhizal fungi live simultaneously in the roots and soil, they provide a link between the two environments and contribute to many water regulation mechanisms (GARBAYE 2000). Fungal hyphae can explore a considerably larger volume of soil than plant fine roots and, in effect, mine available soil water. Moreover, ectomycorrhizal fungi are involved in whole-plant osmotic regulation and enhance water-use efficiency through increased mineral uptake and transfer and by providing growth regulators such as abscisic acid (ABA) and cytokinins, that result in a reduction in the water potential gradient between the soil and plant. Mycorrhizal fungi differ in their efficiency in water-regulation mechanisms and tolerance to water deficit, depending on the properties of the fungal mycelium in soil. Two main types of mycorrhizal fungi can be distinguished. The first type consists of individual or poorly aggregated mycelial hyphae with a hydrophilic surface, absorbing water along their entire length when the soil is wet. This type of mycelium is characteristic for the black mycorrhizas developed by the fungus *Cenococcum geophilum*, common and

abundant in dry soils or during drought (PIGOTT 1982; GARBAYE 2000). The second type of mycorrhizal mycelium consists of hyphae that are hydrophobic along their whole length except for the tips. These hyphae are aggregated in strands (rhizomorphs), are densely branched in the soil, and conduct water internally from moist and nutrient-rich microsites during drought periods. This type of mycelium is characteristic of numerous fungi, including the genera *Boletus*, *Suillus*, *Paxillus*, *Scleroderma*, and *Rhizopogon* (GARBAYE 2000).

10.2.2.2. Temperature

Temperature influences the development and maintenance of ectomycorrhizas through direct effects on the mycobiont and indirectly through regulation of translocation of carbohydrates from shoot to root (HELLMERS *et al.* 1970; MARKS and FOSTER 1972). The temperature difference between above-ground and belowground plant parts significantly influences the rate of carbon translocation. Increased temperatures in the rooting zone results in increased translocation of carbon to roots and enhanced root growth, including the finest root tips which are mycorrhizal (LAWRENCE and OECHEL 1983 a,b). Temperature also influences the quantity and composition of root exudates, which are essential for the formation and maintenance of mycorrhizal symbioses (ROVIRA 1969). Under natural conditions, the development of ectomycorrhizas begins in spring when the temperature of the upper soil layer is 10–11°C; however, under some conditions root growth and mycorrhizal colonization may be observed at temperatures as low as 3 to 9°C (ORLOV 1957). Although mycorrhizal formation may occur at low temperatures, higher temperatures accelerate this process.

Species and strains of ectomycorrhizal fungi grown in pure culture have differing temperature requirements (MOSER 1958; LAIHO 1970; DENNIS 1985; CLINE *et al.* 1987). The temperature minimum is between 1 and 5°C (LAIHO 1970) and even 0–1°C (TIBBETT *et al.* 1998). Temperature maxima are about 30°C (LAIHO 1970), although for some fungal isolates of *Thelephora terrestris* and *Pisolithus tinctorius*, the maximum temperature was higher (32–35°C, CLINE *et al.* 1987). Temperatures ranging between 15 to 25°C promoted the optimal growth of pure cultures, depending on species (e.g. LAIHO 1970; CLINE *et al.* 1987). The temperature requirements seem to depend on the species and also on the geographic origin of the fungal strains. Ecotypes of some fungal species (*Paxillus involutus*, *Suillus variegatus*, *S. plorans*) isolated from mountains exhibited growth optima at lower temperatures than strains originating from low elevations (MOSER 1958). The temperature minima of strains of *P. involutus* and *S. variegatus* isolated from a valley were between 2 and 8°C, whereas strains isolated from mountains exhibited lower temperature between –2 and –4°C. Moreover, the strains originating from mountains were able to survive for 2 months at –11°C (MOSER 1958). A comparison of geographically distinct isolates of some ectomycorrhizal species showed that

strains of *Thelephora terrestris* and *Cenococcum graniformae* originating from northern stands were better adapted to lower temperatures than strains from southern stands (CLINE *et al.* 1987).

Temperature also governs the development and maintenance of ectomycorrhizas of spruce. In laboratory conditions, the mycorrhizal fungus *Thelephora terrestris* developed ectomycorrhizas with seedlings of white spruce (*Picea glauca*) under three temperature ranges: 5–8°C, 15–17°C and 25–29°C, whereas *Hebeloma crustuliniforme* formed mycorrhizas only between 15 and 17°C (HUSTED and LAVENDER 1989). The extramatrical mycelium of *T. terrestris* grown *in vitro* culture with seedlings of Sitka spruce (*Picea sitchensis*) was able to survive the winter at a minimum temperature about 1°C, but the extramatrical mycelium of *Laccaria proxima* disappeared already in November at 8°C (COUTTS and NICOLL 1990). It can be assumed that temperature may similarly influence the mycorrhizal symbiosis of Norway spruce. Temperatures suitable for the development of mycorrhizal symbiosis under field conditions are not always favorable for the mycobiont grown *in vitro*. The mycelium of the ectomycorrhizal fungus *Pisolithus tinctorius* grown in axenic culture dies at a temperature of 41°C (HARLEY and SMITH 1983), yet ectomycorrhizas developed by this fungus on seedling roots were able to tolerate high soil temperatures, which on mine-heaps exceeded 60°C (SCHRAMM 1966; MARX 1977). The temperature requirements of the species and strains of ectomycorrhizal fungi should be a criterion in the selection of fungi for inoculation of seedlings appropriate for afforestation.

10.2.3. Anthropogenic stresses

Anthropogenic impacts alter ectomycorrhizal colonization and plant community structure. Various stress factors, such as acid deposition, nitrogen deposition and fertilization, heavy metals, and ozone may decrease the biomass, length, and degree of branching of tree fine roots, reduce ectomycorrhizal colonization of tree fine roots, decrease the abundance of ectomycorrhizal sporocarps, and reduce ectomycorrhizal diversity. Anthropogenic stresses are known to influence mycorrhizal symbiosis through at least three mechanisms via: 1) direct effects on ectomycorrhizal fungi and ectomycorrhizas; 2) direct effects on the uptake of mineral nutrients by roots and whole-plant nutrition; and 3) indirect effects mediated by a reduction in rates of net photosynthesis and reduced allocation of carbohydrates from shoots to roots and mycorrhizas (ANDERSEN and RYGIEWICZ 1991). Ectomycorrhizal species differ in their sensitivity to environmental pollution. Reductions in mycorrhizal diversity and altered community structure could, in turn, influence tree growth and health.

10.2.3.1. pH

Norway spruce is typically found growing in acidic soils and is thought to be adapted to low soil pH (READ 1991). However, in many regions acid deposition arising from anthropogenic air pollutants, such as SO₂ and NO_x, may result in acidic inputs that exceed the natural buffering capacity of the soils (MAZZARINO *et al.* 1983). Within 23 years (1959–1982) forested areas in Central Germany exhibited a drop in pH of the upper mineral soil from 4.2–5.0 to 3.0–4.5 (FRÖHLICH 1988). A decline in root growth and function has been observed in forest stands of Norway spruce influenced by acid deposition. The symptoms of root decline include: a reduction in secondary roots, an inhibition in fine root growth (a decrease in root diameter, length, and area) (BLASCHKE *et al.* 1985), an increased fraction of dead fine roots (MURACH 1984; LISS *et al.* 1984; BLASCHKE 1986a; MATZNER *et al.* 1986), an inhibition in mycorrhizal symbiosis (BLASCHKE 1986a, b; 1990; GÖBL 1986; MEYER 1987a, b), an abnormal morphology of ectomycorrhizal root tips (BLASCHKE 1990; METZLER and OBERWINKLER 1986), and changes in the chemical composition of the fine root fraction (MURACH 1984). Anatomical studies of *Picea abies* fine roots showed cell wall degradation of the external cells of the roots, destruction of the root cap, and breakdown of meristematic cells (VOGELEI and ROTHE 1988).

Ectomycorrhizal fungi differ in their response to growth substrate acidity. Most ectomycorrhizal fungi can grow throughout the pH range from 3.5 to 5.5 (LAIHO 1970; DENNIS 1985; WILLENBORG *et al.* 1990). However, many fungal species and strains tolerate high acidity, and some prefer higher pH. For instance, strains of *Piloderma bicolor*, *Paxillus involutus*, *Pisolithus tinctorius*, *Scleroderma aurantium*, and *Suillus bovinus* grow equally well in the pH range of 2.5–5.5 (WILLENBORG *et al.* 1990) and strains of *Suillus tomentosus* showed the best growth rate at pH 2.0 (DENNIS 1985). The optimum pH for ectomycorrhizal fungi *Hebeloma crustuliniforme*, *Hygrophorus eburneus*, and *Laccaria laccata* was in the range 6–7 (DENNIS 1985).

In field conditions, a decline in production of ectomycorrhizal sporocarps and diversity with increasing soil acidification was observed among a number of Norway spruce stands (e.g. AGERER 1989; AGERER *et al.* 1998; ARNOLDS 1991). AGERER *et al.* (1998) found a decrease of *Hygrophorus pustulatus* and *Russula ochroleuca* in 16-year-old spruce stands and a reduction of *Amanita crocea*, *A. vaginata*, *Russula cyanoxantha*, and *R. olivacea* in 76-year-old stands in Germany. The ectomycorrhizal fungus, *Russula mustelina*, was selected as a biological indicator of acid deposition in montane and piedmont Norway spruce stands in central Europe (FELLNER 1989). In addition, an alteration in ectomycorrhizal morphotypes of Norway spruce was reported in response to acid deposition (e.g. GRONBACH and AGERER 1986; QIAN *et al.* 1998). The total number of ectomycorrhizal morphotypes may be reduced (ERLAND and TAYLOR 2002), but the abundance of some morphotypes, such as the black

mycorrhizas developed by the fungus *Cenococcum geophilum*, may increase or remain unaffected in acidified forest stands (MEIER *et al.* 1989).

Soil acidification can change the quantity and quality of mycorrhizal roots. The response of the symbiosis depends on the fungal species and strain as well as buffering capacity of the soil. Treating 8-year-old seedlings of Norway spruce with acid water (pH 4.0) for five growing seasons resulted in a decrease in mycorrhizal colonization of seedling roots compared to seedlings grown in soil at about pH 5.6 (BLASCHKE 1990). Reduced numbers of mycorrhizas were observed, especially in the mineral soil layer (BLASCHKE 1986b). NOWOTNY *et al.* (1998) reported that the abundance of mycorrhizal root tips remained unaffected in the humus and upper mineral soil in response to soil acidification. However, two years after soil acidification was stopped, the percentage of mycorrhizal roots in the humus decreased.

The liming of forest soils may counter the effects of soil acidification on mycorrhizal symbiosis. In Höglwald forest in southern Germany, liming of the humus layer significantly increased the pH (ROTHE 1994). JONSSON *et al.* (1999) found increased ramification in *Picea abies* roots and higher numbers of fine roots per root length after liming. Six years after liming there was a two-fold increase in the average annual amount of mycorrhizal roots in the humus. Changes in the belowground ectomycorrhizal community in spruce stands and an increase in fine root density have been observed (e.g. LETHO 1994; ANDERSSON and SÖDERSTRÖM 1995; JONSSON *et al.* 1999). ERLAND and TAYLOR (2002) reported a significant increase in the abundance of some ectomycorrhizal morphotypes of *Picea abies* (*Piceirhiza nigra*, *Amphinema byssoides*, *Tuber puberulum*) in limed forest plots. Liming increased pH from 3.3 to 4.5 and resulted in increased mass of mycorrhizal roots in the humus as well as a higher mass of living mycorrhizal roots in the upper soil layers compared to the untreated plot (NOWOTNY *et al.* 1998).

10.2.3.2. Aluminium toxicity

The mobilization of aluminium ions from Al-containing minerals (aluminosilicates) in acid forest soils can be accelerated by atmospheric inputs of sulphur and nitric acids. The toxicity of aluminium is one of main factors that can restrict root growth of forest trees in heavily acidified soils (ULRICH *et al.* 1980; HÜTTERMANN and ULRICH 1984). The upper mineral soil layers of many forest ecosystems are now in the aluminium buffer range (pH 4.2–3.8) (ULRICH and MEYER 1987). Soils in the aluminium buffer are characterized by extremely low molar (Ca + Mg + K)/Al ratios. At pH 4.0 the concentration of biologically active aluminium ions (Al^{3+} , AlOH^{2+} and $\text{Al}(\text{OH})^{2+}$) may reach concentrations that are toxic to plants (KINRAIDE and PARKER 1989). Ratios are considered critical for Norway spruce. It is likely that other monomeric and polymeric forms of aluminium are also very toxic to plants, but their activity under natural conditions is not clear (ALVA *et al.* 1986; PARKER *et al.* 1989).

Non-mycorrhizal seedlings of *Picea* spp. grown in laboratory conditions are usually more sensitive to the impact of aluminium ions than are seedlings of *Pinus* spp. (Table 1); however, the literature findings differ among studies. INGESTAD *et al.* (1985) reported a 20% reduction in biomass of *P. abies* seedlings in the presence of 1.0 mM aluminium. However, comparable growth reductions were observed at Al concentrations of 0.3 mM (ROST-SIEBERT 1983) and 0.74 mM (ABRAHAMSEN 1984). JORNS and HECHT-BUCHHOLZ (1985) noted a rapid response of spruce roots after only three days of treatment of seedlings with 0.52 mM Al. They observed brown, discolored root systems and cracks in the bark of long roots. A concentration 9.0 mM Al^{3+} was reported as lethal to roots of Norway spruce (GÖRANSSON and ELDHUSET 1991). At the same time, they observed increased vacuolization in cells of the root cap, meristems, and root cortex. An enhanced accumulation of phenolic compounds in cells of the root cap and external layers of root bark was found in declining roots of *P. abies* (HÜTTERMANN 1985). In later stages, the damage to the meristematic cells may be followed by the induction of new, lateral meristems and, finally, characteristic forked forms of the fine roots (METZLER and OBERWINKLER 1986).

Aluminium ions may also injure the mycorrhizal fungi. Mycelia of various ectomycorrhizal species and strains cultivated in vitro differ greatly in tolerance to aluminium. Aluminium tolerant strains include *Suillus luteus*, *S. bovinus* (HINTIKKA 1988; LESKI *et al.* 1995; KIELISZEWSKA-ROKICKA *et al.* 1996), *S. variegatus*, and *Paxillus involutus* (HINTIKKA 1988), whereas as aluminium sensitive strains include species of the genera *Amanita* and *Tricholoma* (HINTIKKA 1988) as well as *Pisolithus* and *Rhizopogon* (KIELISZEWSKA-ROKICKA *et al.* 1996). LESKI *et al.* (1995) found that strains of ectomycorrhizal fungi originating from forest sites characterized by high concentrations of available aluminium in soil solution, showed a higher tolerance to aluminium ions when grown in laboratory conditions than did strains originating in forest sites of low aluminium availability.

The detrimental effects of aluminium ions on plant roots may be ameliorated by mycorrhizal symbiosis. Laboratory experiments revealed that mycorrhizas of spruce seedlings developed with the ectomycorrhizal fungus, *Paxillus involutus*, accumulated aluminium and reduced the translocation of toxic ions to plant tissues (WILKINS and HODSON 1989; HENTSCHEL *et al.* 1993). Polyphosphates present in the rhizosphere or in the fungal hyphae bind Al, producing insoluble complexes (VÄRE 1990; KOTTKE 1991; TURNAU *et al.* 1993; MARTIN *et al.* 1994). The aluminium complexes formed with phosphate ions may result in a decrease in accessible phosphorus in the fungal hyphae and soil substrate and decreased phosphorus transport to aboveground parts (CUMMING *et al.* 1985). However, ectomycorrhiza do not always provide a plant protection against toxic aluminium ions. JENTSCHKE *et al.* (1991) found that ectomycorrhizas developed on spruce roots with *Lactarius rufus* and *L.*

Table 1. Concentrations of Al causing statistically significant reductions of root growth of seedlings of *Picea* spp. and *Pinus* spp. grown in sand, soil, or solution culture. Growth was measured in terms of root biomass, unless otherwise noted.
(after: RAYNAL *et al.* 1990)

Species	Culture	Concentration of Al mM L ⁻¹	Citation
<i>Picea abies</i>	Solution	1.50	EVERS (1983)
<i>Picea abies</i>	Solution	0.30*	ROST-SIEBERT (1983)
<i>Picea abies</i>	Solution	0.74**	ABRAHAMSEN (1984)
<i>Picea abies</i>	Sand	3.33	VAN PRAAG <i>et al.</i> (1985)
<i>Picea abies</i>	Sand	2.96	MAKKONEN-SPIECKER (1985)
<i>Picea abies</i>	Solution	1.00	INGESTAD <i>et al.</i> (1985)
<i>Picea rubens</i>	Solution	3.70*	SCHIER (1985)
<i>Picea glauca</i>	Sand	0.37	HUTCHINSON <i>et al.</i> (1986)
<i>Picea rubens</i>	Solution	0.25*	THORNTON <i>et al.</i> (1987)
<i>Picea glauca</i>	Sand	0.05	NOSKO <i>et al.</i> (1988)
<i>Picea rubens</i>	Sand	0.37	
<i>Picea rubens</i>	Soil	0.54	OHNO <i>et al.</i> (1988)
<i>Picea rubens</i>	Soil	0.25	JOSLIN and WOLFE (1988)
<i>Pinus radiata</i>	Solution	0.74	HUMPHREYS and TRUMAN (1964)
<i>Pinus rigida</i>	Solution	4.44	MCCORMICK and STEINER (1978)
<i>Pinus sylvestris</i>	Solution	4.44*	
<i>Pinus virginiana</i>	Solution	4.44*	
<i>Pinus clausa</i>	Solution	1.22*	WILLIAMS (1982)
<i>Pinus taeda</i>	Solution	1.22*	
<i>Pinus banksiana</i>	Sand	1.48	HUTCHINSON <i>et al.</i> (1986)
<i>Pinus strobus</i>	Sand	2.96	
<i>Pinus sylvestris</i>	Solution	3.0–5.0	ELDHUSET <i>et al.</i> (1987)
<i>Pinus taeda</i>	Sand	0.19***	PAGANELLI <i>et al.</i> (1987)

* – Growth determined as root elongation

** – Growth determined as whole-plant biomass

*** – Growth determined as relative growth rate

thejogalus did not reduce aluminium uptake and that the primary barrier for Al was the root endodermis. Ectomycorrhizas of spruce seedlings with *P. involutus* diminished the negative influence of aluminium (0.8 mM Al) on the content of chlorophyll in needles only during the first 5 weeks of growth of the seedlings in presence of the metal. However, after 10 weeks the chlorophyll content in the mycorrhizal and nonmycorrhizal seedlings was similar (MARSCHNER *et al.* 1992). The protective role of mycorrhizal symbiosis depends mainly on the proprieties of the mycobiont.

10.2.3.3. Heavy metals

Elevated concentrations of heavy metals in the soil may have toxic effects on soil microorganisms (e.g. FRITZE *et al.* 1989; FROSTERGÅRD *et al.* 1993) and mycorrhizas of forest trees (e.g. SMITH and READ 1997; CAIRNEY and MEHARG 1999). Heavy metals that accumulate in the organic layer of forest soils may inhibit numerous soil processes mediated by soil microorganisms such as respiration, nitrification, and ammonification. As a result, decreased decomposition rates and restricted nutrient availability is often observed (TYLER 1972; TURNAU *et al.* 1993). Since mycorrhizal fungi provide a link between the soil and roots, it is thought that detrimental effects of heavy metals on trees are often mediated by dysfunction of the fine roots. In severely polluted areas in the Czech Republic (Krušné Hory), where the concentrations of cobalt, copper, iron, lead, and zinc in Norway spruce roots were elevated compared to a control forest stand (Šumava), the biomass of both living and dead roots was significantly lower than at the non-polluted site: Krušné Hory – biomass 70–170 kg ha⁻¹, necromass 920–1490 kg ha⁻¹; Šumava – biomass 340–500 kg ha⁻¹, necromass 7410–8770 kg ha⁻¹ (KOCOUREK and BYSTRČAN 1989).

Heavy metals may be toxic to plants when concentrations in soil solution exceed certain levels, which depends upon the physico-chemical proprieties of the metal, on environmental factors, and on tolerance of the organism (GADD 1993). Increased concentrations of zinc, cadmium, and lead, greatly inhibited the growth of non-mycorrhizal roots of Norway spruce in hydroponic culture (GODBOLD *et al.* 1987). Heavy metals are also toxic to mycorrhizal fungi; however, high variability in the response to heavy metal availability in the growth medium was observed among fungal species, strains, growth stage, as well as between the vegetative and reproductive forms of the same organism (GADD 1993). A 60% reduction in fungal biomass was observed in forest areas polluted with high levels of copper and zinc compared to unpolluted forest stands, and the number of fungal species which produced fruiting bodies decreased at the polluted sites from 35 to 15 (RÜHLING *et al.* 1984). The following species are considered Cu tolerant: *Amanita muscaria*, *A. porphyria*, *Cantharellus tubaeformis*, *Laccaria laccata*, *Leccinum scabrum*, and *Tricholoma imbricatum*. Sensitive species, which exhibit declining populations with increasing concentrations of Cu in soil are: *Cantharellus cibarius*, *Paxillus involutus*,

Tricholoma portentosum, and species belonging to the genera: *Cortinarius*, *Lactarius*, and *Russula*. *Amanita muscaria*, *Leccinum scabrum*, and *Paxillus involutus* are tolerant to high concentrations of Pb and Cd in soils in the vicinity of a lead production plant, whereas species belonging to the genus *Russula* seemed to be sensitive (LEPŠOVÁ and MEJSTŘÍK 1989).

Ectomycorrhizal fungi in pure cultures exhibit a wide range of responses to elevated concentrations of heavy metals. *Amanita muscaria*, *Hebeloma crustuliniforme*, and various *Suillus* spp. are considered relatively tolerant (MCCREIGHT and SCHROEDER 1982; WILLENBORG *et al.* 1990). Cd, Ni, and Pb inhibited the growth of *Suillus luteus* 5–10 times more than the growth of *S. brevipes* and *S. grevillei* (MCCREIGHT and SCHROEDER 1982). *H. crustuliniforme* was more tolerant of Hg and Cd than was *A. muscaria*, *Piloderma bicolor*, *Paxillus involutus*, *Pisolithus tinctorius*, *Scleroderma aurantium*, *Suillus bovinus*, and *S. grevillei* (WILLENBORG *et al.* 1990).

Heavy metals can negatively influence the formation and maintenance of ectomycorrhizas of spruce (GÖBL and MUTSCH 1985; KOCOUREK and BYSTRČAN 1989; KROPAČEK *et al.* 1989). On the other hand, mycorrhizal colonization could, in effect, prevent metal transport from soil to shoots. Various mechanisms of metal detoxification may influence mycorrhiza response to heavy metals. Metal ions may form complexes with organic exudates from mycorrhizal hyphae, such as organic acids (CROMACK *et al.* 1975), or with pigments such as melanin (GADD and DE ROME 1988). Detoxification of heavy metals can also take place inside fungal cells. Ectomycorrhizal fungi relatively tolerant to heavy metals, such as *Pisolithus tinctorius*, contained induced peptides (cadistin) or proteins (metallothionein) that were not found in metal-intolerant fungi, such as *Cenococcum graniformae* (MORSELT *et al.* 1986). Heavy metals may also be detoxified when complexed by phosphate ions in vacuoles (TURNAU *et al.* 1993). Mechanisms of detoxification of heavy metals inside the fungal mycelium require carbon and result in a significant increase in allocation of carbohydrates to roots and mycorrhizas (ERNST 1976). The availability of carbon can be a limiting factor in detoxification mechanisms (TINGEY and ANDERSEN 1991).

10.2.3.5. Ozone

Ozone is considered a contributing factor in forest decline (e.g. POLLE *et al.* 1993). Yet species may vary in response to the impact of this toxic gas. Norway spruce was reported to be more sensitive to the effects of ozone (O₃) than Scots pine (*Pinus sylvestris*) (SKEFFINGTON and ROBERTS 1985). The negative effects of elevated concentrations of ozone on Norway spruce include decreased root growth and reduced mycorrhizal colonization (e.g. BLASCHKE 1990; BLASCHKE and WEISS 1990; MEIER *et al.* 1990). The decreased growth of roots and mycorrhizas are an early indicator of the detrimental impacts of ozone on trees, occurring prior to visible responses of aboveground parts. The

effects of ozone on root systems are mediated through changes in stomatal function, photosynthesis, respiration, and allocation of carbohydrates from shoots to roots (COOLEY and MANNING 1987; DIGHTON and JANSEN 1991; SHAW *et al.* 1992).

Reports concerning the effects of ozone on mycorrhiza of forest trees are equivocal. Short-term impacts of ozone in concentrations that slightly exceed ambient levels of O_3 include stimulated photosynthetic activity of spruce seedlings (WALLIN *et al.* 1990) and increased mycorrhizal colonization (WÖLLMER and KOTTKE 1990; HOLOPAINEN and RANTANEN 1992; RANTANEN *et al.* 1994). At the same time, a decrease in the shoot/root weight ratio was observed, indicating that an initial effect of O_3 could be increased allocation of carbon from shoots to roots (RANTANEN *et al.* 1994). Increased mycorrhizal colonization stimulated the uptake of water and mineral nutrients and, in turn, increased seedling growth. However, the long-term influence of ozone (several seasons) at concentrations typical of a summer day ($100\text{--}200\ \mu\text{g m}^{-3}$) caused a decrease in translocation of assimilates to roots (WILLENBRINK and SCHATTEN 1993). After five seasons of growth in the presence of elevated ozone concentrations (annual mean concentration $100\ \mu\text{g m}^{-3}$, maximum concentrations $130\text{--}360\ \mu\text{g m}^{-3}$), Norway spruce seedlings had fewer mycorrhizal root tips and an abnormal mycorrhizal morphology compared to control plants (BLASCHKE 1990). A reduction in the number of fine roots and mycorrhizas resulted in decreased water and nutrient uptake and limited drought resistance. The response of roots and mycorrhizas to ozone often depends upon other co-occurring environmental stress factors, such as high SO_2 concentration in the atmosphere and low soil pH. ROTH and FAHEY (1998) studied the effects of ozone and acid precipitation on mycorrhiza of red spruce (*Picea rubens*) and found no effect of ozone treatment on the percentage of mycorrhizal colonization or the composition of the ectomycorrhizal community. However, the combined effects of ozone and acid precipitation altered the ectomycorrhizal community in the organic horizon after one year of treatment.

10.2.3.6. Elevated CO_2

Elevated concentrations of CO_2 in the atmosphere may increase tree growth, including root biomass. Increased CO_2 concentrations also indirectly influence mycorrhizal fungi, which are dependent on plant carbohydrates (REY and JARVIS 1997). Trees, including coniferous species, grown under a CO_2 -enriched atmosphere often exhibit increased ectomycorrhizal colonization (see KUBISKE and GODBOLD 2001, for review). It is reasonable to assume that *Picea abies* may also respond to elevated CO_2 with an increased abundance of mycorrhizas, although there is no evidence to date. Most studies with other tree species report an increased percentage of ectomycorrhizal fine roots, increased numbers of ectomycorrhizas, increased growth of the extramatrical

mycelium, and changes in the ectomycorrhizal species in response to CO₂ enrichment (KUBISKE and GODBOLD 2001). Several authors have suggested that changes in ectomycorrhizal colonization may arise from changes in root carbohydrates. The species composition of ectomycorrhizal fungi colonizing a root system changes over the lifespan of a tree. Under elevated CO₂ there was an increase in the frequency of *Leccinum* sp., *Paxillus involutus*, and *Laccaria* sp., whereas the most abundant fungi under ambient CO₂ were *Laccaria* sp., *Hebeloma sacchariolens*, and *Thelephora terrestris* (REY and JARVIS 1997; TINGEY *et al.* 1997). The increased amounts of carbon allocated belowground under elevated CO₂ may be a controlling factor that results in a shift in ectomycorrhizal community structure toward fungi typically observed in later stages.

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11. OUTLINE OF ECOLOGY

JERZY MODRZYŃSKI

11.1. ECOLOGY

11.1.1. Environmental adaptation

Norway spruce migrated from several refugia following the last ice age (Fig. 11.1). The geographic range expanded throughout the current interglacial period and includes primarily higher mountain regions and lowlands. In the lowlands, the range of Norway spruce expanded in conjunction with significant increases in precipitation (SCHMIDT-VOGT 1977; RALSKA-JASIEWICZOWA 1983). During the last millennium, the range expansion of spruce has been assisted by human activity. The species has spread from its ecological mainstays to areas following fire, land clearing, or extensive logging. In the XIX and XX centuries Norway spruce was introduced into lowlands and lower mountain zones. Human activity also resulted in a lowering of the high-altitudinal limit of the species in European mountains, locally by as much as 200–400 m a.s.l. (SCHMIDT-VOGT 1977).

11.1.1.1. Physiological and ecological optimum

The physiological optimum is defined in Norway spruce by vigorous growth, abundant seed crops, natural regeneration, high tolerance to biotic and abiotic factors, and longevity. However, co-occurring species may out compete the species in areas otherwise suited to its physiological optimum. Consequently, the ecological optimum and physiological optimum do not always coincide. For example, Norway spruce is often dominant in the upper forest zones in relatively unfavorable ecophysiological conditions. In general, Norway spruce occupies sites close to optimal conditions in the central part of the species range, whereas conditions become increasingly less favorable toward its distributional limits (ELLENBERG 1978). Consequently, the biomass of individuals and reproductive output decreases, whereas tolerance and resistance against limiting factors increases. However, the homeostatic capacity of the trees is eventually exceeded as the species reaches its distributional limit.

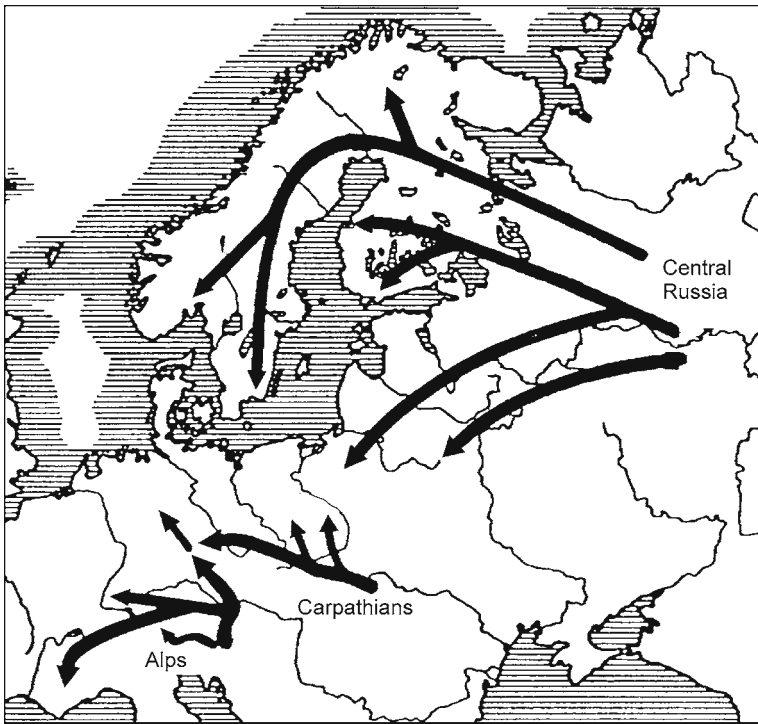


Figure 11.1. Migration of Norway spruce into Europe after the last ice age (based on SCHMIDT-VOGT 1977, 1978)

Soil quality may have very little impact on the growth of Norway spruce in environments near its distributional limit (NEBE 1968). Edaphic factors become increasingly important approaching the climatic optimum of the species. According to NEBE (1968), Norway spruce has an optimal macroclimate, for example, in the Bavarian Alps, where the mean annual temperature is 6°C, the annual amplitude of mean monthly temperatures exceeds 19°C and the growing-season precipitation totals 490–580 mm. According to SCHMIDT-VOGT (1977), Norway spruce exhibits its physiological optimum in the lower elevations in Switzerland, Upper Swabia (Germany) or in Great Britain. This optimum is associated with growing-seasons that exceed 150 days with temperatures above 10°C in continental climatic zone or 250 days with temperatures above 5°C in the maritime climatic zones. The growing-season precipitation totals 300–400 mm in Great Britain and 490–580 mm at the continental optimum. SCHMIDT-VOGT considered the annual temperature amplitude (continentality of climate) rather unimportant for Norway spruce.

11.1.2. Clinal variation and ecotypes

The migration history and the vast natural geographic range of Norway spruce are evidence for its ability to adapt to a variety of habitats, differing in terms of climatic, edaphic, and biotic factors (SCHMIDT-VOGT 1977; ŚRODON 1977; HOLZER 1988). Adaptation is the result of evolutionary processes that lead to changes in the genetic structure of a species. Adaptations result from the existence of a species in environments undergoing temporal and spatial change (STEBBINS 1958; WEISCH 1977). Individual genetic variation, arising from mutation and genetic recombination, is the basis of natural selection. In Norway spruce, the most important selective factors are droughts, late frosts, snow damage, reduced growing season length, and competition with co-occurring beech (*Fagus sylvatica*) (HOLZER 1967a, 1981a; MAYER 1969; BOUVAREL 1974; ELLENBERG 1978). An opposing factor to directional selection is gene flow resulting from open pollination and the long-distance transport of wind-borne pollen. However, as a result of strong directional selection, significant genetic differences are observed even in neighboring populations (MODRZYŃSKI 1989, 1995). Thus, adaptation gives rise to specialized populations, often suited to a specific habitat. If these populations are reproductively isolated, they are termed ecotypes (TURRESSON, cit. LANGLET 1971). The mechanisms underpinning the formation of ecotypes are also responsible for clinal variation (genoclines), defined as the genetic differentiation of populations arrayed along a continuous gradient of ecological factors, such as along latitudinal or altitudinal gradients (ENDLER 1977).

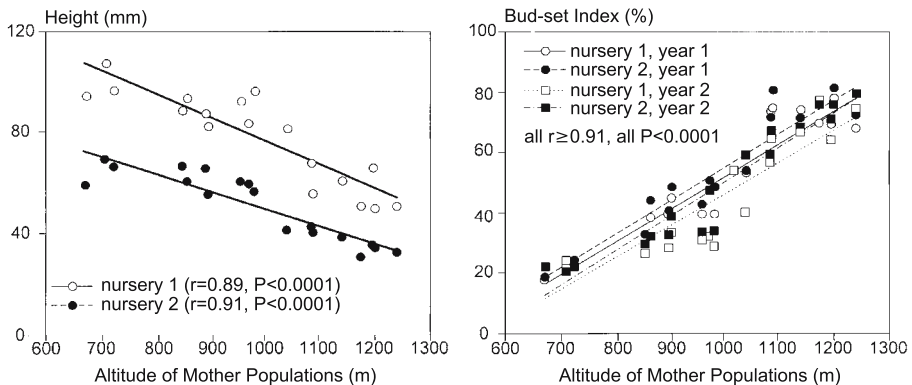


Figure 11.2. Relationship between height (after the second growing season) and bud-set (during the first and second growing season for Norway spruce seedlings grown in two different nurseries) and the altitude of mother tree populations. The bud-set index was calculated as an average proportion of seedlings with developed terminal buds in ten observations from July to October. The altitude of the mother tree population is the average altitude of all trees on the experimental plot (after MODRZYŃSKI 1995)

Clinal variation is well documented for many Norway spruce traits. For example, with increasing altitude of origin, Norway spruce trees set buds earlier and exhibit decreasing growth rates (HOLZER 1964, 1966; MODRZYŃSKI 1995) as shown in Fig. 11.2. Norway spruce seedlings of populations adapted to higher altitudes exhibit: a) higher concentrations of nitrogen, chlorophyll, and carotene in needles, b) higher net photosynthetic capacity and dark respiration rates, c) higher dry mass partitioning to roots (OLEKSYN *et al.* 1998), d) higher tolerance to UV-B radiation (PUKACKI and MODRZYŃSKI 1998), and higher tolerance to drought (MODRZYŃSKI and ERIKSSON 2002) compared to lower altitudinal populations.

11.1.3. Identification of ecotypes

In the past, especially in the period from 1840–1925, imported Norway spruce seeds of unknown origin were used to establish forest stands in Europe (FANTA 1974; SCHMIDT-VOGT 1975; LÜDEMANN 1978). Consequently, identification of the genetic origin and ecological race (ecotype) of many Norway spruce stands is an important issue. Most identification methods are based on observed clinal variation of key adaptive traits of Norway spruce (e.g. bud set or other growth parameters), with the assumption that a cline is a sequence of overlapping ecotypes. The quantitative traits of a population are used to indicate its position along the cline.

The above-mentioned approach was used to test 72 Norway spruce stands in the Sudety and Carpathian Mts. Progeny of most stands exhibited adaptation to the habitats occupied today (influenced largely by altitude), despite the probable foreign origin of many of the stands. HOLZER (1966, 1975) reported similar findings in the Austrian Alps. Thus, it seems that the risks associated with introduced populations are likely overestimated in the forestry practice. An explanation for the well-adapted progeny of Norway spruce populations of unknown origin may be related to the inherent genetic variation both within and among populations. The ecotypes transferred into a drastically alien habitat were usually completely destroyed by frost, snow, wind or other selective factors. Only relatively well-suited populations could survive. In addition, open pollination assured the domination of native populations. Norway spruce is an evolutionarily young species, distinguished by a high degree of genetic polymorphism, which enables effective natural selection (MODRZYŃSKI 1989, 1991, 1995; OLEKSYN *et al.* 1998; MODRZYŃSKI and ERIKSSON 2002). In addition to natural selection and gene segregation (genotype), preconditioning during seed formation (phenotypic gene expression) may play a role as well (SKRØPA, personal communication). Whatever the mechanism of clinal variation among the investigated Norway spruce stands, their progeny appear to be well-adapted to many sites occupied today, implying that they should be naturally regenerated and that collected seed may be used for artificial regenera-

tion. However, altitudinal seed transfer zones should be respected. Transfer zones range from 150–250 m a.s.l. (PRAVDIN and ROSTOVTSEV 1979) or 200–300 m a.s.l. (HOLZER 1985).

11.1.2. Ecological requirements

This chapter is focused, with few exceptions, on the average requirements of the species; however, it should be noted that the ecological amplitude of Norway spruce is the sum of the ecological amplitudes of its individual populations and ecotypes.

11.1.2.1. Light requirements

The ability to survive under a canopy, to retain many needle-age cohorts in a dense crown, or to exhibit relatively long crowns in a dense and closed stand indicate the high degree of shade tolerance of Norway spruce. However, it should be stressed that Norway spruce has a broad amplitude of light requirements. It is maximally shade tolerant in the juvenile stage and in optimal site conditions. On relevant sites in the lower elevation forest zones, it can even compete with silver fir (*Abies alba*) or European beech (*Fagus sylvatica*). Under the canopy of these species, abundant natural regeneration of Norway spruce can sometimes be found. The shade tolerance of Norway spruce decreases with increasing age and in poorer site conditions. Older trees in higher elevations of the upper forest zone have high light requirements.

Many authors regard Norway spruce as a moderately shade tolerant species (RUBNER 1960; OBMIŃSKI 1977; SCHMIDT-VOGT 1977; PUCHALSKI and PRUSINKIEWICZ 1990). RUBNER (1960) reports that Norway spruce twigs with needles required at least 3–4% of full light to survive, whereas those of European beech required 1–2% and those of Scots pine (*Pinus sylvestris*), 10%. GIA (1927) found that 1-year-old Norway spruce seedlings required at least 2–3% of full light, whereas European beech required about 1%, silver fir 2%, Scots pine 7–10% and European larch (*Larix decidua*) 10–14%. The light requirements of Norway spruce in the northwestern Carpathians are illustrated in Fig. 11.3.

Some authors stress the morphological impacts of light on Norway spruce. SCHMIDT-VOGT (1977) states, for example, that in the shaded, lower portion of the spruce crown, the branches appear flattened, even if in the middle portion of crown they are brush- or comb-like in appearance. PISEK and WINKLER (1959) describe the shaded spruce twigs as flaccid, covered with dark, thin and relatively soft needles, loosely distributed in a single layer; whereas the high-light twigs are described as stiff and covered with olive-colored, thick and hard needles, distributed densely in multiple planes.

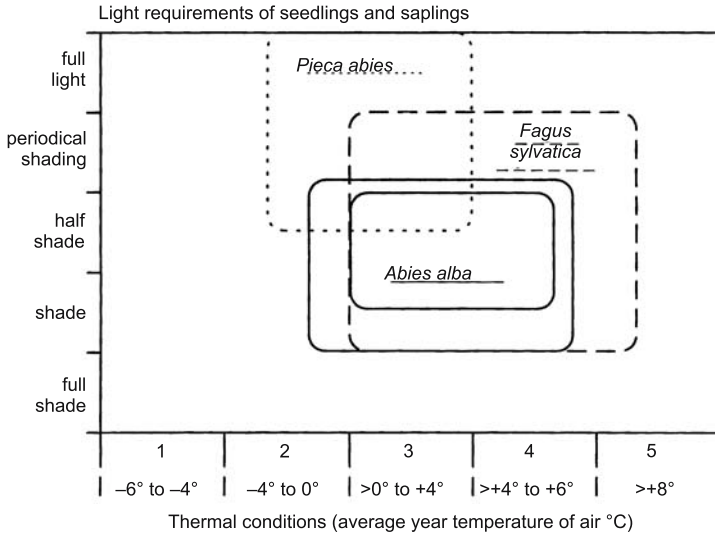


Figure 11.3. Temperature and light requirements of Norway spruce, silver fir, and European beech in the northwestern Carpathians and adjacent regions (after ZARZYCKI, cit. JAWORSKI and ZARZYCKI 1983)

11.1.2.2. Temperature requirements

The temperature or heat sum requirements of Norway spruce are relatively low. This is evident from the natural geographic range of the species, which reaches its limits far in the north and high in the mountains. In the southern part of the range, Norway spruce occurs only in the higher elevations, creating both upper and lower species range limits (tree lines), below which the temperatures are already too high.

According to RUBNER (1960), Norway spruce in the north grows on sites with a growing season of 60 days with temperatures above 10°C, whereas SCHMIDT-VOGT (1977) reports about 150 days with the same temperature as a maximal growing season for the Norway spruce in the south. In Figure 11.3 it can be seen that in the northwestern Carpathians, Norway spruce stands occur in the -4 to +4°C interval of annual mean temperatures (ZARZYCKI 1984). The average January temperature at the upper limit of the Norway spruce range in the Alps is about -8°C, whereas the limit of European beech is -4°C and European larch is -10°C (ELLENBERG 1978). Norway spruce tolerates maximal temperatures up to +46°C. SCHMIDT-VOGT (1977) reports that in Siberia, Norway spruce occurs on sites with an average January temperature of -35°C, but is able to tolerate temperature drops up to -60°C. Although very tolerant to low winter temperatures, Norway spruce is rather sensitive to early and late frosts during the growing season. According to ELLENBERG (1978), it can resist growing season frosts up to -7°C.

11.1.2.3. Water requirements

Despite its xeromorphic appearance and tolerance of winter desiccation, the moisture requirements of Norway spruce are relatively high. SCHMIDT-VOGT (1977) compares it to European beech and silver fir, which have average water demands. The soil moisture requirements of Norway spruce in the northwestern Carpathians are shown in Figure 11.4. More mesic sites are prevalent in the lowlands (ZARZYCKI 1984).

Water requirements can be estimated on the basis of the amount of water used by whole stands. SCHMIDT-VOGT (1977, cit. STALFELT and LAGEFOGED) reports that a 1 ha Norway spruce stand during 24 h transpired 19 metric tons of water on a rather dry site and 34 tons on a moist site. According to SCHMIDT-VOGT (1977, cit. EIDMANN and SCHWENKE), Norway spruce is vulnerable to drought because of its limited ability to reduce water uptake when it is scarce. In one experiment, Norway spruce required 251 ml of water to produce 1 g of dry mass in a water-saturated soil, whereas Scots pine used 294 ml. At 42% of saturation (drought conditions), Norway spruce reduced water use to 204 ml per gram dry mass and Scots pine to 117 ml per gram. Thus, during

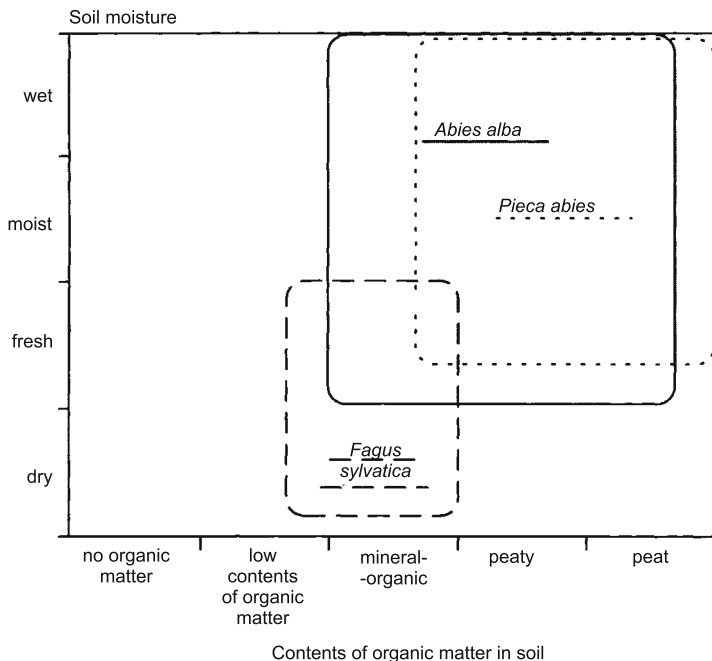


Figure 11.4. Requirements of Norway spruce, silver fir, and European beech in the northwestern Carpathians and adjacent regions in relation to soil moisture and organic matter (after ZARZYCKI, cit. JAWORSKI and ZARZYCKI 1983)

drought periods Norway spruce uses water much less efficiently than Scots pine.

WEIHE (1984) suggests that the extensive and shallow rooting depth and large number of fine roots in Norway spruce is well suited to use precipitation as its primary water source. In contrast, many other forest tree species are better suited for acquiring ground water. MITSCHERLICH (1971) underscores the fact that in the mountains, Norway spruce stands obtain a large share of water from canopy interception, including fog and rime.

11.1.2.4. Significance of wind

Wind usually has an indirect physiological impact on trees. Wind acts to cool soil and trees, removes humid air, and prevents ground frosts by mixing air masses. The physiological response of Norway spruce to wind is relatively minor compared to other species (TRANQUILLINI 1979). A high tolerance to wind may be advantageous on exposed sites in the mountains or in the coastal zone (MITSCHERLICH 1971). Important for the Norway spruce is the biological consequences of wind for reproduction. Wind may transport spruce pollen over several hundred kilometers (SKRØPA personal communication) and seeds for many hundred of meters. Thus, wind is critical to the population genetics and range expansion of the species. The migration rate of Norway spruce is estimated at 250 m/year (FABIAN 1991).

11.1.2.5. Soil requirements

According to OBMÍŃSKI (1977), Norway spruce is not able to attain its full growth potential on very rich sites and succumbs to the competitive pressure of eutrophic species. It develops optimally on soils that are mesic, loamy, medium rich in nutrients and with a relatively shallow depth to water table. Its optimal pH lies between 5.3 and 6.0; however, it can grow on soils with pH values ranging from 3.4 to 6.7.

The soil requirements of Norway spruce, silver fir and European beech differ in terms of soil moisture and humus contents (Fig. 11.4) as well as soil texture and soil trophic classification (Fig. 11.5). ZARZYCKI (1984) considers oligotrophic and mezotrophic soils as characteristic of Norway spruce sites. According to SCHMIDT-VOGT (1977), Norway spruce usually obtains adequate amounts of Ca, K, and P from the soil. Only on marshes or alluvial sands may the contents of K and P be too low for Norway spruce. Typically Norway spruce is found to be N deficient, often owing to a high C/N ratio, resulting from the slow decomposition of its own litter (see also Chapter 7.2).

Norway spruce typically forms an extensive, shallow dish-like system of first order roots in the upper layer of soil (up to 30 cm in depth). The development of second order roots depends upon soil conditions and determines the rooting depth. On well-aerated, moist, and fertile soils, lateral roots arising from the first order roots extend to a depth of 1 to 2 m (KÖSTLER *et. al.* 1968). A

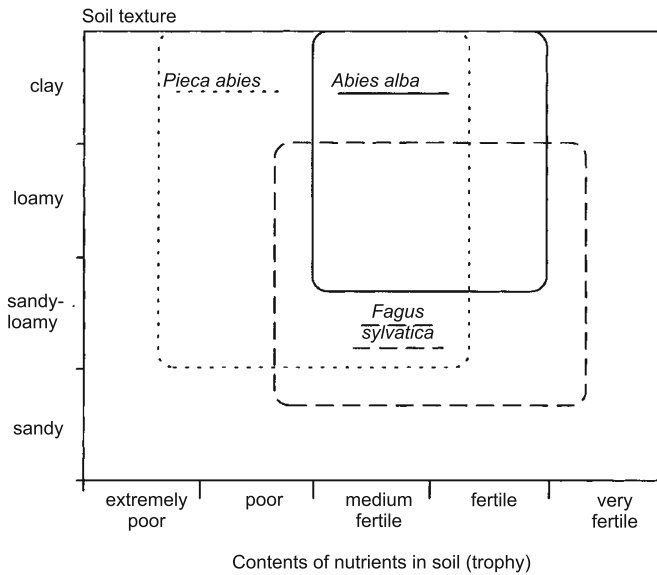


Figure 11.5. Requirements of Norway spruce, silver fir, and European beech in the northwestern Carpathians and adjacent regions in relation to soil texture (after ZARZYCKI, cit. JAWORSKI and ZARZYCKI 1983)

shallow dish-like root system seems not to be a species trait (as many believe), but a consequence of the frequent occurrence of Norway spruce on soils that restrict the full development of roots. Other tree species such as silver fir, European beech or Scots pine on restrictive soils (i.e. poorly aerated, gleyed, compact, stony, dry, oligotrophic) are not able to develop deep root systems either. In contrast, the ability to root more effectively on such soils gives Norway spruce an advantage in expanding to extreme sites.

11.1.2.6. Significance of mycorrhizae

Norway spruce is a mycotrophic species and the fungal symbiosis is necessary for its proper growth and development (see Chapter 10). Norway spruce mycorrhizas include at least one hundred ectomycorrhizal fungi, belonging mainly to the following genera: *Amanita*, *Boletus*, *Cortinarius*, *Lactarius*, *Russula*, *Suillus*, *Tricholoma*, and *Xerocomus*. The fungi obtain carbohydrates from the trees and the trees are supplied water and nutrients from the fungi with high efficiency. The fungi also protect the spruce trees against diseases or harmful impacts of heavy metals and other pollutants (RICHARDS 1979; SCHÖNHAR 1989).

11.1.3. Environmental stresses

SCHMIDT-VOGT (1989) states that among the important European forest tree species Norway spruce is possibly the most susceptible to biotic and abiotic factors. Storms, snow, and insects are among the agents causing major disturbance in Norway spruce stands. Drought, frost, fungal diseases, and herbivores also cause a significant amount of damage. All of the above-mentioned factors are considered key plant stresses in Norway spruce (see Fig. 11.6).

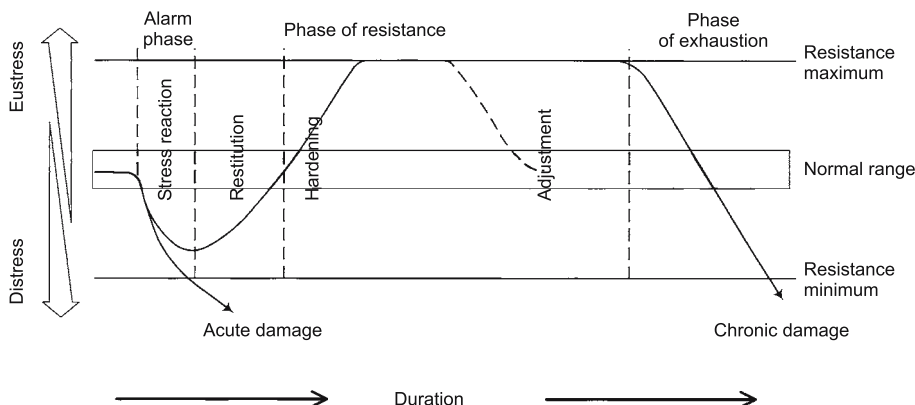


Figure 11.6. A phase model of stress events and responses. The impact of stress factors destabilizes vital structures and functions, including an “alarm phase”, in which there are functional declines (stress response); these are offset by counteractions which may lead to over-compensation (hardening). Under prolonged exposure to a constant stress, a higher degree of resistance is developed and this may result in restabilization (adjustment). If an organism is overtaxed either by acute or chronic stress, irreversible damage occurs. (after SELYE and STOCKER, cit. LÄRCHER 1995)

11.1.3.1. Excessive insolation and enhanced UV radiation

According to LÄRCHER (1995), excessive light intensities may result in pigment destruction, parenchyma damage, and reduced net assimilation rates. LAATSCH and ZECH (1967) observed chlorotic needles on spruce trees in fall and winter, likely resulting from chlorophyll degradation via photo-oxidation.

Atmospheric pollution has resulted in a gradual reduction of the stratospheric ozone layer. This, in turn, has resulted in increased ground-level ultra-violet radiation, which in the wavelength range 280–315 nm (UV-B) is considered harmful for living organisms (MADRONICH 1993). According to BORNMAN and TERAMURA (1993), UV-B causes changes in nucleic acids, proteins, and membrane lipids, leading to mutations as well as organism-level responses in growth and morphology. Typical protective reactions in terrestrial plants are increased contents of polyamines, flavonoids, and isoflavonoides in

leaves, as well as higher production of wax and tomentum. ROBAKOWSKI (1997), applying UV-B doses up to 22.64 kJ/m^2 , observed an increase in flavonoid, anthocyanin, and chlorophyll contents in needles as well as a decrease in an index of relative vitality of young Norway spruce trees. PUKACKI and MODRZYŃSKI (1998) also observed a decrease in the relative vitality index, a significant reduction in biomass, and an increased concentration of flavonoids in needles of Norway spruce seedlings exposed to increased UV-B irradiation (up to 20.1 kJ/m^2) compared to controls.

11.1.3.2. Low temperatures

Norway spruce cold tolerance is entrained to an annual temperature cycle (Fig. 11.7). When properly conditioned in late summer and hardened in fall, Norway spruce trees tolerate temperatures to about -40°C (MITSCHERLICH 1971) or even -60°C (SCHMIDT-VOGT 1977) during winter dormancy. On the other hand, even a brief period of exposure to temperatures below 0°C during the growing season may result in serious injury to photosynthetic membranes and young, un lignified shoots. CHRISTERSSON (1985) and CHRISTERSSON and FIRCKS (1990) observed seedling injury rates of 50% in Norway spruce seedlings tested at -3°C and 100% at a temperature of -4°C . Especially dangerous for young spruce trees are the advective frosts in early spring after growth flushing. However, the native ecotypes, well adapted to the local climatic conditions usually flush later, when the frost risk has passed (GIERTYCH 1972; SCHMIDT-VOGT 1977; SAKAI and LÄRCHER 1987).

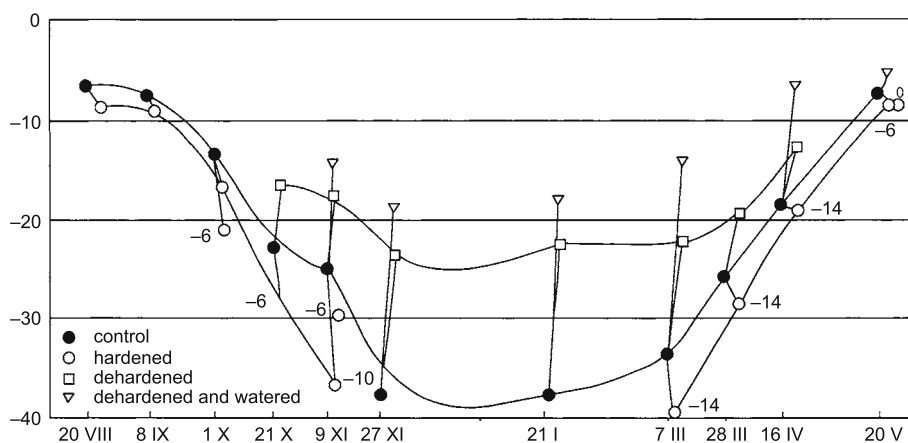


Figure 11.7. Tolerance of Norway spruce needles to low temperatures from summer through spring, following different treatments. The highest tolerance was exhibited in the trees hardened in late summer, the lowest in trees dehardened and simultaneously watered in autumn (after PISEK and SCHIESSEL, cit. MITSCHERLICH 1971)

Reductions in temperature induce physiological changes in the trees, resulting in increased hardening (SAKAI and LÄRCHER 1987; JONES 1992; LÄRCHER 1995). It is generally assumed that increased concentrations of solutes in the cell solution provides tolerance to temperatures not lower than -5°C . Together with the modification of membranes and enzymes, cold tolerance reaches -15°C . Supercooling of cell water provides additional protection up to -40°C . The level of cold tolerance of trees typically exceeds the decreasing air temperatures by some $10\text{--}20^{\circ}\text{C}$ (MITSCHERLICH 1971). For example, an air temperature of about -10°C induces a tolerance to temperatures between -20°C and -30°C . After periods of warming, the level of hardening decreases, but hardening increases again when air temperatures subsequently decline. These adjustments in hardening typically require several days. The tolerance of Norway spruce to low temperatures declines rapidly with the onset of the growing season.

11.1.3.3. High temperatures

In its native environments Norway spruce is exposed to high temperature stress far less frequently than by exposure to subzero temperatures. According to SCHMIDT-VOGT (1977), the harmful impact of high temperatures occurs mostly in young needles and un lignified twigs. The death of mature trees rarely occurs. However, young Norway spruce seedlings are frequently exposed to high temperature stress at the soil surface (up to 65°C). Such temperatures cause protein denaturation in the hypocotyl cells and seedling mortality. KREEB (1979) reports that Norway spruce seedlings can tolerate a temperature of 45°C for about 3 hours, whereas exposure to a temperature of 55°C results in death after 10 minutes.

When Norway spruce trees growing in stand interiors are suddenly exposed to strong direct solar radiation, the cambium covered with a thin bark layer may quickly overheat and die, resulting in sun scald (blistering and bark sloughing). Often trees that seemed to survive a surface fire, later die because the cambium was killed by the high temperature (SCHMIDT-VOGT 1977; KREEB 1979).

Acclimation of trees to heat stress usually is triggered after crossing a temperature threshold of 35°C and is reached within few hours. During hot days, the tolerance to high temperatures is significantly higher in the afternoon than in the morning. High temperature tolerance is increased, in part, through the dehydration of tissues and the synthesis of heat shock proteins (HSP). Subsequent reductions in heat tolerance in Norway spruce trees occur over several days (KREEB 1979; JONES 1992; LÄRCHER 1995).

11.1.3.4. Droughts

Drought-induced mortality in Norway spruce is observed mostly in nurseries and young stands. In developed and older stands, drought damages are rela-

tively minor. However, drought losses are typically higher in Norway spruce than in Scots pine or European beech (SCHMIDT-VOGT 1977). Drought stress begins in Norway spruce with a 5% loss in tissue water. The stomata close when the tissue water deficit approaches 18%. To about a 33% water deficit, subtle and reversible changes occur in the tree. Above this threshold, the changes become irreversible and a water deficit of 65% kills the tissues and whole trees. The physiological responses to drought in Norway spruce include a decrease in gas exchange rates and peroxidase activity or an increase in proline contents and carbohydrate exudation from roots. Drought stress accelerates needle loss, seed ripening, and aging in Norway spruce trees (TESCHE 1989; LÄRCHER 1995).

The protective mechanisms induced in Norway spruce trees during drought stress lead to a shift in the critical dehydration boundary of the protoplasm. Among the most important mechanisms are: regulated transpiration, increased osmotic pressure, and increased nitrogen metabolism. According to LÄRCHER (1995), Norway spruce immediately responds to the onset of drought. With increasing water deficits, transpiration rates decline first in the shaded twigs, followed by the high-light twigs at the bottom of the crown, and finally the high-light exposed shoots at the top of the crown (Fig. 11.8). Under a prolonged drought, the stomata remain closed and transpiration occurs only through the cuticle. TESCHE (1989) reports that the increase in osmotic pressure in the cells of Norway spruce trees is not only the result of water loss, but also a consequence of the synthesis of osmotically active compounds (e.g. sugars). Consequently, the ability to absorb and maintain tissue water is sustained. SCHMIDT-VOGT (1989), TESCHE (1989), and LÄRCHER (1995) indicate, that when the cell turgor in Norway spruce trees declines, nitrogen metabolism is increased. Nitrogen accumulation increases in shoots and roots with increasing tree age. MODRZYŃSKI and ERIKSSON (2002) found that Norway spruce populations from higher elevations, which exhibit higher nitrogen concentrations in needles (OLEKSYN *et al.* 1998), also exhibited higher tolerance to simulated drought stress.

Winter frost results in dehydration of Norway spruce tissues, similar to

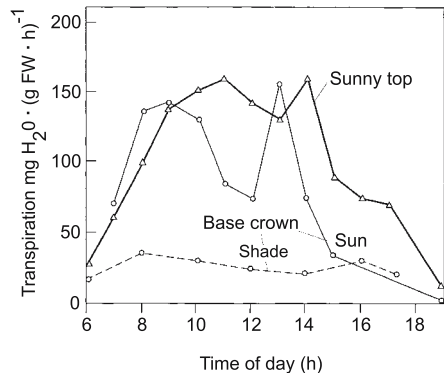


Figure 11.8. Daily fluctuations in the transpiration of Norway spruce shoots on a sunny August day. As the water supply declines, the shoots in the shade at the base of the crown are the first to reduce their water loss, followed by the twigs in the sun at the lower margin of the crown, and finally the shoots in the top of the crown (after PISEK and TRANQUILLINI, cit. LÄRCHER 1995)

the effect of drought. During prolonged winters, Norway spruce trees cannot take up water from frozen soil. The water stored in the trunk and branches is used initially, but upon freezing, even well developed needles are subject to desiccation. Winter desiccation is increased by dry and cold winds, especially after warming periods (SAKAI and LÄRCHER 1987; SCHMIDT-VOGT 1989).

11.1.3.5. *Excess water*

A rise in the level of ground water or flooding are both detrimental to Norway spruce trees. Under reduced aeration and anoxic soil conditions, toxic substances may increase and some pathogens are activated, especially those of the genus *Phytophthora*. As a consequence, the root systems of trees gradually degenerate. The development of reproductive and vegetative organs ceases, and under prolonged stress the trees die. The flooding of roots by standing water for longer than a few weeks is the most harmful. Flowing water contains more oxygen and is tolerated by some tree species, including Norway spruce (KOZŁOWSKI *et al.* 1991). Near wetlands, excessive soil moisture and anoxia serves as an ecological barrier for Norway spruce trees. Norway spruce tolerates excess water relatively well (almost as well as European alder, *Alnus glutinosa*), but prolonged oxygen deficiency is lethal (ELLENBERG 1978).

11.1.3.6. *Snow hazard*

Norway spruce is frequently damaged by ice, rime, or snow, forming heavy loads on the branches. Disturbances of this type often result in extensive damage to Norway spruce stands (ROTTMANN 1983; SCHMIDT-VOGT 1989). The most serious is precipitation in the form of wet snow, forming layers on the twigs and branches. If the crown becomes overloaded, the trunk may bend and break at different points from the top to the bottom of the crown (ROTTMANN 1983; ZAJĄCZKOWSKI 1991). According to SCHWERTDFEGER (1970), the critical load of snow is about 50 kg/m². ZAJĄCZKOWSKI (1991), however, reports that Norway spruce sustains loads of 40–50 kg/m² only for a short time. For prolonged snow loading, the critical load amounts to 20–30 kg/m². ROTTMANN (1983) reports that Norway spruce trees with long crowns resist critical loads exceeding 100 kg/m². SCHMIDT-VOGT (1989) indicates that the longer the crown, the better the h/d index (relationship of tree height and DBH). With h/d < 80, Norway spruce trees are relatively resistant to snow damage. A beneficial h/d index and a relatively high stability of Norway spruce stands can be attained through regular thinning, beginning in young stands (CHROUST 1980).

11.1.3.7. *Wind hazard*

Chronic winds at speeds above 3 m/s negatively impact the physiology and morphology of spruce trees, and are one of the limiting factors at the range limits of Norway spruce. Spruce stands are seriously threatened, however, only by strong

windstorms. Indeed, windstorms often result in catastrophic damage in Norway spruce, recognized in Europe as the most sensitive species to windthrow (SCHMIDT-VOGT *et al.* 1987; SCHMIDT-VOGT 1989). Damage in Norway spruce stands begins at wind speeds of 15 m/s and are catastrophic at 25 m/s (SCHMIDT-VOGT 1989, ZAJĄCZKOWSKI 1991). The severity of wind disturbance also depends on soil conditions. Norway spruce trees are much more vulnerable to wind damage on low quality soils or in wet soils after rainfall. The risk of wind damage is also increased in trees with a high h/d index and short, relatively broad crowns (Fig. 11.9). Wide spacing beginning in young stands, enables the development of an extensive root system, tapered trunk with an elastic top and long crown, and thereby increases the resistance of Norway spruce trees to windstorms (MITSCHERLICH 1971; SCHMIDT-VOGT 1989; ZAJĄCZKOWSKI 1991).

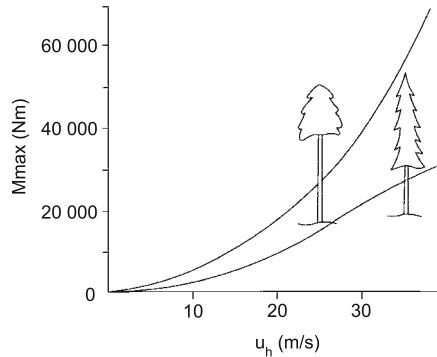


Figure 11.9. Maximal bending moment (M_{max}) in Norway spruce trunks, as dependent upon wind velocity (u_h) and crown shape. Values are greatly reduced in narrow crowns, especially during high winds (after MLINSEK, cit. ZAJĄCZKOWSKI 1991)

11.1.3.8. Pollution

Air and soil pollution have both direct and indirect impacts on trees. According to KELLER (1978a, 1989), air pollutants can cause various anatomical and physiological injuries in the aboveground organs of Norway spruce trees. Among other injuries, the protective cuticular wax layer is eroded and stomatal function is impaired. Inside the needles, hypertrophy of resin canals, delignification of cell walls, degeneration of the chloroplasts, and deposition of phenol-like substances in the mesophyll are common observations. Pollutants disrupt the gas exchange and water balance of Norway spruce trees and induce a number of biochemical responses (see Chapter 14).

For the roots of Norway spruce, soil acidification is especially harmful. The acidification of soil, primarily from SO_2 deposition, results in the leaching of important nutrients (Mg, K, Ca), the release of aluminium ions (Al^{3+}), and deposition of heavy metals. These elements impair the function of the mycorrhizas and induce fine root mortality (SCHMIDT-VOGT 1989; SCHÖNHAR 1989; KUHN *et al.* 1995). The injury of needle and root tissues and impaired physiological function decreases the resistance of Norway spruce trees to abiotic stress. The weakened trees are also an easy target for the invasion of fungal, bacterial, and viral pathogens as well as for insects and other pests.

Finally, these factors together contribute to the decline of Norway spruce forests (SCHMIDT-VOGT 1989; SKRE and MORTENSEN 1990; SAXE 1993; MODRZYŃSKI 1996).

According to SCHMIDT-VOGT (1989) for Norway spruce in high altitudes and latitudes, the toxic effects of SO_2 in the air are initiated at 20 mg/m^3 for chronic impacts and 80 mg/m^3 for acute impacts. On optimal sites, the critical concentrations are 50 and 200 mg/m^3 for chronic and acute impacts. For fluorine (HF) pollution on average sites, the relevant thresholds are 0.3 and 0.9 mg/m^3 . The critical concentrations for NO_2 are similar to those of SO_2 . For O_3 the critical doses are 100 mg/m^3 for 1 h and 120 mg/m^3 for 0.5 h. The average deposition rates of several toxic metals should not exceed: $400 \text{ mg/m}^2/\text{day}$ for Zn, $100 \text{ mg/m}^2/\text{day}$ for Pb, and $2 \text{ mg/m}^2/\text{day}$ for Cd.

11.1.3.9. Biotic hazards

The primary cause of disease in Norway spruce is fungi, which affect its cones, seeds, buds, needles, twigs, and other organs. The most problematic fungi are pathogens of roots and trunk. The roots of Norway spruce trees are frequently infected by *Armillaria* spp. Especially vulnerable are Norway spruce trees weakened by drought, or trees on fairly rich soils with relatively high pH. The resistance of Norway spruce to these fungi also decreases after herbicide treatments. A second important pathogen of Norway spruce roots is *Heterobasidion annosum*, although the primary mode of action of this pathogen is trunk decay. Its spores are dispersed long-distances by wind. Ideal infection sites are stumps left after thinning, through which the roots of neighboring trees are infected via root grafts. The spores carried in precipitation may also cause the infection of roots (SCHÖNHAR 1989). These and other important pathogens are discussed in Chapter 12.

Animal-related losses in Norway spruce stands are several times greater than those caused by fungi, but generally several times less than those caused by abiotic factors. The most harmful are insects and game animals. The insects *Lymantria monacha* and *Ips typographus* are the highest threat to older spruce stands. Plantations are often targets for *Hylobius abietis*. Dense stands are often affected by *Pityogenes chalcographus*. Insect invasion is often triggered by droughts, windthrow, or pollution. Different insect species specialize in attacking needles, buds, twigs, cambium, wood, roots, cones or seeds (KLIMETZEK and VITÉ 1989).

Among game species, roe deer (*Capreolus* spp.) and red deer (*Cervus* spp.) cause the greatest damage. Besides the direct damage to bark and wood, chaffed cambium acts as infection sites for fungi. In stands affected by large game activity, the older trees often are broken because of wood rot. Birds feed on seeds or seedlings, which locally may cause significant damage. More harmful are rodents that gnaw the buds and bark around the stems of young Norway spruce trees (KLIMETZEK and VITÉ 1989).

11.1.4. Ecological patterns in growth and development

11.1.4.1. Growth patterns

Temperature and precipitation are the most important climatic factors for the growth of Norway spruce (NEBE 1968). In central Europe, the optimal combination of these factors was found in the elevation zone 450–750 m a.s.l. Above this optimum, the diameter increment of spruce trees correlates positively with temperature, and below – with precipitation (KOCH 1958). Clonal Norway spruce trees planted at an elevation of 1900 m a.s.l. in the Alps exhibited a height growth rate five times slower than counterparts planted at 1250 m a.s.l. (TRANQUILLINI *et al.* 1980). The decrease in height growth observed when approaching the distribution limits of Norway spruce appears to be independent of stand density, whereas DBH often shows a clearer response to stand density than altitude (MODRZYŃSKI 1988a). Optimal soil moisture is essential for the normal growth of Norway spruce (KRAMER and KOZŁOWSKI 1979). The impact of soil fertility seems to be less important, although in the same climatic zone, soil conditions significantly influence the growth of the Norway spruce (KÜNSTLE 1962; FIEDLER *et al.* 1981; INGESTAD and KÄHR 1985).

According to TYSZKIEWICZ and OBMİŃSKI (1963), Norway spruce attains heights up to 50 m and timber volumes of 1000 m³/ha in the Beskid Mts and over 50 m height and 1.5 m DBH in the Białowieża Primeval Forest in Poland. SCHMIDT-VOGT (1986) reports a spruce tree 63 m in height and 1.65 m DBH in Bosnia. According to SCHMIDT-VOGT (1986), the volume of the largest Norway spruce trees is about 40 m³ and the most productive stands attain a timber volume of 1670 m³/ha at an age of 100 years.

11.1.4.2. Developmental patterns

Environmental factors influence all developmental stages of Norway spruce from germination and seedling stages through reproductive maturity and decline. For example, seed crop abundance in Norway spruce depends upon weather conditions during the two years prior to flowering as well as during flowering and cone ripening. The amount of solar radiation in the month of June and the temperature of July in the year prior to flowering are both very important environmental factors, as they stimulate the setting of flower buds (CHAŁUPKA 1975a; 1975b). Under optimal conditions, Norway spruce has a good seed crop every 3 or 4 years. With increasing latitude or altitude, the interval between seed crops increases (CHAŁUPKA and GIERTYCH 1973). Under extreme conditions at the distributional range limits of Norway spruce, the trees never bear sound seeds and exclusively reproduce vegetatively.

The length of the growing season in Norway spruce depends upon photoperiod and temperature. Bud set is associated with shoot growth cessation and initiation of dormancy, and is induced by increasing night length. The response to photoperiodic cues is, in essence, an adaptation to temperature

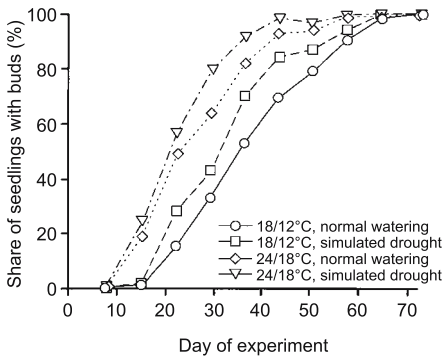


Figure 11.10. Impact of four combinations of temperature and watering on the rate of bud-set in Norway spruce seedlings.

The experiment was conducted in a phytotron on 24 Norway spruce populations from the Sudety and Carpathian Mountains. In the legend, initial day/night temperatures are shown; daylength was regulated continuously

(DORMLING *et al.* 1968; EKBERG *et al.* 1979). In addition to critical night length, other factors, such as temperature and moisture (Fig. 11.10) also influence bud set. The onset of deep dormancy occurs only after temperatures fall to about 0°C. The release from dormancy in spring is governed initially by the photoperiod, but growth resumes following a specified degree-day accumulation (WORRAL and MERGEN 1967). Needles and shoots begin to develop when the average daily temperature exceeds 5°C. Cambial activity begins at temperatures near 10°C. Shoot growth typically begins in May followed by diameter growth in June in many regions of Europe. Peak biomass production occurs in June and July (RUBNER 1960; FELIKSIK 1972).

11.1.4.3. Disturbances of growth and development and the biological costs of tolerance

Damage caused by frost, snow, wind, insects, and animals often results in a reduction in leaf area and photosynthetic carbon gain. The production of new needles, shoots, and branches requires assimilates that otherwise could be used for growth (LÄRCHER 1995). Insect outbreaks may cause a 50% reduction in biomass in a Norway spruce stand (SCHMIDT-VOGT 1986). Drought and other stresses accelerate bud set, cone ripening, and aging (BOYER 1980; WIEBE 1980; KOSKI 1983).

In response to environmental stress a number of defense mechanisms may mitigate the harmful effects. All these mechanisms, however, require assimilates. The reduced production or altered partitioning of assimilates is disadvantageous for the aboveground organs (SCHMIDT-VOGT 1982; WARING 1991; LÄRCHER 1995). For example, under unfavorable climatic conditions, Norway spruce trees initially cease shoot growth, whereas the growth of roots may continue. Thus, during dormancy the trees may increase their potential frost and drought resistance (SCHMIDT-VOGT 1982; LÄRCHER 1995). As a defense against herbivory, Norway spruce produces substances that inhibit herbivore development or the palatability of needles and other organs. These compounds include antibiotics, phenols, terpenes, resins, tannins, and alkaloids (SPURR and BARNES 1980; WARING 1991). Investment of assimilates in defen-

sive mechanisms involves a trade-off in terms of reduced growth potential. In contrast, weak defenses may entail a higher risk of mortality. The adaptations of Norway spruce to stress-dominated environments, however, seem to favor traits that confer increased survival at the cost of a more rapid growth and development (HOLZER 1967a; MODRZYŃSKI 1989; LÄRCHER 1995).

11.1.5. Natural regeneration

Through natural regeneration Norway spruce may sustain viable populations through successive generations. Range expansion of this species is enhanced by wind dispersal of seed and seedling shade tolerance. In natural stands Norway spruce begins producing seed crops at the age of 50–60 years. The seeds require an average temperature above 10°C between June and September for proper development. The seeds usually ripen in the middle of September and are released from the cones when their moisture content falls below 18%. This may happen already in autumn or winter, but 80% of the seeds fall during the spring, between April and June. Their relatively low rate of descent (on average 0.83 m/s) enables the wind to transport the seeds for considerable distances. Although most seeds fall within a radius of 50 m from the mother tree, 10% may land up to a few hundred meters away. Only about a half of the seeds produced leave the cones, and only 30–50% of the falling seed is viable. Even so, the number of seeds reaching the forest floor during an average seed year is about 100–200/m² and is typically sufficient for successful regeneration (SCHMIDT-VOGT 1991). The periodicity of seed years in Norway spruce, usually every 3 to 5 years, in effect, suppresses the population sizes of seed consumers (insects, birds, rodents and others). Consequently, during a seed year enough seeds remain to support natural regeneration (SPURR and BARNES 1980).

The optimal conditions for the germination of Norway spruce are high and stable substrate moisture contents, a pH of about 5.5, and temperatures between 15 and 25°C (PUCHALSKI and PRUSINKIEWICZ 1990; SCHMIDT-VOGT 1991). Light does not influence the germination of the Norway spruce, but is very important in subsequent growth stages. The light requirements of spruce seedlings increase rapidly with age. Between 1 and 5% of full sunlight is necessary to initiate natural regeneration. To regenerate seedlings under a canopy, light levels should be about 10–15% of full sun. With increasing age, light requirements increase to 30% of full light or more (FABIJANOWSKI *et al.* 1974; PUCHALSKI and PRUSINKIEWICZ 1990; SCHMIDT-VOGT 1991).

A Norway spruce understory may remain under the canopy for many years prior to release through improved light conditions. If this does not happen, however, the trees will eventually lose the ability to develop into normal trees. Under sustained shade conditions, Norway spruce initially reduces shoot growth then root growth, maintaining leaf area and photosynthetic capacity

(KÜNSTLE 1962; SCHMIDT-VOGT 1991). Temperature is not as important as light in affecting the growth rate of understory seedlings, although at the peripheries of its geographic range distribution, temperature gains in importance. Figure 11.11 illustrates the decrease in height of naturally regenerating Norway spruce along gradients of altitude and aspect, which determine temperatures and heat sums in montane environments. In addition, the overstory influences height growth of regenerating Norway spruce differentially with increasing altitude. The height increment of young spruce trees growing near the edge of the stand decreases with altitude much more slowly than that of the young spruce trees growing in adjacent open areas about 10–15 m from the stand edge (MODRZYŃSKI 1979).

High and stable soil moisture is very important for the proper growth of naturally regenerated spruce trees (MOSER 1965; ANDERS 1974). The type and state of the humus is also critical. Norway spruce regenerates optimally on humus of the moder type, followed by mull and mor types (MOSER 1965; MODRZYŃSKI 1978, 1979). Soil chemistry is much less important than soil physical properties for the natural regeneration of Norway spruce. The amount of nutrients, however, often determines the occurrence of competing plant species, which on rich soils are very high (WIEDEMANN 1936; PUCHALSKI 1972; ANDERS 1974, 1976). Norway spruce regenerates on rotting stumps (Fig. 11.12) and logs which provide the seedlings with adequate moisture and temperature conditions and an advantage in environments with high herbaceous competition. In addition, the seedlings are better protected against snow. The physical advantages of stumps and logs for Norway spruce regeneration are much more important than their chemical insufficiencies. This type of natural regeneration of Norway spruce is especially common in the north and in higher elevation zones. Norway spruce regeneration is also influenced by microtopography. Regeneration often occurs on small mounds formed by the

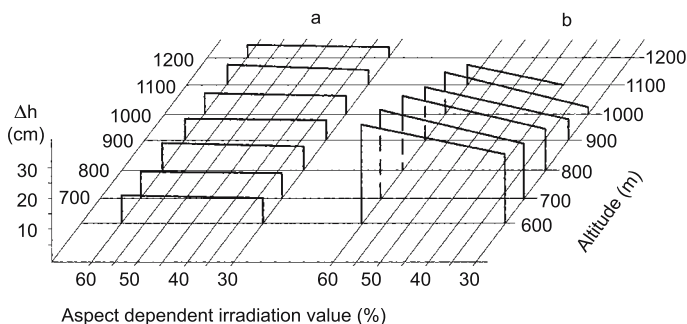


Figure 11.11. Impact of altitude and aspect on the height increment of young spruce trees regenerating naturally at the edge of a stand (a) and 10–15 m from the edge (one-half of stand height) of the mother stand (b). Irradiation values were calculated according to JUNGHANS (1967) (modified from MODRZYŃSKI 1979)



Figure 11.12. Seedlings of Norway spruce on rotting (spruce) wood and mounds of wind-fallen trees (photo A. BORATYŃSKI)

A–B – about 10-year-old seedlings on the top of mounds of wind-fallen trees; C – rotting log covered with mosses – a common site colonized by Norway spruce seedlings in the upper montane (subalpine) forest belt; D – Norway spruce seedling at the base of a dead old tree; E – seedlings on a stump; F – seedlings in a crevice of a Norway spruce stump

root systems of fallen trees (EICHRODT 1969; SCHMIDT-VOGT 1991). Often spruce seedlings are found close to the trunks of older trees, on the down-slope side. In this case the trunk protects the young tree not only against sliding snow masses and wind, but also provides water from stem flow down the trunk (PUCHALSKI 1972).

Natural stands of Norway spruce begin to produce seed when reproductively mature just prior to the stage of optimal stand development. At this stage, natural regeneration occurs infrequently, when individual dominant trees fall and form canopy gaps. Natural regeneration is synchronized in the old-growth forest during the stand decline phase at an age of about 200–250 years. At this stage, light and water availability approach levels optimal for regeneration. Protected by the remnant overstory, the new generation develops and matures (KORPEL 1989a). Some silvicultural cutting systems attempt to emulate this process.

11.1.6. Effects of Norway spruce on the environment

11.1.6.1. Microclimate within stands

The microclimatic conditions within a Norway spruce stand differ from those of nearby open areas, and may also differ from the microclimate of stands of other tree species. On average, the understory of a closed, shaded spruce stand receives light levels of about 10% of full sun. In dense young stands, the relative irradiation may fall to 1%. However, light levels are typically about 20 % in 80-year old and 30 % in 120-year-old stands (MITSCHERLICH 1971; SCHMIDT-VOGT 1986). Ambient temperatures are comparatively stable and exhibit low annual amplitudes inside Norway spruce stands compared to the surrounding environment. In winter, the temperature in a Norway spruce stand is somewhat higher, and in the summer, lower than in adjacent open areas or in comparable stands of trees such as pine, larch, or oak. Under the canopy of Norway spruce, the effective radiant energy loss is very low, because of the reflective radiation of the canopy. This prevents frosts (MITSCHERLICH 1971). The wind speed is greatly reduced in closed spruce stands at a distance of a few dozen meters. Air circulates between the ground and canopy, owing to temperature gradients between them (PUCHALSKI and PRUSINKIEWICZ 1990). The average relative humidity in a Norway spruce stand is typically 80% in summer and 90% in winter, and generally about 10% higher compared to adjacent open areas. The high humidity results from transpiration of tree crowns and ground vegetation, as well as from reduced wind speeds (MITSCHERLICH 1971). Norway spruce canopies intercept large fractions of precipitation. On average, the throughfall in a Norway spruce stand is about 65% of the bulk precipitation, compared to 78% in European beech. In addition, the high needle surface area arrayed on the twigs of Norway spruce is well suited to intercept fog or cloud water. At higher elevations, canopy interception may

comprise about 50% of the bulk precipitation (STALFELT 1961; MITSCHERLICH 1971; WEIHE 1973; SCHMIDT-VOGT 1986; LÄRCHER 1994).

11.1.6.2. Effects on local climate

At a landscape scale, vast areas of Norway spruce stands may have a significant effect on local climate. This effect is mainly associated with the evapotranspiration of large amounts of water vapor, between 9.8 and 48.8 metric tons of water/ha/day, depending upon stand density and site conditions (SCHMIDT-VOGT 1986). Evaporation raises the relative humidity, and in turn may modify the local light, thermal, and precipitation conditions. Increasing water vapor in the air increases the dispersion of solar radiation. Humid air, having a higher heat capacity, both warms and cools more slowly than dry air. Increased water vapor content in the atmosphere contributes to precipitation. In addition, Norway spruce stands are very effective in mitigating winds. A few rows of Norway spruce trees may reduce wind speeds to about zero. The zone of decreased wind speed leeward of a 25 m high stand extends for about 500 m (BAUMGARTNER 1982; PUCHALSKI and PRUSINKIEWICZ 1990). Norway spruce canopies may intercept large amounts of dust and gases via dry deposition (SCHMIDT-VOGT 1986). According to BAUMGARTNER (1970, 1982) a one hectare stand of Norway spruce over the course of a single year assimilated 45.7 tons of CO₂ and lost 19.4 through respiration, resulting in a net gain of 26.3 tons of CO₂ in biomass as well as about 20 tons of O₂ produced via photosynthesis.

11.1.6.3. Effect on soil

Norway spruce effects on soil conditions are mediated through the amount and quality of aboveground litter, stand structure, associated flora and fauna, and water and nutrient cycling (SCHMIDT-VOGT 1986; PUCHALSKI and PRUSINKIEWICZ 1990). Norway spruce stands may produce between 1 and 7 tons of aboveground organic matter litter every year (SCHMIDT-VOGT 1986). The decomposition rate of Norway spruce litter is very low. However, the type of humus formed in Norway spruce stands also depends on soil type. On alkaline soils, rich in nitrogen and phosphorus with a diversified and active edaphon, humus of the mull type is formed. On acid, poor soils, often dry or too wet, where fungi and mites dominate the edaphon, humus of the moder or mor type is developed (KUNDLER 1963; SCHLENKER 1967; FIEDLER 1979). Soil acidification in Norway spruce stands may occur through increased deposition of acidic compounds present in air pollution, especially SO₂ intercepted by canopies (ELLENBERG 1978). Precipitation redistributes compounds intercepted by canopies as dry deposition to the forest floor and soil. Sulfate ions may increase the leaching of significant amounts of Al, Ca, K, and Mg, increasing acidification in poorly buffered soils.

Many authors report that Norway spruce introduced on sites previously occupied by European beech or pedunculate oak (*Quercus robur*) results in decreased activity of the edaphon, increased formation of humus of the mor type, reduced pH up to 50 cm deep, and other altered physical and chemical soil properties (NIHLGARD 1971; SCHLENKER and DENNO 1971; FIEDLER 1979). Soil porosity appears not to be affected. Planted on previous agricultural land or pasture, Norway spruce improves the soil structure in a manner comparable to that of pedunculate oak (CHALLINOR 1968). Generally, little to no change in site productivity is observed on strongly alkaline, well-buffered eutrophic soils even after many stand rotations or generations of Norway spruce. On the other hand, on slightly alkaline and poorly buffered substrates, the intensification of podzolization process should be taken into account (SCHLENKER 1967; MIEHLICH 1971; ELLENBERG 1978; SCHMIDT-VOGT 1986). Using silviculture, this process can be mitigated by including silver fir or European beech in the Norway spruce stand (ELLENBERG 1978).

11.1.6.4. Retention, erosion prevention, and hydrology

The capacity of Norway spruce stands to retain water depends on the amount intercepted by the tree crowns, ground vegetation (especially mosses), litter, humus, and soil. The canopy, ground vegetation, and litter together cover the surface of the forest soil, mitigating surface runoff. The soils tend to be porous and well drained by the extensive root systems that, in effect, promote the infiltration of rainwater and snowmelt. Consequently, subsurface flow (at greatly reduced flow rates compared to surface runoff) dominates water movement in Norway spruce stands. In this manner the forest prevents erosion and flooding. Norway spruce acts to protect mountain slopes and regulates the local hydrology across its range of geographic distribution. Norway spruce stands are important in governing mountain stream flow as well as the river systems of small and large catchments fed by mountain springs (HESMER and FELDMANN 1953; KULIG 1955; KELLER 1968; SCHMIDT-VOGT 1991). A frequent consequence of excessive surface runoff is reduced water quality. During slow subsurface percolation, characteristic of forested areas, water is filtered and enriched in mineral salts, which improves its clarity and taste (HÜSER 1979; ULRICH 1981; SPOREK and WOŹNIAK 1993). However, in heavily polluted regions, some harmful compounds may pollute the water, owing to the high interception capacity of Norway spruce crowns (SCHMIDT-VOGT 1986).

11.1.6.5. Biocenotic role

Norway spruce is present in many phytocenoses as well as biocenoses, and the ecosystems to which they belong. In some plant communities Norway spruce occurs as an admixture, in others it is an important or even dominant species. The habitats modified, or sometimes created by Norway spruce are home to numerous associated species of fungi, plants, and animals. Many organisms

are indirectly associated with Norway spruce through their ecological linkages through symbionts or parasites (PACZOSKI 1930; MAYER 1976; MYCZKOWSKI 1977; ELLENBERG 1978; SPURR and BARNES 1980; SCHMIDT-VOGT 1986).

11.1.7. Ecological prospects

According to ŚRODON (1977) the fact that the contemporary geographic range of Norway spruce vastly differs from that of past interglacial periods is evidence of an incomplete redistribution of the species since the last ice age (see also Chapter 1). Present day climatic conditions resemble that of the final phase of the Eemian-interglacial, favoring the range expansion of Norway spruce under natural conditions (CZERWIŃSKI 1977). Lowland range expansion will likely displace Scots pine since Norway spruce regenerates very well in the understory of Scots pine stands. However, according to MAYER (1969) and ELLENBERG (1978), the range of Norway spruce will contract and be replaced by the more tolerant European beech along the western range limits and in lower montane sites.

Superimposed on the legacy of the postglacial history of Norway spruce, spanning several millennia, human impacts throughout the last few centuries appear to play an increasingly important role. In many regions artificial regeneration has replaced natural regeneration. Seeds have been transferred to distant sites often out of range of the species. The geographic range of the species has been artificially expanded. Human activities have resulted in the modification of the chemical and physical properties of atmosphere. These are but a few of the changes influenced by human activities. What will be the final effect of these impacts?

Norway spruce, as an evolutionarily young species, is characterized by high genetic polymorphism and plasticity. Populations generally exhibit sufficient adaptation to habitats into which it has been transferred, already in the second generation (HOLZER 1988; MODRZYŃSKI 1995; MODRZYŃSKI and ERIKSSON 2002). The artificial expansion of the range of Norway spruce into adjacent areas should be considered an acceleration of its natural expansion (ŚRODON 1977; MODRZYŃSKI 1999). The introduction of Norway spruce outside of its natural range is sometimes very effective, as was the case in Denmark and Great Britain (SCHMIDT-VOGT 1986).

The most serious threat to Norway spruce today seems to be air pollution, which in combination with other harmful agents, initiated a rapid decline of this species in Europe in the decade 1970–1980. Predictions based on the rate of forest decline observed in the eighties suggested a total elimination of some spruce stands in several decades. However, the rate of decline of Norway spruce fell by the end of the eighties. Presently, one can observe the regeneration of many Norway spruce stands throughout Europe. However, forest decline continues regionally, especially in the mountains and in older stands

(SCHMIDT-VOGT 1991; MODRZYŃSKI 1996, 2003). Improvement in the state of Norway spruce stands is largely dependent upon marked reductions in environmental pollution.

Air pollution has also important indirect impacts via enhancement of UV radiation or global warming. Experiments indicate that Norway spruce is sensitive to elevated doses of UV-B and that high-altitude ecotypes exhibit better-developed defense mechanisms (ROBAKOWSKI 1997; PUKACKI and MODRZYŃSKI 1998). Global warming may influence Norway spruce-dominated ecosystems. Predictions, based in part on rates of fossil fuel combustion, forest fires, and land-use change, suggest a doubling of atmospheric CO_2 concentrations and associated temperature increases of about 2.5°C within the next century. Climate changes of this magnitude would result in a shift of vegetation zones by about 250 km to the north (Fig. 11.13), comparable to the warm period of Holocene some 6000 years ago (FABIAN 1991; SCHMIDT-VOGT 1991). Under this scenario, the range of Norway spruce would retract in the south and in lower elevations and expand into present-day tundra or alpine thickets and meadows. Estimates of the rate of climate warming and its regional effects differ among the simulation models, and some models predict regional cooling mediated by air pollutants (SCHMIDT-VOGT 1991).

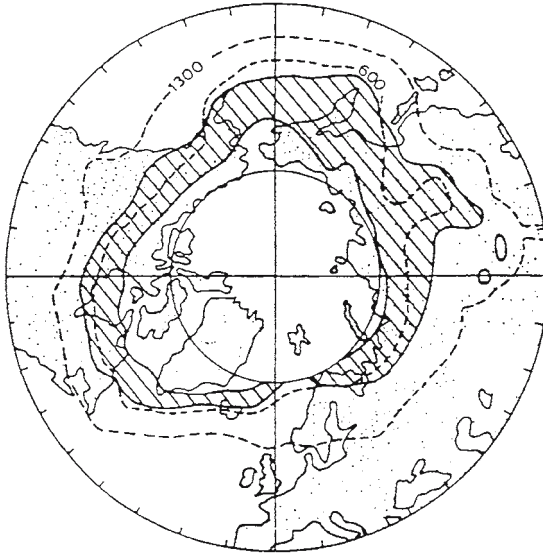


Figure 11.13. Circumpolar boreal zone defined by the contemporary temperature sums (dotted lines) and by the predicted climatic conditions resulting from a doubling of CO_2 concentration in the atmosphere (dashed area). The contemporary temperatures sums are: northern minimum – 600, southern maximum – 1300 degree-day units (after KAUPPI and POSCH, cit. SCHMIDT-VOGT 1991)

In summary, there remain many unanswered questions concerning the ecological prospects of Norway spruce. However, it seems that Norway spruce is a species of high adaptive potential, and that despite the many hazards, remains one of the most important forest tree species of the temperate and boreal zones.

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11.2. COMMUNITY DYNAMICS OF NORWAY SPRUCE

11.2.1. Forest types and plant associations

11.2.1.1. Norway spruce and its community associations

Contrary to expectations, defining the presence and role of Norway spruce in plant communities is a difficult task. Despite advances in the phytosociological exploration of Central European woodlands, a uniform system of classification of forest communities is yet to be developed, and classification proposals advanced by various authors often differ widely. The problems involved in the classification of Norway spruce forests are in part due to the contrasting historical origins of spruce-dominated stands. Norway spruce occurs in stable natural and semi-natural communities that develop and persist in response to certain forest management practices, as well as in communities *in statu nascendi*, which result from the expansion of its geographical and phytocoenotic range.

In a survey of plant communities involving Norway spruce that are described below, an effort was made to accommodate all Norway spruce-forest communities as well as the major communities in which this species is found in Poland (Fig. 11.14). Other details concerning the taxonomic classification and rank of some communities are outside the scope of this paper.

Norway spruce forests in which *Picea abies* is the natural dominant tree species are usually included in the alliance *Piceion abietis* in the order *Vaccinio-Piceetalia* and the class *Vaccinio-Piceetea*, which encompasses the Euro-Siberian acidophilic, oligo- and mesotrophic forest communities with a predominance of coniferous tree or shrub species, understory shrubs, and mesophilic mosses. The range of communities grouped in this alliance is distinctly continental-boreal, and the central part of the range covers the coniferous zone of northern and eastern Europe as well as upper mountain regions of

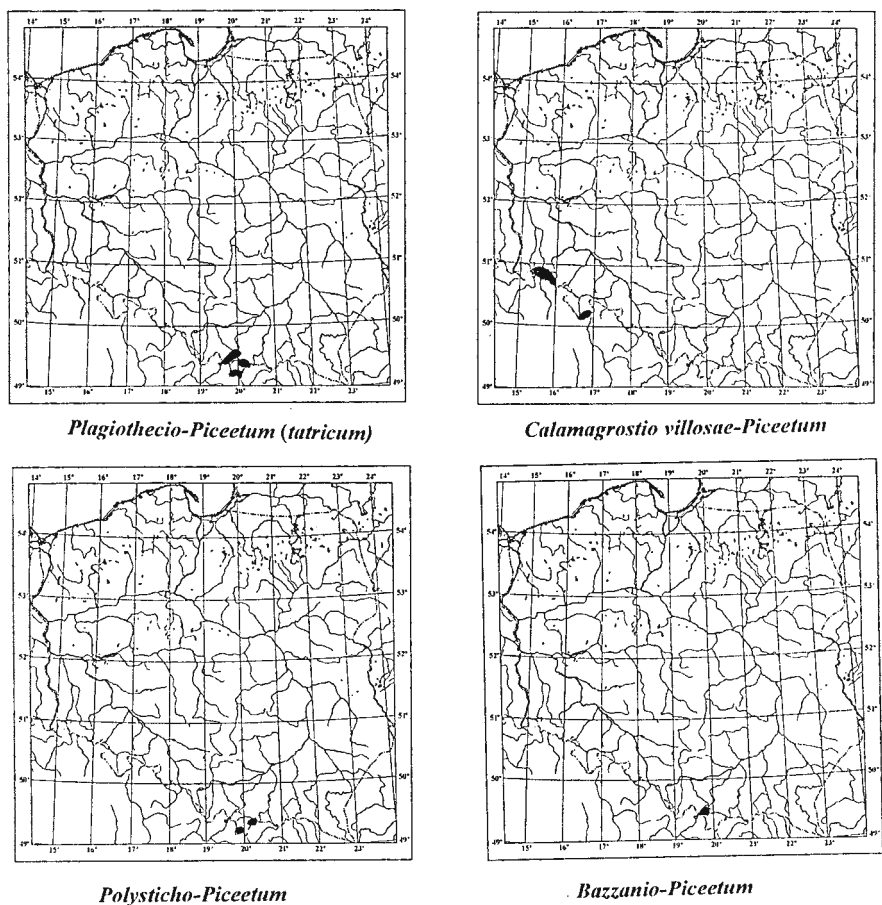


Figure 11.14. Distribution of coniferous forests including Norway spruce in Poland (after MATUSZKIEWICZ W. 2001)

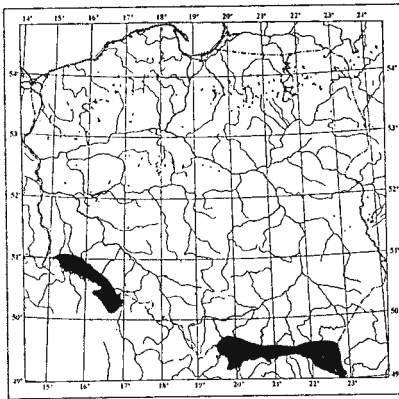
central Europe. The alliance is divided into two suballiances: *Vaccinio-Piceenion*, encompassing the mountain and boreal oligotrophic communities with a dominance of spruce and no beech and fir among the tree species; and *Vaccinio-Abietenion*, to which belong the mesotrophic mountain spruce communities with fir and beech as well as numerous lowland-piedmont species originating, in part, from the class *Quercio-Fagetea*.

The systematics of Norway spruce forests occurring in Poland¹:

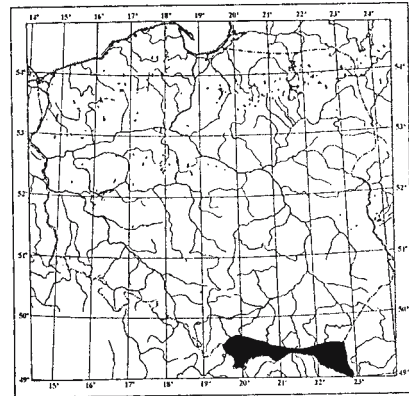
Class: *Vaccinio-Piceetea* BR.-BL. 1939

Order: *Vaccinio-Piceetalia* BR.-BL. 1939

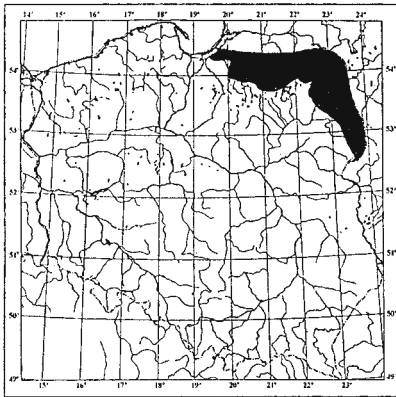
¹ Plant community names follow those of MATUSZKIEWICZ W. (2001)



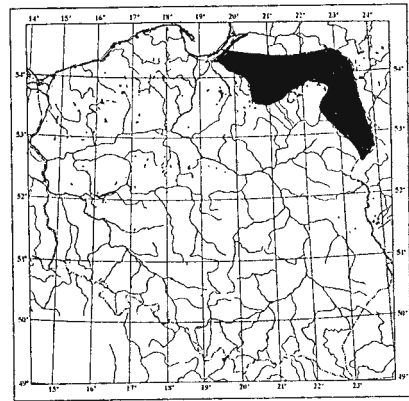
Abieti-Piceetum



Galio-Piceetum



Sphagno girgensohnii-Piceetum



Quercus-Piceetum

Alliance: *Piceion abietis* PAWL. et al. 1928

Suballiance: *Vaccinio-Piceenion* OBERD. 1957

Association: *Plagiothecio-Piceetum (tatricum)* (SZAF. PAWL. et KULCZ. 1932) BR.-BL., Vlieg. et SISS. 1939 em. J. MAT. 1977)

Association: *Calamagrostio villosae-Piceetum* (R.TX. 1937) HARTM. ex SCHLÜTER 1966)

Association: *Bazzanio-Piceetum* BR.-BL. et SISS. 1939

Association: *Sphagno girgensohnii-Piceetum* POLAK. 1962

Association: *Querco-Piceetum* (W. Mat. 1952) W. MAT. et POLAK. 1955)

Suballiance: *Vaccinio-Abietenion* OBERD. 1962

Association: *Polysticho-Piceetum* (SZAF., PAWL., KULCZ. 1923) W. MAT. (1967) 1977

Association: *Abieti-Piceetum (montanum)* SZAF., PAWL. et KULCZ. 1923 em. J. MAT. 1977

Association: *Galio-Piceetum* J. MAT. 1977

11.2.1.2. Natural montane Norway spruce forests

The main areas of occurrence of montane spruce forests are the Alps, Carpathians, and mid-elevation ranges to the south created by the Hercynian uplift. The European center of occurrence and diversity of the montane Norway spruce forests is the Alps. In the Alps, the largest mountain chain in the continent, the diversity of forest habitats reflects the differing climatic condi-

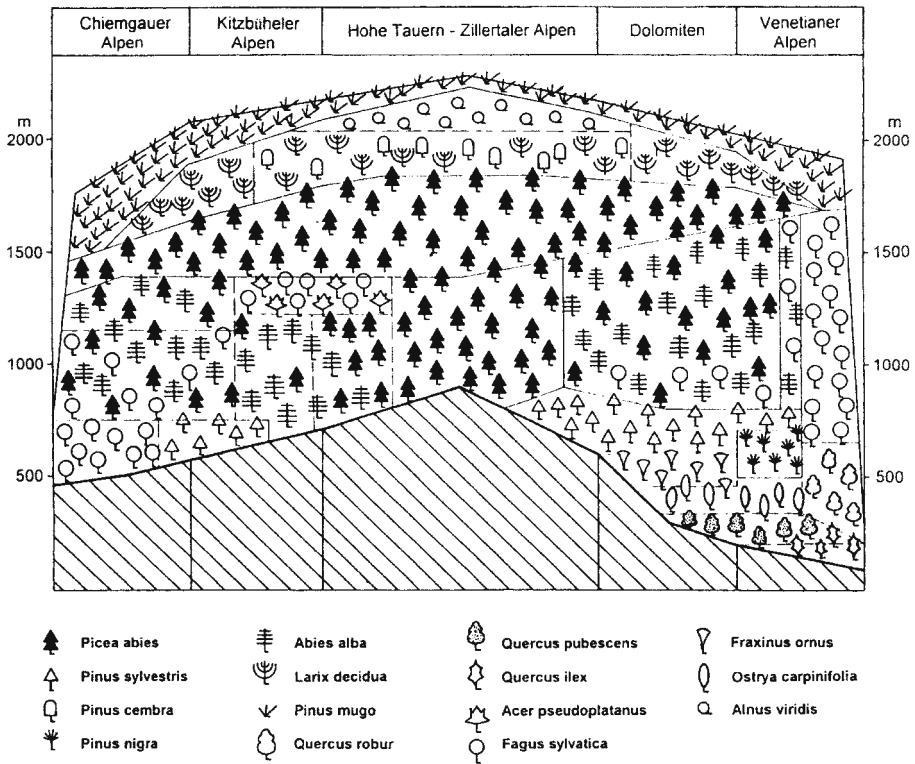


Figure 11.15. Role of Norway spruce in the landscapes of the eastern Alps (after MAYER 1984, modified)

tions among the mountain ranges. In the northern and southern parts, the climate is generally maritime, while in the central part, where the forest-forming role of spruce predominates, the climate has distinct continental features. Despite regional differences in the altitude-related vegetation zones of the Alps, spruce forests are a stable component of the subalpine and upper montane zones. At lower elevations, an increasing proportion of *Picea abies* is observed in forest communities, which transition into mixed coniferous forests with fir and beech (Fig. 11.15).

11.2.1.2.1. *The group of upper subalpine communities*

The upper subalpine zone is the main area of occurrence of the alliance *Piceion abietis* in Poland. Spruce forests occupy a range of habitats there and represent vegetation zones conditioned by altitude and climate. The dominant element of the vegetation of the West Carpathians and Sudety Mts is Norway spruce forest of the suballiance *Vaccinio-Piceenion*. On the basis of geographic floristic differences, two variant regional associations have been distinguished: *Plagiothecio-Piceetum* (*tatricum*) in the Carpathians and *Calamagrostio villosae-Piceetum* in the Sudety Mts.

1. *Plagiothecio-Piceetum* (*tatricum*)

This association is present on shallow, acidic soils with a mor-type humus. They include podzols and gley podzols on a substratum of non-carbonaceous rock. In terms of moisture content, they are classed as moist (MATUSZKIEWICZ J. 1977). The floristic composition of the association, as in the analogous upper subalpine forest of the Sudety Mts, includes many species from the class *Vaccinio-Piceetea* and the order *Vaccinio-Piceetalia*, such as: *Vaccinium myrtillus*², *V. vitis-idaea*, *Lycopodium annotinum*, *Barbilophozia lycopodioides*, *Trientalis europaea*, *Melampyrum sylvaticum*, *Ptilium crista-castrensis* and *Bazzania trilobata*. Of the species characteristic of the alliance *Piceion abietis* (besides *Picea abies*), those commonly found are: *Homogyne alpina*, *Plagiothecium undulatum*, *Sphagnum girgensohnii*, *Luzula luzulina*, *Rhytidadelphus loreus*, and *Listera cordata*, and rarer are: *Hylocomiastrum umbratum*, *Pinus cembra*, and *Moneses uniflora*. The characteristic species of the association include *Plagiothecium undulatum* and *Barbilophozia floerkei* (MATUSZKIEWICZ J. M. 2001). In the spruce-dominated stands there is usually an admixture of mountain ash and, in the Tatras, occasionally *Pinus cembra*, *Betula pubescens* subsp. *carpatica*, and *Larix decidua*. Phytocoenoses with a large proportion of those species used to be assigned to a separate association named *Cembro-Piceetum* (MYCZKOWSKI and LESIŃSKI 1974).

An example of the stand structure of the *Sorbo-Aceretum* among the complex of *Plagiothecio-Piceetum* on Mount Babia is shown (Fig. 11.16A).

The *Plagiothecio-Piceetum* (*tatricum*) found in the western Carpathians as a regional association of upper subalpine spruce forest on a silicate substratum

2 Names of vascular plant species follow MIREK *et al.* (2002), the mosses, OCHYRA *et al.* (2003)

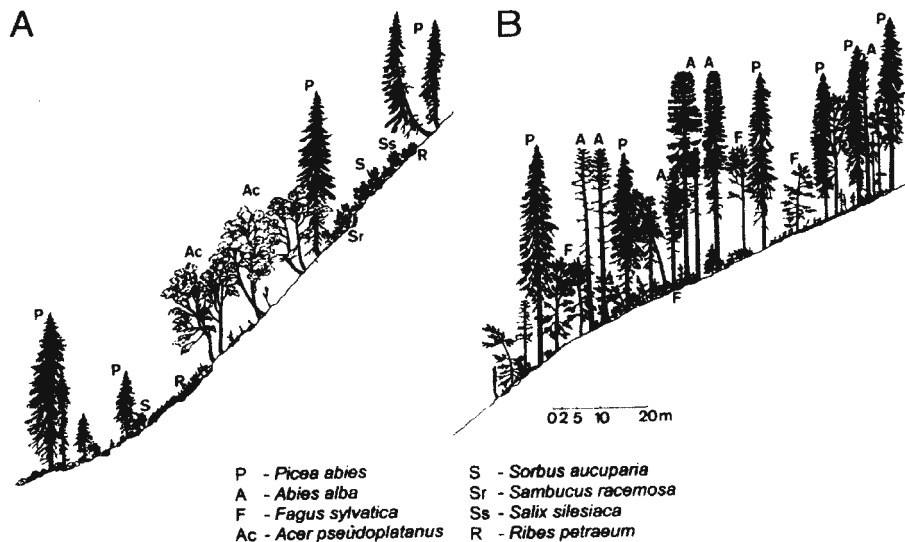


Figure 11.16. Structure of forest stands in mountain communities of Norway spruce. The Mount Babia (after WOJTERSKI and KASPROWICZ 1985)

A – complex *Plagiothecio-Piceetum* and *Sorbo-Aceretum*; B – *Abieti-Piceetum*

differs from that of the Sudety Mts in that it includes a few endemic Carpathian species, e.g. *Luzula flavescens* and *Soldanella carpatica* (MATUSZKIEWICZ W. 2001). The association can be divided into four sub-associations:

- *P.-P. typicum* (syn. *P.-P. myrtilletosum*),
- *P.-P. calamagrostietosum villosae*,
- *P.-P. filicetosum* (syn. *P.-P. athyrietosum alpestris*), and
- *P.-P. sphagnetosum*.

In Poland, *Plagiothecio-Piceetum* phytocoenoses largely occur in the Tatras (SZAFAER *et al.* 1923; SZAFAER and SOKOŁOWSKI 1926; PAWŁOWSKI and STECKI 1927; PAWŁOWSKI *et al.* 1928; MYCZKOWSKI 1955; MYCZKOWSKI and LESIŃSKI 1974; Fig. 11.17). The range of this association also includes the Beskid Sądecki (PAWŁOWSKI 1925), Gorce (MEDWECKA-KORNAŚ 1955), Wzniesienie Gubałowskie (PANCER-KOTEJOWA 1965), Beskid Żywiecki (WALAS 1933, CELIŃSKI and WOJTERSKI 1961, 1978; KASPROWICZ 1996) and Beskid Śląski (WILCZEK and CABALA 1989; WILCZEK 1995).

2. *Calamagrostio villosae-Piceetum*

The association *Calamagrostio villosae-Piceetum* (syn. *Plagiothecio-Piceetum hercynicum*) is the only climate-conditioned, stable forest community in the upper subalpine zone of the Sudety Mts (Fig. 4.5). Apart from the Sudety Mts,



Figure 11.17. Upper montane (subalpine) Norway spruce forests on siliceous substrata

A–B – *Plagiothecio-Piceetum* in the Tatras (Carpathians) (photo K. JAKUSZ)

C–D – *Calamagrostio villosae-Piceetum* on the slopes of Śnieżnik Kłodzki Massif (Sudetes)
(photo A. BORATYŃSKI)

it also occurs in the Ore Mts, the Thuringian forest, the mountains of eastern Franconia, and the Harz.

The altitudinal distribution of this association in the Sudety ranges from about 1000 (840) m a.s.l. to about 1250 (1340) m a.s.l. This association occurs on almost all habitat types on a substratum of crystalline, non-carbonaceous rock, partly metamorphosed to a varying extent, on which develop podzolic soils, and in certain topographic positions, on peat soils with a thick layer of mor-type humus (MATUSZKIEWICZ J. 1977).

Compared with its western Carpathian variant, *Plagiothecio-Piceetum (tatricum)*, this association is marked by a much higher frequency of *Trientalis europaea* and *Melampyrum sylvaticum* as well as the occurrence of *Galium saxatile*. In addition, *Luzula luzulina* is absent and *Luzula sylvatica* is rarely found (MATUSZKIEWICZ J. 1977). Depending on the moisture conditions of the habitats, the association can form any of the three sub-associations:

- *C.-P. typicum* – on fresh and moderately moist soils,
- *C.-P. filicetosum* – on moist soils, and
- *C.-P. sphagnetosum* – on a peat substratum.

In Poland, the association of the Sudetan upper (subalpine) spruce forest can be found in the Karkonosze Mts (MATUSZKIEWICZ W. and MATUSZKIEWICZ A. 1960, 1967, 1975; BORATYŃSKI *et al.* 1987; Figs. 4.5, 4.6, 11.17, 11.18), the Iżera and Orlice Mts (MATUSZKIEWICZ J. 1977), the Sowie Mts (PENDER 1975), the Śnieżnik Kłodzki Massif, and the Bialskie Mts (FABISZEWSKI 1968). The stands of that association in the Sudetes were severely disturbed due to forest decline (Fig. 11.19, 11.20) during the last decades of the 20th century.

3. *Polysticho-Piceetum*

The phytocoenoses of the upper, subalpine spruce forests colonize rendzinas and podzolic soils on a carbonaceous substratum if the limestone layer is covered with silicate deposits. In their upper horizons, the soils tend to be highly acidic, but are neutral or weakly alkaline at greater depths (MATUSZKIEWICZ J. 1977).

A distinctive feature of this community is the co-occurrence of two groups of plant species. The first group includes those characteristic of the class *Vaccinio-Piceetea* and order *Vaccinio-Piceetalia*. They largely constitute the same plants that comprise the core floristic composition of other spruce communities in upper subalpine forests. The other group includes species characteristic of broadleaved forests of the fertile, lower subalpine beech forests, e.g. *Galeobdolon luteum*, *Phyteuma spicatum*, *Epilobium montanum*, *Primula elatior*, *Chrysosplenium alternifolium*, *Dentaria glandulosa*, *Dryopteris filix-mas*, *Carex digitata*, *Adoxa moschatellina*, *Poa nemoralis*, *Paris quadrifolia*, and *Polystichum aculeatum* (MATUSZKIEWICZ J. 1977; MATUSZKIEWICZ J. M. 2001). In the upper subalpine zone of the limestone Tatras, *Polysticho-Piceetum* is the only forest association growing at an altitude of 1,000–1,500 m

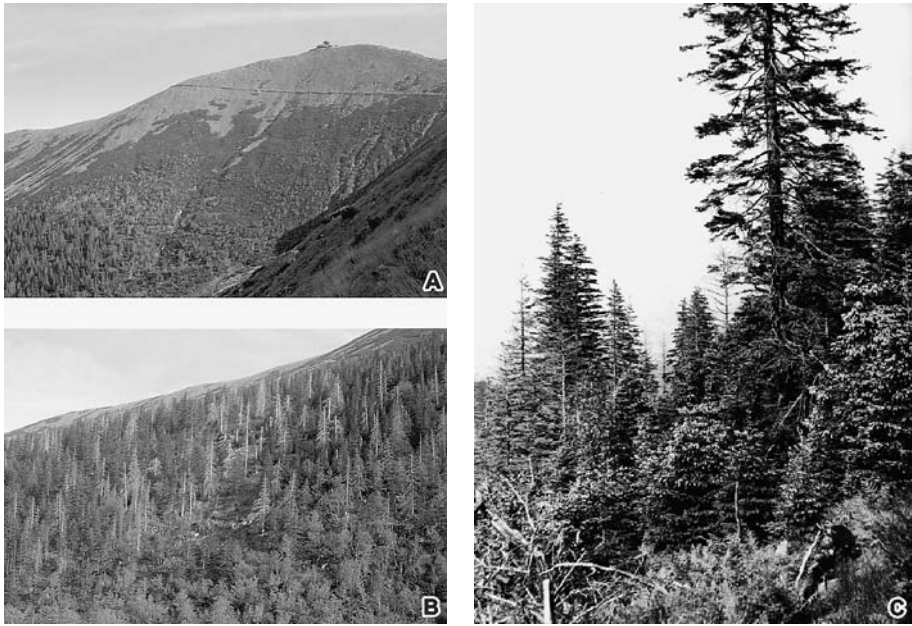


Figure 11.18. *Calamagrostio villosae-Piceetum* in the Karkonosze Mts (Sudetes)
(photo A. BORATYŃSKI)

A–B – N slopes of the Śnieżka Mts. (visible groups of dead trees)
C – trees of various age in the Kocioł Łomniczki glacial cirque

(MATUSZKIEWICZ W. 2001). A small phytocoenosis of this association has also been found in the Pieniny Mts (KULCZYŃSKI 1928; PANCER-KOTEJOWA 1973).

11.2.1.2.2. Lower subalpine communities

The forest-forming role of Norway spruce is less important in the lower subalpine zone mountains than in the upper zone throughout Poland. Beech forests serve as an indicator woodland type in this altitudinal zone. Natural spruce-dominated associations are limited to habitats whose edaphic or microclimatic conditions give spruce a competitive advantage over beech.

1. *Bazzanio-Piceetum*

The only place in Poland where a montane Norway spruce forest occurs on peat (the association *Bazzanio-Piceetum*) is the lower subalpine zone of the Mount Babia massif (BUJAKIEWICZ 1981). A detailed characterization of this association has been given in KASPROWICZ (1996). The *Bazzanio-Piceetum* phytocoenoses develop on the margins of raised and transitional bogs. Norway spruce forms two- or more typically, single-story stands, occasionally with some fir. In the shrub layer, in addition to the natural regeneration, one can find sporadic occurrences of *Sorbus aucuparia* and *Salix caprea*. The herba-



Figure 11.19. Norway spruce decline in the Sudetes during 1980–1985
(photo A. BORATYŃSKI)

A–C – dead stands of *Calamagrostio villosae-Piceetum* in the Karkonosze National Park (1982–1984)

D – dead stand of Norway spruce on the peat-bog in the Izerskie mountains (1988)

E – dead stand of *Calamagrostio villosae-Piceetum* at the forest line in the Karkonosze National Park (1988)

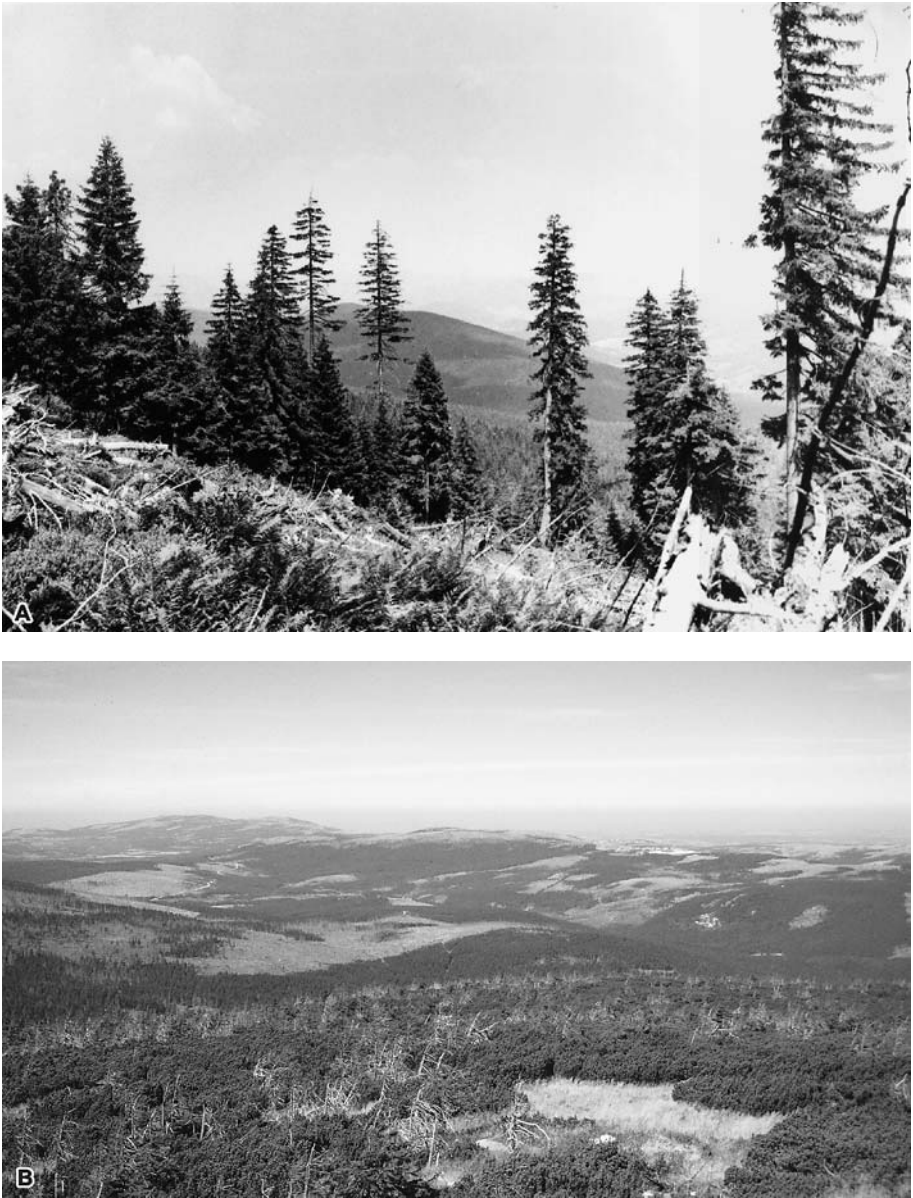


*Figure 11.20. Deforestation of the Sudetes in the last decade of 20th century
(photo A. BORATYŃSKI)*

A – wind-throw area on N slopes on Śnieżnik Kłodzki Massif (1995)
B – deforestation of S slope of Wysoki Grzbiet (Izerskie Mts), view from Szrenica Mt. (1997)

ceous layer is dominated by *Vaccinium myrtillus* and *V. vitis-idaea* along with *Equisetum sylvaticum*, *Carex brizoides*, and *Calamagrostis villosa*. The permanent constituents of the well-developed ground cover include the widespread *Sphagnum girgensohnii* and *Polytrichum commune*, as well as less common *Bazzania trilobata*, *Plagiothecium curvifolium*, and *Dicranum scoparium*. A more mesic version of this association is *B.-P. caricetosum fuscae*, and a drier one, *B.-P. equisetetosum silvaticae*.

2. *Abieti-Piceetum (montanum)*

Despite differences in the definition of *Abieti-Piceetum* among various authors (cf. CELIŃSKI and WOJTERSKI 1978; MEDWECKA-KORNAŚ 1977; MATUSZKIEWICZ J. 1977, MATUSZKIEWICZ W. 2001; DZWONKO 1986; KASPROWICZ 1996), this association includes phytocoenoses with fir and spruce, and typically a small proportion of beech or sycamore maple (Fig. 11.16B). Because of their marked coniferous character, they have more in common with the acidophilic, upper subalpine spruce forests than with the beech forests predominant in the lower subalpine zone. In natural conditions, lower subalpine fir-spruce forests usually colonize flat terraces, upper topographic positions, and hilltops formed by silicate rocks covered with acid, poor soils that are highly susceptible to podzolisation (MATUSZKIEWICZ J. 1977; MEDWECKA-KORNAŚ 1977; CELIŃSKI and WOJTERSKI 1978). In the cool valley floors of deeply cut river valleys, the occurrence of this association is linked to thermal conditions (MATUSZKIEWICZ J. 1977). It is likely that some *Abieti-Piceetum montanum* phytocoenoses are of human origin and arise from the cultivation of spruce and fir on acid, beech forest sites, *Luzulo nemorosae-Fagetum*.

The major forest tree species of this association (i.e. spruce and fir) attain impressive heights. For example, on Mount Babia, trees often exceed 40 m in height with a breast-height diameter near 100 cm (CELIŃSKI and WOJTERSKI 1978; KASPROWICZ 1996). The proportion of fir in the stands varies. It is usually smaller in the highest locations, and generally greater in the Carpathians than the Sudety Mts.

Abieti-Piceetum differs from the upper subalpine spruce forest in that it is comprised of a group of lower subalpine species, e.g., *Athyrium filix-femina*, *Fagus sylvatica*, and *Abies alba*, and lacks subalpine plants. The differences between the association *Abieti-Piceetum* and communities belonging to the sub-association *Vaccinio-Abietenion* consist largely of the absence or sporadic occurrence of species from the class *Querco-Fagetea*.

Two sub-units are distinguished in this association in the Carpathians: a poor *A.-P. m. typicum* and a more fertile *A.-P. m. galietosum* (DZWONKO 1986). The variability of the poor form extends to two variants described from Mount Babia: a typical one with a rare occurrence of beech, and one with *Fagus sylvatica*, perhaps a bit more fertile, with a substantial proportion of this species in both the overstory and shrub layer (KASPROWICZ 1996).

Abieti-Piceetum montanum phytocoenoses occur in the Carpathians at altitudes ranging from about 590 m to about 1 200 m (DZWONKO 1986 and the literature cited there). In the Sudety Mts this community was recorded in the Śnieżnik Kłodzki Massif (FABISZEWSKI 1968), the Karkonosze Mts (MATUSZKIEWICZ W. and MATUSZKIEWICZ A. 1975), the Stołowe Mts (MATUSZKIEWICZ J. 1977), and the Opawskie Mts (KUCZYŃSKA 1972).

3. *Galio-Piceetum*

This community, which exhibits floristic similarities to fir forests of the alliance *Fagion silvaticae* and the sub-alliance *Galio-Abietion*, occurs in the Carpathian lower subalpine zone on a carbonaceous or silicate-carbonaceous substratum. While similar to *Abieti-Piceetum montanum*, especially in its tree and shrub composition, *Galio-Piceetum* is comprised of a larger number of species characteristic of broadleaved forests of the class *Quercio-Fagetea*, such as: *Fagus sylvatica*, *Prenanthes purpurea*, *Eurynchium zetterstedtii*, *Viola reichenbachiana*, *Galeobdolon luteum*, *Dentaria glandulosa*, *Phyteuma spicatum*, *Epilobium montanum*, *Dryopteris filix-mas*, *Carex digitata*, *Atrichum undulatum*, *Paris quadrifolia*, and *Sanicula europaea* (MATUSZKIEWICZ J. 1977). The association has been recorded in many places in the Carpathians, e.g. in the Gorce Mts, Gubałówka Massif, the Tatras, and the Bieszczady Mts (MATUSZKIEWICZ J. 1977).

11.2.1.3. Natural sub-boreal Norway spruce forests

The boreal zone of coniferous forests in Europe encompasses most of the Scandinavian Peninsula with the exception of its northern- and southernmost portions, as well as the northern part of the eastern European Plain. Norway spruce and Scots pine are among the most important forest tree species in this region.

Taiga is the dominant vegetation type in the European boreal zone, which includes communities of dense spruce forests and open pine forests. Spruce forests constitute the climax communities of the boreal zone and occupy most meso- and eutrophic habitats. Only on extreme soil substrates do these communities give way to other types of vegetation. For example, in extremely oligotrophic habitats, dry pine forests predominate, whereas marshy broadleaved forests develop on wet soils, and rich mesic habitats support herbaceous communities.

The phytosociology of the boreal spruce forests of northeastern Poland is well understood, but their taxonomic classification remains controversial. Two separate associations are commonly recognized: a peatland spruce forest *Sphagno girgensohnii-Piceetum* and a lowland, mixed coniferous forest *Quercio-Piceetum*. Other types of spruce-dominated forests described by various authors in ranked associations (CZERWIŃSKI 1977, 1978, 1995; ENDLER 1979, 1987, 1991; SOKOŁOWSKI 1968a, 1968b, 1974a, b, 1980, 1993; SOKOŁOWSKI and KAWECKA 1970) are usually treated as geographic races of assorted

associations of mixed coniferous forest or even hornbeam-oak forest, or as degenerated forms of hornbeam-oak forest (MATUSZKIEWICZ J. 1977, 1988; MATUSZKIEWICZ W. 2001; MATUSZKIEWICZ W. and MATUSZKIEWICZ J. M. 1996).

1. *Sphagno girgensohnii-Piceetum*

Peatland Norway spruce forests develop as a rule on acidic, mesic sites of shallow depressions filled with sedge-moss peat of the blanket-bog or transition type, and occasionally on *Sphagnum* peat. This community is less commonly found on mineral deposits, usually on flat terrain near alder carrs and marshy coniferous forests. The most dynamic and main forest-forming species is Norway spruce, accompanied in the overstory canopy layer by pine and downy birch or, less frequently, by oak, aspen, and sometimes black alder. Some *Sphagno-Piceetum* phytocoenoses have developed as a result of autogenic or human-influenced succession in alder carrs, riparian alder woodlands, or marshy coniferous forests (CZERWIŃSKI 1978, 1995).

In addition to the ubiquitous *Vaccinium myrtillus*, the herbaceous layer includes species typical of Norway spruce forests, such as *Lycopodium annotinum*, *Stellaria longifolia*, *Listera cordata*, *Moneses uniflora*, *Corallorhiza trifida*, *Huperzia selago*, *Sphagnum girgensohnii*, *Ptilium crista-castrensis*, and *Dicranum majus*.

The first to describe this association was POLAKOWSKI (1962), who employed the term *Piceo-Sphagnetum*, later corrected by CZERWIŃSKI (1966). Of all the spruce forest types of lowland Poland, the association *Sphagno girgensohnii-Piceetum* displays most clearly its membership in the alliance *Vaccinio-Piceion* (CZERWIŃSKI 1983). The association *Sphagno girgensohnii-Piceetum* is divided into two subunits: an oligotrophic *S.-P. typicum* and a more fertile *S.-P. thelypteridetosum*. Boreal peatland spruce forests usually occupy small areas in the forests of northeastern Poland in the Mazurian lake region, and the Elbląg upland.

2. *Quercu-Piceetum*

The sub-boreal marshland mixed forest of oak-spruce occurs in Poland on brown podzolised soils, crypto-podzols, or podzols that have largely developed from loamy sands and poorer loams. This forest type is found in local topographic depressions where the groundwater table fluctuates considerably throughout the year, from depths exceeding 1 m to seasonal inundation (MATUSZKIEWICZ J. 1977). The phytocoenoses of this association are usually adjacent to alder carrs or floodplain woodlands occupying the upper topographic positions. They can also be found in hornbeam-oak complexes in locations with the poorest runoff and drainage, occasionally forming a transition zone between alder carrs and coniferous forests (CZERWIŃSKI 1978). In the spruce stands of *Quercu-Piceetum*, there is usually an occasional oak, aspen, silver birch, downy birch, black alder, and rarely Scots pine. There is a well-developed shrub layer in which, apart from saplings of Norway spruce, mountain

ash, and alder buckthorn, one can find hazel and hornbeam typical for more fertile broadleaved forests. The herbaceous vegetation is comprised of coniferous woodland species, such as *Vaccinium myrtillus*, *Pteridium aquilinum*, *Calamagrostis arundinacea*, *Hylocomium splendens*, and *Pleurozium schreberi*, whereas species associated with the class *Querc-Fagetea* include species such as *Anemone nemorosa*, *Carex digitata*, *Melica nutans*, *Corylus avellana*, *Hepatica nobilis*, and *Galeobdolon luteum* (CZERWIŃSKI 1973, 1978).

In addition to the typical forms, one can also find those that are closer to marshy hornbeam-oak forests (*Tilio-Carpinetum calamagrostiestosum*), or to spruce forests with *Sphagnum* peat (*Sphagno girgensohnii-Piceetum*), which are closely related to the *Querc-Piceetum* phytocoenoses (SOKOŁOWSKI 1980). According to CZERWIŃSKI (1978, 1995), this association subdivides into a typical (dry) *Q. -P. typicum* and a humid *Q. -P. sphagnetosum*.

Despite the lack of indicator species, the *Querc-Piceetum* association is the most typical form of Norway spruce forest on mineral soils in countries of the eastern part of, European Plain (CZERWIŃSKI 1978, 1995). In the forests of the geobotanical Northern Division, it occupies some 5.2% of the land area (CZERWIŃSKI 1973).

In northeastern Poland, the following spruce forest associations have been recorded:

Vaccinio myrtilli-Piceetum (SOKOŁOWSKI 1980),
Betulo pubescentis-Piceetum (SOKOŁOWSKI 1980),
Calamagrostio arundinaceae-Piceetum (SOKOŁOWSKI 1968a),
Myceli-Piceetum (CZERWIŃSKI 1978),
Carici digitatae-Piceetum (CZERWIŃSKI 1978),
Corylo-Piceetum (SOKOŁOWSKI 1973),
 and *Piceo-Alnetum* (SOKOŁOWSKI 1980).

11.2.1.4. Other natural communities including Norway spruce

Within the limits of its geographic range, Norway spruce occurs in almost all types of woodland communities. However, its forest-forming role varies with geographic location (Figs. 11.21, 11.22). Above the upper subalpine forests, spruce is a common element of subalpine thicket associations, such as *Pinetum mugo (carpaticum)* and *P.-m. (sudeticum)*. It occurs sporadically in subalpine communities of broadleaved thickets, such as *Pado-Sorbetum* in the Karkonosze Mts (MATUSZKIEWICZ W. and MATUSZKIEWICZ A. 1975), *Salicetum silesiacae* (PARUSEL 1991), and *Athyrio-Sorbetum* on Mount Babia (BORYSIK 1986).

The communities in which Norway spruce is an important species include montane and upland broadleaved forests and fir forests. In the Carpathians they are represented by communities of the sub-alliance *Galio rotundifolii-Abietenion*, which belong to the alliance *Fagion sylvaticae*, and in the up-

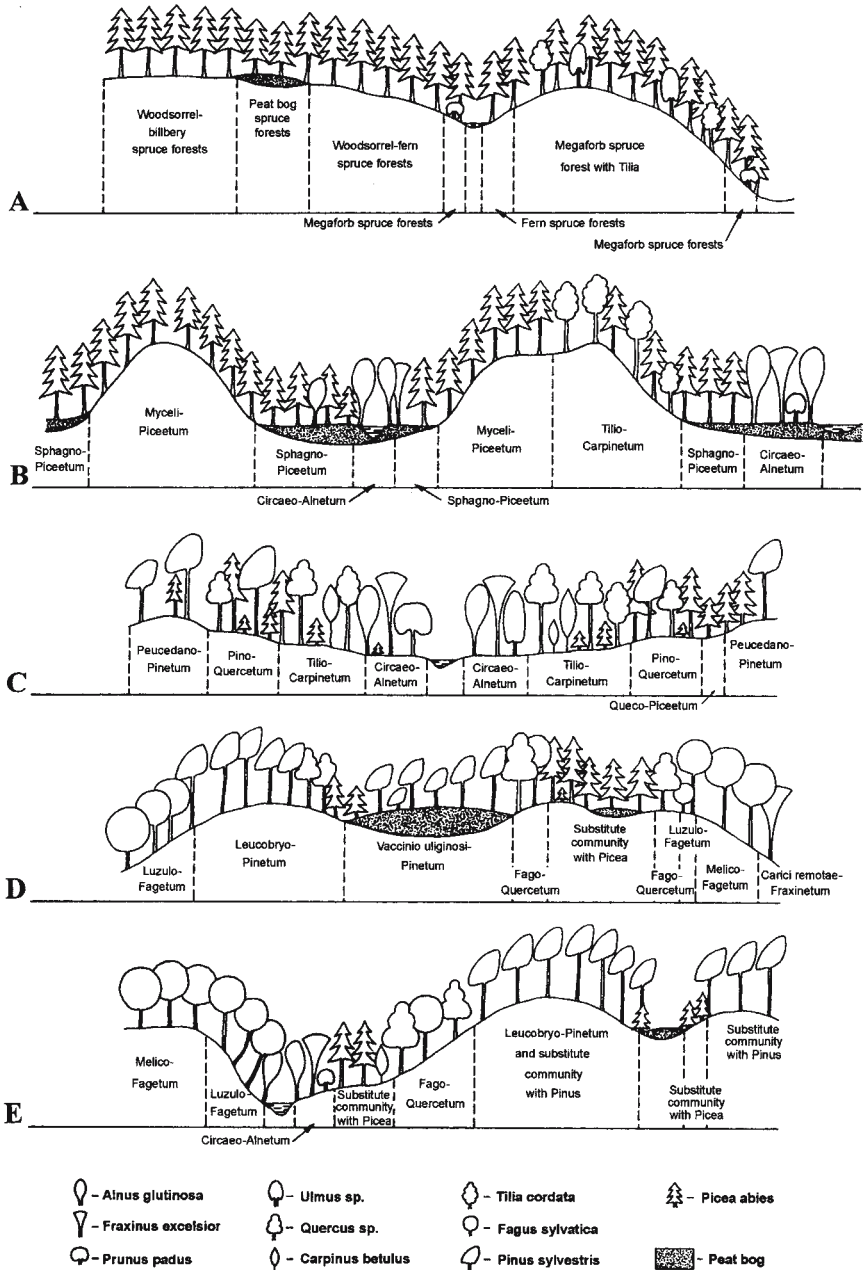


Figure 11.21. Role of Norway spruce in the landscapes of the European Plain (based on A – ABATUROV et al. 1988, B – KWIATKOWSKI 1986, C – FALIŃSKI 1977, D – HERBICH 1982, E – PAWLACZYK unpubl.)

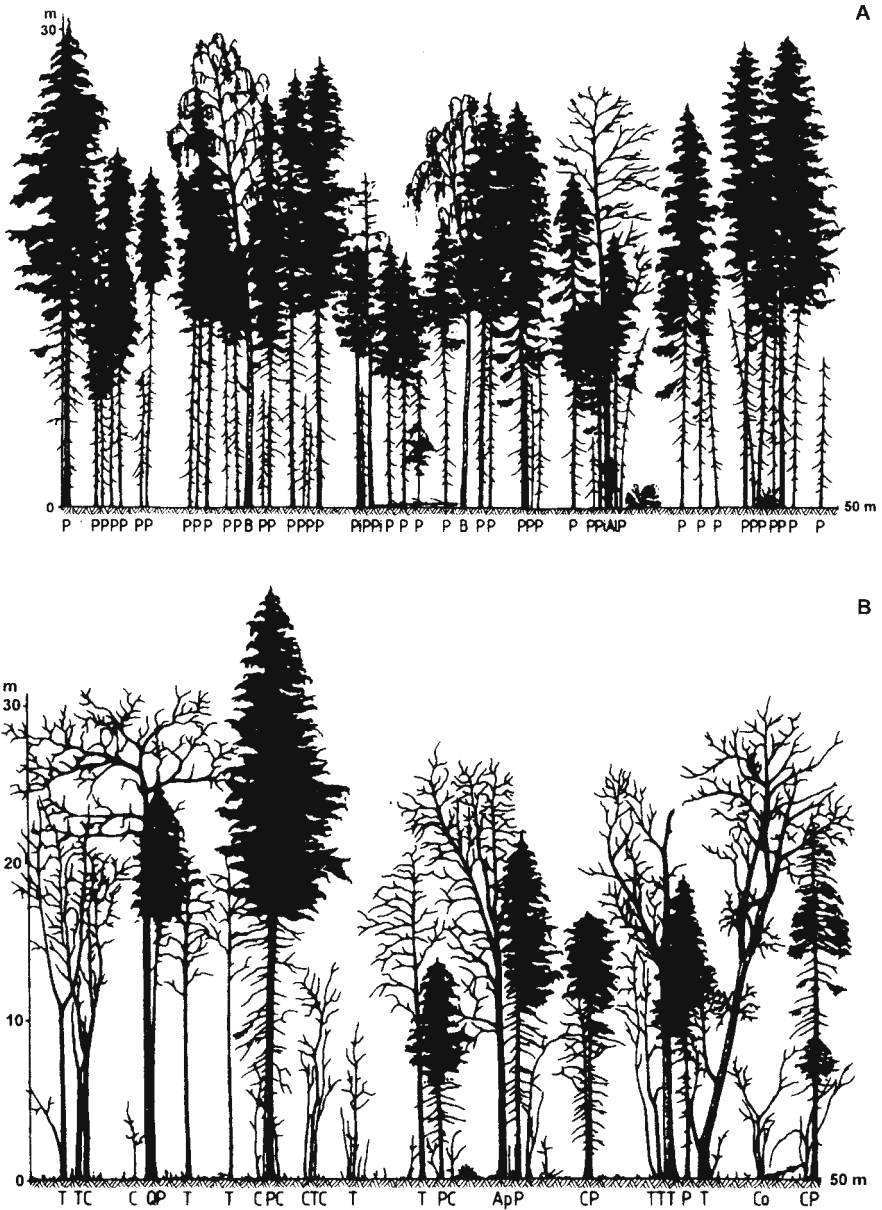


Figure 11.22. Structure of forest stands in selected lowland communities of Norway spruce: A – *Vaccinio myrtilli-Piceetum* spruce forest, B – spruce in *Tilio-Carpinetum* hornbeam-oak forest; P – *Picea abies*, Pi – *Pinus sylvestris*, B – *Betula pendula*, Al – *Alnus glutinosa*, T – *Tilia cordata*, C – *Carpinus betulus*, Q – *Quercus robur*, Ap – *Acer platanoides*, Co – *Corylus avellana* (after SOKOŁOWSKI 1993)



Figure 11.23. Norway spruce in the oak-hornbeam woodland in the Białowieża Primeval Forest (photo J. HEREŻNIAK)

land parts of Poland, by the endemic association *Abietetum polonicum*, described from the Świętokrzyskie Mts by DZIUBAŁTOWSKI (1928).

The ranges of spruce and beech coincide mostly in the lower mountain zones in the foothills and adjacent lowland areas, as well as the western parts of the East-Baltic Lakelands. In these regions Norway spruce is a component of almost all beech forests. The proportion of Norway spruce increases in the mountains and in the higher elevations of the lower subalpine zone.

A complete list of the forest communities including Norway spruce is extensive. Norway spruce can be found in the following associations: fertile broadleaved forests (*Tilio-Carpinetum* (Fig. 11.23), *Galio-Carpinetum*, *Potentillo albae-Quercetum*), mountain and lowland floodplain forests (*Caltho laetae-Alnetum*, *Alnetum incanae*, *Carici remotae-Fraxinetum*, *Circae-Alnetum*, *Ficario-Ulmetum minoris*), alder carrs (*Ribeso nigri-Alnetum* and *Sphagno squarrosi-Alnetum*), mixed coniferous forests and acid oak forests (*Serratulo-Pinetum*, *Quercu roboris-Pinetum*, *Luzulo luzuloidis-Quercetum petraeae*, *Molinio arundinaceae-Quercetum roboris*, *Molinio caeruleae-Quercetum*, *Calamagrostio arundinaceae-Quercetum*), and pine forests (*Cladonio-Pinetum*, *Peucedano-Pinetum*, *Leucobryo-Pinetum*, *Molinio caeruleae-Pinetum*, *Vaccinio-uliginosi-Pinetum*, *Calamagrostio villosae-Pinetum*). Further details are provided in DANIELEWICZ and PAWLACZYK (1998).

11.2.1.5. Norway spruce plantations

Owing to the commercial value of spruce forests and the choice of this species in forest management (see below), pure spruce plantations are a common sight in both mountain and lowland landscapes. Plantations of pure *Picea abies* stands produce various phytocoenotic effects, ranging from a species composition close to those of natural communities to the formation of phytocoenoses with a labile floristic composition impossible to identify with any of the natural forest associations.

Such substitute forest communities with stands of Norway spruce occur in many European montane and lowland landscapes, sometimes occupying a substantial proportion of their area. Moreover, some of these communities represent new plant associations *in statu nascendi*, e.g., Norway spruce-dominated communities developing outside the limits of its natural range.

11.2.2. Ecological properties of Norway spruce affecting stand structure and dynamics

11.2.2.1. Tendency towards a clustered spatial structure of populations

In almost all forests, Norway spruce populations tend to form a clustered spatial structure, termed the biogroup (MYCZKOWSKI 1964; PLESNIK 1971; WOJTERSKI *et al.* 1982; WOJTERSKI and KASPROWICZ 1985; PRUŠA 1985; AWZAN *et al.* 1986/87; SZYMAŃSKI 1989; SCHMIDT-VOGT 1991; ZUKRIGL

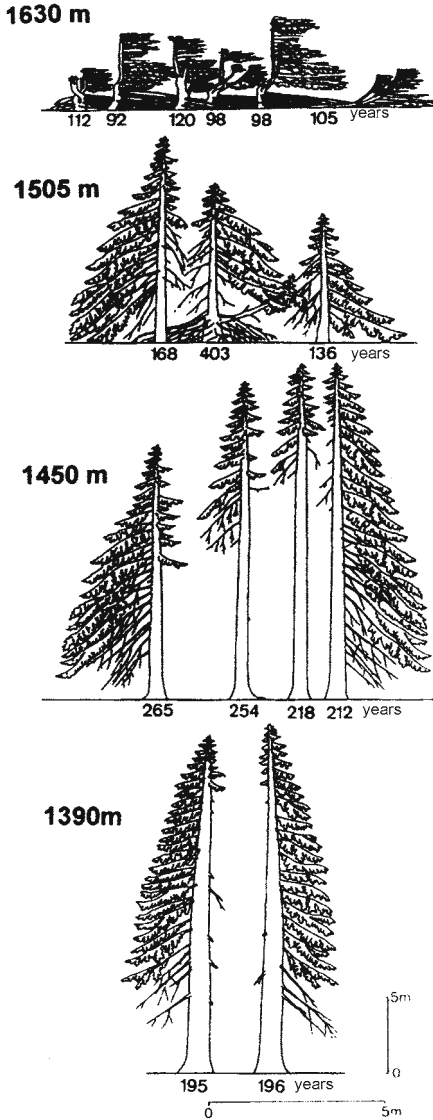


Figure 11.24. The growth habit of Norway spruce biogroups and differences in tree age depending on altitude: above the timberline, at the timberline, in the open-forest, and dense forest zones in the Tatra Mountains (after MYCZKOWSKI 1964)

1991a,b; HOLEKSA 1998; Fig. 11.24, see also Figs. 4.5 and 4.6). This tendency is most striking in extreme ecological conditions, e.g., in the timberline zone. Spruce biogroups there often have the form of polycormons, although sexual reproduction is also favorable to their development. Favorable seedbeds for the germination of seeds and early survival occur close to existing trees or their clusters, since they modify the local microclimate and reduce competition. The structure of the biogroups (the number of stems, their height and diameter) depends on the altitudinal zone and type of timberline. In the compact belt of the upper subalpine forest in the Tatras, biogroups usually number two or three trees with crowns set relatively high and straight rather than tapering. In contrast, Norway spruce form rows within dwarf mountain pine stands and include up to a dozen trees arranged in the direction of the prevailing winds with numerous flag forms, with the lower parts of the stems surrounded by a tangled mass of thick, trailing branches (MYCZKOWSKI 1964).

A clustered structure, although less marked, is also characteristic of compact spruce forests at lower altitudes in the mountains. The size of the biogroups, the number of trees in them, and the distance between groups are strongly dependent on ecological conditions, e.g. the elevation above sea level (MYCZKOWSKI 1964). A biogroup pattern of tree distribution has also been recorded in the spruce forests of lowland Europe (ANTONOV 1988).

The natural clustered structure of Norway spruce stands is so evident that a proposal has been put forward to incorporate this phenomenon in forest stand management. The formation of biogroups is suggested as a means of afforestation at high elevation mountain sites (KARAŚ 1995; MIKUŁOWSKI 1995a,b). In addition, the maintenance of Norway spruce biogroups is accommodated in silvicultural practices in lower mountain elevations and on lowland sites (ANTONOV 1988; ZAJĄCZKOWSKI 1994).

11.2.2.2. Formation of a sapling bank

A characteristic feature of Norway spruce is its highly variable rate in development, depending largely on growth conditions. A relatively frequent occurrence is a substantial lengthening of the juvenile stage of spruce saplings on the forest floor, especially under low light conditions. The period of suppressed growth and survival in unfavorable light conditions can be very long, sometimes exceeding 100 years (ABATUROV *et al.* 1988; KWIATKOWSKI 1986; STEIJLEN and ZACKRISSON 1987). Consequently, there is often a very poor correlation between the age and size of mature trees (see, e.g., KOOP 1989; STEIJLEN and ZACKRISSON 1987). An ecological consequence is an accumulation of individuals ready to respond with accelerated growth to any amelioration in the conditions, e.g. the appearance of a gap in the tree stand due to the death of a mature tree (a seedling bank – GRIME 1979, a sapling bank – WHITMORE 1982). Seedling or sapling banks have been reported in a variety of woodlands including: upper subalpine spruce forests (FISCHER 1992), spruce forests on mineral soils in eastern Europe (ABATUROV *et al.* 1988), and pine-spruce forests of Scandinavia (STEIJLEN and ZACKRISSON 1987).

11.2.2.3. Regeneration on the forest floor and on dead wood

An ecological characteristic specific to Norway spruce seedlings is the relationship between survival and microtopography. The probability that a spruce seedling will survive and be recruited into successive growth stages is much higher on micro-elevations than in forest floor depressions (ABRAZHKO 1989; ABATUROV *et al.* 1988; HOLEKSA 1998). A special case is the commonly noted linkage between the regeneration of young spruces and the pit and mound topography resulting from tip-up mounds of old fallen individuals (SKVORTSOVA *et al.* 1983; HOFGAARD 1993a). Seedling spruces are most abundant on such windthrow mounds and on decaying logs; they are absent in the hollows (Figs. 11.25, 11.28). The density of young trees is also much higher on the mounds and in their vicinity than on an undisturbed forest floor (HOFGAARD 1993a).

A clear relationship exists between the distribution of young spruces and decaying coarse woody debris. Clusters of seedlings growing on decomposing logs on the forest floor are a characteristic feature of both natural mountain forests of the high Alps and Carpathians (Fig. 11.25) or spruce forests of Scandinavia and, e.g., the Białowieża hornbeam-oak forest in eastern Poland.

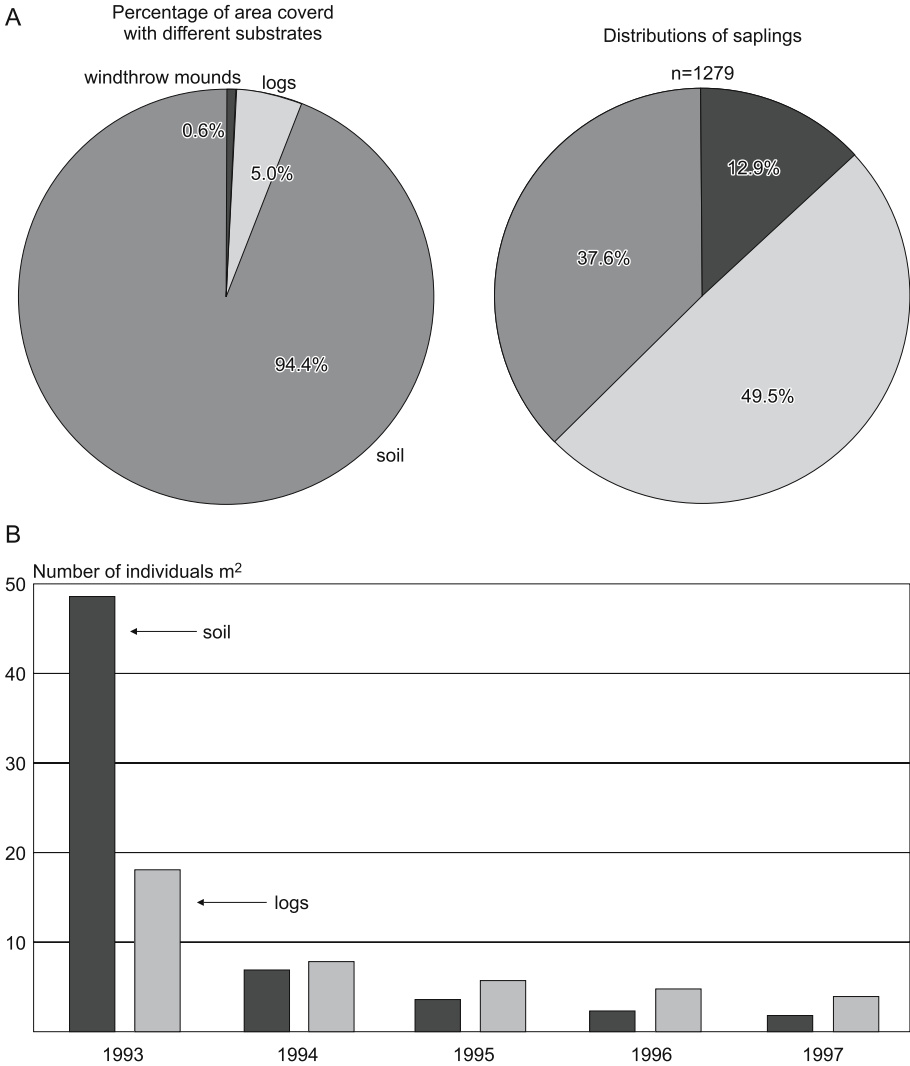


Figure 11.25. The importance of the micro-habitats of decaying logs for Norway spruce regeneration in the upper subalpine coniferous forests of Mount Babia (after HOLEKSA unpubl. data)

A – distribution of Norway spruce saplings on various substratum; B – changes of individual density of a seedling cohort established in 1993, depending on substratum

Norway spruce originating in a decaying wood micro-habitat will very likely reach maturity. Where log decay rates are very slow, such an origin can be recognized even in 200-year-old trees (HOFGAARD 1993a). One consequence is

the development of a characteristic, stilt-like tree form (PRUŠA 1985) arising from root growth in the most decomposed, outer parts of a fallen log. This often produces a linear arrangement of trees, sometimes erroneously suggesting a man-made origin of the stand and often described from mountain spruce forests (PRUŠA 1985; KORPEL 1989a; KASPROWICZ 1996). The removal of dead spruce logs from upper subalpine forests can seriously impact the regeneration of this species (HOLEKSA *et al.* 1996; HOLEKSA and CIAPAŁA 1998).

11.2.2.4. The role of vegetative propagation

Norway spruce sometimes reproduces vegetatively. The basic mechanism is layering, or root formation on lower branches that contact the soil, often additionally pressed down by snow or accumulated litter. Such bent branches grow adventitious roots rather easily. As this secondary root system develops, the tip of the branch gradually changes its originally plagiotropic growth direction to orthotropic. Depending on the development of its rootstock and the strength of the connection with the maternal tree, the new individual quickly becomes more or less independent. Greater growth is commonly observed in the thickness of a rooted branch beyond the rooting junction than in the section connecting it with the maternal tree (LOKVENC 1959/60; KUOCH and AMIET 1970).

In certain ecological conditions, e.g., the timberline zone, this type of propagation is widespread and determines the stability of an entire population. In alpine conditions, the rooting of tree branches is one of the main mechanisms of spruce biogroup formation. It is a key factor enabling the population to survive in extreme conditions in which the efficiency of sexual reproduction *via* seed, drops almost to zero (KUOCH and AMIET 1970; TRANQUILINI 1979; PAWLACZYK 1991).

11.2.2.5. Norway spruce windthrow mounds

Norway spruce trees are highly susceptible to being broken or felled by the wind. As a result, it is the major species contributing to the development of windthrow mounds in boreal forests of the European Plain. For instance, in the Białowieża hornbeam-oak forest in eastern Poland, nearly 80% of the total number of mounds are those produced by the blowdown of Norway spruce (FALIŃSKI 1976, 1978).

The development of windthrow mounds, and hence a microrelief consisting of associated pits and mounds, is one of the major disturbance factors in a natural forest ecosystem (SKVORTSOVA *et al.* 1983; SCHÄTZL *et al.* 1989; JONSSON and DYNESIUS 1993). By disrupting the continuity and mixing of soil horizons, the mounds modify the process of soil formation. The scale of the phenomenon can be large. For example, in the spruce forests of the Kologrivskij Les Nature Reserve in Valday, VASENEV and PROSVIRINA (1988) estimate that the windthrow pit and mound microrelief of up to 300 years in

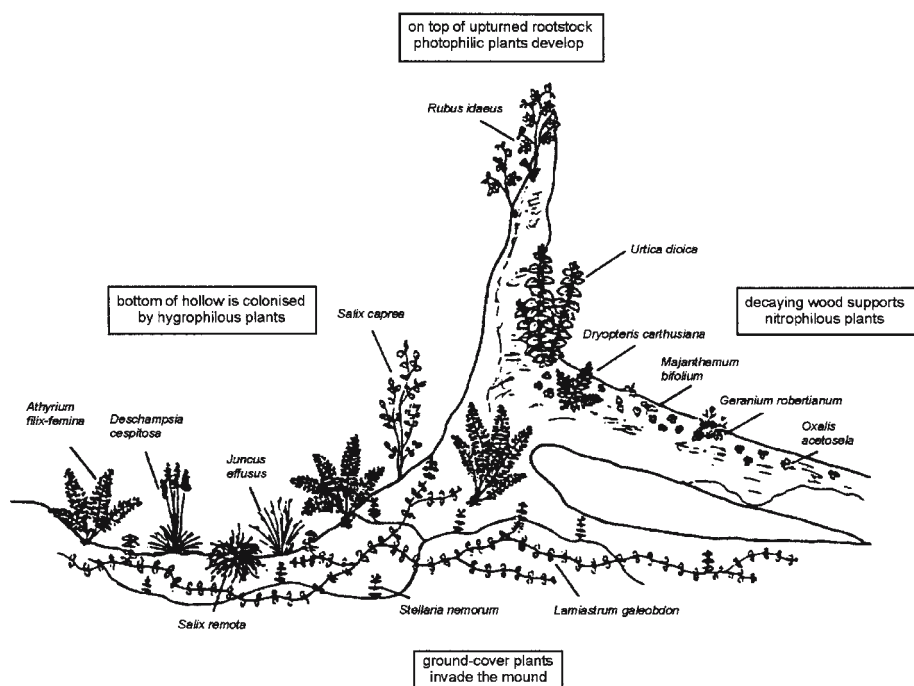


Figure 11.26. Colonization of Norway spruce tip-up mounds by plants. The Białowieża National Park (after MASALSKA unpubl. data)

age can occupy 10–30% of the forest floor surface area. Moreover, the entire forest floor has been disturbed in this manner several times during its Holocene history. The situation is similar in other forests with Norway spruce in the boreal zone (SKVORTSOVA *et al.* 1983).

The mixing of soil horizons is not the only way in which windthrow mounds affect forest ecosystems. Equally important is the amount of dead wood deposited and decaying on the forest floor. An inventory taken by FALIŃSKI (1976) in the Białowieża hornbeam-oak forest estimated 200 to 450 broken trees and associated windthrow mounds per 100 ha accumulated over the year on the floor of this type of forest, most of which were spruce-related. The volume of the mounds was $60\text{--}70\text{ m}^3\text{ ha}^{-1}$. Over a 10-year period, two-thirds of the forest area had intensive accumulation and decomposition of fallen trees.

Decaying logs and associated root plates are gradually colonized by vascular and nonvascular plants (HACKIEWICZ-DUBOWSKA 1936; MASALSKA unpubl.; Fig. 11.26). Norway spruce seedlings are among the species favoring such habitats. The role of windthrow mounds in a forest ecosystem is one that is hard to overestimate.

11.2.3. Structure and dynamics of forests including Norway spruce

11.2.3.1. Structure and dynamics of Norway spruce forests

There is ample evidence that Norway spruce forests can persist and function owing to the dynamics of a mosaic of small-scale canopy gaps. Single or small group tree falls form canopy gaps that are filled with the next generation of trees. Many authors believe that this is the basic process of vegetation dynamics occurring under natural conditions, both in high-elevation spruce forests (ZUKRIGL 1991a, b) and in the boreal zone (STEIJLEN and ZACKRISSON 1987; HYTTEBORN *et al.* 1987; LEEMANS 1991; QINGHONG and HYTTEBORN 1991; HOFGAARD 1993a,b; HÖRNBERG *et al.* 1995). Gap replacement dynamics are also suggested indirectly by data on the stand structure of Norway spruce forests in eastern Europe (KARPOV 1983; JAROSLAVTSEV 1986; GUSEV and JAROSLAVTSEV 1988; ABATUROV *et al.* 1988).

The Central European school of forest ecology, while not denying the role of canopy gaps in regeneration and recruitment, also takes into account differences in the properties of forest communities at larger spatial scales, ranging from 0.5 ha to more than 10 ha. A forest is conceived as a mosaic of structurally fairly homogeneous patches representing the particular stages of a developmental cycle termed: initial, optimal, and final. Within each stage, developmental sub-stages are distinguished. The differences in the properties of tree stands reflecting the forest developmental stages have often been described and mapped in the spruce forests of the central European mountains (e.g. KORPEL 1981, 1989a,b; CEITEL *et al.* 1989, 1992–94; SANIGA and SKLENDER 1989; JAWORSKI and KARCZMARSKI 1989; PARUSEL and HOLEKSA 1991; HOLEKSA 1998; JAWORSKI 1998; Fig. 11.27). The absence of similar maps and descriptions from other geographical regions where Norway spruce forests occur is due to the limited range of this conception of forest dynamics, rather than to a lack of suitable empirical data.

Stand-replacing disturbances are of major importance in forest dynamics (Figs 11.28, 11.29). In high-mountain conditions, these disturbances are typically windthrows, and sometimes outbreaks of leaf- and wood-boring insects that usually occur when trees have been weakened by other stress factors. Under natural conditions, such disturbances seem to be episodic, but natural events in the life of a subalpine forest, posing no threat to the forest as a plant formation. As a rule, the stand-replacing disturbances initiate vigorous regeneration. A key species, at least in Poland, is the mountain ash (*Sorbus aucuparia* var. *glabrata*), normally a minor species in the community. Throughout the course of regeneration it assumes a dominant role (LOCH 1991, 1992, 1998; CEITEL 1994a). Alternative regeneration pathways may occur. For instance, direct regeneration of a Norway spruce forest may occur *via* the 'sapling bank' growing on the forest floor, or through a successional pathway whose stages are dominated by the birch, *Betula pendula* (FISCHER *et al.* 1990).

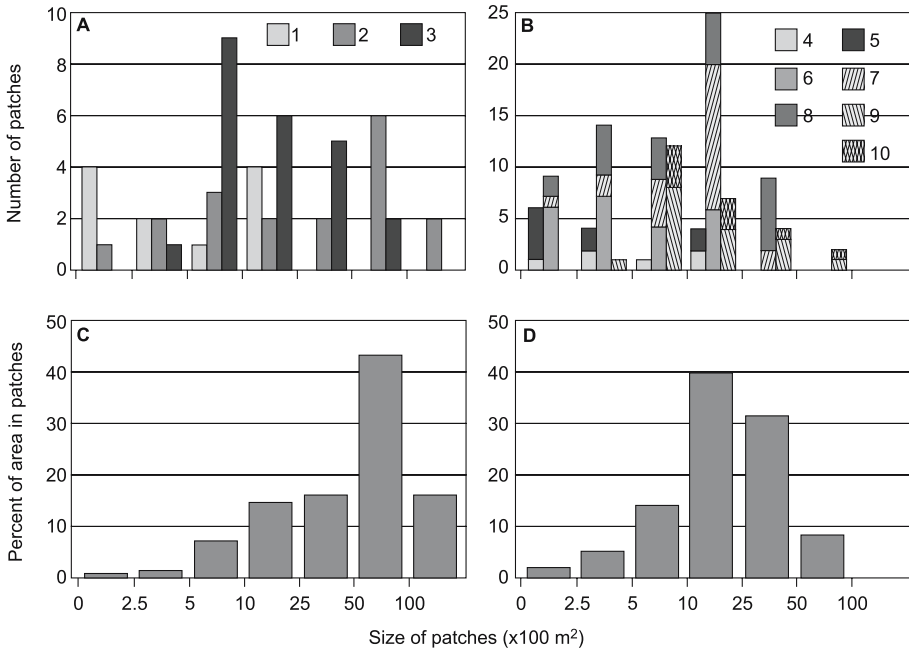


Figure 11.27. The structure of an upper subalpine Norway spruce forest – a mosaic of developmental stages of the tree stand, Mount Babia (after HOLEKSA 1998)

Regeneration following large-scale disturbance can be relatively easily disrupted or even stopped by human activities. For instance, it is not well understood what role is played by remnant dead trees, both standing (cf. suggestions of LOCH 1991, 1992 concerning their part in the dispersal of ornithochorous mountain ash) and those decaying on the forest floor.

11.2.3.2. Structure and dynamics of pine-spruce forests

Mixed pine and spruce coniferous forests are common in the eastern part of the European Plain. However, while seemingly very similar, such communities may differ widely in origin (PACZOSKI 1925, 1930; ŻYBURA 1983; STEIJLEN and ZACKRISSON 1987; ASTROLOGOVA 1990). The results of some Scandinavian research (STEIJLEN and ZACKRISSON 1987) suggest that in these geographic conditions, pine-spruce forests form a stable ecological system. The regeneration and hence the perpetuation of both pine and spruce populations is possible. The age structure of the two populations is diversified and indicates that there were periods in the past that alternately favoured the establishment and survival of individuals of one or the other species. Such 'pulsating' development of spruce and pine regrowth may be due to climatic fluctuations.

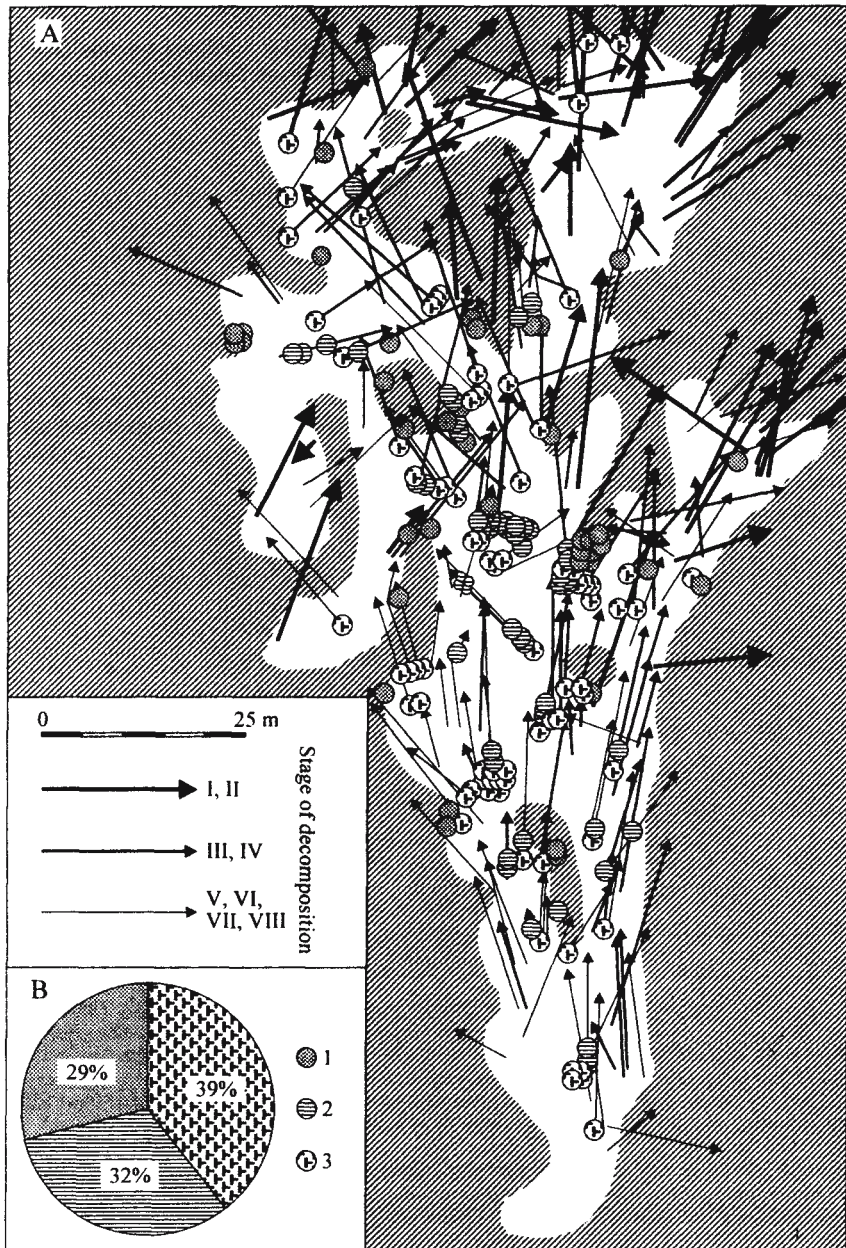


Figure 11.28. The role of windthrow in the dynamics of the upper subalpine Norway spruce forest. A windthrow gap, the distribution of spruce logs in various stages of decay, the distribution, and the proportion of saplings growing on different substrate types. Mount Babia (after HOLEKSA 1998)

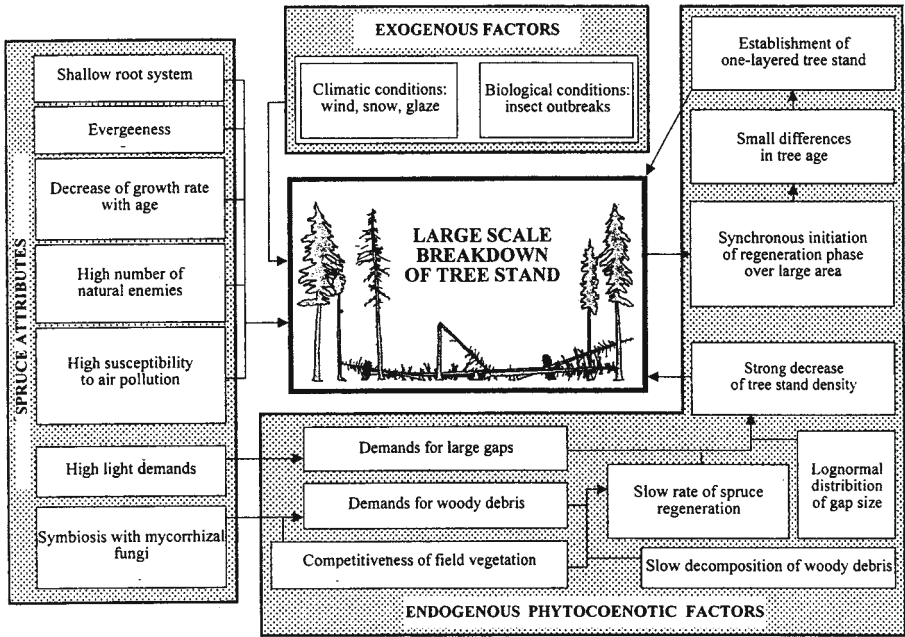


Figure 11.29. The role of various factors in a large-scale decline of forest stands in an upper subalpine Norway spruce forest (after HOLEKSA 1998)

However, the structure of pine-spruce forests is usually different. It is common to find stands with an almost even-aged pine population lacking young individuals in combination with a younger and more age-diversified population of spruce (CZERWIŃSKI 1967, 1978; JAKUBOWSKA-GABARA *et al.* 1991). Such a stand structure suggests that these communities have developed as a result of the colonization of pine stands by Norway spruce. Spruce can gradually come to dominate the entire stand structure of a community (cf. the simulation by LEEMANS and PRENTICE 1987). Thus, a coniferous forest, with the participation of pine, might be merely one of the stages of succession leading to a spruce forest. The fact that such systems are a permanent and recurring element of the landscape would then seem to be the result of a repeating action of a factor blocking succession by disturbing the structure of the forest ecosystem. Several proposals have been put forward as to what this factor may be, e.g.:

- recurrent surface fires that destroy the spruce population, but leave the pines unharmed owing to differences in the biology of these two species;
- mass outbreaks of insects, primarily Norway spruce cambium-feeders, such as the eight-toothed bark beetle *Ips typographus*, which may result in a repeated destruction of the spruce population, thus allowing the pine population to regenerate;

- the action of pathogenic fungi, especially the white root-rot fungus, *Fomes annosus*, which spreads when the spruce population has attained suitable density; and
- human impacts, arising from clear cutting or transitional agricultural use; pine is the first tree species to colonize an area during the course of succession.

In North America there are two species, jack pine, *Pinus banksiana* and black spruce, *Picea mariana*, which follow the same pattern. The spruce colonizes the interior of even-aged stands of jack pine that have developed after fire and gradually dominate the stand, unless there is another disturbance favorable for pine regeneration (CARLETON 1982).

11.2.3.3. *The role of Norway spruce in the dynamics of mixed forests*

Owing to its ecological and biological properties, Norway spruce often plays a larger role in the dynamics of mixed forests than expected based on its proportional contribution to a forest stand (Fig. 11.30). The process of degeneration and regeneration of forest phytocoenoses with an admixture of spruce can lead to changes in the frequency of this species. In the Białowieża Primeval Forest in eastern Poland, the maintenance of a large deer population for hunting has altered forest structure by increasing the proportion of Norway spruce at the expense of other tree species. Many hornbeam-oak forests became spruce-dominated in recent history. The regeneration that occurred after the game impacts had diminished gradually began re-establishing the former species composition. However, the forests still suffer secondary effects in the form of a higher incidence of windthrow, since the Norway spruce have attained heights in excess of the canopy of the hornbeam-oak forest, thus becoming more susceptible to the wind. However, the impact of large herbivores is not always favorable to Norway spruce establishment. SMIRNOV (1981) has shown that in eastern Europe, the bark scraping of young Norway spruce by elk inhibits the invasion of this species into stands of birch and aspen by opening the way to pathogenic fungi.

A mass disappearance of spruce from a stand can initiate processes that act as a temporary disturbance in the structure and function of the phytocoenosis, i.e., its transitory degeneration, or even regression. For instance, in the Białowieża National Park in Poland, one can observe the disappearance of Norway spruce from phytocoenoses in a mixed *Pino-Quercetum* forest, possibly in response to a change in water conditions. This development has led to the destruction of the entire structure of these phytocoenoses (FALIŃSKI 1988). Mass blowdown of Norway spruce in *Tilio-Carpinetum* hornbeam-oak forests, in turn, leads to quantitative changes in the structure of the phytocoenosis and initiates the processes of regeneration (KAWECKA and GUTOWSKI 1988; KAWECKA 1991). Thus, in those forests where Norway spruce forms part of the stand, the species tends to initiate both changes in and

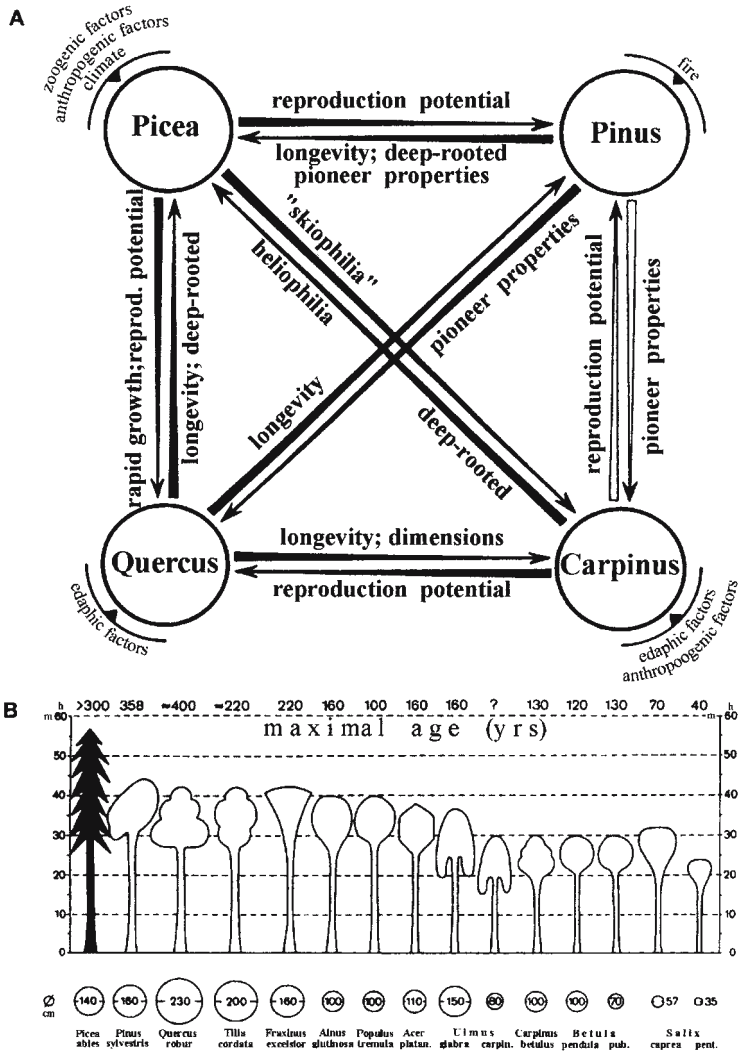


Figure 11.30. Properties of Norway spruce determining its role in multi-species forest stands in the lowlands. A: Biological properties and external factors determining the role of major forest-forming species (FALIŃSKI 1986). B: Maximum sizes and ages attained by particular species (FALIŃSKI 1977)

possible degeneration of the phytocoenoses. The dynamics of this species is often the factor governing the dynamics of the entire forest.

11.2.3.4. The timberline zone as a dynamic ecological system

Norway spruce is one of the few European tree species whose range extends to the farthest woodland and shrubland zones in the north as well as up to high-elevation mountain sites. It also plays a basic structural role in forest communities up to the tundra and timberline limits of its occurrence.

The timberline, like other range limits of a forest, is controlled by a number of abiotic and biotic factors associated with the climate, soil, and the biological properties of species. These factors affect vegetation in a complex way, influencing the species composition and physiognomy of tree stands and their altitudinal boundaries (cf. WARDLE 1993, after HEIKKINEN *et al.* 1995). The Norway spruce populations at the range limits are in a dynamic equilibrium: their existence and function depend on a complex web of factors, including the efficiency of sexual reproduction, growth, and vegetative propagation, as well as pollen and seed dispersal from lower elevations.

A characteristic feature of the forest physiognomy at the timberline is the decreasing stem density of tree stands with increasing altitude above sea level. A forest community generally maintains its floristic composition up to the point where the forest structure fragments into dispersed groups of individuals numbering fewer than several dozen trees (SOKOŁOWSKI 1928; MYCZKOWSKI 1964). Above this zone only single trees can usually be found. With an increase in altitude there is a decrease in the average height and diameter of trees, and an increase in the length of their crowns (ZIENTARSKI 1989). There are also changes in other morphological features of Norway spruce, e.g., the size of needles and cones, or the thickness of the outer bark (LEWICKI 1985). Flag forms of spruce typical of the timberline zone are an indicator of the prevailing wind direction (GAŚNICA-BYRCYN and KOT 1987). A reduction in the sexual reproduction potential in the timberline zone is compensated by an increased ability of Norway spruce to regenerate vegetatively. Consequently, the species can adapt to environments extremely unfavorable to trees, forming characteristic tree islands known as biogroups.

11.2.3.5. Norway spruce in successional processes

Norway spruce is not a pioneer species, but several of its life history traits, such as a high reproductive potential and capacity for seed dispersal, render it an active player in both primary and secondary succession. An example of primary succession is the spread of Norway spruce to raised bogs undergoing succession to forest. This occurs in one of the final stages of succession, determined by the prior development of habitats providing 'safe sites' for spruce saplings. Such habitats are usually the basal parts of trunks, windthrow mounds, and fallen pine logs, the first tree species to colonize peat bogs (KUKIER 1992). Spruce colonization of peat bogs is usually greatly accelerated by wetland drainage caused by human activities (NEUHÄUSL 1975).

Both at high elevations and in the lower subalpine zone, Norway spruce, together with birch and mountain ash, are among the first tree species to colonize scree (OSTAPENKO and CHRISTIUK 1982) and rock outcrops. Norway spruce is the key species taking part in secondary succession in clearings in the Carpathians following cessation of sheep grazing (MICHALIK 1990; CHMIEL, personal communication; Fig. 4.4). The invasions of Norway spruce on the abandoned pastured lands above tree line can also result from global warming (DULLINGER *et al.* 2003, 2004). This process also occurs in clearings in the lower subalpine zone in the primary habitats of beech forest. In these conditions, Norway spruce is an important facilitator in the process of succession, radically altering the floristic composition of the community. The expansion of spruce onto clearings is observed even when they are still being grazed. The trees develop characteristic pasture forms in response to sheep browsing.

Norway spruce appears relatively early in succession of lowland oligotrophic and mesotrophic habitats of abandoned agricultural lands. Some Norway spruce forests, such as those in Scandinavia whose present-day structure resembles that of natural communities, have developed over a mere 200 years of succession on former pastures (BRADSHAW and HANNON 1992, SZWAGRZYK 1994).

Norway spruce plays a special role in secondary succession following the stand-replacing fires common in coniferous forests. There is an interesting hypothesis that the two-layered pine-spruce stands common in eastern Europe, including northeastern Poland, represent one of the stages of secondary succession after fire (SIRÉN 1955, CZERWIŃSKI 1967). Following fire, the sites were presumably colonized initially by pine, followed by Norway spruce under the pine overstory. Successive stand-replacing fires may occur or surface fires may eliminate the fire-sensitive spruce from under the canopy of pine, which is relatively resistant to a surface fire. This model probably fits the historical dynamics of some pine-spruce forests (CZERWIŃSKI 1967; FALIŃSKI 1986). Changes in the composition of the boreal pine-spruce forests of Sweden are closely correlated with local fire frequency. Norway spruce is dominant where such disturbances are fairly rare (ENGELMARK 1987). However, in Scandinavia, the colonization of burned-over sites by Norway spruce precedes the development of a pine population (ENGELMARK 1993).

Norway spruce also takes part in the succession of low-lying wetland ecosystems, especially as a result of changes in hydrological conditions. In northeastern Poland, Norway spruce commonly invades alder carrs (NOGOWICZ 1990), eventually forming a spruce forest. This process is greatly accelerated as a result of the drying of alder carr habitats and the initiation of peat formation. The establishment of a dense spruce forest in these conditions occurs in less than 100 years. This is the origin, for instance, of many patches of the association *Sphagno girgensohni-Piceetum* in the Romincka Forest in northeastern Poland (KWIATKOWSKI 1986). Equally susceptible to Norway spruce expan-

sion are the marshy coniferous forests, especially upon drying. Even outside its natural geographic range, in the Kashubian Lakeland, Norway spruce may invade the dry edges of raised bogs to establish spruce-dominated communities (HERBICH 1982).

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12. TREE HEALTH

MAŁGORZATA MAŃKA

12.1. MAJOR INFECTIOUS DISEASES

12.1.1. Diseases of seeds and seedlings

12.1.1.1. Cone rusts [*Pucciniastrum areolatum* (FR.) OTTH. and other species]

In Norway spruce, female flowers that are infected in the spring time form cones with whitish pycnia (spermogonia) on the inner side of the cone scales. During the summer the cones develop numerous spherical brown aecia (Fig. 12.1). At high relative humidity, the scales of affected cones appear ruffled, whereas the healthy cones remain closed. The affected cones develop few seeds if any.

The causal agent is a fungus – *Pucciniastrum areolatum* (Basidiomycota, Uredinales), which produces spores of stages 0 and I on Norway spruce, II and III on leaves of various bird cherry species (uredinia on upper and telia on the lower side) (Fig. 12.1). Basidiospores (stage IV) infect female flowers of the

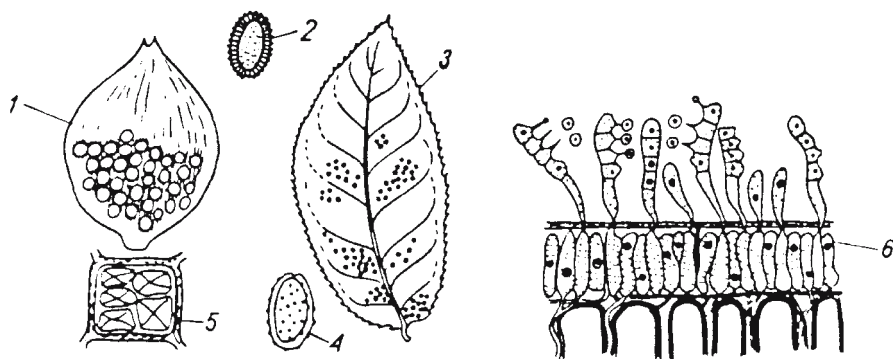


Figure 12.1. Cone rusts caused by *Pucciniastrum areolatum* (K. MAŃKA 1998): 1 – cone scale with aecia; 2 – aeciospore; 3 – leaf of *Prunus padus* with uredinia and telia; 4 – urediniospore; 5 – epidermis cell with teliospores inside; 6 – stratum of germinating teliospores

first host (Norway spruce). A similar disease of Norway spruce can be caused by another teliomycete, *Chrysomyxa pyrolae* ROSTR. (with stages II and III on *Pyrola* spp.). According to data from Norway (ROLL-HANSEN 1974), *P. areolatum* is also a cause of young shoot malformation in Norway spruce, resembling shoots of young Scots pine infected with *Melampsora pinitorqua* ROSTR. No control measures have been applied so far.

12.1.1.2. Seed mold [different species of fungi]

Abundant mycelium occurring on seeds is initially not a threat; however, prolonged exposure may destroy the seed. The mycelium may differ in color, structure, and effects depending on fungal species. The causal agents may be many species of fast-growing fungi, particularly from the Zygomycetes (Zygomycota) and Hyphomycetes (Deuteromycota i.e. *mitosporic fungi*), mostly from the genera of *Mucor*, *Rhizopus*, *Botrytis*, *Trichoderma*, *Verticillium*, *Penicillium*, *Aspergillus*, etc.

The disease is promoted by incorrect seed preparation and poor storage conditions (particularly high humidity, lack of ventilation, and high air temperature). Mechanical damage favors seed mold as well. Seeds should be properly extracted and stored (optimum temperature of -4°C). Prior to storage, seed moisture content should be slowly reduced to 10–15%. Surface sterilization of seeds by chemical or physical methods is also recommended.

12.1.1.3. Seedling damping-off [various species of fungi]

Seedling damping-off causes considerable losses in forest nurseries in the field and in glasshouses. Norway spruce seedlings are affected from germination until about 6 weeks following emergence. Two types of the disease are recognized: pre-emergence damping-off, when germinating seeds are affected, and post-emergence damping-off, when roots and seedlings are affected after emergence. The threat from damping-off is highest during the first 3 weeks after emergence (to the 6th week at the latest), after which the seedlings become resistant. Symptoms of post-emergence damping-off consist of a blackening of the main root and loss of side roots. Affected seedlings are easily extracted from the soil. Stem narrowing and blackening at the base eventually cause the diseased plantlets to fall over (Fig. 12.2). Seedlings lost to excessive heat usually have undeveloped epicotyls and no apical bud, whereas seedlings affected by fungi always have apical buds, even if poorly developed.

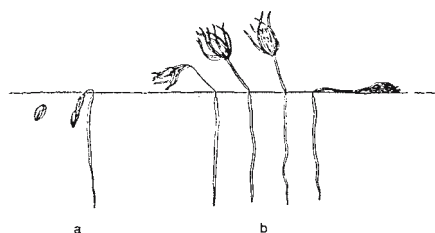


Figure 12.2. Post-emergence damping-off of coniferous seedlings (K. MAŃKA 1998):

- a – pre-emergence damping-off;
- b – damping-off after germination

The causal agents are various fungi and rarely nematodes. In Poland and central Europe, the agents are mainly *Rhizoctonia solani* Kühn, *Fusarium* spp. (*F. oxysporum* SCHLECHT., *F. solani* (MARTIUS) APP. et WOLLENW., etc.), and *Cylindrocarpon* spp., e.g. *C. destructans* (ZINSS.) SCHOLTEN (teleomorph: *Nectria radicola* GERLACH et NILSSON), less frequently *Phytophthora* spp. and *Pythium* spp. Recently damping-off is also attributed to fungi known earlier as 'weakness parasites', such as *Alternaria alternata* (FR.) KEISSLER, *Botrytis cinerea* PERS., etc. The phenomenon may occur in degraded soils following long-term application of fungicides.

The disease symptoms are not specific. Nevertheless, the identity of the pathogen is important, particularly if combined with adverse environmental factors. *Fusarium oxysporum* may be a threat to conifer tree seedlings at fairly low temperature (e.g. 12°C), whereas *R. solani* at the same temperature is nearly harmless, and during warm weather (e.g. 23°C) much more harmful than *Fusarium oxysporum*. *Cylindrocarpon destructans* often infects forest tree seedlings and can also infect roots of older trees, unlike the other fungi discussed above. *Fusarium* spp. and *Cylindrocarpon* spp. after invading the roots overtake the stems, cotyledons, and needles. In contrast, *R. solani* only affects the stem. These fungi differ in their epidemiology. Infected seedlings are scattered in the case of the fusarioid fungi, whereas they occur in patches in the case of *R. solani*. *Rhizoctonia solani* more frequently causes pre-emergence damping-off.

The occurrence of damping-off is favored by the predisposition of seedlings to the disease. The predisposition is temporary, but occurs during the first several weeks as young plants transition from utilizing resources contained in the seed to autotrophy. In conifers, the transition occurs during the first 6 weeks, typically about 2 weeks after emergence. The predisposition to damping-off increases with unfavorable environmental conditions, such as high humidity and low soil temperature (slowing seedling development), or excessive soil drying (diminishing root tissue turgor and inhibiting seedling development), or in response to excess soil nitrogen, which stimulates seedling growth and accelerates the transition to autotrophy.

The biotic and abiotic environment also influences pathogen inoculum. Saprotrophic fungi dominate the biotic environment. Usually, the longer a particular nursery is used, soil conditions are created for increasing pathogen inoculum. Likewise, in nurseries established on sites previously occupied by old Norway spruce stands, the first years of nursery use are typically free from damping-off. The saprotrophic and mycorrhizal fungi suppress pathogen growth.

The most important abiotic environmental factors are humidity and temperature. The pathogenicity of *R. solani* is favored by a fairly high temperature (ca 20°C), relative humidity below 70%, and soil pH below 5.8, whereas *Fusarium* spp. are a threat at lower temperatures, particularly in moist condi-

tions. *Pythium* spp. and *Phytophthora* spp. are favored at temperatures below 20°C, relative humidities over 70%, and a soil pH higher than 5.8.

The control of damping-off is based on prevention aimed at increasing seedling resistance. In this regard, establishing a nursery on a proper site is of great importance. Heavy, wet soils should be avoided, as well as light sands, in which shortages of soil moisture and nutrients may occur. In both cases, unfavorable soil structure may be improved by the addition of *Sphagnum* peat. Soil pH should range from 4.5–5.5 for conifer seedlings. Nurseries should be sheltered from wind and located so as not to be exposed to water loss. Standard sowing practices should be followed, avoiding over-fertilization with nitrogen.

Reducing or removing inoculum from a nursery decreases infection risk. Treatment of seeds with preparations based on Thiram or Benomyl is a common practice. Mixtures are commonly recommended, as the spectrum of fungal pathogens is wide and their sensitivity to fungicides varies widely.

Chemical or physical soil disinfection is also recommended. The latter is rarely applied in forest nurseries (steam treatment of soil or burning). The chemical method of soil disinfection is based on fungicide application. Recommended soil disinfectants are often based on Thiram and Previcur. These treatments are effective in soils contaminated with fusarioid fungi, and particularly the *Phytophthora* and *Pythium* genera. Previcur, Dithane M-45, Nemispor and formaldehyde are commonly used. Where possible, the disinfection should be performed before soil or other substrate is introduced or prior to seeding. Isolation of the substrate in containers or with polyethylene sheeting under soil is recommended in plastic tunnels and glasshouses. These methods prevent migration of pathogens from deeper soil levels to the upper layer in which seedlings grow.

A biological method of seedling protection is based on the application of antagonistic saprotrophic fungi and mycorrhizal fungi. They may be added or the soil environment modified to improve conditions for the beneficial fungi. Antagonistic fungi may be introduced in preparations containing spores (e.g. *Trichoderma* spp.) or by mixing the upper layer of nursery soil with forest litter and soil from an old Norway spruce stand where the fungi occur naturally (see Chapter 10). Repeated application of fungicides in nurseries has resulted in biological degradation of soils by eliminating antagonistic fungi as well as beneficial mycorrhizal fungi. Avoiding unnecessary chemical treatments (e.g. soil disinfection) may aid in restoring the composition of a soil fungal community.

Treatment involves spraying or watering diseased seedlings with chemical preparations immediately after the first symptoms appear. When the disease occurs in patches, removing diseased seedlings together with neighboring healthy looking ones is recommended. The remaining plants should also be treated with fungicides. Recently, instead of disinfecting the soil before sowing, watering the emergent seedlings with fungicides is recommended. If nec-

essary, the treatment should be repeated every 7–10 days depending on the spread and intensity of disease.

12.1.1.4. Smother (seedling blight)

[*Thelephora terrestris* EHRH. ex FR.]

Seedling blight is a disease of minor economic importance, only occasionally affecting forest nurseries. Sporocarps of *Thelephora terrestris* (Basidiomycota, Thelephorales) are chocolate-brown in color, soft, semi-circular, funnel- or cup-shaped, with rugged and ciliate edges, and gray-brown verrucous hymenophore. The sporocarps grow on the host plant and can encompass and shade the young seedlings, impeding gas exchange (Fig. 12.3). The disease is favored in damp environments. The disease may be mitigated by transplanting healthy individuals to drier microenvironments or – in young plantations – by transplanting to artificial beds or mounds.

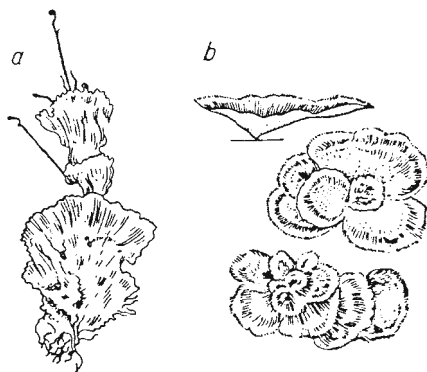


Figure 12.3. Smother (strangling disease) caused by *Thelephora terrestris*: a – Norway spruce seedling overgrown with a fruit body; b – fruit bodies (after K. MAŃKA 1998)

12.1.2. Needle diseases

12.1.2.1. Mountain needle-cast

[*Lophodermium macrosporum* (HART.) REHM.]

In dense mountain stands of Norway spruce, the previous year's needles turn yellow in spring and then brown as a symptom of this disease. The discoloration starts at the tip or middle part of the needle before covering the entire needle. Apothecia are formed in September or October mostly on the lower side of the needles, in the form of brown and later, black shiny elongated swellings (Fig. 12.4). The majority of dead needles stay on the shoots until the following spring when

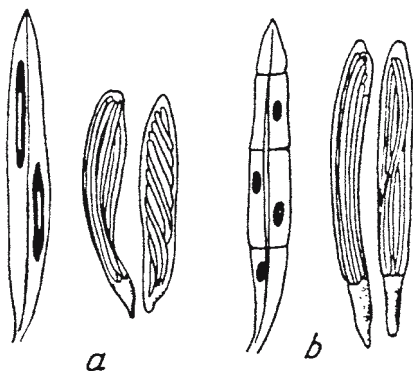


Figure 12.4. Needle-cast caused by *Lophodermium macrosporum* (a) and *L. piceae* (b); affected needles of Norway spruce and asci with spores (after K. MAŃKA 1998)

the apothecia ripen and the ascospores are released. If the diseased needles are shed in the same year of infection, the apothecia ripen and release ascospores on the forest floor. Picnidia are sometimes formed in addition to the apothecia. The causal agent of the disease is the fungus *Lophodermium macrosporum* (Ascomycota, Rhytismatales). Infection occurs through the germination of hyphae that penetrate the stomata on the needle surfaces. No control measures are undertaken owing to the minor importance of this disease.

12.1.2.2. Lowland needle cast [Lophodermium piceae (FCKL.) V. HÖHN = L. abietis ROSTR.]

Lowland needle cast is a disease of Norway spruce and other spruce species (e.g. *Picea sitchensis*, *P. canadensis*), as well as Douglas fir (*Pseudotsuga menziesii*), silver fir (*Abies alba*), and yew (*Taxus baccata*). Infected needles turn yellow-brown and are shed prematurely. Elongated black apothecia are formed on the fallen needles on the forest floor (Fig. 12.4). The apothecia appear circular in cross section in the case of *L. piceae* and triangular in *L. macrosporum*.

Lowland spruce needle cast is caused by *Lophodermium piceae* (= *L. abietis*; taxonomy as above) with the conidial form of *Hypodermina abietis* (DEARNESS) HILITZER (Deuteromycota, Sphaeropsidales). The disease is a threat only at high relative humidity. Under moist conditions, the needles may also be colonized by the fungus *Sphaeridium candidulum* (Deuteromycota, Hyphomycetales), which suppresses the development of the pathogen by promoting rapid decomposition of needles on the forest floor prior to formation of apothecia. Both diseases are favored by high stand density in young spruce stands and control is based primarily on thinning and removal of diseased trees.

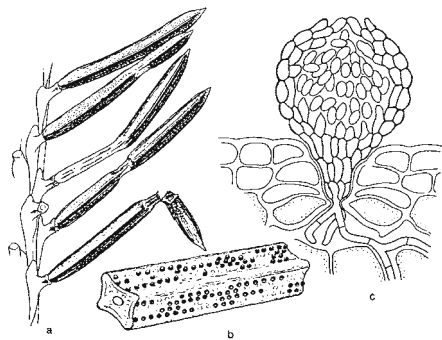


Figure 12.5. *Rhizosphaera* needle-cast (after M. MAŃKA 1998): a – symptoms on Norway spruce needles; b – part of needle with picnidia; c – a cross-section through a picnidium with conidiospores

12.1.2.3. Rhizosphaera needle-cast [Rhizosphaera kalkhoffii BUB.]

This disease is not a threat to Norway spruce, but a serious problem in other spruce species (*P. pungens*, *P. engelmannii*), particularly in nursery production and Christmas tree plantations. In spring, typically in May, affected Norway spruce needles turn purple-brown in color and prematurely senesce. Black spherical picnidia are formed in the stomata, which in turn, produce oval-shaped

conidiospores (Fig. 12.5). Dead needles are subsequently shed, leaving bare twigs. The causal agent is *Rhizosphaera kalkhoffii* (Deuteromycota, Sphaeropsidales), sometimes considered a saprotroph or parasite, occasionally competing with *Lophodermium piceae*. The disease is not controlled in the practice of forestry.

12.1.2.4. *Chrysomyxa needle rust* [*Chrysomyxa abietis* (WALL.) UNGER]

This disease of Norway spruce needles, occasionally occurring on other *Picea* species (e.g. *Picea pungens*), is present throughout the European lowlands and in mountain regions up to an altitude of about 1700 m. Dense spruce stands, aged 10–20 years, are most susceptible to the disease, though it is of minor economic importance.

At the end of June, wide transverse stripes appear on the needles – dull at first, then turning bright yellow. With a severe infestation, the stands look golden yellow from a distance. In May the following year, orange red protuberant spots (telia) of several mm in length occur on the discolored parts of needles (Fig. 12.6). Shortly afterwards, the needles turn yellow, necrotic, and fall prematurely.

The pathogen – *Chrysomyxa abietis* (Basidiomycota, Uredinales), is a single-host microcyclic rust. It completes its entire life cycle on spruce, producing only teliospores and sporidia. A mass of teliospores is built up in elongated red cushions that protrude through the needle epidermis. In May the teliospores ripen and germinate into multicellular basidia on which sporidia are formed. The latter are carried by the wind to new shoots, forming intercellular mycelium and haustoria in young needles. According to some authors, the fungus *Darluka filum* CAST. (Deuteromycota, Sphaeropsidales) occasionally parasitizes the telia of *C. abietis*.

The disease is favored under high relative humidities in young spruce stands from 10–20 years old. Consequently, regular silvicultural thinnings and the introduction of other species to the stands may reduce the incidence of the disease. If necessary, diseased branches may be removed, but only before the bright-colored telia appear. In most cases only lower branches are infected.

Other spruce needle diseases worth mentioning are spruce and wild rosemary (marsh tea) rust occurring in the European lowlands and rhodo-

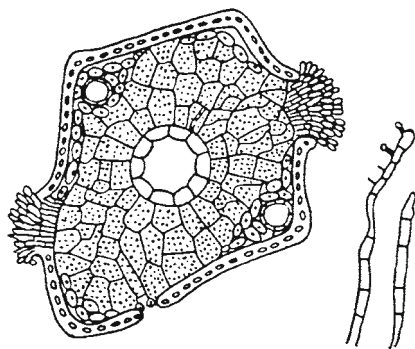


Figure 12.6. Cross-section of a Norway spruce needle affected with *Chrysomyxa abietis*; two telia visible on the needle and on the right – germinating teliospores (after K. MAŇKA 1998)

dendron rust in the Alps. Both diseases are caused by two-host macrocyclic rusts. The wild rosemary rust is caused by *Chrysomyxa ledi* (ALB. et SCHW.) DE BARY, the rhododendron rust is by *C. rhododendri* (DC.) DE BARY. The alternate host of the latter is *Rhododendron* and the former, *Ledum palustre*. Both rusts are of minor economic importance and control is not recommended as control measures may conflict with ecological and conservation goals.

12.1.2.5. Brown felt blight [*Herpotrichia juniperi* (DUBY) PETR.]

The brown felt blight disease occurs mainly in higher elevations in the mountains of Europe and North America, affecting the needles and shoots of spruce, dwarf mountain pine, and juniper (and also other conifer species in America). It also occurs in the lowlands of northern regions of Europe and North America. In Poland the disease occurs in the Beskidy and Karkonosze Mts (southern Poland). Occasionally it may cause serious losses.

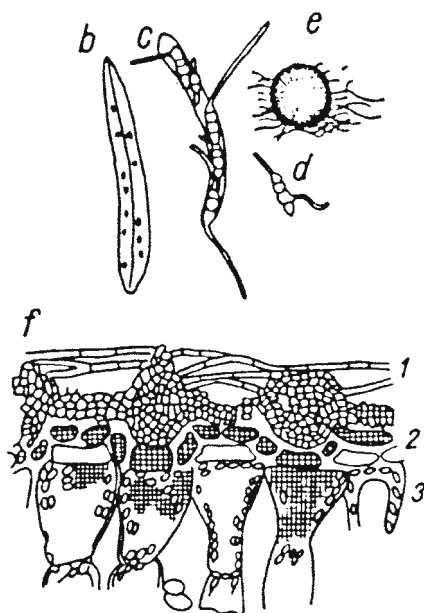


Figure 12.7. Snow mold caused by *Herpotrichia juniperi* (after K. MAŃKA 1998): b – Norway spruce needle with perithecia; c – ascus with germinating ascospores; d – germinating ascospore; e – perithecium; f – affected needle cross-section: 1 – mycelium blocking stomata; 2 – haustoria penetrating epidermal cells; 3 – mesophyll

Needles and shoots are wrapped in an abundant brown-black mycelium (mold). Affected needles and shoots die. The disease develops in winter and early spring under the snow pack. Consequently older, taller trees are infected only below the snow cover. The disease stops developing shortly after snow melt. Brown snow mold often infects dwarf mountain pine thickets and spruce plantations. It is also a threat to spruce in nurseries. Following snowmelt, shoots are covered with the black mycelium of the pathogen.

The pathogen is *Herpotrichia juniperi* (Ascomycota, Pleosporales), although similar symptoms may be caused by *Neopectria coulteri* (PECK) BOSE. Both pathogens are found in the Carpathians (SAVULESCU and RAYSS 1928) and in North American pines. A brown mycelium winds around the needles and is concentrated above the stomata. After contacting the surface of needle, haustoria penetrate the epidermal cells. The parenchyma is penetrated adjacent to stomata. In autumn,

spherical, black-brown perithecia are formed in an aerial mycelium. A mass of horizontal, undulating, and sometimes, branched hyphae grow from the surface (Fig. 12.7).

High relative humidity is essential for the disease. Below 90% relative humidity, growth of the fungus is inhibited. The optimum temperature is ca 15°C. At 0°C the mycelium growth rates are reduced by half and growth stops below -5°C (GÄUMANN *et al.* 1934). Its pathogenic activity is promoted at sub-optimum temperature and high humidity under snow cover. Thus, the disease is a threat to trees covered by snow.

The control of this disease in young plantations and stands is difficult. Trees should be planted, if possible, in microsites protected from excessive snow depths. Ideally, snow-flattened trees should be straightened as quickly as possible.

12.1.3. Shoot and trunk diseases

12.1.3.1. *Scleroderris* canker (= shoot dieback, *Brunchorstia* defoliation and dieback) [*Gremmeniella abietina* (LAGERB.) MORELET] and *Cenangium* dieback [*Cenangium ferruginosum* FR.: FR.]

Formerly the disease was not important in central Europe, but became a threat in recent decades. In Western Europe it has a long history (over 100 yrs) and in the USA it was first detected in the late 1960s. This disease affects various species of spruce, recently also pine, and rarely other conifer species. Spruce in Scandinavian countries, as well as Austrian pine (*Pinus nigra*) and Scots pine (*Pinus sylvestris*) in Poland are particularly impacted. Trees are affected throughout their life cycle, but most severely at the age of 5 to 25 yrs (GREMMEN 1972).

Necrosis of the previous year's shoots and red discoloration of needles are the first symptoms in spruce (BARKLUND *et al.* 1984). These symptoms appear in the spring before shoots start to develop. The shoots often die, but if they survive, the growth flush is delayed or the young shoots are short. New shoots develop the following year from twigs bearing dead shoots. However, the new infected shoots are asymptomatic. The latent infection predisposes the tree to environmental stress. Numerous necrotic, needle-free shoots appear in the upper parts of the crown and on side branches, and in severe cases, the entire tree dies. Elongated cankers appear on affected trees in spring before shoots start to develop (BARKLUND *et al.* 1984). Elongated cankers on main and side shoots are characteristic of the disease. Cankers formed on live shoots are gradually covered with callus tissue. After surviving the first stages of the disease, trees may recover and regenerate. In recent decades, the disease has been epidemic, resulting in the loss of entire stands. LAFLAME (1993) considers symptoms on spruce nonspecific (as opposed to those occurring on pine)

and requiring pathogen fruit bodies (picnidia or apothecia) for identification of the disease.

The main pathogen is a fungus currently named *Gremmeniella abietina* (*Ascomycota*, *Helotiales*); anamorph *Brunchorstia pinea* (KARST.) V. HÖHN (*Deuteromycota*, *Sphaeropsidales*). Picnidia of the fungus emerge in spring and summer on dead shoots infected in the previous year, and on necrotic needles (mostly at the base). The apothecia, if present, appear the following year (Fig. 12.8). Black spheroid picnidia (ca 1 mm diameter) are formed mainly on needle abscission scars, but also on and between scales. In humid conditions, conidia emerge to form pink bands covered with slime. The spores of two or more cells are sickle shaped with a pointed apex, hyaline, measuring $2.5\text{--}3\text{ }\mu\text{m}$. Apothecia (Fig. 12.8) are larger than the picnidia with diameters ranging from 0.5–2 mm. The ascospores are oval 2–3-septate, hyaline, measuring $4\text{--}20 \times 3.5\text{--}5\text{ }\mu\text{m}$. The mycelium of *G. abietina* is loose, cottony, grayish yellow green, and grows very slowly. Growth is active even at temperatures near 0°C , though its optimum growth temperature is above 20°C . Nevertheless, it requires very high relative humidity.

Gremmeniella abietina is divided into at least two races: European and American. The former is considered more pathogenic (particularly in America) and produces apothecia only occasionally. It has a wider range of host plants and infects trees in a wider range of environmental conditions. Until recently the fungus *Cenangium ferruginosum* FR.: FR. (*Ascomycota*, *Helotiales*) was considered a co-pathogen. At present it is considered a saprotroph that may colonize dead shoots.

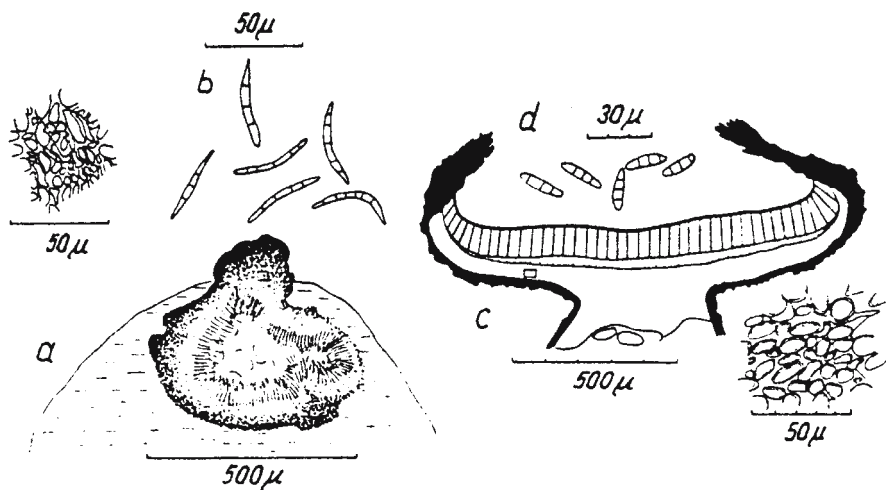


Figure 12.8. *Gremmeniella abietina*: a – picnidium; b – picnidiospores; c – apothecium; d – ascospores (after K. MAŃKA 1998)

Infection is accomplished by conidia and ascospores when new shoots are produced in spring, and not later than early July. The sites of infection are buds (particularly at the base) and shoots, although wounds may be infected as well. The incubation period is long and symptoms appear at the end of the year. The first symptoms are resin exudates from some of the infected buds and brown-colored necrosis of their inner tissues, mainly at the base.

The disease is promoted mainly by host susceptibility, the pathogenicity of the fungus, and favorable environmental conditions. Norway spruce seems more resistant than Scots pine, at least in Poland. High humidity and low temperature promote the disease by increasing pathogen activity. *Gremmeniella abietina* can grow at temperatures near 0°C (e.g. under snow cover) with high humidity. Consequently, the disease is more acute in stands growing in sheltered environments in deep shade, near topographic depressions, or water bodies. Conditions favoring infection occur in seaside and mountain regions, in excessively dense stands and high humidity.

The control of this disease is based on use of less susceptible species and varieties of trees and proper stand management to avoid accumulation of inoculum that could contribute to an epidemic outbreak. Broadleaved species are immune to the disease and may be introduced in stands or through filling gaps in existing conifer stands. In Poland, these practices result in decreases in the infestation by *G. abietina*. Fir and larch are more resistant than spruce and pine.

Control measures are particularly important in areas favorable for the disease (i.e. high relative humidity and low temperature). Wide spacing and early thinning may be effective in conifer plantations. Sanitary cutting should be immediately applied when the first disease spots are discovered to prevent growth losses and stem defects. Planting a belt of broadleaved species may serve as an effective barrier between older stands and newly established plantations. In addition, thinning may protect against *Heterobasidion* root rot (MAŃKA K. 1986).

12.1.3.2. *Nectria* canker [*Nectria cucurbitula* (TODE ex FR.) FR.]

Nectria canker occurs mainly in spruce species, particularly in young, dense stands. The disease is less frequently observed in other conifer species, such as pine or fir. Branches are infected in young trees; whereas in older trees, the trunk, and often stumps and dead wood are the infection sites. MAŃKA K. (1998) observed the pathogen on 40–60 year-old Norway spruce weakened by an *Armillaria ostoyae* infestation.

Small to large segments of bark tissues die on infected trunks and branches, resulting in a browning of the bark tissue. On the dead bark and in its fissures (when not too dry), a small white cushion-like mycelium appears (conidial stromata of the pathogen) in which dark red nodules (apothecia) are later formed. When the dead bark tissues girdle the trunk or branch, the upper part

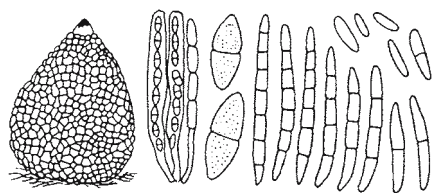


Figure 12.9. *Nectria cucurbitula*: from left to right: perithecium; asci with a paraphysis; ascospores; conidia (after K. MAŃKA 1998)

of the crown turns yellow and dies. Infested bark segments may be isolated from the healthy tissues through production of a cork layer by adjacent living tissues during the growing season.

The disease-causing agent is *Nectria cucurbitula* (Ascomycota, Hypocreales); anamorph *Cylindrocarpon cylindroides* Fr. (Deuteromycota, Hyphomycetales) (Fig. 12.9), a facultative parasite living primarily on dead twigs of conifer trees. Its mycelium is active in living

bark only after the growing season, growing ca 10 cm upwards on the trunk and up to 3–4 cm perpendicularly to its axis, resulting in characteristic strips of dead bark. Ascospores are released in winter and early spring. Infection of trees occurs only through wounds.

The disease is promoted through wounds to the tree arising from insects, game, hailstorms, as well as high stand density, and low temperatures. Weakening of the host by other diseases, e.g. *Armillaria* root rot, also increases the susceptibility of trees. The disease is considered a threat to Norway spruce when occurring simultaneously with the tortricid *Laspeyresia pactolana*. Careful management of young spruce stands and an admixture of broadleaved species are recommended.

12.1.3.3. Spruce twig blight (= Spruce shoot dieback) [*Ascochyta piniperda* LIND.]

Spruce twig blight is a disease known in Europe and North America that infests the current-year shoots of young spruces (*Picea abies*, *P. sitchensis*, *P. pungens*), and recently also a pine species (*Pinus contorta*) in Scottish nurseries.

At the beginning of summer, needles of infected current-year shoots turn brown at the base (sometimes also in the middle) and fall prematurely. The remaining needles are abscised and the bare stems die. Occasionally the disease spreads to the base of neighboring shoots. The necrosis starts from the base and middle part of the shoot, unlike the dieback caused by late ground frost that covers the entire shoot, including the tip.

Tiny black dots appear as the picnidia of the pathogen – *Ascochyta piniperda* (Deuteromycota, Sphaeropsidales). Observation may require careful searching between scales at the base of affected shoots (LAGEBERG 1933). The picnidia are like those of many saprotrophic fungi (e.g. *Cytospora pinastri*, *Scleropycnium abietina*). They may be distinguished by microscopic analysis of the conidiospores, which are elongated, 2-celled, measuring $9\text{--}15 \times 1.5 \mu\text{m}$ in the case of *A. piniperda*. Disease control is possible by removing and destroying affected trees when the disease intensity is high.

12.1.3.4. Red ring rot, white pocket rot of conifers [Phellinus pini (THORE ex FR.) PILÁT]

The disease often occurs in Europe, North America, and Asia in the lower (and valuable) portions of spruce trunks in stands older than 60–70 yrs. The only diagnostic symptoms are the pathogen's fruit bodies (sporocarps, Fig. 12.10), which occur on the outside of an infested trunk, usually protruding from broken branches. The sporocarp is a woody bracket with sharp edges and a diameter ranging from 8–16 cm. The upper side is brown-black or almost black, with concentric zonation and perpendicular cracks. The body of the conk (trama) is cinnamon-yellow or rusty dark brown. The multi-layer hymenium on the lower side is olive-yellow or yellow-brown, with tube outlets of differing size and shape.

The softwood at the base of a conk ceases growth and the trunk surface becomes flattened with time and characteristically sunken. When a conk becomes detached, a small depression is visible on the trunk and the remains of the dark brown conk substance (trama) is occasionally dusty in appearance, also a diagnostic feature. Other external symptoms are the so-called blind conks (small swellings containing compact dark brown mycelium), numerous hollows in the trunk, and resin exudates.

Internal symptoms are visible inside the bole in the form of a rot called cavernous white rot (*Heterobasidion annosum* rot), occurring exclusively in the heartwood. In cross section, the rot forms nearly regular circles or rings, most often crescents. The first rot stage, called early rot, is pale rose in color, turning red to pale cocoa. At this stage the wood becomes friable, and the first caverns filled with white cellulose may appear. In the late rot stage, the wood turns red-



Figure 12.10. Typical fruit body of Phellinus pini on Scots pine: a – upper surface, b – bottom (photo M. MAŇKA)

dish or cocoa, and cracks appear along the annual increment rings and vascular rays, and the cellulose caverns occur regularly. The wood easily crumbles when handled and eventually is pulverized. The rot is usually most advanced at the bottom of the trunk.

The pathogen, *Phellinus pini* (Basidiomycota, Hymenochaetales), spreads through basidiospores that are single-celled, yellow-brown, and measure $4\text{--}6 \times 4\text{--}5 \mu\text{m}$. They are produced in large quantities in conk hymenophores. The maximum basidiospore release in central Europe takes place in moist periods of February and March, and in larger quantities at the end of summer and beginning of autumn. Scots pine and other coniferous species are affected to an even greater extent than Norway spruce. Spores are airborne. Infection is complete only when a spore contacts the heartwood – mainly in wounds resulting from broken branches.

Owing to the dependence of infection on the presence of heartwood, infection is possible only after the trees reach 30-yr old. The pathogen mycelium grows slowly through branch and trunk heartwood (maximum ca 18 cm per year). When the tree is cut and the wood starts to dry, the growth of the pathogen ceases. The probability of infection, rot intensity, and rate of spread increases with tree age. Eventually, the rot growth surpasses the volume of yearly wood growth increment in a diseased individual.

Heavily branched trees of low softwood/heartwood ratios and thick branches are considered particularly susceptible to the disease. The threat of infection increases with an abundant inoculum source (i.e. many conk-bearing trees in the stand). The infection process is favored by wet weather, as the pathogen basidiospores require at least 96% relative humidity for germination. Trees growing on poor sites are generally more resistant.

Disease control, if deemed necessary, is based on proper stand management and appropriate logging practices at harvest. During thinnings, wolf trees should be removed, as they are easily infected through broken branches. In thinning stands over 40-yr old, trees with external symptoms of *P. pini* infestation should be removed first. Pruning of trees in 25–35 year-old stands may also aid in disease prevention.

12.1.4. Root diseases

12.1.4.1. *Armillaria* root rot [*Armillaria* spp.]; Honey fungus (GB), Shoestring fungus (US)

The disease occurs in temperate climatic zones worldwide. Numerous woody plant species are affected, including Norway spruce and Scots pine in central Europe. The causal agents are species from the genus *Armillaria*, predominantly *A. obscura* (*A. ostoyae*).

Forest trees are affected from ca 3-yr old to advanced ages. The greatest losses are observed at ca 10–30 yr when roots and stem bases are infected.

Armillaria root rot is of great economical importance in Poland, as it occurs as an epidemic in some parts of the country (e.g. in the Carpathians and in the Olsztyn region). In the lowlands, young pine stands are often affected, requiring regeneration. The first symptom is often a delayed shoot, leaf or needle growth. In coniferous trees, a marked response of the main shoot is observed. Occasionally, an attack is so sudden and intense that needle discoloration (pale to brown) is the first symptom. The necrotic needles are easily shed. Sometimes green dead needles are shed prematurely.

In the final phase of the disease, abundant resin exudates appear on the lower trunk (Fig. 12.11). The resin flows are mixed with soil, litter, and needles forming dirty irregular lumps or encrusting the soil near the trunk base. Often, the resin solidifies in the space created under the bark.

On dying and dead trees affected by *Armillaria*, sheets of the creamy-white mycelium spread between the bark and wood of roots and trunks (Fig. 12.11). In old trees, the mycelium may extend up to a dozen or so meters up the trunk in infected Norway spruce, and to the butt of the trunk in pine. Under the mycelium, the surface of the wood is dark brown. The mycelial sheets spread under the bark and into the soil in the form of dark brown or almost black, branching, and string-like mycelium called rhizomorphs. Rhizomorphs grow considerable distances in the soil, spreading the pathogen and infecting other roots. After the trees are dead, the mycelial sheets under the loose bark turn into flat, branched rhizomorphs. These rhizomorphs are capable of growing apically, reaching higher portions of the trunk than the mats.

Armillaria fruit bodies (sporocarps, Fig. 12.12) are another etiological symptom. They appear in autumn, mainly on or at the bases of dead trees and stumps. The roots and infested parts of the trunk develop a white rot, mostly in

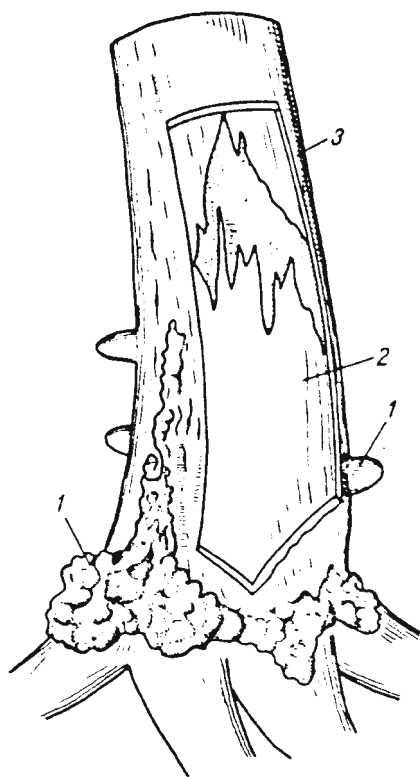


Figure 12.11. Stem basis of 8-yrs-old Norway spruce affected with *Armillaria*: 1 – solidified resin exudates; 2 – mycelium sheet; 3 – brown discoloration of wood surface above mycelium mat range (after K. MAŃKA 1998)

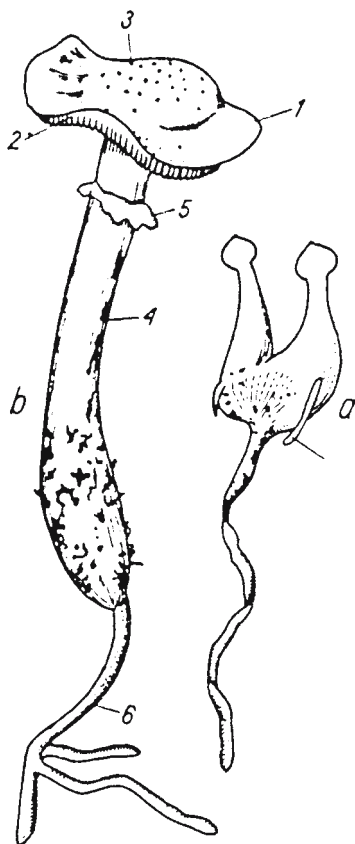


Figure 12.12. *Armillaria* fruit bodies: a – young fruit body; b – mature fruit body: 1 – cap (pileus); 2 – gills (lamellae); 3 – squamules (small scales) on the cap surface; 4 – stipe; 5 – ring (annulus) on stipe; 6 – rhizomorph (after HARTIG 1874); 7 – *A. obscura* basidiocarps (photo P. MŁODKOWSKI)

the sapwood. Only the wood of the roots may be entirely rotted (including the heartwood), as the soil environment is suitable for the fungus. In time, the infested wood exhibits irregular dark brown or black lines, called zone lines or sclerotia, in cross section. Eventually the wood is reduced to a stringy sodden mass.

In Europe the following species of the *Armillaria* (Basidiomycota, Agaricales) genus are considered pathogenic (KORHONEN 1978a):

1. *Armillaria mellea sensu stricto* (VAHL ex FRIES) KUMMER,
2. *Armillaria obscura* (SCHAEFF.) HERINK = *A. ostoyae* (ROMAGNESI) HERINK
3. *Armillaria bulbosa* (BARLA) KILE et WATLING,
4. *Armillaria borealis* MARXMÜLLER et KORHONEN, and
5. *Armillaria cepistipes*, in which two forms are defined: *A. cepistipes* f. *typica* VELENOVSKY and *A. cepistipes* f. *pseudobulbosa* ROMAGNESI et MARXMÜLLER.

In Europe the honey fungus (*A. mellea*) affects mostly broadleaved trees, particularly fruit trees, although it was recently found in forests (ŁAKOMY 2001). *Armillaria bulbosa* is quite common on coniferous and broadleaved trees that are weak or dead. *Armillaria borealis*, is rather rare in central Europe (found on Norway spruce), and more common in northern Europe (e.g. Finland). *Armillaria cepistipes* also occurs in central Europe.

The fruit bodies and rhizomorphs are the most distinctive features of the above-mentioned species of the *Armillaria* complex. The former are edible, appearing in late summer and autumn in clusters, sometimes numerous, at the base of diseased trees, on stumps, roots, and occasionally several meters up the stems of dead trees.

The fruit bodies (basidiomes) are formed at the ends of the rhizomorphs to which they are connected throughout their development. The fruit bodies consist of pilei (caps) on stipes, usually 5–10 cm high and 15–25 mm thick. A ring/annulus (pronounced or rudimentary) occurs in the upper part of the stipes. The pileus is at first protuberant, almost spherical, later on increasing to a diameter of 5–10 cm with a thin layer of white trama. On the upper surface of the *A. ostoyae* pileus, there are numerous brown-black squama (scales). Basidia bearing basidiospores are located under the pileus lamellae (gills) (Fig. 12.13), appearing yellowish-white at first, and later reddish. The basidiospores measure $7-9 \times 5-6 \mu\text{m}$ and are produced in mass, covering the surrounding area with white powder when released.

The rhizomorphs are mycelial structures resembling branching strings, 0.5–3 mm thick, dark colored outside and white inside. They infect tree roots and transport gases and metabolites. The youngest, apical, and infective part of the rhizomorph has a different morphology. It is 2–3 mm long, white, parabolic, and covered with adhesive hyphae excreting sticky slime in moist soil (Fig. 12.14). The rhizomorph elongates due to the fast apical growth of the hyphae.

Conditions favoring the disease are associated with the host, pathogen, and the environment. In the case of *Armillaria obscura*, live deciduous trees are rather resistant to the pathogen, whereas the stumps or dead wood of deciduous trees are highly susceptible. It is the perfect food source for *Armillaria* and an abundant source of infectious mate-

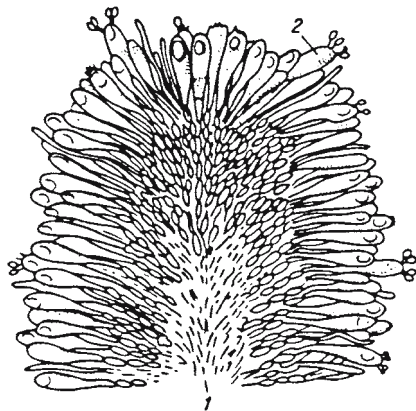


Figure 12.13. Cross-section of *Armillaria* fruit body lamella (after HARTIG 1874):
1 – trama; 2 – basidium bearing basidiospores

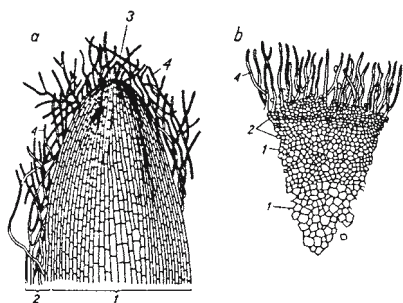


Figure 12.14. Apical part of rhizomorph on longitudinal (a) and cross (b) sections (after K. MAŃKA 1998): 1 – core part; 2 – cortex part; 3 – apical meristem of rhizomorph; 4 – adhesive hyphae

rial – threatening coniferous trees, which are very susceptible when alive. The disease is also promoted by environmental factors – air pollution, unsuitable soil microbial communities, or root conditions (MAŃKA K. 1961).

Severely affected or threatened Norway spruce stands in the submontane and lower montane belts of the Carpathians and other mountain regions (MAŃKA K. 1953) should be replaced with heterogeneous stands, composed mainly of fir and beech, with a varying admixture of larch, Norway spruce, and other tree species. When stand regeneration is

not an option, young stands should be carefully managed, according to following guidelines:

- 1) local seed material should be used for reforestation,
- 2) establishing coniferous stands after harvesting deciduous stands should be avoided, unless stumps are removed, which is currently not recommended for ecological reasons,
- 3) thinnings should be properly performed and dying or dead trees removed,
- 4) trees should be removed in late spring or summer and the stumps debarked (to dry them and to avoid resin flux that delays drying),
- 5) the stumps of deciduous trees should be treated with a preparation of *Pleurotus ostreatus* to speed up their decomposition.

The guidelines mentioned above should be adjusted in practice to match the extent of an *Armillaria* threat. The threat can be evaluated based on stand health, the quantity and quality of infectious material, and the role of local environment in the disease process. In many countries of central Europe, Norway spruce is considered the most susceptible species, followed by Scots pine and larch. Deciduous trees are less susceptible, unless the pathogen is *Armillaria mellea* s.s. Environmental factors modify the threat significantly. In the upper mountain forest belts (e.g. mount Romanka at elevations above 1300 m), Norway spruce stands are free from *Armillaria* infestation, as the pathogen does not occur there because of low temperatures (MAŃKA K. 1998).

12.1.4.2. *Heterobasidion* root rot [*Heterobasidion annosum* (FR.) BREF. = *Fomes annosus* (FR.) CKE]

The disease is a threat mainly to coniferous trees, including Norway spruce. It occurs in forests throughout the northern hemisphere on trees of all age

classes. Its cause is a root pathogen that spreads to the stem base and trunk (Fig. 12.15), producing white pocket rot in spruce. In pine and several other conifer species, the pathogen stops at the root-stem junction. In spruce, part of the root system is killed and the trunk wood is degraded. The early rot stage in spruce is visible as a violet-red discoloration of the wood, later turning brown and displaying numerous cavities filled with white cellulose (often with a black spot inside; Fig. 12.16). The lower portion of an infested spruce trunk appears swollen and bottle-shaped.

Young infected trees, up to ca 10-year-old, turn pale green, then brown and die. Unlike infections with *Armillaria* sp., resin exudates from the trunk are not observed. Between the loose bark and wood, a delicate white mycelium with conidia (Fig. 12.17) may appear, and fruit bodies (sporocarps) of the pathogen can be produced at the root junction (Fig. 12.18). Upon felling older trees, the disease symptoms appear as a white pocket rot in root and trunk wood (Fig. 12.16). In advanced stages, the trunk base swells and is bottle-shaped.

The causal agent is *Heterobasidion annosum* = *Fomes annosus* (Basidiomycota, Russulales). Three intersterile groups are recognized within the species (KORHONEN 1978b): S (infecting mainly Norway spruce), P (infecting pine), and F (occurring on fir, considered saprotrophic). The P group has a wide range of host plants, including

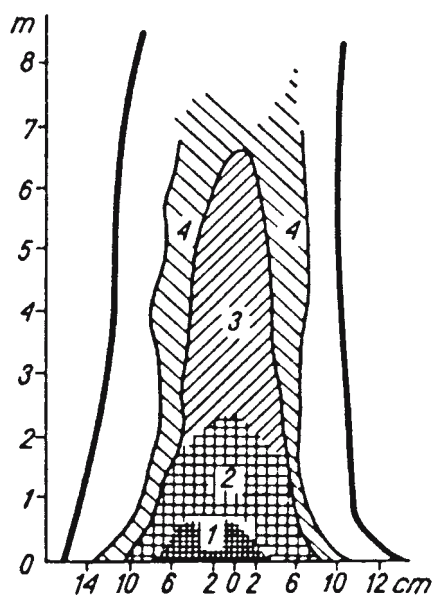


Figure 12.15. Basal part of a Norway spruce trunk affected by *Heterobasidion annosum* (after K. MAŇKA 1998):
1–4 – degrees of wood rot

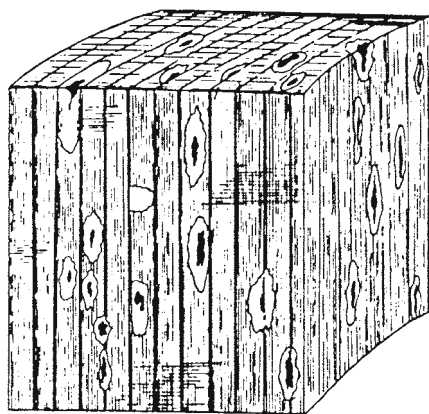


Figure 12.16. A cube of Norway spruce wood destroyed by *Heterobasidion annosum* (after H. M. WARD 1909 in K. MAŇKA 1998)

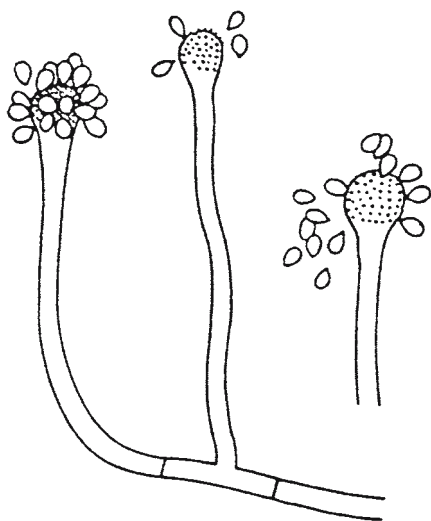


Figure 12.17. Conidiophores and conidia of *Heterobasidion annosum* (after K. MAŃKA 1998)

mm long with round or slightly angular outlets of 0.3–0.6 mm diameter. At first, the outlets are white, then creamy white in color. The spores are usually released between May and November. On artificial media and on infected wood in humid conditions, the pathogen produces abundant conidiophores, spherically swollen at the end and single-celled oval conidia of $2.5\text{--}3.0 \times 3.5 \mu\text{m}$ (Fig. 12.17).

There are a number of infection pathways in trees (RISHBETH 1950, 1951a, 1951b). The pathogen may penetrate wounds or spread from a diseased root to



Figure 12.18. Fruit body of *Heterobasidion annosum* at the base of a Sitka spruce stump (photo M. MAŃKA)

spruce, juniper, birch, alder, heather, and other species. This is the most frequently occurring group in Poland.

The pathogen fruit bodies (basidiocarps) display white hymenophores that are cushion like or resupinate in appearance (Fig. 12.19). They are formed mainly in the dark, e.g. on roots. They may also appear as brackets, occurring at the base of the stem or on stumps. The dimensions are $3\text{--}15 \times 5\text{--}30 \times 1\text{--}2 \text{ cm}$. The upper side is red brown at first, later turning dark brown, with faint concentric rings. In a growing conk, the edge is whitish, and not very sharp, with white trama up to 10 mm thick. The hymenophore is multilayered, with tube layers of different years often only partially covering the entire hymenophore area. The tubes are 3–7

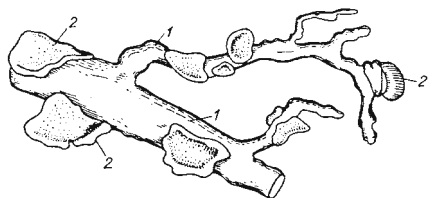


Figure 12.19. Norway spruce root (1) with resupinate fruit bodies (2) of *Heterobasidion annosum* (after K. MAŃKA 1998)

a healthy root through adjacent or grafted roots. Stumps are of great importance in infecting stands. The basidiospores germinate on the cut stump surface and the growing mycelium overtakes the stump and roots as well as roots of trees growing nearby. This results in the death of groups of trees and the formation of gaps in the stand. Root infection may occasionally occur through the deposition and infiltration of the soil by the pathogenic spores (conidia and basidiospores) in rainfall.

Monocultures of Norway spruce and Scots pine are particularly susceptible to the disease, especially when stands are even aged. Younger stands are vulnerable and often subjected to more pathogenic forms of *Heterobasidion*. Environmental conditions should also be considered. First- and second-generation conifer stands on post-agricultural land exhibit higher incidences of the disease (usually with fairly high soil pH; SIEROTA 1995). In older forested areas, environmental conditions may also affect the disease. The effect is mediated by the fungal communities inhabiting soil and stumps. For example, in the Zielonka Forest District in Poland, where there is no *Heterobasidion* threat, pine stumps are inhabited by fungal communities that suppress the growth of *H. annosum*, and at the same time support the growth of *Phlebiopsis gigantea* (Fr.: Fr.) JÜLICH, an antagonist of the pathogen. In the Laski forest district in Poland, a region of high incidence of the disease, pine stumps of the same age (30 yrs) are inhabited by fungal communities that suppress *H. annosum* growth only slightly and do not support the growth of *P. gigantea* (PRZEZBÓRSKI 1974b).

Formerly it was recommended to remove stumps and roots of affected trees when establishing new stands. Currently, the introduction of broad-leaved species into young conifer stands is a recommended silvicultural practice. The most suitable species seem to be birch, sycamore maple, and red oak, as their rhizosphere fungal communities are highly antagonistic to the pathogen (MAŃKA K. 1990; MAŃKA K. *et al.* 1993b). The broadleaved species may be removed later (e.g. when stands are over 30-yr old and the coniferous trees become more resistant), depending on the form planned of the stand. In the early thinnings, dead trees should be removed together with roots. Thinning also promotes the formation of soil fungi communities antagonistic to *H. annosum* (MAŃKA K. *et al.* 1991; MAŃKA M. *et al.* 1993a; MAŃKA M. and ŁAKOMY 1995). Experiments on Scots pine in central Poland show that after early spring thinning (just after the disappearance of the snow cover) stumps are better protected against infection than after summer thinning (MAŃKA K. *et al.* 1972; MAŃKA K. and PRZEZBÓRSKI 1974). Small diameter trees should be removed (diameter at trunk base of 7–8 cm; MAŃKA K. *et al.* 1974). When the remaining stumps are larger in diameter, and thinnings are performed in summer or autumn, biological, chemical, or physical protection of stumps must be preformed.

Biological control is based on preparations containing *P. gigantea* spores (e.g. Polish biopreparation PgIBL, British PG suspension, Finnish Rotstop). Physical protection is based on de-barking fresh stumps, which is effective mostly in the summer and at the beginning of autumn, particularly with taller stumps, e.g. 15 cm (MAŃKA K. and PRZEBÓRSKI 1972, 1974). Shorter drying times of the stump promote better protection against *H. annosum* infection. Partially dried wood also favors the activity of *P. gigantea* and not of *H. annosum*. Mechanical protection of stumps is based on cutting off slices 5–10 cm thick after the thinning operation. The time of cutting depends on local conditions – it should be short when the weather is warm and humid, and when the stands are young – and may range from 2 weeks to 2 months (PRZEBÓRSKI 1974b). The aim of the slice cut is to remove the pathogen, which may be present in the upper part of stump. The remaining part of stump is free from the pathogen and has dried in the meantime so that it is no longer an optimal substrate for *H. annosum*, but remains a substrate for saprotrophic antagonistic fungi. Removing dead trees and stumps with roots is also an element of mechanical protection.

Chemical methods are based on treating stumps with prepared compounds, e.g. borax, sodium sulfamate, Agrico (RYKOWSKI and SIEROTA 1973) and Sodium nitrate. The latter is inexpensive and effective, applied as a 10% water solution with methyl violet stain. Urea is most often applied with the chemical method. According to integrated pest management principles, the control of *Heterobasidion* root rot should be based on non-chemical methods, preferably biological, using chemical methods only when necessary.

12.1.4.3. *Schweinitz conk* (= brown root rot) [*Phaeolus schweinitzii* (FR.) PAT.]

The disease results in brown rot of wood in roots and butts of conifers (spruce, pine, Douglas fir, eastern white pine (*Pinus strobus*)) and occasionally broad-leaved species (oak, sour cherry), mainly in trees older than 60 yrs.

Infested wood turns red brown, starting from the roots to the trunk to above 2 m. In the early stage, the wood becomes friable. Thin yellow-white mycelium mats appear in the crevices between the rectangular blocks that form in the wood. The rotting wood smells of turpentine. Before a tree is cut, the disease may only be identified by the presence of the pathogen's fruiting bodies. They usually form on or near the butt and on the ground, growing from infested roots.

The causal agent is *Phaeolus schweinitzii* (Basidiomycota, Polyporales), which produces basidiocarps in June and July. They are annual, circular to bracket-like (or calycinal), and sometimes possessing a short stalk (Fig. 12.20). The conk is 10–40 cm in diameter and is thick and showy. The upper surface is plush-like and velvety ("velvet top"), rusty brown, with a yellow rim (when active). The hymenophore has tubes 3–6 mm long with yellowish-green angular

pores (0.3–2.5 mm diameter), often irregular. Later the fruit bodies turn dark brown to black and crumble. Infection occurs through wounds and by root contact. The pathogen can also develop in cut wood when suitably damp and cease development in drying wood only to become active again when the substrate is rewetted. Protection measures are presented below, as they are identical for both *P. schweinitzii* and *Mucronoporus circinatus*.

12.1.4.4. White pocket root rot of spruce [Mucronoporus circinatus (FR.) ELL. et EV.]

The disease is similar to that caused by *Phaeolus schweinitzii*. Infested trees show no external symptoms. In cross section, the butt heartwood is distinctly discolored. Its outer part in the early stage is dark red-brown, whereas it is much paler in color compared to the very similar red-ring rot caused by *Phellinus pini*. In its final stage, the wood is dotted by small oval pits full of white cellulose. The rot spreads to the trunk up to ca 5 m. The diagnostic feature of the disease is the fruiting body of the pathogen, *Mucronoporus circinatus* (Basidiomycota, Hymenochaetales), occurring on the ground or more often on stumps. The basidiocarps are formed between July to September. They are annual, delicate, and small (3–8 cm diameter), mostly bracket-like, calycinal with a short stalk. Their upper surface is tomentous, pale rusty, with a whitish or yellowish rim. Short tubes (1–5 mm) with irregular, rugged pores (0.25–0.8 mm diameter) cover the lower surface. The fruit bodies are very similar to those of *P. schweinitzii*, but always smaller and not as brightly colored.

The disease is important in older spruce and pine stands, where attention should be paid to proper harvest time, as the susceptibility of trees to both diseases increases with tree age.

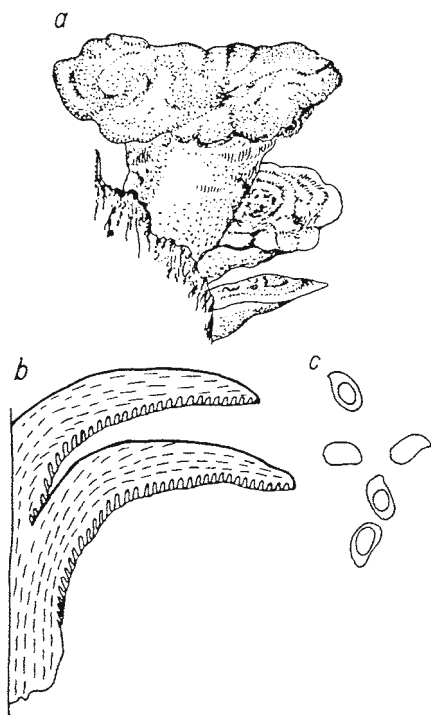


Figure 12.20. Fruit bodies of *Phaeolus schweinitzii* (after K. MAŃKA 1998):
a – group of fruit bodies; b – longitudinal section of fruit bodies; c – basidiospores

12.1.4.5. *Group death of conifers [Rhizina inflata (SCHAFF.) SACC. = R. undulata FR.]*

The disease occurs mainly in areas following fire, where it makes reforestation with coniferous species (in particular, Scots pine and Austrian pine) difficult or even impossible. It is not a threat to Douglas fir or broadleaved species. However, in western Europe (Great Britain, The Netherlands, France), it is a cause of group death in pole-sized conifer stands (20–30 yrs), and in Poland in plantations 2 to 5 yrs old (ORŁOŚ 1952).

The fruiting bodies of *Rhizina inflata* are produced on the forest floor, particularly after a forest fire or in campfire pits. They first appear as small brown buttons with yellow edges. Mature specimens are irregular, chestnut-brown hummocks, 2–6 cm in diameter, occasionally up to 12 cm (MAŃKA K., MAŃKA M. 1993), retaining the yellowish edges, which darken with age (Fig. 12.21). The sporocarp has fine cream-colored or yellow mycelial strands (rhizoctoniae, 1–2 mm thick) on the undersides. The mycelial strands grow through the soil, forming a network on the surface of infested roots.

Fruiting bodies are distributed on the ground singly or in crust-like groups or rows. When an infestation is large, several sporocarps may occur per square meter. They appear in the late summer beginning in August and usually decay during the winter. Sometimes only their blackened remains can be seen on the ground the following year. In areas where sporocarps have appeared after a fire, a dieback of conifer transplants may be expected at reforestation. Some foresters have noticed that 1-year-old transplants suffer more than 2-year-olds.

The pathogen is also a common saprotroph (facultative parasite) that occurs in conifer wood, but causing no disease. It is known as a pyrophilic fungus (fire loving), as its development is associated with fire and high temperature.

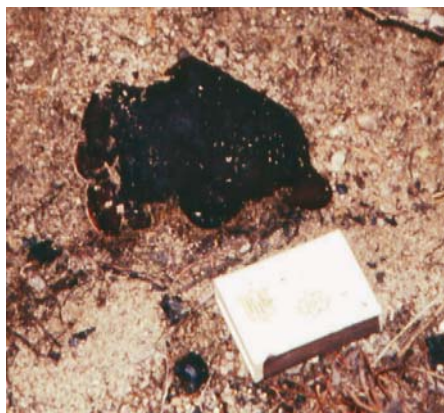


Figure 12.21. Fruit bodies of *Rhizina inflata* (photo M. MAŃKA)

Rhizina inflata (Ascomycota, Pezizales) produces fruit bodies (described above) with the upper (brown) surface covered entirely with hymenium of asci and paraphyses. Unicellular and fusiform ascospores ($22\text{--}40 \times 8\text{--}11 \mu\text{m}$) are formed in club-shaped asci (ca $400 \times 20 \mu\text{m}$) (Fig. 12.22). The spores may lie in the soil for several years and their optimum temperature for germination is $35\text{--}45^\circ\text{C}$. Germination is promoted by exudates of live coniferous trees.

The food source for the mycelium consists of new stump roots (e.g. near camp-fires), but the fungus may also

use roots of living trees. The disease is promoted by a low pH and the presence of live conifer roots, and particularly by high temperatures (35–45°C) which allow the pathogen to survive in soil, while other species of fungi (including anatonistic ones) disappear for some time from the soil.

Recommended protection measures include:

1. Delaying the reforestation of post-fire areas by two years; exceptionally by one year.
2. Avoiding the burning of woody debris in cut over areas, except in winter.
3. Prohibiting campfires in high-risk areas.
4. When reforestation is the immediate goal, removing the stumps along with the roots, placing the remaining post-fire woody debris in piles, and deep ploughing are recommended.

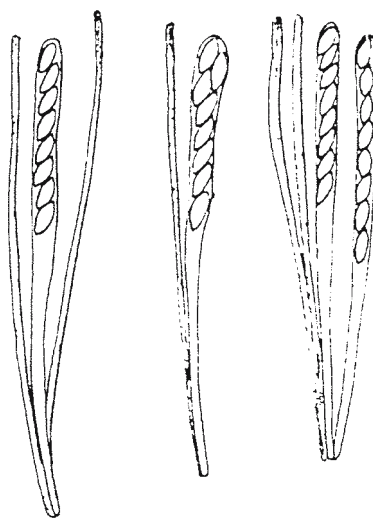


Figure 12.22. *Rhizina inflata* asci with ascospores and paraphyses (original M. MAŇKA)

12.1.5. Wood stain

A diagnostic characteristic of wood stain is a change in the natural color of the wood without associated decomposition of wood cell walls.

12.1.5.1. Blue stain of wood [*Ceratocystis* spp., *Discula pinicola* (NAUM.) PETRAK, *Sclerophoma pythiophila* V. HÖHN and other species]

Blue stain is widespread in North America, Europe, and Asia. Downed or felled timber of conifers are affected and seldom broadleaved trees. The disease occurs almost exclusively in sapwood, appearing as blue-black and black stripes or spots of varying size and shape. Blue stain may also occur in mechanically chipped wood. When the disease originates in the forest it is termed raw material blue stain; whereas after sawing, it is called lumber blue stain.

The main causal agents are fungi of the genus *Ceratocystis* (Ascomycota, Microascales) (Fig. 12.23), and numerous species form Deuteromycotina, e.g. *Discula pinicola* and *Sclerophoma pythiophila* (Deuteromycota, Sphaeropsidales). Some, such as *Hormodendron cladosporioides* (FR.) SACC., are active only in the surface layer of wood at high humidity.

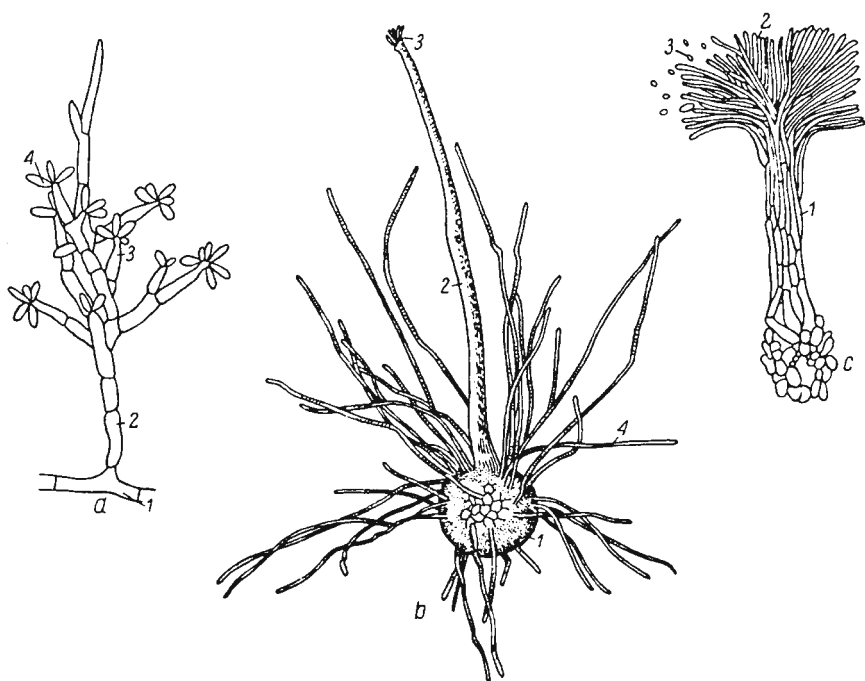


Figure 12.23. Types of sporulation of several species of *Ceratocystis* causing blue stain of Norway spruce wood (after MEYER 1953): a – *Cephalosporium*-type sporulation of *C. pini*: vegetative hypha (1); conidiophore (2); conidiophore branch (3); conidia (4); b – perithecium of *C. coerulescens*: perithecial wall (1); neck (2); setae (3); appendices (4); c – *Coremium*-type sporulation of *C. comatum*: coremial stalk (1); coremial head (2); conidia (3)

The most important pathogens are: *Ceratocystis coeruleum* (MUNCH) BAKSH. – in Norway spruce and pine; *Ceratocystis pilifera* (FRIES) MOREAU. – in pine; *Ceratocystis coerulescens* (MUNCH) BAKSH. – in spruce and pine wood; *Ceratocystis pini* (MUNCH) BAKSCH. – mostly in Scots pine; *Discula pinicola* – mainly in pine, active at fairly low temperature (a few degrees above 0°C) when other blue stain species are no longer active.

Spores of blue stain fungi are borne by the air, raindrops, bark beetles, human activities (transport of diseased wood), etc. The spores germinate only at high relative humidity and high temperature. Infection occurs only on uncovered wood. The mycelium of *Ceratocystis* spp. grows entirely in the vascular rays and wood parenchyma. Although the fungi feed mainly on cellular contents, they can also decompose cell walls to a limited extent.

The disease is promoted by wounds in trees and at a defined range in water content of wood. At water contents below 20% or above 80%, blue stain does

not develop. Warm weather also promotes the disease (20–25°C), except for some fungal species, as *D. pinicola*, which tolerates much lower temperatures. High relative humidity and tree-damaging bark beetles increase the risk of disease. Frozen wood, both solid and chipped, is more susceptible when defrosted, compared to unfrozen wood. Wood of Austrian pine (*Pinus nigra*) is considered particularly susceptible.

Blue stain deteriorates wood in different ways, limiting its quality, and several structural properties (particularly impact strength). Wood saturability is also limited. The value of wood as a construction material remains almost unchanged.

Protection is focused almost entirely on preventative measures as follows:

1. Reducing the time between felling trees and sawing (maximum 6 weeks).
2. Treating sapwood (on cross cuts) and trunk wounds with fungicides at high concentrations prior to leaving logs in the forest or wood yard.
3. Careful piling of lumber in fresh air to facilitate rapid air drying (the spacers should be free of blue stain).
4. Chemical protection of lumber (when air drying is not sufficient). Newly sawn lumber should be submerged/dipped in a fungicide solution for 10–60 seconds. According to BOYCE (1961) following fungicides are effective: Dowcide G (sodium chlorophenolate, 4%), Lignosan (copper-ethylic phosphate, 0.8%).
5. Submerging, dipping, or continuous spraying the timber with water to maintain the water content of the wood above 80% prevents infection by blue stain fungi.

12.1.5.2. Brown stain of wood [*Discula brunneo-tingens* MEYER]

The sapwood of Norway spruce, Scots pine, and Siberian larch is affected. The phenomenon is similar to blue stain; however, the sapwood turns coffee brown in color. The causal agent is *Discula brunneo-tingens* (*Deuteromycotina*, *Sphaeropsidales*), a fungus that produces dark irregular picnidia on the surface of the infected wood. The picnidia are irregular, multilocular, about 1–4 mm. The conidia are hyaline, elongated $5.2 \times 2.5 \mu\text{m}$, and are formed on branched conidiophores, 20–40 μm long. The optimum and minimum temperatures for the fungus are ca 30°C and 5–10°C. In central Europe, the pathogen appears to be a uniform species; no recognized races are known. A reservoir of the pathogen may be the knots (branch and stem junction) of healthy trees (BURKOT-KLONOWA 1971). Control of the disease follows the methods used for blue stain.

12.1.6. Quarantine diseases of spruce (EPPO/EC)

Most of the following diseases described here do not yet occur in Europe. Yet because of the likelihood of their introduction and because of the present Eu-

ropean and Mediterranean Plant Protection Organization (EPPO) regulations, they are presented here in brief. The descriptions below are based on Quarantine Pests of Europe (ANONIM 1994). The codes following the disease names denote the quarantine object classification scheme, according to the EPPO and European Community (EC).

12.1.6.1. Root and crown rot (foot rot) EC II/B) [Phytophthora cinnamomi Rands]

The disease occurs in almost all continents and affects many plant species, including conifers. Its most common symptoms are: seedling damping-off, transplant dieback, thin root rot, and irregular-shaped necrotic discolorations on aboveground parts of plants. Trees several years old and older may exhibit wilting, stem cankers (resulting in sudden tree death), yield reduction, fruit atrophy, gummosis, and various rots. The disease-causing agent, *Phytophthora cinnamomi* (Oomycota, Peronosporales), infects roots with zoospores and can survive in plant residues and soil up to 6 years.

In the climatic conditions of central Europe, the disease is a minor threat particularly in nurseries of ornamental trees and shrubs. Control techniques follow those recommended for damping-off. Systemic fungicides are recommended for soil drenches, spraying, and for trunk injections. When the soil is infested by the pathogen, resistant plants should be grown there for 4 years.

12.1.6.2. Common yellow witches broom rust, sprucebroom rust (EC I/A1, EPPO A1/8) [Chrysomyxa arctostaphyli Dietel]

The disease occurs in North America on *Picea abies* and other *Picea* spp. and on *Arctostaphylos uva-ursi*. Current-year needles are infected in early summer and turn chlorotic. The resting buds produce witches brooms with chlorotic needles bearing spermogonia under the epidermis. They are followed by ecia, which render the brooms orange in color. The needles senesce and are shed in autumn and the broom remains bare through the winter (as opposed to witches brooms caused by other factors). The brooms are usually large and infrequent in the tree crowns. Swollen fragments and cankers on branches seldom occur. The trees lose vigor, and branch and the crown dieback is observed.

Symptoms on bearberry appear in late spring as purple-brown spots on the lower leaf surfaces. Orange-brown waxy telia are formed there. The disease is a rust caused by *Chrysomyxa arctostaphyli* Dietel (Basidiomycota, Uredinales), an alternate-host, invalid life-cycle (lacking uredium). The pathogen occurs on spruce in stages 0 and I (pycnium/spermogonium and ecium) and on *Arctostaphylos uva-ursi* in stage III (telium). Sporidia produced from teliospores infect spruce early in the summer. Pycnia and ecia are abundant on current-year needles. Eciospores infect bearberry on which telia and sporidia are

produced. The disease causes considerable losses in *Picea engelmannii* and *P. pungens* stands in the US, and since the conditions in Europe are favorable, it is considered a potential threat to spruce stands in Europe.

12.1.6.3. Laminated butt rot, yellow ring rot (EC I/A1, EPPO A1/19) [Inonotus weirii (MURRILL) KOTLABA et POUZAR]

The disease occurs on various coniferous species in Japan and North America, affecting trees from the age of 1–2 yrs. Disease spots are noticeable when a stand is 10–15 years old and gaps or infection centers form. Between 5–15 years after infection, aboveground symptoms appear as growth decreases, needle loss, windthrow, and dieback. Yellow laminated rot spreads from roots of diseased trees to 4 m high in the trunk. In the butt and roots, brown crust-like sporophores are formed with white or cream-colored edges.

The disease is caused by *Inonotus weirii* (Basidiomycota, Hymenochaetales). Infection occurs through root contact with mycelium, which survives in roots and stumps for long periods (e.g. in Douglas fir ca 50 yrs). The sporophores (fruiting bodies) produce basidiospores on decomposed wood, but the spores are not responsible for infection.

The disease is considered a potential threat to European spruce forests. Control is difficult. Effective control of the mycelium in snags may result from the joint application of antagonistic fungi of *Trichoderma* spp. and chemical treatments that are more effective against the pathogen than the antagonistic fungi. A change in stand structure is recommended, increasing the share of resistant or less susceptible tree species. Only wood without bark may be imported into Europe. The import of bark itself is not permitted.

12.1.6.4. Dwarf mistletoes (EC I/A1, EPPO A1/24) [Arceuthobium spp.]

Dwarf mistletoes, occurring in North America, Central America, and Asia, parasitize many tree species of *Abies*, *Tsuga*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, and *Juniperus* genera. The symptoms vary depending on the host plant. At first the twigs swell, then witches brooms grow on successive branches or are limited to the infection point, depending on the pathogen. After the lower part of crown is infested, crown growth is inhibited, the needles turn yellow, the top dies, and eventually the whole tree dies.

The higher plants from the genus *Arceuthobium* cause the disease. Their shoots are tiny, smooth and vary in color with leaves reduced to very small scales. Male and female flowers appear (diameter of 2–4 mm) on young shoots. The female flowers produce two-colored, slimy oval berries containing a single seed that is explosively dispersed as far as ca 15 m. There are nine *Arceuthobium* species on the European quarantine list. Their biology is similar to that of the common mistletoe. Twigs younger than 5-yr old are infected most often.

Dwarf mistletoes are extremely harmful, as they cause a reduction in growth increment, seed production, wood quality, and eventually tree death. The threat to European stands is considered great because of the wide host range in central, eastern, and northern Europe. Due to the slow spread of seeds, sanitary cutting and removal of infested trees is considered effective. According to the general regulations, the import of transplants and branches of *Abies*, *Larix*, *Picea*, *Pinus* and *Tsuga* from North America and Asia is not permitted, whereas the import of seeds and tissue cultures are allowed.

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JACEK MICHALSKI

12.2. BARK BEETLES

Introduction

The bark beetles – *Scolytidae*, are among the most important pests of Norway spruce. These insects require trees with intact bark for their development. In natural conditions, they use the trunks of trees broken or thrown by wind or snow. They also attack trees weakened as result of other pest damage or by abiotic stress. For these reasons, a large majority of weakened Norway spruce trees in the forest ultimately succumb to bark beetles.

Scolytidae are characterized by a very high reproductive potential. Depending on the species, they can have one, two, and even three generations each year under favorable conditions. However, the main factor that initiates a large outbreak is an abundance of fallen spruce trees with intact bark in the forest.

Ips typographus (L.) (Fig. 12.24.) is the most important bark beetle species damaging Norway spruce. It is a common threat in both lowland and mountain forests. Its aggressiveness increases significantly with increasing population size. In these conditions, *I. typographus* also attacks healthy trees. It is a main constituent of the bark beetle species complex that affects *Picea abies*.

12.2.1. The biology of bark beetles

The species of *Scolytidae* are cambium and/or xylem feeders. They occur naturally in forests ecosystems. Their population sizes are not large under normal, stable conditions, but they increase in numbers, when the amount of broken, fallen or otherwise damaged Norway spruce trees increase in the forest stand.

The trees damaged in the winter, broken or thrown by wind or snow, are a common source of breeding material for the bark beetles (OKOŁÓW 1982; CAPECKI 1983, 1993).

Outbreaks of *I. typographus* occur often and this species is responsible for the greatest damage to Norway spruce stands both in the mountains and lowlands. The imago (adult) is 4–6 mm long, cylindrical, stocky, brown, glittering and rusty haired, especially on the sides of pronotum and elytra. The back elytral declivity is visibly hollow and dull (Fig. 12.24). The back edges of elytra in adults of both sexes have four teeth. The third tooth is the largest and knobby at the top (Fig. 12.25). The pronotum has parallel sides extending about two-thirds of its length, and is beveled on both sides towards the front, which is rough (with bumps). The epiphysial portion is smooth, shiny, and dotted. The elytra exhibit punctured stria, and wide smooth interstriae.

I. typographus swarms in April – May in Europe with a second generation in July – August. It normally has two generations every year, which can significantly increase the population numbers. In favorable climate conditions, e.g. an early warm spring and warm and late autumn, a third generation appears, which additionally increases the population size. It is a polygamous species. The maternal gallery is regular, bored along the wood fibres, about 6–15 cm long and begins with a nuptial chamber (Fig. 12.26). The number of maternal galleries depends on the number of females (1–4), because each of them bores one maternal gallery. When there are three maternal galleries, two of them are bored toward the bottom of the trunk; in case of two galleries, one is bored toward the top, and the second toward the bottom. Each single maternal the gallery is bored to the top. The egg niches, numbering 20–100, are bored on both sides of gallery at irregular distances. The

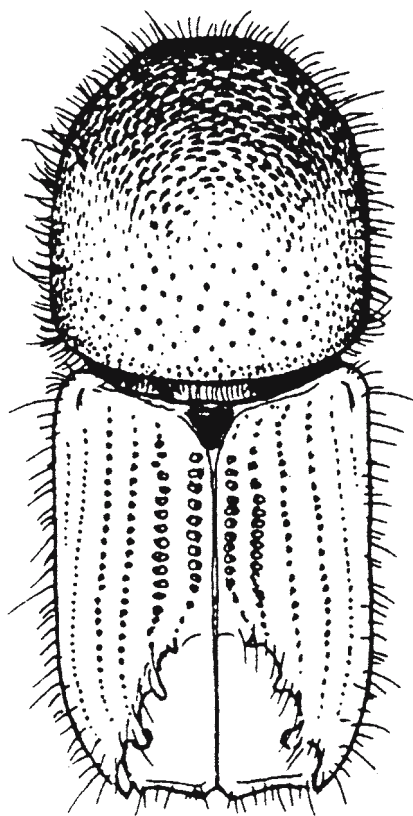


Figure 12.24. A schematic view of *Ips typographus* (L.) body shape, a lateral view with the characteristic four teeth, the third of which is the largest and capitate at the end (by A. MAZUR)

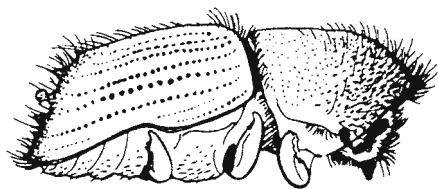


Figure 12.25. The profile of the *Ips typographus* (L.) body. The front edge of the pronotum in the shape of a trapezium with rounded angles is characteristic for this species and distinguishes it from the other *Ips* species, such as *I. amitinus*, in which the front edge of pronotum is softly rounded (by A. MAZUR)

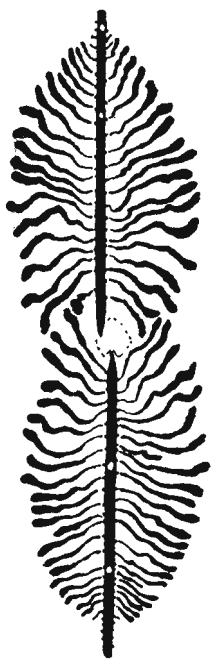


Figure 12.26. The scheme of the *Ips typographus* (L.) gallery system. There are usually two maternal galleries coming from the nuptial chamber situated inside the bark. Maternal galleries are parallel to the wood fibres and are straight for almost their entire whole length (by A. MAZUR)

eggs are always covered by sawdust. The hatched larvae bore their own larval galleries, initially perpendicular to the maternal gallery, then more or less along the wood fibers, 4–6 cm long, and clogged with thick, brown sawdust. The larvae pupate in oval cradles. The beetles carry out supplementary regeneration feeding. This species can also bore bay-like caves or galleries on branches. The young individuals of the 1st generation leave the gallery system in mid July or later, depending on weather conditions.

The mature beetles continue to feed. The adult females extend the maternal galleries, and males widen the nuptial chamber. New galleries can also be bored by the adults and used by a second hatching (sister brood), which numbers about 60% of the first one. In the middle of July, the young beetles initiate a second generation, sometimes along with the sister generation. A third generation is possible when autumn is sufficiently warm. The adults of the second generation, along with the larvae and pupae of second and third generations can overwinter in galleries in various stages of development.

Several other species occur along with *I. typographus*, increasing damage to forest stands. The most common and important are *Ips* species: *I. amitinus* EICHH., which occurs both in the mountains and lowlands, and *I. duplicatus* SAHLB., characteristic mostly of the lowland portions of the range of Norway spruce, but reported recently also in the uplands and mountains (GRODZKI 1997a, 2003). All three species appear together, fre-

quently overlapping and intergrading in their ranges. In numerous Norway spruce stands *Pityogenes chalcographus* (L.) is also considered as an important and dangerous species accompanying *I. typographus* (GRODZKI 1997c). Another dozen or so species of *Scolytidae* also are known to co-occur. Together these species form a “bark-beetle complex”, to which belong *Polygraphus poligraphus* (L.), *Xylechinus pilosus* (RATZ.), *Pityophthorus pityographus* (RATZ.), *P. micrographus* (L.), *Dendroctonus micans* (KUG.), and *Xyloterus lineatus* (OLIV.). This group of species is most often associated with *I. typographus*. Several other species that appear less often with this species include: *Hylurgops palliatus* (GYLL.), *H. glabratus* (ZETT.), *Cryphalus abietis* (RATZ.), *Dryocoetes autographus* (RATZ.), and *D. hectographus* (REITT.). The above-mentioned species sometimes occur separately, but all of them occur with *I. typographus*, *I. amitinus*, and *I. duplicatus*, depending on the climatic conditions and stand age. *I. typographus* and other bark beetles inhabit various parts of spruce trunks, from its lowest parts to the top and even branches (Fig. 12.27).

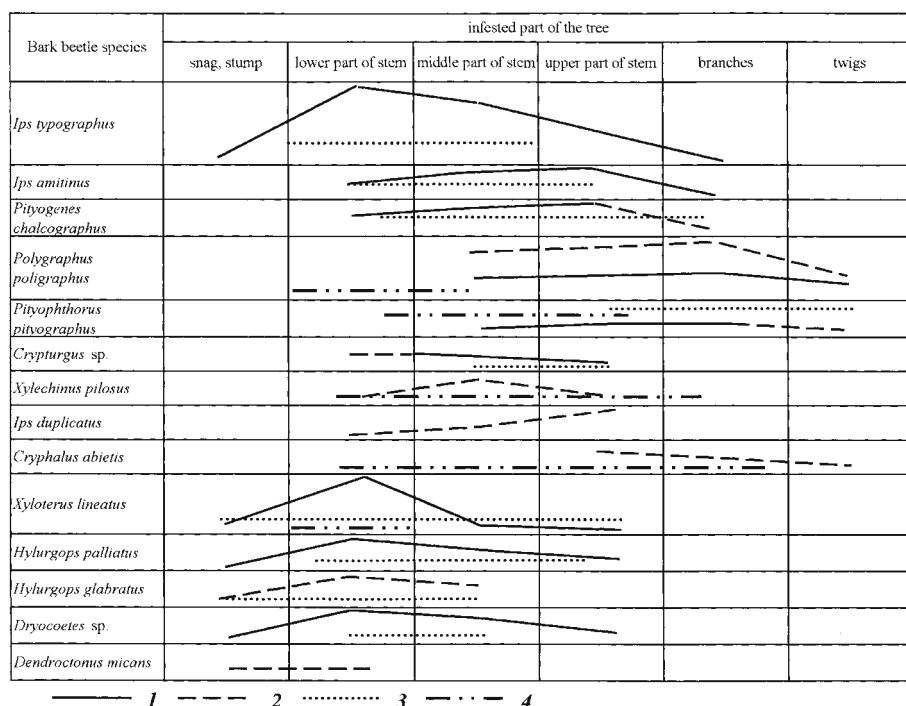


Figure 12.27. Infestation by bark beetles on standing (after CAPECKI 1978) and fallen (modified by MICHALSKI) trees: 1. after CAPECKI; 2. modified and supplemented by MICHALSKI; 3. fallen trees of IV–V age classes; 4. standing trees of younger age classes

12.2.2. Bark-beetle outbreaks and control measures

Norway spruce forms natural forest communities that extend to the upper elevations of the mountains of Central Europe (see Chapter 4). The species exhibits the greatest growth increment and wood production in the environmental conditions of central Europe and has been an important forest tree species for at least two centuries in this region. The large-scale planting of Norway spruce in the past is one reason that this forest type dominates many parts of central Europe.

Monospecific and especially even-aged and older forest stands of *Picea abies* may give rise to numbers of injured or weakened trees that increase the probability of a bark-beetle outbreak. In general, the forest should be well managed during all seasons of the year. Any dying or weak trees, trees with broken tops or larger branches left in the forest serve as a food source for the bark-beetles, sufficient to increase the population to a critical size.

Outbreaks of *Scolytidae* are promoted by the presence of spruce trees with intact bark. The sources of such material include all logging residues left after cutting, i.e. the remaining branches, trunks, stumps, and even aboveground parts of root systems. Broken trees are also a common food and breeding source, but weakened trees are the second source of material suitable for the bark beetles. Stressed, weakened, and dead trees may appear following drought, low temperature, air pollution, and as a result of injury caused by fungi, defoliating insects, herbivorous mammals, etc. (CAPECKI and GRODZKI 1998; GRODZKI 1998; GRODZKI *et al.* 2004). Forest stands of even age, especially when not sufficiently managed, are of concern.

Prevention measures include proper stand management. Trunks and remaining coarse branches should be removed from the stand immediately after cutting. The trunks should be peeled and stored in open areas for drying. Where allowed, chemical treatment can be used to protect against the bark beetles. The bark should be burned, especially when insect pupae are present. The branches should be burned when they cannot be removed from the forest in a timely manner.

Careful observation of growing trees is another very important preventive measure. Each weakened tree can be the prey of *I. typographus*. The insects produce sawdust when boring out the galleries in cambium between the wood and bark. The presence of sawdust indicates that the tree has already been attacked by *I. typographus* or other species of bark beetle. The infested trees in Norway spruce stands should be cut down and the bark peeled before the new generation of *Ips* spp. pupate and disperse.

An effective control method is the use of trap trees, set in the stands in early spring. Broken or fallen trees can be used to control of presence and quantity of the bark beetles in a forest stand. The number of galleries on such trees indicates the potential for a bark beetle outbreak. The trap trees should be peeled before the new generation pupates and infests other spruce trunks. This is a

traditional, but very efficient way to control *Ips* population sizes. Populations can also be monitored with artificial pheromone traps.

Compared to the effective measures against other insect outbreaks, such as leaf-eating insects, there is limited possibility to successfully control a massive bark beetle outbreak. The only effective method is to keep forest stands and ecosystems in good health and to remove any broken, fallen and weakened trees before they become the feeding grounds of bark beetles.

12.2.3. Natural enemies of bark beetles

The bark beetles have many natural parasites or predators, which act to control population sizes at low population densities. The majority of bark-beetle parasites are other insect taxa. However, parasites from the *Acari*, *Nematoda*, and even *Protozoa*, which develop on the various stages of *Scolytidae* are also common (MICHALSKI 1998). Birds are natural predators of bark beetles too.

Several dozen species of hymenopterous insects, predominantly from the families *Braconidae*, (*Ichneumonidae*), *Eurytomidae*, *Pteromalidae*, and *Eulophidae* (*Chalcidoidea*) parasitize the larva and pupa of most of the above-mentioned *Scolytidae* taxa (Fig. 12.28). Also the imagines of *I. typographus* are frequently parasitized by hymenopters as end-parasites or even hyperparasites (SITOWSKI 1930; MOKRZECKI 1933; KARPIŃSKI 1935; NUNBERG 1930; KARPIŃSKI and STRAWIŃSKI 1948; WIĄCKOWSKI 1956; SZCZEPAŃSKI 1960; KRÓL and MICHALSKI 1961; BAŁAZY and MICHALSKI 1962; BAŁAZY 1965, 1966, 1968; BAŁAZY *et al.* 1967; CAPECKI 1967, 1978; MICHALSKI and RATAJCZAK 1989, 1994; MAZUR 1996, GRODZKI 1997b, MICHALSKI 1998).

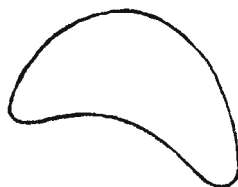


Figure 12.28. The characteristic shape of a Chalcid (*Chalcidoidea*) larva, often found in the larval or maternal galleries of the bark beetles (by J. MICHALSKI)

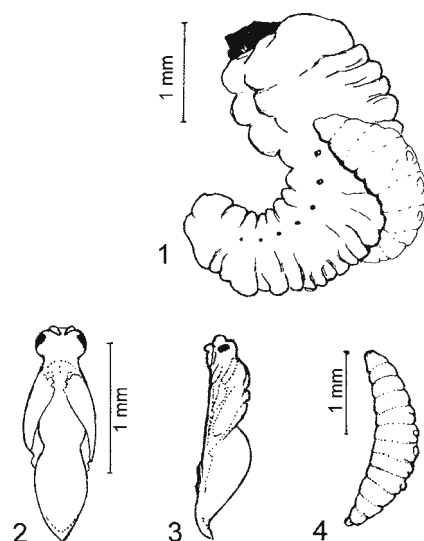


Figure 12.29. Parasites of bark beetles (by A. MAZUR): 1. bark beetle larva with parasitizing Chalcid larva; 2 and 3. free pupae of parasites found in the bark beetle galleries; 4. parasite larva

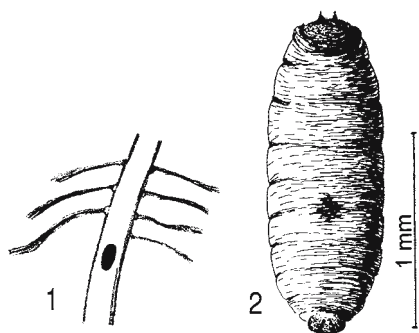


Figure 12.30. A portion of the bark beetle galleries with the typical pupa of the genus *Lonchaea* (1) (by J. MICHALSKI) and this pupa enlarged (2) (by A. MAZUR)



Figure 12.31. Predatory larva of *Raphidia* (by A. MAZUR)

A large group of predatory insect species also destroys the eggs, larvae, pupae, and adult bark beetles. Species from *Coleoptera*, *Diptera*, *Raphidioptera*, and also *Odonata* and *Heteroptera* are among the typical predators of *Scolytidae*. *Coleoptera* from the families *Staphylinidae*, *Histeridae*, *Cucujidae*, *Nitidulidae*, *Rhizophagidae*, *Tenebrionidae*, *Carabidae*, and *Cleridae* are the most numerous among them. The larvae and imagines of these insects (Fig. 12.29, 12.30, 12.31) are important predators of the various developmental stages of bark beetles (MOKRZECKI 1933; KARPIŃSKI 1935; WIĄCKOWSKI 1956; KINELSKI and SZUJECKI 1959; BAŁAZY and MICHALSKI 1960, 1977, 1982, 1983; SZUJECKI 1960, 1976, 1978, 1980, 1996; OKOŁÓW 1963, 1982; NUNBERG 1967, 1976; BAŁAZY 1966, 1968; SENICZAK 1968; BAŁAZY *et al.* 1974; CAPECKI 1978; DOMINIK and STARZYK 1989; MICHALSKI and RATAJCZAK 1989, 1994; MAZUR 1996, GRODZKI 1997b, MICHALSKI 1989, 1996, 1998).

The important predators and parasites of *Scolytidae* larvae are the larvae of the *Diptera*, mostly from the families *Dolichopodidae* and *Lonchaeidae* (MOKRZECKI 1933; KARPIŃSKI 1935; KARPIŃSKI and STRAWIŃSKI 1948; KRÓL and MICHALSKI 1961; BAŁAZY 1968; MICHALSKI 1982, 1988; MICHALSKI and BANASZAK 1994; MICHALSKI and RATAJCZAK 1989, 1994). There are a number of *Acari* species, which are associated with *Scolytidae* as parasites or predators. Many species have been frequently observed in the bark-beetle galleries (MICHALSKI 1998 and literature cited therein). The predatory *Acari* species from the *Mesostigmata* are considered among the most important in regulating the population size of the bark beetles (KIELCZEWSKI and MICHALSKI 1962; LINDQUIST 1964, 1967, 1969, 1970; KIELCZEWSKI and BAŁAZY 1966; KIELCZEWSKI *et al.* 1973; KIELCZEWSKI and WIŚNIEWSKI 1983; BAŁAZY and WIŚNIEWSKI 1986, 1987; KACZMAREK *et al.* 1992; KACZMAREK and MICHALSKI 1995a, b).

The several genera of *Nematoda* also contain species that parasitize the *Scolytidae*. Infection leads to the degeneration of some organs of the bark beetles, reproductive dysfunction, and sometimes death (MICHALSKI 1984; MICHALSKI and TOMALAK 1984; TOMALAK *et al.* 1984). *Nematodes* from the orders *Tylenchida* and *Rhabditida* are the most frequent parasites of *Scolytidae* (WEISER 1954; RÜHM 1956; BAŁAZY 1966, 1968; NICKLE 1967; MASSEY 1974; MICHALSKI 1982, 1989; RIMMELT 1994; MICHALSKI 1998). The nematode parasites are frequently specialized to particular bark-beetle species (MICHALSKI 1998).

12.2.4. Historical outbreaks of bark beetles

Outbreaks of bark beetles have been noted many times in the historical record in central Europe. The most spectacular took place in the years 1774–1798, 1808–1809, 1845–1858, and 1918–1922 (WOLSKI 1966; CAPECKI 1986a,b; SZWAŁKIEWICZ 1996). These outbreaks and more recent ones are correlated with the occurrence of wars and explained as the result of many Norway spruce trees being cut down and left in the forest. In the mountain regions, outbreaks also follow stand blow-downs resulting from foehns (and other strong winds), as occurred in the years 1921 and 1925 in the Tatra Mts in southern Poland. The very cold winter in 1929 also caused many injuries in the spruce stands, both in the lowlands and in the mountains and was the reason for the bark beetle outbreak noted in many regions of central Europe.

The outbreaks of the *Ips* spp. complex in Poland during the past 50 years also tend to follow various forest stand disturbances. The most spectacular outbreak occurred in 1984–1988 as a result of drought and an outbreak of

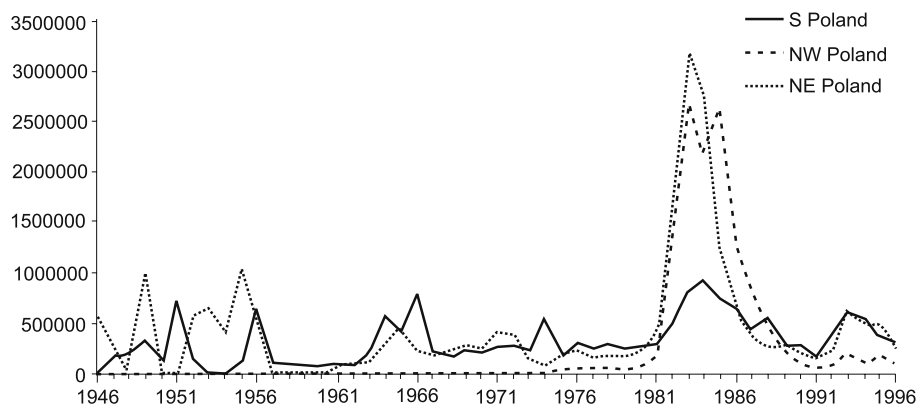


Figure 12.32. The volume (cubic meters) of spruce trees infested by bark beetles, and felled in the stands of individual regions (southern – mountains, north-western and north-eastern) of Poland, following the II World War

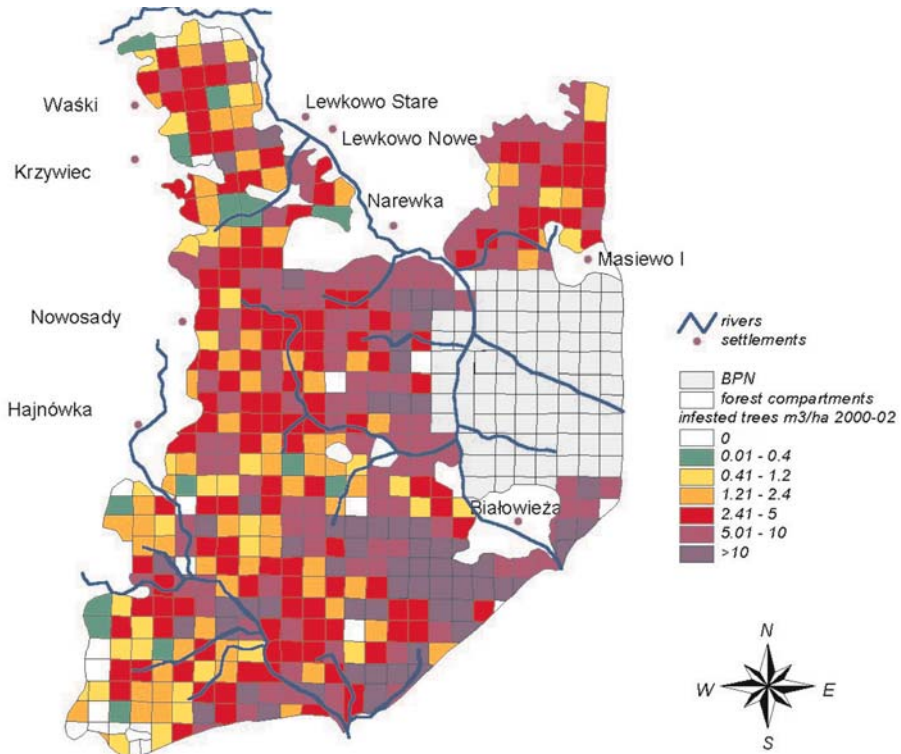


Figure 12.33. Total volume of trees infested by bark beetles (m³/ha), removed from individual forest compartments in three Forest Inspectorates of the Białowieża Forest (Białowieża National Park excluded) 2000–2002 (MICHALSKI et al. 2004)

Lymantria monacha (Fig. 12.32). Damage was much higher in northern Poland than in the mountain regions, but a large outbreak severely damaged Norway spruce stands damaged by *Zeiraphera griseana* HB. in the Sudetes (CAPECKI and GRODZKI 1998). The quantities of Norway spruce wood transported off the forests in the northern part of Poland after this event were 3–4 times larger than in any previous outbreak. As a result, some Norway spruce forest stands completely disappeared from the northwestern part of Poland. The historical record underscores the importance of prevention as the best method to control bark beetle outbreaks.

In recent years several bark beetle outbreaks have occurred in both the northern and southern Norway spruce ranges in Poland. In the last decade, two subsequent outbreaks took place in Białowieża Forest (Fig. 12.33) (MICHALSKI et al. 2004), but the largest outbreaks were observed in the Tatra Mts on both sides of Polish-Slovak state border (GRODZKI et al. 2003), as well as in the Western Carpathians in Polish, Slovak, and Czech territories

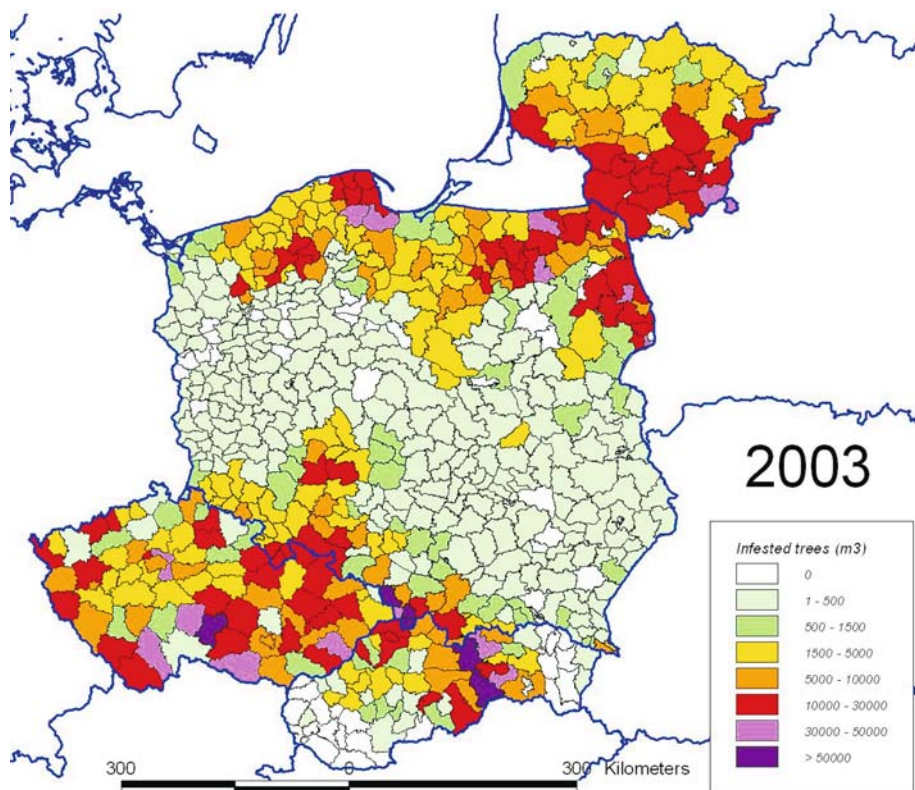


Figure 12.34. The volume of trees infested by bark beetles in 2003 in individual forestry or state administration area units in four adjacent Central European countries: Poland, Czech Republic, Slovakia, and Lithuania (GRODZKI and JACHYM 2004)

(GRODZKI 2004). In the last several years, new bark beetle outbreaks are developing in several, distant areas with Norway spruce stands throughout Central Europe (Fig. 12.34) (GRODZKI and JACHYM 2004).

Acknowledgements: I would like to thank Prof. dr hab. Adam Boratyński for the English translation of the text, and dr Wojciech Grodzki for his help in preparation of the final version of the text and figures, and supply of color maps.

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13. SILVICULTURE OF NORWAY SPRUCE

STANISŁAW SZYMAŃSKI

13.1. THE IMPORTANCE OF NORWAY SPRUCE

Norway spruce [*Picea abies* (L.) KARST.] is second only to Scots pine (*Pinus sylvestris*) as the most important forest tree species in European forestry. It is comparatively easy to cultivate, and its wood products are very valuable for high-quality pulpwood and lumber. Its wood is broadly used in carpentry and as a construction material. Narrow-ringed wood without defects, termed resonant wood, is highly prized for manufacture musical instruments (see Chapter 6.2.3). Young Norway spruce trees are used as Christmas trees and its boughs are used for decorative purposes.

13.1.1. Growth and yield in Norway spruce

Norway spruce is among the top five most productive forest tree species. A ranking of the most productive stands at age 100 years are: fir (*Abies alba*),



Figure 13.1. A 95-year-old, even-aged Norway spruce stand in the “Butorza” Nature Reserve (Rycerka Forest District, western Carpathians, Poland)
(photo S. SZYMAŃSKI)



Figure 13.2. A seed stand of the Istebna ecotype of Norway spruce (age 140 years) in compartment 149 h, Bukowiec Forest Division, Wisła Forest District (western Carpathians, Poland)
(photo S. SZYMAŃSKI)



Figure 13.3. The crown form of 140-year-old Istebna spruce in compartment 149 h, Wisła Forest District (western Carpathians, Poland) (photo S. SZYMAŃSKI)

spruce, Scots pine, beech (*Fagus sylvatica*), and oak (*Quercus robur*) (PUCHALSKI 1968). Spruce stands containing 750 to 800 m³/ha age 100 years are common (Fig. 13.1). Some over-mature seed stands of a valuable provenance, i.e. Istebna (Poland), approached 900 m³/ha at age 140 years (SZYMAŃSKI 1973, 1975) (Figs 13.2 and 13.3). The standing volume of the stand shown in Fig. 13.2 exceeded 1000 m³/ha at 170 years and had a mean height of 45 m.

13.1.2. Norway spruce as a forest tree in Poland

Norway spruce, as a typical hygrophyte with a shallow root system, appears adapted to sites with a high soil moisture content and high annual precipitation. Consequently, its natural distribution in Poland covers the cooler northeastern regions of the country and the montane regions in the southwest, where precipitation increases with altitude (see Chapter 4.2).

Intensive cultivation of Norway spruce in those regions is shown in Fig. 13.4, where the percentages of Norway spruce stands in the individual provinces of Poland are presented. However, increasing pollution loads from the large urban and industrial centers of Poland and Western Europe may restrict its cultivation, even in the northeastern parts of the country. Further details on the distribution of Norway spruce in pure and mixed stands in Poland are presented by ŻYBURA (1990) (Table 13.1). According to ŻYBURA (1990), the forest area of spruce stands is ca 483, 000 ha, comprising 7.3% of the total forest cover in Poland. This species is found most often in mixed-species stands. ŻYBURA (1990) in his summary of the role of Norway spruce in forestry in Poland stated:

1. Three regions within the range of Norway spruce are: the northern and southwestern regions, where spruce has a very important role; the central and western region, where it plays a minor role in forestry; and the central and southeastern region, where it is largely insignificant (Fig. 13.5).



Table 13.1. The total forested area of dominant and mixed Norway spruce stands of various stand age classes in Poland (in thousand of hectares) (after ŻYBURA 1990)

Age class	Area of Norway spruce stands								Total
	Dominant	Mixed stands of tree species						Other tree species	
		<i>Pinus sylvestris</i>	<i>Fagus sylvatica</i>	<i>Quercus robur</i>	<i>Betula pendula</i>	<i>Abies alba</i>	<i>Alnus glutinosa</i>		
I, 1–20	97.0	160.8	4.0	30.1	11.9	4.1	10.4	0.2	318.9
II, 21–40	47.9	34.7	2.4	5.0	16.8	2.9	3.3	0.6	113.6
III, 41–60	107.9	76.1	8.5	6.6	22.0	4.7	5.9	1.6	233.3
IV, 61–80	109.3	73.7	8.9	7.1	9.1	5.2	5.6	0.8	219.7
V, 81–100	61.3	66.4	8.9	9.3	1.4	3.1	3.5	0.6	154.5
VI, 101–120	20.2	26.9	4.6	6.3	0.0	1.2	1.3	0.5	61.0
VII, 141–160	11.1	21.3	2.2	5.8	0.0	0.6	0.3	0.4	41.7
stands re-generated with the seed tree method	26.1	6.2	8.1	2.5	0.5	5.5	2.2	0.6	51.7
sparsely timbered areas	1.4	0.4	0.1	0.1	0.0	0.0	0.1	0.0	2.1
	482.6	466.5	47.7	72.8	61.7	27.3	32.6	5.3	1196.5

usually regenerated in canopy gaps following the removal of beech. Consequently, fir typically occurs in patches in mixed stands with spruce. ATTENBERGER (1954) and ASSMANN (1961, 1968) observed higher productivity in the mixed stands than pure stands of spruce or fir. Prior studies in Germany indicated that volume production in the mixed stands was higher in some cases, whereas in others it was equal to the productivity of pure stands of individual species. The presence of fir within spruce stands is advantageous because of its stable root system, increasing stand resistance to windthrow. Additionally, the admixture of fir litter in the stand improves the decomposition of the acidic litter of Norway spruce. To maintain fir within spruce stands, it is necessary to regenerate it in the understory earlier than other species and follow with intensive further tending. The most desirable compositions of mixed fir-spruce stands are established by group selection silvicultural techniques. The silvicultural management of mixed stands is effective only when the percentage of fir in the forest is high and the seedlings are protected from large herbivores.

Pine-spruce stands are common in many regions in northern Europe, Asia and North America. In Poland, pine-spruce stands result from either natural or artificial regeneration. Within such stands the maintenance of the pine component is very important, even if the pine trees are not economically valuable.

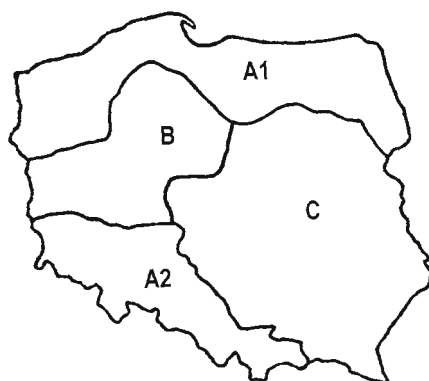


Figure 13.5. Division of Poland into regional zones differing in importance of Norway spruce forests (adapted from ŻYBURA 1990)



Figure 13.6. A natural spruce stand in the upper region of Mt. Pilsko (western Carpathians, Poland) at an altitude of 1250 m (photo S. SZYMAŃSKI)

Beech-spruce stands, usually with an admixture of fir, were once common in the mountain regions of central Europe. However, clear-cutting reduced the extent of this forest type. In many forest sites, a mixture of beech within the Norway spruce stand is highly profitable. On most forest sites suitable for both species, Norway spruce grows faster than beech until age 10 years. Consequently, beech must be established early and regenerated in either small or large groups. Subsequently, beech requires protection during the silvicultural tending treatments.

The beech-fir-spruce forest type is the natural forest cover in lower mountain regions throughout central Europe, especially in the Alps, Black Forest, Sudety Mts, Dynarian Alps, and Carpathians. DENGLE (1943) wrote that a mixed forest consisting of these three species is the optimal forest type to produce the highest volume of large-diameter timber. This species composition creates ideal conditions for natural regeneration. The silviculture systems in Bavaria originate from the management of this forest type.

Birch-spruce stands are established in the same manner as pine-spruce stands, i.e. through the natural seeding of the pioneer birch species in the spruce stands. Formerly, removal of these seedlings was advised owing to the "whipping" of spruce by birch branches. At present, it is known that fast-growing birch in the juvenile stage acts as a shelter against frosts occurring in open areas, where young spruce are susceptible to ground-level frosts.

Oak-spruce stands are rather rare in central Europe because spruce is a shade – intolerant species compared to the broadleaved forest trees species.

Larch-spruce stands are characteristic of many upper elevation mountain sites, where they are naturally established. In the lower elevations, they are rarely observed and originate from artificial seeding or planting. Larch is maintained in the stand as an admixture only in large patches of 0.15–0.25 ha. Currently, it is still possible to find mixed stands of larch and spruce of natural origin in the Sudety Mts in Poland.

13.2.2. Natural and artificial regeneration of Norway spruce

Norway spruce is small-seeded tree species that can regenerate naturally under shelterwood cuts and in openings near adjacent mature stands. Spruce readily regenerates along the northern edge of mature stands, likely owing to the increased soil moisture that is key to successful its regeneration.

In the practice of forestry, several silvicultural systems have been developed to regenerate Norway spruce stands. The uniform shelterwood system is used for stands situated in protected mountain valleys or in areas lacking strong winds. This system sometimes consists of preparatory cuts to create the proper soil and seedbed conditions. Alternatively, a late thinning may prepare both the stand and soil for natural regeneration. In this case, the preparatory cuttings are not necessary and the system begins with the next stage, called the

seed-tree cut. Seed-tree cuttings are conducted in a year with an abundant seed crop. These cuttings open up the canopy of the parent stand and provide enough light for new seedling growth during the subsequent 2–3 years. Norway spruce growth may be further enhanced by light thinnings. Following the natural regeneration and recruitment of spruce, the remnant trees of the parent stand are felled with a removal cut. Concomitantly, the regeneration success in the stand is surveyed. In the spring, artificial over-plantings may be established using light-demanding forest tree species (e.g. larch, pine). These species should be planted in either small or large groups. The introduction of the admixture enriches the species composition and biodiversity of the forest and stabilizes the shallow-rooted spruce stand against damage from wind and snow.

Another silvicultural system is the progressive shelterwood and group selection system, known as the Bavarian irregular shelterwood system. This system is the combination of the improved Swiss *femel* cutting system (CARL GAYER) and shelterwood strip or border cutting system. The aim of this system is to increase the percentage of valuable spruce timber in spruce stands composed of fir and beech. It is often applied in mixed stands of spruce, beech, and fir. Initially, small openings in the stand are created in the foreground of the regeneration zone to naturally regenerate fir and beech. These openings occupy about 30% of the strip under regeneration. After the fir and beech have regenerated and the sapling height exceeds 70 cm, a seed cut on the whole strip is carried out in a seed year of Norway spruce. The remaining 70% of the strip area, not yet regenerated, is then seeded in naturally by spruce. To stimulate Norway spruce growth, low intensity thinnings between the openings of fir and beech are conducted. When the trees exceed 70 cm in height, the remaining canopy layer is harvested by a removal cut. In this manner, a mixed stand of fir, beech, and spruce, resulting from natural regeneration, is formed with the Norway spruce as the dominant species (70%). Owing to the lack of adequate light and temperature and because of strong competition for water and nutrients under the shelterwood, the removal cuttings are conducted rather early, but only after the requirements of the natural regeneration have been met.

The optimal method for the natural regeneration of spruce is the strip selection cutting system, synonymous with WAGNER'S system (1923). This silvicultural system is based on the most advantageous ecological conditions for the natural regeneration of spruce along the northern edge of the stand. This method is based on peripheral strip cuttings with decreasing intensity inside the stand. The cuttings thin an outside strip (Fig. 13.7) and continue inside the stand following the appearance of fir, beech, and spruce regeneration. This system gives the best results in regenerating pure Norway spruce stands and mixed stands comprised of fir, beech, spruce, pine, and larch, but with a dominant spruce component. The management area consists of two strips extend-



Figure 13.7. Natural spruce regeneration along a stand edge in the “Butorza” Nature Reserve (Rycerka Forest District, western Carpathians, Poland) (photo S. SZYMAŃSKI)

ing along the edge of the stand (Fig. 13.8) as follows: a) an outside strip, the width of 1/2 to 1 times the height of the stand; and b) an inside strip, the width of 1/2 to 2 times the height of the stand. Thus, the width of the management area may approach 1 to 3 times the height of the stand. At the border between the two strips, one can distinguish the “stand edge”, a narrow area about 10 m wide (1/3 of the stand height) and extending 5 m to the outside and inside along the stand. Within the inside strip, the shade tolerant species (fir and beech) are the first to naturally regenerate.

Norway spruce regenerates at the edge of the stand. Light-demanding species occur in the outside strip by self-seeding or artificially as needed. This

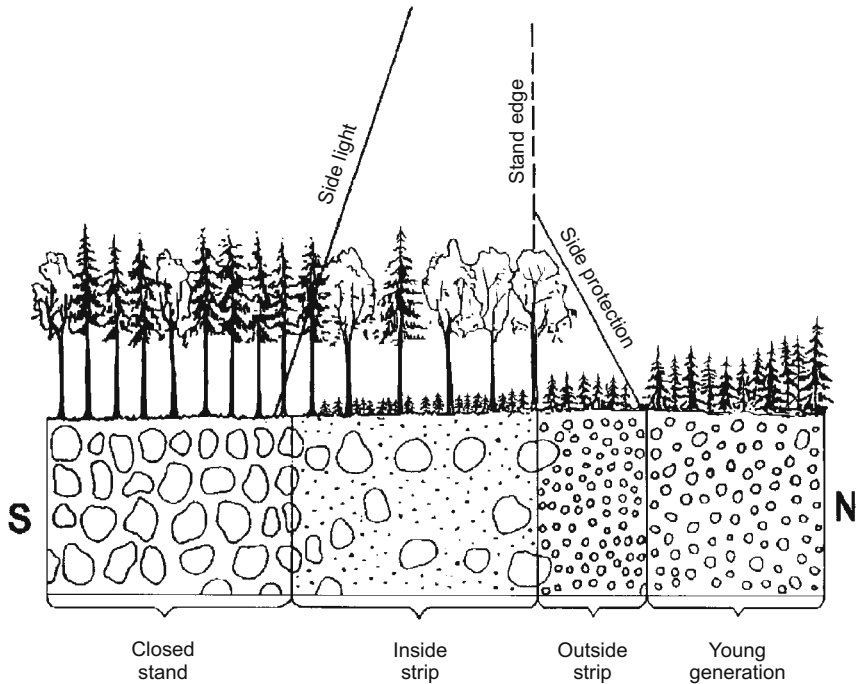


Figure 13.8. Natural regeneration along the northern edge of a stand using the stepwise cutting (strip-selection cut) method (WAGNER, after VANSELOW 1943)

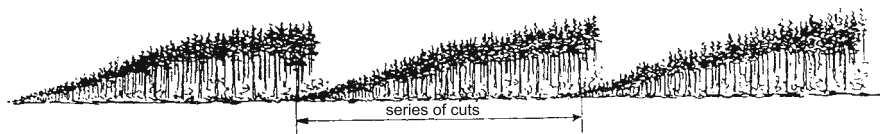


Figure 13.9. A stand profile showing a series of cuts in the strip selection method (by WAGNER)

silvicultural system is effective in reducing light levels inside the stand. The regeneration occurs under the canopy of the parent stand (the inside strip), extending through the cuts, across the stand edge, and within the shade along the edge of the stand. Finally, the regeneration extends out of the stand into the open area.

The progress of the cuts is slow in this system and the regeneration interval is long (30–40 years). Throughout a 10-year period, the regeneration “wave” moves about 20–30 m inside the stand (2–3 m per year). To accelerate natural regeneration, the stand is divided into separate zones and strip cuts are made simultaneously on all strips of each zone, creating a “sawtooth” stand profile arising from the cutting series (Fig. 13.9). A strip selection cutting system should be continued without interruption. TWARÓG (1990) stated that this silvicultural system does not guarantee the “overtaking” of fir and beech adequately in the inside strip.

The artificial regeneration of Norway spruce through clear-cutting and planting is a common forestry practice. Two- to five-year old, bare root seedlings are used as the planting stock; however, containerized plants are increasingly being used.

The growth and quality of the bole depends on the amount of growing space, e.g. the initial spacing. According to PUCHALSKI (1968), the optimal square spacing ranges from 1.3 m to 2.0 m. PUCHALSKI (1968) recommended a 1.5×1.5 m initial spacing in the lowlands and lower altitudes in the mountains, 1.75×1.75 m in the intermediate altitudes, and 2.0×2.0 m spacing at the higher altitudes. Re-



Figure 13.10. A Norway spruce stand in the Zdroje Forest District in Poland, a typical example of rectangular spacing with a 2.5 m distance between rows

cently, rectangular spacing is used commonly with the distances between rows of 2.0 m and 3.0 m (CEITEL 1994a) (Fig. 13.10). The initial growing space should not exceed 3.0 m² in the lowlands and the optimal number of seedlings is 4000–5000 per hectare (CEITEL 1994b) with an initial spacing of 2.0 m × 1.0 m or 1.5 m × 1.5 m. Because of the high costs of row planting in the mountains, this method is not practical in forestry there.

As an alternative to the use of clear-cutting systems over large areas, a number of variants, such as strip clear-cutting or strip-like clear-cutting are used in forestry. In Norway spruce stands, east-west oriented strip cuts are made typically 15–30 m in width and equal to the height of the stand. Owing to the shade cast along the northern stand edge, Norway spruce grows better there than under the shelterwood of the parent stand.

13.2.3 Tending and thinning principles in spruce saplings and older stands.

Owing to the high density of spruce stands, the tending treatments are quite different from those of beech, oak, and pine saplings. According to PUCHALSKI (1968), this difference arises from the fact that Norway spruce stem growth is always straight and does not form wolf trees. The dominant and codominant trees are the most valuable individuals in the stand. During the juvenile stage, Norway spruce requires wide spacing in order to form a long and regular crown, which promotes intensive growth. Branching is not important; however, if the younger branches are suppressed, the number of trees within the stand should be reduced immediately by removing the smaller trees. This renders the stand less susceptible to the negative impacts of climatic factors, such as snow and wind, and it is the most important purpose of the thinning treatments. This aim is achieved by appropriately tending the tree crowns. For this purpose, the best spruce stands are those in the first age class (up to 20 years); however, older stands (age classes II and III) respond well to strong thinning operations. This objective, according to PUCHALSKI (1968), is best achieved by heavy thinning in the juvenile stage when the tree height is 5–10 m. This type of thinning achieves better tree growth and higher volume in the pole stand. A more intensive thinning should be carried out in stands on drier sites to promote crown and root system development. Table 13.2 presents results obtained by WECK (1955). Understory trees, while maintained in the stand, do not contribute to the volume increment. At most forest sites, the understory trees negatively influence the decomposition of litter, especially on the poorer, drier sites.

There are several tending treatments that reflect the ecology and biology of Norway spruce. One example is the thinning method described at the end of the nineteenth century by BOHDANECKY (1880) and developed especially for pure spruce stands. In this method, the stand is thinned early before an age of 30 years. The number of remaining trees per hectare depends on the forest

Table 13.2. Tree crown classes as a percentage of the total number (stand density) and basal area of trees within a well-thinned Norway spruce stand (from WECK 1955)

<i>Crown class</i>	<i>Percentage</i>	
	<i>Number of trees</i>	<i>Basal area</i>
Dominant	25	58
Codominant	45	37
Intermediate	20	4
Suppressed	8	1
Dead	2	—

site: 2000–2500 on the better sites and 3000–3500 trees on the poorer sites. The large reduction in canopy density is aimed at promoting increased crown length in the remaining spruce. When the trees begin to compete, a thinning is conducted at the higher layers of the stand. At the same time, any damaged, infected, branched, and curved trees are removed from the stand. Three years after the thinning treatment, the crown cover should equal that prior to the treatment. This thinning method led to a shortening of the production cycle of large-diameter, valuable spruce timber. According to BOHDANECKY (1880), the determination of the timing of the cuttings depends on the stand-tending method and not on site quality. BOHDANECKY established the rule that during the first half of the production period, volume increment should be favored. During the second half, greater attention should be paid to stem quality.

GEHRHARDT (1924) developed another thinning method, based on the premise that the highest volume of timber is obtained during the shortest production period, if the tree crown lengths are as long as possible. The thinning cycle should be short, of high intensity, and should not exceed 3 years. The contact of adjacent trees is permitted only in young stands until the age of 40 years. Then, neighboring trees should not suppress the crowns of one another in order to produce trees of the highest volume (diameters).

The most appropriate thinning method for Norway spruce is WIEDEMANN'S thinning method (1936). In this method, the spruce stand is prepared for thinning by reducing canopy closure during the initial stages of stand development and selecting evenly distributed, well-shaped trees. In the pole stage, WIEDEMANN recommended moderate thinning from below in a 5-year thinning cycle. This kind of tending tends to form a single-layered stand with horizontal crown closure. During the thinning, selection is based on tree height. Trees in the uppermost stand layer as well as trees with the highest volume increment are retained. Individuals from the lower stand canopy layers (from the lower KRAFT classes) are removed successively. Thus, this method belongs to a group of methods that thin from below; however, it begins with intensive thinning from above. In this method, the spruce stand should consist of the two

dominant KRAFT classes, e.g. the dominant and codominant trees. This method of thinning does not contradict the selective thinning approach of SCHÄDELIN (SCHÄDELIN 1934; PUCHALSKI 1970, 1972).

The method of thinning from above, recommended by some foresters, and always leading to stands with vertical crown closure, results in losses in volume increment. Stand volume losses increase with increasing thinning intensity. In addition, in Norway spruce stands, the secondary stand dies early, prior to an age of 40–50 years. Consequently, thinning from above is restricted until after this period. It is unnecessary to use this type of thinning in spruce stands, because spruce usually forms a straight trunk without thick branches.

Another method of tending spruce stands has the production of the highest wood quality, e.g. resonant wood, as its main objective. This is possible only when the spruce trees grow under uniform light conditions throughout the stand. This can be attained only in even-aged pure stands, growing under optimal climatic and edaphic conditions (e.g. montane forest sites) and originating through natural regeneration at a high initial density. In such stands, silvicultural activities are limited to the pre-commercial thinning of suppressed trees. Several good examples of stand management of this type in Poland are located in the Śląski and Żywiecki Beskidy Mts in the western Carpathians. A seed stand of Norway spruce located in compartment 149h in Bukowiec Forest District in Istebna (shown in Fig. 13.2 and Fig. 13.3) resulted from careful tending cuts, while maintaining crown closure in the young stands, and using light or moderate thinning from below. Stand treatments of this type should result in high wood quality.

For safe tending of spruce stands, they must be located in an area where they are not exposed to strong winds. The most important aim of tending is the maintenance of open-crown closure in the young stands to be followed by a heavy thinning in the pole stage. Moderate and light thinning should be conducted in the mature stand. The most valuable timber in Norway spruce stands is obtained from the most vigorous trees with high and even growth and volume increments. Thus, within such stands, natural stand development processes can be used to benefit silviculture. Consequently, human activities are minimized to control only the self-thinning process.

13.2.4 The potential for Norway spruce silviculture outside its natural range

As mentioned above, the natural range of Norway spruce in central Europe depends largely on the amount of precipitation. In central Poland and in northwestern Ukraine, for example, where the extremes of the continental climate increase and the precipitation is lower, the silviculture of this species is much more difficult on dry sites. Norway spruce can be planted on mesic forest sites, where the ground water is within reach of the root systems or where other factors act to provide continual access to water and nutrients. In drier re-

gions, the most suitable sites for Norway spruce cultivation are alluvial soils and the ash-alder swamp forest type or mesic forest sites. In mixed species stands, Norway spruce can grow in the moist micro-sites with the exception that there be no standing water or frost pockets. In such cases, the suitable locations for this forest tree species are on the lower slopes, whereas at the bottom of the depressions, alder can grow quite well (JEDLIŃSKI 1928; MEL'NYK 1993). The introduction of Norway spruce in mixed groups on the slopes of small depressions enriches the biodiversity of the forest. It also permits management of the microhabitat conditions of such areas. In general, Norway spruce can be planted in mixed stands on drier sites where the precipitation is not high enough.

13.2.5 Norway spruce silviculture in polluted areas

Norway spruce is among the most sensitive forest tree species to the effects of air and soil pollutants, especially by sulfur dioxide (SO_2) deposition and acid precipitation caused by industrial emissions (see Chapter 14). Increasing levels of pollutants and toxins that negatively impact vegetation, cause injury and negative effects in Norway spruce stands. A number of negative synergistic interactions with pollutant stresses involve: the proximity of the emission point source, the occurrence of periodic droughts, and fungal diseases.

In lowlands outside the natural range of Norway spruce, the occurrence high industrial pollutant loads does not bode well for the successful silviculture of this forest tree species. It would seem reasonable to modify the species composition of stands containing spruce, replacing it with other, less-sensitive forest tree species. In the mountain regions, especially at higher elevations, and within the northern natural range of Norway spruce, the species will likely continue in cultivation, owing to the lack of a suitable replacement. As a rule, in extreme conditions or on stressful, optimal silvicultural methods should be applied. In such cases, tree vigor and natural genetic variation at the population scale should be considered.

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14. NORWAY SPRUCE FUNCTION IN POLLUTED ENVIRONMENTS

PIOTR KAROLEWSKI

14.1. SENSITIVITY TO ENVIRONMENTAL POLLUTION

The economic importance of Norway spruce (*Picea abies*) is a key reason why this species has been the subject of numerous studies of the impacts of toxic pollutants on forest trees (BENNETT and BUCHEN 1995). Experiments with Norway spruce are also justified owing to a large intraspecific variation in tolerance to environmental pollutants. Genetic variation may, in part, explain contrasting findings among published results of pollution tolerance. In addition, genetic variation enables selection of individuals, clones (KRIEBITZSCH *et al.* 1996; LONGAUER *et al.* 2001) or whole populations (HAVRANEK *et al.* 1990; GEBUREK and SCHOLZ 1992) that are relatively tolerant to the influence of toxic compounds.

It is generally believed that coniferous trees are more sensitive to industrial pollution than broad-leaved trees (BIAŁOBOK *et al.* 1984; SLOVIK 1996; OSZLANYI 1997). However, there is a large amount of variation in tolerance among conifers. Norway spruce is usually regarded as a highly sensitive species. ROHMEDEK and SCHÖNBORN (1965) and WENTZEL (1968) ranked coniferous trees with respect to sensitivity to fluorine (F) compounds as follows: Norway spruce, European silver-fir (*Abies alba*), Scots pine (*Pinus sylvestris*), Austrian pine (*Pinus nigra*). HORNTVEDT and ROBAK (1975) found that in areas polluted with fluorine compounds, Norway spruce trees had fewer injured needles than Scots pine and European silver-fir. Those authors also reported that pines (*Pinus* spp.) usually retain seriously injured needles, whereas spruce (*Picea* spp.) typically shed even slightly injured needles. KAROLEWSKI *et al.* (2000) show that the higher F tolerance of Norway spruce trees compared to Douglas-fir (*Pseudotsuga menziesii*), does not result from a lower fluorine uptake, but from a higher resistance of spruce needles to absorbed fluorine. The researchers also noticed that needles of Scots pine are injured to a similar extent as those of Norway spruce, despite an even greater accumulation of fluorine in the Scots pine needles. Hydroponic experiments on the influence of

NaF on seedlings (WULFF and KÄRENLAMPI 1996) revealed that fluorine accumulation in Norway spruce needles is 2 to 10 times higher than in Scots pine needles.

Most field observations and controlled-environment studies show that Norway spruce is highly sensitive to the influence of sulphur dioxide (SO_2). RANFT and DÄSSLER (1970) found that Norway spruce sensitivity to SO_2 is comparable to that of Scots pine and European larch (*Larix decidua*). BUCHER-WALIN *et al.* (1979) report that Norway spruce is more tolerant than Scots pine and European silver-fir, whereas KELLER (1977a) and SLOVIK (1996) suggest that it is similarly or slightly more sensitive than Scots pine, but more tolerant than European silver-fir. Field observations made over 15 years by BALCAR (1996) indicate that Norway spruce is more sensitive than European silver-fir and lodgepole pine (*Pinus contorta*).

Many attempts have been made to assess the potential for Norway spruce cultivation in areas polluted with toxic gases, mainly sulphur oxides and nitrogen oxides. On the basis of published results, non-governmental organizations such as the International Union of Forestry Research Organizations (IUFRO), United Nations (UN-CE), and World Health Organization (WHO) suggest that the annual mean concentration of sulphur dioxide in the air should not exceed $0.027\text{--}0.063\text{ mg SO}_2\text{ m}^{-3}$ under optimal soil conditions and $0.022\text{--}0.037\text{ mg SO}_2\text{ m}^{-3}$ for trees grown on poor and acidic soils (SLOVIK 1996). KNABE (1976) cites maximum concentrations of sulphur dioxide recommended for planting of various tree species in Germany, dividing the species into three groups: most sensitive, sensitive, and least sensitive. *Picea* spp. have been assigned to the first two groups. The maximum annual mean concentrations and mean concentrations during the growing season are 0.06 and $0.05\text{ mg SO}_2\text{ m}^{-3}$ for the most sensitive species, and 0.09 and $0.08\text{ mg SO}_2\text{ m}^{-3}$ for sensitive species, respectively. For the group of tolerant species, which does not include any conifers, the values are more the two-fold higher than that of the most sensitive species: 0.13 and $0.12\text{ mg SO}_2\text{ m}^{-3}$. MANNINEN and HUTTUNEN (2000) suggest that Norway spruce, like Scots pine, can exist in areas polluted with SO_2 if the mean concentration during the growing season does not exceed $0.005\text{--}0.010\text{ mg SO}_2\text{ m}^{-3}$. According to those authors, the respective range for nitrogen dioxide is $0.010\text{--}0.015\text{ mg NO}_2\text{ m}^{-3}$. The differences between the threshold values for Central Europe and Scandinavia reflect the greater threat posed by sulphur dioxide to boreal forests.

As far as gaseous pollutants are concerned, Norway spruce is least sensitive to ozone (SUCHARA 1980; BIAŁOBOK *et al.* 1984; WIESER and HAVRANEK 1996; WULFF *et al.* 1996b). LANDOLT *et al.* (2000) suggest that compared to Norway spruce, several broad-leaved species, such as beech (*Fagus sylvatica*) and ash (*Fraxinus excelsior*) are more sensitive to ozone. In contrast, the findings of KLAP *et al.* (2000) demonstrate a relatively high sensitivity of Norway spruce to ozone. According to RANTANEN *et al.* (1994), spruce saplings are re-

sistant to ozone at concentrations of 1.5 times normal ambient concentrations for no more than two growing seasons. In addition, SKEFFINGTON and ROBERTS (1985) showed that Norway spruce seedlings are more sensitive to ozone than are Scots pine in controlled-environment studies.

Norway spruce is also sensitive to non-gaseous pollutants. Comparable concentrations of aluminium ions caused greater growth reductions in Norway spruce seedlings than in Scots pine (AROVAARA and ILVESNIEMI 1990). GODBOLD *et al.* (1985) ranked metal cations with respect to their toxicity to Norway spruce seedlings as follows: Hg, Pb, Cd, Zn. Toxicity was based on the inhibition of root and shoot elongation and dry mass gain, and reduction in photosynthetic rate, dark respiration, and transpiration. Norway spruce is also relatively sensitive to cement dust (CZAJA 1962; MANDRE 2002), but slightly less so than Scots pine (OTS and RAUK 2001). MANDRE *et al.* (2000), in analysing the morphological changes in coniferous trees (e.g. reductions in height growth, decreases in shoot length and biomass), found that Norway spruce is more sensitive to the influence of cement dust than Douglas-fir, but more tolerant than Scots pine.

A polluted environment is often comprised of various toxic gases and metals. For example, visible injuries to trees planted close to copper smelters emitting large amounts of sulphur dioxide and toxic metals (Cu, Zn, Cd and Pb) showed that although Norway spruce is more sensitive than Colorado spruce (*Picea pungens*) and most broad-leaved trees, it is less sensitive than many *Pinus* spp., including Scots pine, white pine (*Pinus strobus*), and Austrian pine, which is regarded as relatively tolerant (RACHWAL 1983). Norway spruce seedlings are less sensitive than Scots pine seedlings to mixtures of nitrogen and sulphur oxides containing fluorine and ammonium compounds (HUTTUNEN 1978; BALSBERG-PÅHLSSON 1989). Other studies indicate that Norway spruce is much more sensitive to air pollutant mixtures than Scots pine (WULFF and KÄRENLAMP 1996). However, such results are uncommon and are based on seedling experiments.

An increasingly important problem is the harmful influence of excessive nitrogen fertilization. Application of high amounts of artificial fertilizers with a narrow range of components, results in altered uptake of required elements, and has a negative effect on the mycorrhizal colonization of roots. Experiments with 3-year-old seedlings of Norway spruce (LUMME and SOMOLANDER 1996) show that foliar N uptake is lower than N uptake by roots, and that ammonium N is taken up through needles more readily than nitrate N. SETZER and MOHR (1998) conclude that for coniferous trees, an excess of ammonium N is more harmful than an excess of nitrate N. Experiments conducted under controlled conditions with ammonium solutions at concentrations typical for regions with high deposition rates of this compound (2–5 mM), demonstrate that Norway spruce is more tolerant than European silver-fir.

Although reported findings are somewhat conflicting, in general, Norway spruce is highly sensitive to acidifying pollutants (sulphur dioxide, hydrogen fluoride, and other fluorides), to alkaline compounds (e.g. cement dust), and to the salts of toxic metals. By contrast, Norway spruce is relatively tolerant to oxidizing pollutants such as ozone and nitrogen oxides.

14.1.1. Sensitivity of Norway spruce compared to other *Picea* spp.

Among species of the genus *Picea*, Norway spruce is one of the most sensitive to industrial pollution. Compared to other *Picea* spp., Norway spruce is more sensitive to fluorine and chlorine compounds, sulphur dioxide, and ammonia,

Table 14.1. Estimates of the susceptibility of Norway spruce to the effects of industrial pollutants relative to other *Picea* species (*S* – sensitive, *I* – intermediate, *T* – tolerant; *L* – laboratory conditions, *F* – field study).

Species	Pollutants	Exp. Type	Tolerance estimation	References
<i>P. abies</i>	HF	L	S	MOOI 1982
<i>P. engelmannii</i>			S	
<i>P. glauca</i>			I-T	
<i>P. omorica</i>			S	
<i>P. abies</i>	HF, F ₂	F	S	ROBAK 1969
<i>P. engelmannii</i>			S	
<i>P. omorica</i>			S	
<i>P. abies</i>	F	L	S	DÄSSLER <i>et al.</i> 1972
<i>P. pungens</i>			S	
<i>P. abies</i>	F	F	I	HORNTVEDT and ROBAK 1975
<i>P. engelmannii</i>			I	
<i>P. omorica</i>			S	
<i>P. abies</i>	F	F	I	KLUCZYŃSKI 1975
<i>P. pungens</i>			I	
<i>P. abies</i>	SO ₂	L	S	MOOI 1982
<i>P. alba</i>			I	
<i>P. engelmannii</i>			S-I	
<i>P. glauca</i>			I-T	
<i>P. mariana</i>			S	
<i>P. omorica</i>			S	

<i>P. abies</i>	SO ₂	L	S	RANFT and DÄSSLER 1970
<i>P. omorica</i>			S	
<i>P. pungens</i>			I	
<i>P. abies</i>	SO ₂	F	S	HÜVE <i>et al.</i> 1995
<i>P. pungens</i>			I	
<i>P. abies</i>	SO ₂	F	S	BALCAR 1996
<i>P. omorica</i>			I	
<i>P. pungens</i>			I	
<i>P. abies</i>	O ₃	F	T	MOOI 1982
<i>P. glauca</i>			T	
<i>P. abies</i>	O ₃	F/L	T	LUCAS and DIGGLE 1997
<i>P. sitchensis</i>			S	
<i>P. abies</i>	SO ₂ , O ₃ , SO ₂ +O ₃	F/L	T	PEARCE and MCLEOD 1995
<i>P. sitchensis</i>			T	
<i>P. abies</i>	SO ₄ ²⁻ + NO ₃ ⁻ + NH ₄ ⁺ + F ⁻	F	S	BEDNAROVÁ 1999
<i>P. pungens</i>			I	
<i>P. abies</i>	SO ₂ , SO ₄ ²⁻ + Al ³⁺ + F ⁻ , low pH	F	S	KOBAYASHI <i>et al.</i> 1997
<i>P. jezoensis</i>			T	
<i>P. abies</i>	SO ₂ +toxic metals	F	S	RACHWAŁ 1983
<i>P. pungens</i>			I	
<i>P. abies</i>	SO ₂ +other	F	S	RYŠKOVÁ 1977
<i>P. mariana</i>			T	
<i>P. omorica</i>			I	
<i>P. pungens</i>			I	
<i>P. abies</i>	Cement dust	F	T	MANDRE <i>et al.</i> 2000
<i>P. glauca</i>			I	
<i>P. mariana</i>			S	

and less sensitive to ozone (Table 14.1, SUCHARA 1980; BIAŁOBOK *et al.* 1984). Norway spruce is relatively more tolerant to alkaline particulates, such as cement dust, than white spruce (*P. glauca*) and black spruce (*P. mariana*) (MANDRE and OTS 1999; MANDRE *et al.* 2000).

One of the factors determining sensitivity is the buffering capacity (BC) of the cytosol, linked to neutralization of excessive acidification or alkalization caused by pollution. PASUTHOVÁ (1981), studying trees from an SO₂-polluted

area, ranked four spruce species with respect to BC as follows: Norway spruce, Colorado spruce, Serbian spruce (*P. omorika*), black spruce. However, in an experiment with 4-year-old saplings planted in a polluted site, SO₂ caused a decrease in BC in all species except Serbian spruce after 1 year, and Serbian spruce after 2 years of pollutant exposure. This suggests that BC is not a significant determinant of tolerance and not useful for assessment of differences in pollution tolerance between tree species.

The amount of toxic gases absorbed by leaves increases with higher rates of gas exchange. However, it seems that the greater sensitivity of Norway spruce to gaseous pollution, compared to other *Picea* spp., is not caused by differences in gas exchange rates. Spruce species have low assimilation rates, ranging from 3–6 mg CO₂ h⁻¹ g⁻¹ dry mass (LÄRCHER 1969) to 11–20 mg CO₂ h⁻¹ g⁻¹ dry mass in Sitka spruce (*P. sitchensis*) (KRUEGER and RUTH 1969; CORNIC and JARVIS 1972). Interestingly, Sitka spruce is more tolerant to gaseous pollutants than Norway spruce (Table 14.1). Although Norway spruce needles absorb relatively small amounts of SO₂, one possible explanation for the high sensitivity of the species to sulphur dioxide is its low efficiency in assimilating SO₄²⁻ into organic compounds compared to other conifers (MANNINEN and HUTTUNEN 2000).

14.1.2. Intraspecific variation in sensitivity

Research indicates genetic differences among trees in sensitivity to industrial pollution. In Norway spruce, variation in pollution sensitivity has been observed among populations (HAVRANEK *et al.* 1990; GEBUREK and SCHOLZ 1992), among families (ROHMEDER and SCHÖNBORN 1965; SAXE and MURALI 1989a,b), and among individuals (BÖRTITZ and VOGL 1972; LONGAUGER *et al.* 2001).

Most studies show that the sensitivity of spruce trees to industrial pollution depends on provenance. Experiments on the influence of excessive acidification on Finnish populations of Norway spruce revealed that a low pH (pH 3, H₂SO₄ + HNO₃) causes the most serious needle injury in populations of southern origin, less so among northern populations, and the least injury in populations originating in the central part of Finland (BALSBERG-PÄHLSSON 1989). Likewise, exposure to aluminum ions for 12 weeks caused growth inhibitions in Norway spruce seedlings originating from southern Finland at a lower concentration (1.85 mM) than in seedlings originating from the central part of the country (2.78 mM) (AROVAARA and ILVESNIEMI 1990). The greater sensitivity of populations was correlated with higher uptake rates of aluminium by roots. HODSON and WILKINS (1991) showed that Norway spruce seedlings grown from seeds of populations from areas of high soil acidity are more tolerant to aluminum ions than populations originating on calcareous soils. In that study, the differences in Al response are probably due to the fact that Si ions are

more abundant in the cell walls of the root cortex in seedlings of the more tolerant population.

Gaseous pollutants are less harmful to seedlings of populations that have a higher needle xeromorphy and thicker cuticles (HUTTUNEN 1978). TUOMISTO (1988) reports that the structure of epicuticular waxes influences the response of Norway spruce to industrial pollution. In that study, epicuticular wax structure is closely linked with population origin, and the degree of wax structure degradation may be used as an indicator of air pollution (also see Chapter 14.2).

Intraspecific variation in the tolerance of trees to toxic gases depends, in part, on differences in rates of gas exchange. HAVRANEK *et al.* (1990) found that spruce trees with the highest rates of photosynthesis are injured most severely by ozone. Controlled exposure of cut shoots to SO₂ revealed greater reductions in gas exchange rates in Norway spruce clones exhibiting higher intrinsic rates of gas exchange (KRIEBITZSCH *et al.* 1996). In the case of soil pollution, trees with better-developed root systems are more sensitive, owing to greater absorption of toxic substances (e.g. aluminum ions) at higher rates (AROVAARA and ILVESNIEMI 1990).

14.1.3. Factors modifying sensitivity

The sensitivity of Norway spruce to industrial pollution depends on internal factors, such as stage of development and age of individual organs and trees. In addition, external factors, such as air temperature and humidity, soil moisture, insolation, and fertilization affect the pollution sensitivity of Norway spruce.

14.1.3.1. Influence of internal factors

Younger needles are less sensitive to SO₂ than are older needles (FÜHRER *et al.* 1993; HÜVE *et al.* 1995) and O₃ (FÜHRER *et al.* 1993). Moreover, HÜVE *et al.* (1995) found that SO₂ exposure results in a much greater accumulation of sulphates in older needles. These observations support the notion that younger plant tissues, which are more active metabolically, are able to utilize larger amounts of sulphur than older needles with a lower metabolic activity (MALHOTRA and KHAN 1980). KLUMPP *et al.* (1989) found that exposure to gas mixtures (SO₂+O₃+NO₂) increased the free proline content and peroxidase activity, widely used stress indicators, more in 2-year-old than in 1-year-old needles of Norway spruce. However, an increased activity of superoxide dismutase (SOD), an indicator of defense metabolism, was observed only in 1-year-old needles. In addition, younger needles have a greater capacity for transforming absorbed SO₂ into H₂S and releasing it than older needles (SEKIYA *et al.* 1982). WIESER *et al.* (2000) suggest that the age-dependent sensitivity of needles to ozone is due to differences in stomatal conductance and uptake. Those authors report uptake rates of 24 μM O₃ m⁻² s⁻¹ in

current-year needles, $16 \mu\text{M O}_3 \text{ m}^{-2} \text{ s}^{-1}$ in 1-year-old needles, and $12 \mu\text{M O}_3 \text{ m}^{-2} \text{ s}^{-1}$ in older needles (averaged across the four older needle age classes).

In areas exposed to particulate air pollution of toxic metals, metal absorption by Norway spruce needles of various ages depends on the level of pollution. When the pollution level is low, current-year needles accumulate significantly less $\text{Cu} + \text{Zn} + \text{Pb} + \text{Cd}$ than 1-year-old and 2-year-old needles (BALSBERG-PÅHLSSON 1989). In contrast, in heavily polluted areas, the concentration of those metals is the highest in current-year-needles, lower in 1-year-old needles, and lowest in 2-year-old needles. The differences in accumulation of individual metals by needles of various ages depend both on the type of metal and level of pollution. Under the influence of long-term pollution, the Pb content of spruce needles increases with needle age (TUNG and TEMPLE 1996).

Needle sensitivity also depends on developmental stage through the course of the growing season. However, published findings on this subject are inconsistent. The level of absorption of fluorine and the proportional inhibition in CO_2 assimilation in Norway spruce needles is the lowest in June, higher in August, and the highest in September (KELLER 1977b). However, HORNTVEDT and ROBAK (1975) found that recent, fully elongated needles are more sensitive to fluorine compounds than needles in earlier and later periods of the growing season. In contrast, LALK *et al.* (1992) report that very young needles in spring are the most sensitive to SO_2 and NO_2 , whereas the older needles in winter are the least sensitive. VISKARI *et al.* (2000) suggest that the degradation of epicuticular waxes and mesophyll structure by nitrogen oxides is the highest in the youngest spruce needles, which are the most photosynthetically active. In an area contaminated with sulphur and fluorine compounds, WULFF *et al.* (1996a) observed senescence-related changes in cell ultrastructure, such as an increase in the number and size of plastoglobuli and an increase in lipid accumulation with increasing needle age. The disparities among studies of age-dependent sensitivity of needle to pollutants may arise from many factors. First of all, the pollutant type, concentration, and dose are likely important. Other factors important in sensitivity assessment include: visible injury (chlorosis, necrosis), morphological and anatomical changes, changes in rates of physiological processes, and metabolic disturbances.

Needle sensitivity to pollutants also depends upon tree age. KELLER (1977b) found that Norway spruce needles at an early stage of development are more sensitive to pollution with fluorine compounds in younger than older trees. He also reported that rooted cuttings of 40-year-old spruce trees were more sensitive to air pollution with fluorine than cuttings obtained from 120-year-old trees (KELLER 1976). WIESER *et al.* (2000) observed an increased sensitivity of younger Norway spruce trees to ozone, owing to a six-fold greater absorption of ozone by needles of younger trees (aged 17 years) than older

trees (aged 216 years). Of the few studies reported, older Norway spruce trees appear more tolerant than younger trees.

Variation in the extent of SO₂-related injury and in inorganic S content can also be observed within individual needles. Sulphur levels are the highest at the tips of Norway spruce needles, and necrosis proceeds from the tip to the base of the needle (JÄGER 1976).

14.1.3.2. Influence of external factors

The impact of a selected pollutant on plants may critically depend upon the influence of external factors. There are a number of literature examples indicating that concurrent exposure to various toxic substances may have additive, synergistic, neutral, or antagonistic effects. Most frequent are synergistic effects. KLUMPP *et al.* (1989) assessed the tolerance of trees to toxic gases on the basis of free proline content, a sensitive biochemical indicator of the level of plant response to stress factors (KAROLEWSKI 1989). In that study, SO₂ at a concentration of 0.034 ppm for 22 weeks did not cause any significant changes in the free proline content of needles in 4-year-old saplings of Norway spruce. Ozone exposure (0.065 ppm) increased free proline content by about 25 percent. However, a combined exposure of SO₂ (0.034 ppm) and O₃ (0.043 ppm) resulted in a nearly 6-fold increase in free proline content. Thus, the harmful effect of ozone appears amplified by SO₂ exposure. In an experiment on the combined effects of ozone and acid mist (H₂SO₄, pH 3), exposure to acid mist enhanced injury to spruce needles by up to 50% (ROBERTS *et al.* 1987). Nitrogen oxides are the least harmful among pollutant gases, but in combination with other gases, they greatly enhance pollutant injury to trees. In Norway spruce, this has been shown in experiments on the effects of single gases and mixtures including: O₃+NO₂ and O₃+SO₂+NO₂ (GUDERIAN *et al.* 1985) and SO₂+NO₂ (MANNINEN and HUTTUNEN 2000). In contrast, a higher concentration of CO₂ in the air often reduces the negative effects of toxic substances, stimulating synthesis of free oxide radicals through increasing the activity of antioxidant enzymes, including superoxide dismutase, catalase, peroxidase, glutathione reductase, as well as glucose-6-phosphate dehydrogenase, associated with the production of more NADPH necessary for detoxification (SCHWANZ *et al.* 1996; SEHMER *et al.* 1998).

An increased sensitivity of Norway spruce to SO₂ and O₃ is observed during drought (MAIER-MAERCKER and KOCH 1992). According to those authors, enhanced pollutant sensitivity is associated with altered plant water balance, excessive water loss via transpiration, and a lower photosynthetic rate. A moderate drought may result in stomatal closure and a reduced absorption of toxic gases by leaves, but this effect is transitory. Prolonged drought or severe water stress arising from a high water vapour pressure deficit exacerbates the effects of toxic gases. Similar relationships were observed in experiments on the influence of ozone in Norway spruce (WIESER and HAVRANEK 1993).

The sensitivity of plants to pollution depends on the type and rate of mineral fertilization. This is a complex problem. For example, KELLER (1976) found that nitrogen fertilization initially reduced needle injury caused by fluorine compounds in Norway spruce seedlings. However, after 3 years, physiological injuries due to fluorine (e.g. lower chlorophyll level, higher concentrations of soluble carbohydrates, phenols, and free amino acids) were greater in fertilized than in unfertilized seedlings. Nevertheless, the negative effects of excessive amounts of nitrogen salts and especially of ammonia ions are reduced by additional potassium fertilization (SETZER and MOHR 1998).

The influence of multiple stress factors on plant sensitivity is often complicated. For instance, TESCHE *et al.* (1989) and FEILER *et al.* (1989) showed that the type and magnitude of interactive effects (synergistic, additive, antagonistic) of SO₂ and drought on Norway spruce seedlings depends on whether the two factors act at the same time, or which acts first.

Tree sensitivity to pollutants often increases with growth temperature. MANNINEN and HUTTUNEN (2000) observed such a relationship for the effects of SO₂ and NO₂ in fumigation experiments with Norway spruce seedlings in open-top chambers. Greater gas absorption results from higher stomatal conductances with increasing temperature (THOENE *et al.* 1996). Industrial pollution also increases tree sensitivity to low temperatures. LALK *et al.* (1992) found that SO₂ exposure enhances the reductions in water content and photosynthetic capacity of needle tissues occurring in response to freezing temperatures. According to FEILER (1985), the SO₂-related increase in sensitivity of Norway spruce to cold temperatures arises from a greater permeability of cell membranes and the leakage of electrolytes caused by SO₂ exposure. Experiments on the effects of excessive acidification also showed that a low pH (pH 3, H₂SO₄+HNO₃) alters physiological processes (CO₂ uptake, transpiration) and increases cold injury to Norway spruce needles (BALSBERG-PÅHLSSON 1989; ESCH and MENGEL 1998). An increase in frost injury in Norway spruce needles is also observed in plants exposed to gaseous oxidants such as ozone (DAVISON *et al.* 1988).

The absorption of toxic gases by needles is determined by the degree of stomatal opening, which is dependent upon light conditions, temperature, and humidity. WIESER *et al.* (2000) found that shaded needles of Norway spruce absorb about twice as much ozone as sunlit needles. Higher light intensity and relative humidity increased absorption of NO₂ by spruce needles (THOENE *et al.* 1996).

While external factors affect tree sensitivity to industrial pollution, air pollution may also alter tree sensitivity to other abiotic stress factors. As pollution alters plant water relations, additional drought-induced dehydration of plant tissues may enhance the unfavorable metabolic changes. For example, PIERRE and QUIEROZ (1988) showed that SO₂ reduces the activity of important enzymes (isocitrate dehydrogenase, glucose-6-phosphate dehydrogenase, gluta-

mate dehydrogenase) in needles of Norway spruce seedlings exposed to drought. LALK *et al.* (1992) found that under favorable growth conditions, low levels of toxic gases (SO_2 , O_3 , and $\text{SO}_2 + \text{NO}_2$) did not result in any significant changes in free proline content in Norway spruce needles. However, after 14 days of drought, the same levels of the gases resulted in a greater increase in free proline content than the drought itself. FEILER *et al.* (1989) show that SO_2 may stimulate stomatal closure and thus contribute to the maintenance of a higher water content, counteracting the effects of short-term drought. Nonetheless, the capacity to retain water decreases with prolonged exposure to SO_2 .

At high temperatures, coniferous trees emit volatile organic compounds (VOC) from leaves into the atmosphere. This group of substances is dominated by monoterpenes, which participate in reactions that produce ozone and other photochemical oxidants. In Norway spruce, the dominant monoterpenes formed are alpha-pinene, camphene, and to a lesser extent beta-pinene and limonene (FISCHBACH *et al.* 2000). However, in comparison to other *Picea* spp., the emission of isoprene by Norway spruce is relatively low (KEMPF *et al.* 1996).

The examples discussed above reveal the difficulty of predicting the response of Norway spruce trees in regions subjected to industrial air pollution or in degraded environments that are no longer exposed to air pollution. Toxic substances present in the soil may exert a negative effect on trees for long periods of time, resulting in complex interactive effects in combination with other abiotic stress factors.

14.1.4. Disturbances in physiological processes and metabolism

In response to low levels of stress, a number of defense mechanisms are induced in plants, and have been observed in Norway spruce (WIESER *et al.* 1998). These include stomatal closure (MANSFIELD 1998), buffering of excessive acidification or alkalization of the cytosol (KELLER 1982; PASUTHOVÁ 1981), and activation of respiratory processes (SAXE and MURALI 1989a; HOHENDORFF and VOGELS 1990). Enzymes, such as peroxidase, superoxide dismutase, and catalase (KLUMPP *et al.* 1989; BAUMBUSCH *et al.* 1998), and the compounds ascorbate and glutathione (WILD and SCHMITT 1995; BAUMBUSCH *et al.* 1998) play important roles in the initial stages of detoxification of the superoxide and hydroxyl radicals. Any excess nitrate formed in needles and roots as a result of the uptake of nitrogen oxides or excessive nitrate fertilization is eliminated by increased activity of nitrate reductase (HÖGBERG *et al.* 1998; WEBER *et al.* 1998). Through redox reactions some pollutants are transformed into less harmful substances and partially removed from the organism (SEKIYA *et al.* 1982; HÜVE *et al.* 1995).

Long-term exposure to toxic pollutants or short-term exposure to high pollutant concentrations amplifies stress effects and ultimately leads to irrevers-

ible changes in stomatal function (HASEMANN *et al.* 1990; MAIER-MAERCKER and KOCH 1992) and degradation of the needle cuticle and epicuticular wax (BEDNAROVÁ 1999; VISKARI *et al.* 2000). Disturbances in plant water relations are reflected in inefficient water use, higher stomatal conductance, lower water potentials, and consequently insufficient hydration of tissues (FREER-SMITH and DOBSON 1989; VISKARI *et al.* 2000). Unfavorable changes in the ultrastructure of mesophyll cells of Norway spruce needles have been observed in response to ozone stress (HOLOPAINEN *et al.* 1996) as well as of sulphur dioxide, fluorides, and excessive amounts of nitrogen compounds (WULFF and KÄRENLAMPI 1996).

Toxic substances alter basic physiological processes. A decrease in transpiration rate in Norway spruce has been observed in response to SO₂ (BÖRTITZ and VOGL 1972; LALK *et al.* 1992), O₃ (LALK *et al.* 1992; MIKKELSEN and RO-POULSEN 1994), NO₂ (SAXE and MURALI 1989a; LALK *et al.* 1992), and a mixture of SO₂+NO₂ (SAXE 1989; LALK *et al.* 1992). Inhibition of CO₂ assimilation in Norway spruce has been observed in experiments on the influence of SO₂ (FÜHRER *et al.* 1993; PEACE *et al.* 1995), HF (KELLER 1977b), NO₂ (SAXE and MURALI 1989a; LALK *et al.* 1992a), O₃ (MIKKELSEN and RO-POULSEN 1994; PEACE *et al.* 1995), and mixtures of SO₂+O₃ (HOHENDORFF and VOGELS 1990) and SO₂+NO₂ (LALK *et al.* 1992; PEACE *et al.* 1995). The destruction of chlorophyll-protein complexes, reduced concentrations of photosynthetic pigments, and changes in the proportions of pigments in Norway spruce needles have been detected in experiments on the effects of SO₂ (BRECHT and SCHULZ 1989), HF (KELLER 1976), O₃ (MIKKELSEN *et al.* 1995), mixtures of SO₂+O₃ (HOHENDORFF and VOGELS 1990) and NO₂+O₃ (SCHULZ 1989), and alkaline particulates (MANDRE and TUULMETS 1997). Altered physiological responses of Norway spruce seedlings may result from the effects of SO₂, O₃, NO₂, and mixtures of these gases on the light reactions of photosynthesis (LÜTZ *et al.* 1992; SCHMITZ *et al.* 1993), the dark reactions (WEDLER *et al.* 1995; WILD and SCHMITT 1995), as well as dark respiration (GODBOLD *et al.* 1985; SCHLEGEL *et al.* 1987). RUTH and WEISEL (1993) report that the energy ratio of photosystem PSI to PSII is an extremely sensitive indicator of the response of Norway spruce to ozone. As cellular degradation proceeds, the PSII/PSI ratio decreases (BAUR *et al.* 1998).

Sulphur oxides, nitrogen oxides, fluorine compounds, ozone, and toxic metals result in excessive accumulation of a number metabolites in Norway spruce needles, including amino acids (KELLER 1976; LALK *et al.* 1992), soluble carbohydrates and starch (KELLER 1976; BALSBERG-PÅHLSSON 1989), lipids (WULFF *et al.* 1996b; VISKARI *et al.* 2000), and secondary metabolites, including phenols (RICHTER and WILD 1992; WULFF *et al.* 1996b). By contrast, air pollution with cement dust decreases the concentration of starch, and even more so, the soluble carbohydrates in needles (MANDRE and OTS 1999; MANDRE *et al.* 2000).

Environmental pollution with toxic substances results in altered mineral nutrition in Norway spruce needles. This is reflected in deficiencies of nutrients such as Ca, Mg, and K (RANTANEN *et al.* 1994; WEDLER *et al.* 1995). Moreover, a number of metabolic and hydrolytic processes are observed that accelerate needle maturation and aging (WILD and SCHMITT 1995; VISKARI *et al.* 2000). Under extreme conditions or under long-term exposure to industrial pollution, growth is inhibited and permanent injuries to needle and root tissues are observed (VISKARI *et al.* 2000; MANDRE 2002). This often leads to unfavorable changes in the biomass ratio of aboveground parts to roots (GEBUREK and SCHOLZ 1992; RANTANEN *et al.* 1994). Overall, the literature data show that pollution-related disturbances in physiological processes and metabolism of Norway spruce are commonly observed in other tree species, supporting the idea of a common set of responses of trees to various abiotic stress factors (JONES 1978; CHAPIN 1991).

14.1.5. Conclusions

As a tree species within the genus *Picea* and compared to other conifers, Norway spruce is highly sensitive to the effects of toxic pollutants, especially sulphur dioxide, fluorine compounds, and toxic metals. However, the potential exists to select individual clones and populations with an increased pollution tolerance. Norway spruce is less sensitive to ozone and nitrogen oxides than to other pollutants. The sensitivity of Norway spruce to industrial pollutants is dependent upon other potentially interacting climatic factors and soil conditions. Factors such as frost, high temperature, drought, and salinity may enhance the sensitivity of spruce to pollution. The response of spruce to pollutants is dependent on the age of trees and needles. Older trees are more tolerant than younger individuals. Seasonal differentiation in sensitivity may also be important in some cases.

Environmental pollutants, including toxic gases and metals, alter the rates of physiological processes, the activity of enzymes, and the contents of certain metabolites. Under mild stress conditions, defense metabolism may play a key role in plant response. Increases in respiration rates and activity of enzymes such as peroxidase and superoxide dismutase and increased ascorbic acid and glutathione contents constitute important metabolic responses to pollutant stress. In response to high pollutant doses, unfavorable changes occur in the levels of primary metabolites (i.e. pigments, sugars, amino acids, proteins, etc.) and secondary metabolites (phenols). In addition, decreased activity of many enzymes and the inhibition of photosynthesis and respiration are observed in response to pollution stress. Often these metabolic and physiological changes are irreversible and lead to the formation of necroses, the acceleration of aging, and the eventual senescence and death of plants.

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14.2. EFFECTS OF POLLUTANTS ON NEEDLE AND WOOD ANATOMY

14.2.1. *Erosion of epicuticular waxes*

The needles of Norway spruce are covered with tubular wax structures. These long and thin wax rods form a dense cover over the stomata (GRILL 1973a,b; GÜNTARD and WANNER 1982a,b), filling the antechambers with a porous mesh that protects the stomatal aperture from occlusion by dust particles. These waxes can reduce transpiratory water loss by two-thirds, and the diffusion of CO₂ by one-third (JEFFREE *et al.* 1971). Epicuticular waxes mediate cuticular transpiration and restrict the leaching losses of nutrients and organic compounds (JUNIPER and JEFFREE 1983). In addition, waxes protect the epidermis from mechanical injuries, UV radiation, and damage from insects, fungi, bacteria, and viruses (TURUNEN and HUTTUNEN 1990).

The wax structures undergo an aging process and change in response to environmental pollution (GRILL 1973a; GÜNTARD and WANNER 1982a,b; BERMADINGER *et al.* 1988; GRILL *et al.* 1987, 1992). Erosion usually affects the waxes of older needles. GÜNTARD and WANNER (1982a) observed no differences in the structure of waxes between one-year-old needles from polluted and unpolluted areas in the summer, whereas the waxes of older needles from the polluted areas were more eroded. Damage to needle surfaces is frequently used as a criterion for evaluation of the extent of air pollution (GRILL *et al.* 1987). However, the use of changes in epicuticular wax morphology for diagnostic purposes is somewhat controversial. Apart from pollution effects, the structure of epicuticular waxes reflects tree vigor, genetic differences, and even location within the tree crown (TUOMISTO and NEUVONEN 1993). Trees may differ markedly with respect to the mass and structure of waxes and their chemical composition. In addition, the thermal stability of waxes appears to be related to their chemical structure (SCHÜTT and SCHUCK 1972; RADDI and RINALDO 1989).

Pollution causes morphological alterations to the antechamber waxes, such as fusion of the wax rodlets, and degradation of the crystalline structures into an amorphous wax. In extreme cases, these changes lead to an occlusion of the stomatal aperture by an amorphous plate-like wax. Erosion of epicuticular waxes exposes the epidermis (BERMADINGER *et al.* 1988) and facilitates the penetration of toxic substances into the needle (SWIECKI *et al.* 1982). The bare needle surface is quickly eroded, and consequently, cuticular transpiration, nutrient leaching, and the number of necrotic lesions increase (JUNIPER and

COX 1973; SCHÖNHERR 1976; HUTTUNEN *et al.* 1981; HUTTUNEN and LAINE 1983; GLATZEL and PUXBAUM 1983; HUTTUNEN and SOIKKELI 1984). Uncontrolled cuticular transpiration is more detrimental to plants in winter when the stomata are closed (HUTTUNEN *et al.* 1981) compared to summer when stomatal transpiration predominates. Plugs of fused waxes reduce CO₂-exchange and transpiration (JEFFEREE *et al.* 1971; GRILL 1973c). Wax erosion increases needle surface wettability, which favors germination of fungal spores and needle infection by parasites (ELSTNER and OSWALD 1984; HUTTUNEN 1984; MATHE 1985). In a polluted area, HAIN (1987) observed an increase in needle damage by insects. The amino acid content in tissues may increase in response to stress, which enhances their attractiveness to insect pests (WHITE 1984).

Crystalline wax structures are highly sensitive to mechanical injury (VAN GARDINGEN *et al.* 1991). GÜNTHARDT-GOERG *et al.* (1994) observed severe wax damage on young and one-year-old needles of alpine Norway spruce in the spring in unpolluted areas. Wax erosion there was explained by an exposure of the trees to wind, rainfall, and ice damage.

Altered plant metabolism in response to pollution negatively impacts wax synthesis. Spruce needles in polluted areas exhibit alterations in the chain length of the paraffins and esters in the epicuticular waxes (SCHÜTT and SCHUCK 1972; TRIMBLE *et al.* 1982; HUTTUNEN and SOIKKELI 1984). However, changes in the chemical composition of waxes should not be exclusively linked to the direct influence of pollution even though a causal relationship is apparent (BAKER 1982; CAPE *et al.* 1989). GRILL (1973a), KIM and LEE (1990), and TUOMISTO and NEUVONEN (1993) demonstrated negative effects of urban smog on wax structure and needle morphology. In addition, the needle surfaces of sun-exposed branches exhibit faster erosion rates of waxes, owing to a higher thermal instability linked to the chemical structure of the waxes (KIM 1985).

Environmental monitoring based on changes in needle surfaces poses difficulties, especially when the objective is to diagnose the causal factors. The connection between erosion type and the type of pollution has been demonstrated in many coniferous trees (PERCY and RIDING 1978; CARLSSON 1980; KRAUSE and HOUSTON 1983; RIDING and PERCY 1985; HAFNER 1986, KARHU and HUTTUNEN 1986; BARNES *et al.* 1988; BERMADINGER *et al.* 1987). Wax erosion on surfaces of 2-year-old spruce needles from areas polluted by O₃, SO₂, and NO_x leads to the degeneration of cuticular, stomatal, and epidermal structures (HASEMANN *et al.* 1990). BRAUN and SAUTER (1983) found an increase in needle chlorosis with increasing length of exposure to solar irradiance in polluted areas, mainly in spruce growing in UV-exposed mountain areas. In that study, needle chlorosis was thought to arise from photo-oxidative processes induced by the presence of nitric oxides with a possible synergistic effect of SO₂. The evidence concerning the influence of ozone on wax structure is

contradictory (MAGEL and ZIEGLER 1986; GÜNTARD-GOERG and KELLER 1987; BARNES *et al.* 1988; SCHMITT *et al.* 1988; BARNES and BROWN 1990; LÜTZ *et al.* 1990).

14.2.2. Changes in the structure and function of stomata

In contrast to a general assumption, SO₂-acidified water can penetrate the stomata and affect the cells bordering the substomatal cavity (WERNER 1982; 1989; MAIER-MAERCKER and KOCH 1992). SO₂ reacts with the cuticle and dissolves in the liquid phase of the apoplastic water, causing the breakdown of lignins, mainly in the walls of the subsidiary cells. Stomatal control of transpiration was lost in Norway spruce fumigated with SO₂ (MAIER-MAERCKER and KOCH 1986) and O₃ (MAIER-MAERCKER 1989). The dysfunction of stomata appeared simultaneously with a partial delignification of the cell walls of the stomatal complex. The walls of the stomatal complex contain more lignin and release more water to the atmosphere than the surrounding epidermal cells. The higher rate of water loss around the stomatal pore, termed peristomatal transpiration, is closely associated with the mechanism of stomatal control (MAIER-MAERCKER 1983). Compared to other areas of the epidermis, the enhanced water loss from the walls of stomatal guard cells is linked to the abundance of aldehyde groups in their lignin. Due to their high hydration potential, the cell-wall aldehydes may act as wicks for water movement from the apoplastic stream to the atmosphere (MAERCKER 1965). The competing pathways for water flux through evaporation and flux into the vacuole as the osmotic pressure of the cell sap rises, results in the cell walls of the stomatal apparatus acting as a "sensor". Even a slight variation in the balance between evaporation and water influx from the transpiration stream is reflected in a shift in the water potential gradient between the vacuoles of the guard cells and the surrounding apoplast. Guard cell metabolism responds to and signals these slight variations in water potential.

The hygroscopy of cell walls of the stomatal apparatus increases under the influence of SO₂ and probably ozone. Concomitant with a decline in water potential gradient, water transfer through the cell wall ceases. As the cell walls become saturated with water, subsidiary cells cease to absorb water and stop transfer to the stomatal cells. In spite of the changes in needle water content, the stomata remain open. The consequence is excessive water loss, which is especially harmful during drought (KOCH and MAIER-MAERCKER 1986). As a result of uncontrolled transpiration due to stomatal malfunction, the water potential of the entire needle declines. Following several days of intense transpiration and considerable water loss, the needles dry out and the stomata close. During prolonged drought periods, needles that do not control tissue water level will senesce prematurely, turn yellow, and fall.

14.2.3. *Effects of pollutants on the epidermis, hypodermis, and mesophyll*

In the earliest stages of visible injury, a decrease in chlorophyll content in the mesophyll cells results in bleaching of the needle tips. Subsequently, the needle tips turn yellow due to phenolic deposits in the vacuoles. With time, the discoloration spreads toward the needle base. The injured cells eventually collapse and turn brown. Initially, the subsidiary cells of the stomatal apparatus appear less injured than the surrounding epidermal cells. The degree of subsidiary cell injury increases in the necrotic zones. Deformations of the epidermal cells result in a reduction in the distances between individual stomata both within and between rows. Severely injured stomata containing large quantities of phenols are symptomatic of advanced needle surface degradation (HASEMANN and WILD 1990; HASEMANN *et al.* 1990).

As a result of the action of various pollutants, especially SO₂, initial necrosis is observed in the cells surrounding the substomatal cavities and the mesophyll cells below the hypodermis, as well as the cells adjacent to the bundle sheath (SOIKKELI 1981d). The content of phenols increases with the degree of needle injury. This increase is a highly sensitive indicator of metabolic changes within the cell, occurring before microscopic symptoms of injury become apparent (YEE-MEILER 1978).

Needle injury in the field is often the result of many biotic and abiotic factors interacting with the dominant pollutant. Depending on pollutant concentration and dose, some factors may have an ameliorating effect, although synergistic or additive effects are more frequent (SCHLEE and KÖCK 1987). Under the influence of various concentrations of SO₂, O₃, and NO_x, a bleaching of needle tips is typically observed and results from chlorophyll loss. During the initial stages, the consistency of the cytoplasm changes. Plasmolysis and hypertrophy of the epithelial cells frequently leads to the occlusion of resin canals (HUTTUNEN and SOIKKELI 1984). With an increasing pollution concentration or dose, the destruction of the mesophyll cells spreads towards the vascular bundle. The protoplasts of dying cells turn into an amorphous mass and their cell walls collapse. Altered cell wall fluorescence under UV light indicates an accumulation of phenols and cell wall lignification. The brown-colored tissue is primarily restricted to a few cell rows below the hypodermis. Subsequently, necrotic spots encompass the needle tip or form transverse bands along the needle. These changes are often accompanied by hypertrophy and a proliferation of mesophyll cells in the necrotic regions (HASEMANN and WILD 1990).

Ultrastructural changes typically appear long before macroscopic symptoms. Structural differences between mesophyll cells of senescing healthy needles and needles of trees from polluted environments are observed mainly in the chloroplasts (SOIKKELI 1981a; MEYBERG *et al.* 1987). During needle senescence, the presence and number of plastoglobuli increase with increasing needle age (SUTINEN 1987b,c). In contrast, plastoglobuli abundance is only oc-

casionally associated with the degree of pollution (PARAMESWARAN *et al.* 1985). The earliest indications of pollutant effects are changes in chloroplast shape and inner membrane structure, observed as dilating, swelling, curling, or undulating thylakoids, and a reduction in thylakoid numbers. The disintegration of the internal chloroplast membrane indicates large changes at the molecular level and impaired function (LICHTENTHALER and BUSCHMANN 1984). Intracellular membrane destruction leads to decompartmentation (JUNG and WILD 1988), resulting in an aggregation of the remaining organelles. The deleterious effects of SO₂, NO, NO₂, and O₃ on spruce needles is related to an increased number of plastoglobuli, reduced number of thylakoids, decreased size of chloroplasts, membrane rupture, and higher amounts of vacuolar tannins (SUTINEN 1987b,c).

Ultrastructural studies of field-collected needles involve comparisons of the degree of cell injury. In contrast, under experimental conditions, the type and degree of change is associated with the dose of a particular pollutant. Typical SO₂-induced injury to mesophyll cells results in the swelling of the chloroplasts, which become rounded in shape (SOIKKELI and TUOVINEN 1979). The increase in chloroplast volume is accompanied by the swelling of the grana and stroma thylakoids, and frequently a reduction in their number (GODZIK and KNABE 1973). A similar swelling of thylakoids was observed in spruce needles collected from an area with a low concentration of SO₂ between 15 to 20 µg/m³ (SOIKKELI 1981b). In field-collected plant material, the influence of pollution often accelerates the natural aging processes. Plastoglobuli, which in young needles are usually dense, become clearer. In the cytoplasm, an accumulation of lipid-like bodies is observed, sometimes filling all available spaces between the organelles (SOIKKELI 1981a,b,c). This phenomenon is associated with altered lipid metabolism. In long-term experiments, where low SO₂ concentrations are applied in combination with nitrogen salts, initial positive effects can be observed, which are explained as a fertilization effect (WULF and KÄRENLAMPI 1996). The thickening of the grana due to increased nitrogen supply may lead to improved photosynthetic efficiency (SOIKKELI and KÄRENLAMPI 1984a; BÄCK and HUTTUNEN 1992). Opposite effects may be observed with plant exposure to gaseous NO₂ (SCHIFFENS-GRÜBBER and LÜTZ 1992).

WULF and KÄRENLAMPI (1996) did not observe a reduction thylakoid number in chloroplasts of Norway spruce needles exposed to a low SO₂ concentration over three growing seasons. In that study, foliar application of a solution of NH₄NO₃ was likely an ameliorating factor. Often the vacuoles of mesophyll cells become prominent in foliage exposed to acid rain or SO₂ (KÄRENLAMPI and HOUPIS 1986; HOLOPAINEN and NYGREN 1989; BÄCK and HUTTUNEN 1992; BÄCK *et al.* 1994). Vacuoles are believed to be storage sites for protons and sulphite (KAISER *et al.* 1989; HEBER *et al.* 1994). An increased

numbers of vacuoles may indicate an increased metabolism of SO_2 and detoxification.

F and HF treatments result in curling or undulating thylakoids, although without swelling, which is usually ascribed as an effect of SO_2 . It should be noted, however, that similar structural changes of the thylakoids have also been attributed to frost (SOIKKELI and TUOVINEN 1979; SOIKKELI 1981d). Green needles, without any clear visible injury after exposure to high concentrations of SO_2 and HF, contained chloroplasts with unnaturally stretched envelopes. In slightly injured needles, excessive stretching of chloroplast envelopes was a common phenomenon. In cells with a greater degree of visible injury, curled thylakoids and ruptured chloroplasts were also observed (SOIKKELI and TUOVINEN 1979; SOIKKELI 1981a). Changes in chloroplast structure, and especially the reduction in thylakoids, has obvious negative effects on photosystems I and II, and on the light reactions (HUTTUNEN and SOIKKELI 1984). With increasing needle injury, changes may be observed in other cellular organelles (SOIKKELI and PAAKKUNAINEN 1981). Needles originating from areas polluted with SO_2 and HF show a lower number of polyosomes, indicating a significant alteration in protein synthesis.

Occasionally, experiments on plants exposed to a low fluorine concentration yield contrasting results. In needles of Norway spruce treated with a mist of fluoride (NaF) at 50 mg F/L, SO_2 at 100–400 $\mu\text{g}/\text{m}^3$, and nitrogen applied as a spray of NH_4NO_3 at 200 mg N/L, WULF and KÄRENLAMPI (1996) observed thylakoid swelling, an increase in lipid bodies, and mitochondrial injury, but under none of the treatments was thylakoid curling observed. The absence of thylakoid curling, despite high fluorine content in the needles (25–425 μg F/g), suggests that thylakoid curling is not a direct effect of fluorine. Apart from frost, drought may also contribute to this effect (ZWIAZEK and SHAY 1987). A darkening of plastoglobuli, evident in Norway spruce treated with NaF, may result from a decrease in the ratio of saturated/unsaturated fatty acids, since osmium is known to bind exclusively to saturated fatty acids (GOODWIN and MERCER 1983). A pronounced darkening of chloroplast stroma due to an increase of ribosome-like granules as well as a reduction in chloroplast size were both described as effects of ozone exposure (SUTINEN 1987a; SUTINEN *et al.* 1990) and of phosphorus deficiency (PALOMÄKI and HOLOPAINEN 1994). According to WULF and KÄRENLAMPI (1996), these effects appear to be non-specific. Owing to the observed swelling of mitochondria with dilated cristae in response to P deficiency (PALOMÄKI and HOLOPAINEN 1994), an increased occurrence of disintegrated mitochondria, described as the effect of F treatment (PILET and ROLAND 1972; WULF and KÄRENLAMPI 1996), may also be non-specific.

In needles exposed to ozone, structural changes are typically observed within the cytoplasm and plastids. Ozone at concentrations between 40 and 300 $\mu\text{g}/\text{m}^3$, applied for 3–9 hours a day for an extended period induced

ultrastructural changes in mesophyll cells of green needles (SUTINEN 1989). A typical response involved a decreased length and flattening of the chloroplasts. These changes were accompanied by the accumulation of ribosome-like granules and an increase in the number of plastoglobuli in the osmophilic plastid stroma. In more acutely injured needles, degenerating microbodies and a cytoplasm containing clumps of ribosomes were observed (SUTINEN 1987a; SUTINEN *et al.* 1989).

The joint action of O_3 and SO_2 at concentrations ranging between 30 and $150 \mu\text{g}/\text{m}^3$ usually results in changes similar to those observed when ozone is the sole factor. However, the degree of needle injury is markedly higher. In older needles, SO_2 causes additional effects, such as the appearance of irregularly shaped plastids, a reduction in thylakoids, an increase in the number plastoglobuli, an accumulation of lipid-like material in the cytoplasm, and formation of crystals within the plastid stroma. Similar changes were observed in spruce needles exposed to industrial emissions of SO_2 , NO , NO_2 , and O_3 at various concentrations and proportions (PARAMESWARAN *et al.* 1985; SUTINEN 1987c; 1989).

The influence of ozone on the cellular ultrastructure of Norway spruce needles differs in the presence of acid mist (HCl). In spruce exposed for two growing seasons to an acid mist at a pH of 3.0 and ozone at $100 \mu\text{g}/\text{m}^3$ with episodic increases to $130\text{--}360 \mu\text{g}/\text{m}^3$, a delayed export of starch from chloroplasts of older needles was observed in addition to polyphenol accumulation (EBEL *et al.* 1990). An increase in the number of plastoglobuli, typical for senescing needles, always occurred after treating the plants with ozone. The number of grana in the chloroplasts was also reduced. REUTZE *et al.* (1988, 1989), analyzing the effects of long-term exposure to realistic concentrations of SO_2 , O_3 , and NO_2 on the ultrastructure of Norway spruce needles in fumigation chambers, demonstrate a harmful effect of low concentrations of these gases on plant metabolism. Apparent changes, although occurring slowly, affect mostly the cells of the stomatal apparatus, the epidermal and mesophyll cells adjacent to the substomatal cavities, and the mesophyll cells adjacent to the bundle sheath. Thylakoid swelling and disappearance, typical of plant material exposed to SO_2 , occurred in cells exhibiting minor levels of injury.

A number of studies, including HÜTTL and FINK (1988), FINK (1989), SCHMITT and REUTZE (1990), suggest that many types of injury considered typical of direct effects of SO_2 or other pollutants, in fact resemble changes resulting from mineral nutrient deficiencies that may arise from indirect or secondary effects of pollution on plants.

14.2.4. Alterations to the vascular bundle and disruption of water transport

In experiments with high gas concentrations, cells of the vascular bundle typically succumb to pollutant injury, following the deterioration of most of the

mesophyll (SCHMITT *et al.* 1989; REUTZE *et al.* 1989). In response to low concentrations in long-term experiments and chronic pollution levels in the field, pollution indirectly affects mainly the sieve cells (FINK 1983; PARAMESVARAN *et al.* 1985; SCHMITT and REUTZE 1990).

Low ozone concentrations throughout three growing seasons resulted in a marked degradation of organelles in the bundle sheath and albuminous cells (SUTINEN *et al.* 1990). In young spruce trees exposed to a mixture of SO₂, O₃, and acid mist at concentrations similar to those in heavily polluted areas, SCHMITT and REUTZE (1990) observed a large number of phloem cells with collapsed walls and a lack of the typical cell wall thickening. A reduced wall thickness in young sieve cells, identified as a natural aging effect, indicates reduced translocation activity (REUTZE and SCHMITT 1988). An accumulation of starch in the mesophyll may indicate reduced sugar transport caused by phloem dysfunction (GUDERIAN *et al.* 1986; KÜPPERS and KLUMPP 1987; MEYBERG *et al.* 1988; FORSCHNER *et al.* 1989; ZELNING *et al.* 1989). Within geographic regions chronically exposed to SO₂, NO, NO₂, and O₃, the appearance of osmophilic bodies together with large quantities of lipids was observed in the cytoplasm of albuminous cells (SUTINEN 1987c). According to JENSEN and KOZLOWSKI (1975) and GUDERIAN (1977), the translocation and accumulation of assimilates containing sulfur in the albuminous cells negatively affects cellular metabolism and structure. Additionally, in spruce needles from areas chronically polluted by O₃, SO₂, and NO_x, a hypertrophy of the parenchyma of the transfusion tissue and a proliferation of cambial cells is often detected. A common phenomenon is the accumulation of phenols in vacuoles of parenchyma cells of the transfusion tissue and in the bundle sheath cells (HASEMANN and WILD 1990). In addition, hypertrophy of the albuminous cells and the accumulation of osmophilic substances in phloem cells and suberin in their walls have been observed in needles of declining Norway spruce trees (PARAMESWARAN *et al.* 1985).

Unlike the primary root endodermis, the cell walls of the needle bundle sheath do not act as a barrier to water transport. The radial walls of the bundle sheath cells contain lignin and mediate water transport from the bundle through the mesophyll and to the sites of transpiration (MAIER-MAERCKER 1986). After exposure of Norway spruce to SO₂ or O₃, the cell walls of the vascular bundle sheath may collapse, owing to a loss of lignin from the radial walls. Because of their considerable lignification, MAIER-MAERCKER (1986) considers these cells as key sites of apoplastic water transport out of the vascular bundle. Both bundle sheath cells and stomatal cells have chloroplasts filled with large starch grains, suggesting the existence of a common mechanism of osmotic pressure control. The marked increase in phenolic compounds in the bundle sheath cells may arise from numerous altered metabolic processes. Regulation of the radial flow of water and mineral nutrients is also disrupted

owing to cell wall damage in the bundle sheath cells as well as ion binding by phenolic compounds in the vacuole.

14.2.5. Changes in wood structure

Past dendrochronological studies on trees in polluted environments focused on measurement of annual growth rings, whereas less attention has been paid to the ratio of earlywood to latewood. KELLER (1978, 1980) showed that with an increase in SO₂ concentration from 0.05 to 0.2 ppm, the number of rows of tracheids in a radial section decreased. Especially significant was the decrease in latewood in the annual growth ring, although observed only in trees exposed to the highest gas concentration. The annual ring width and the specific gravity of earlywood did not differ from the control. A negative impact of SO₂ on plants in early spring was observed in reduced CO₂ assimilation at the end of May and at the beginning of June. SO₂ exposure had no influence on earlywood production. This is likely because earlywood growth is dependent both on rates of net photosynthesis and on the level of stored carbohydrates at the beginning of the growing season. A marked decline in photosynthesis is typically observed only after several weeks of exposure to low SO₂ concentrations, reflecting injury to the photosynthetic apparatus. Altered photosynthesis adversely influences the activity of the vascular cambium, and consequently leads to a lower proportion of latewood in the annual ring increment and to a lower wood specific gravity.

The reasons for a delayed response of the cambium to stress, manifesting itself as a pronounced reduction in cell division (KELLER 1978, 1980; RADEMACHER *et al.* 1986), should be carefully considered. Frequently, the damage of needles or even tree crowns is not immediately followed by reduced cambial activity (KOZŁOWSKI and CONSTANTINIDOU 1986). Compared to fir, the suppression of wood growth in spruce and pine in response to pollution exposure is typically delayed by one year or more and is strongly dependent on site quality and tree condition (BAUCH *et al.* 1979; FRANZ 1983; FRÜHWALD *et al.* 1984; KENK *et al.* 1984; NAGEL *et al.* 1985; SCHWEINGRUBER *et al.* 1986). Drought, which affected a large part of Germany in 1976, strongly influenced the width of annual growth rings formed in the following year in spruce trees from lowland sites, whereas in declining high-elevation spruce forests, the drought effect was marked by reductions in annual ring widths over many years (RADEMACHER *et al.* 1986).

Studies of declining Norway spruce stands indicate significant root system injury and the disappearance of mycorrhizas. Water transport in the stem, which in heavily polluted areas is disproportionately low in relation to water demand, is often attributed to the presence of numerous compounds and aluminum, cadmium, and lead ions in the soil solution, which compete with other ions at the root uptake sites (KLEIN 1985). In polluted forest areas, the calcium

and magnesium nutrition of trees is often insufficient. This may arise from reduced sapwood volume, which typically constitutes 20–25% of the total stem volume (RADEMACHER *et al.* 1986). Because of a lack of detailed studies on the rate of water and nutrient transport in large trees, our understanding of the role of mineral nutrition in the phenomenon of forest decline remains incomplete.

The level of the soluble sugars glucose, fructose, and sucrose is significantly higher in both xylem and phloem of trunks of diseased trees, whereas the amount of starch present during winter dormancy is lower and is less than 30% of its average level in healthy trees (RADEMACHER *et al.* 1986). A higher content of soluble sugars in the phloem and sapwood of diseased trees is a stress indicator (HÖLL 1985). The annual fluctuation of soluble sugars and starch in healthy spruce trees demonstrated that imbalanced ratios as well as an insufficient quantity of sugars transferred to the active cambium may lead to an inhibition of wood formation and to a change in earlywood and latewood increments in the annual growth ring (HÖLL 1985). A reduced earlywood increment leads to an insufficient supply of water and nutrients to the crown. Trees exhibiting thin crowns produce less carbohydrates and hormones, which negatively influences their root biomass and the quantity of root-derived growth substances.

In healthy trees, the thickness of tracheid cell walls is correlated with annual net assimilation (LARSON 1964). Declining spruce trees with thin crowns exhibit latewood tracheids with thinner walls and wood with lower specific gravity (KELLER 1980; KIENAST 1982). The wood of healthy and pollutant-impacted trees do not differ with respect to the contents of cellulose, hemicellulose, or lignin (PULS and RADEMACHER 1986). Consequently, pollutant-damaged tree crowns have no clear negative effect on wood strength parameters and other wood quality characteristics (FRÜHWALD *et al.* 1984; KNIGGE *et al.* 1985). Apart from a lower extensibility, no significant differences are found with respect to stiffness or torsion resistance between wood from trees with or without crown damage (THORNQVIST 1986).

In addition to SO₂, many other toxins negatively influence the increment and structure of wood, usually leading to a deterioration of wood quality. Sulphite, similar to sulfur dioxide, causes a reduction in the annual growth of wood (WESTMAN 1974). ATHARI (1984) showed a similar influence of potassium hydroxide (KOH). Unlike SO₂, which reduces tracheid wall thickness (BAUCH *et al.* 1986) but not length (KELLER 1978, 1980), hydrogen fluoride reduces tracheid extension growth (WENTZEL 1981). KRAPPENBAUER *et al.* (1985), in a case study of seven spruce growing 2 km from a glassworks plant, described an association between increased NO₂ air pollution and wood structure. When the factory production was changed from soft to hard glass and fuel oil was replaced with natural gas, the trees formed 3–4 rows of short, narrow tracheids with extensive incrustations in the walls and a small number of

bordered pits in the lower trunk segments. The reduction in tracheid length and diameter, and a reduction in the annual ring widths occurred simultaneously with the switch to a higher furnace temperature regime. As a consequence, NO_2 emission to the atmosphere increased, which in the presence of ozone may strongly reduce both CO_2 assimilation and alter the distribution of photosynthates.

Similar changes in wood structure were discovered in spruce trees growing in the proximity of another glassworks factory, which generated mostly fluorine and chlorine pollution (BODNER 1987). Apart from significant differences in the length and width of tracheids and fibers compared to the control material, additional tracheids were formed after the latewood and had exceptionally small diameters, enhanced wall incrustations, and small numbers of bordered pits. In that study, the change of latewood specific gravity turned out to be the most sensitive indicator of air pollution level. With increased pollution levels, tracheids were shorter and their numbers per square millimeter were fewer. As a result, the wood had exceptionally narrow growth rings. JORDAN (1986) demonstrated a significant effect of NaCl on wood increment in Norway spruce growing near a roadway in which the compound is used as a deicer.

LIESE *et al.* (1975) in a study of the effect of SO_2 and magnesite dust on spruce wood structure, observed reduced wood increments that coincided with the opening of a magnesite processing plant. The tracheids had reduced diameters and lengths and greater numbers of bordered pits. In contrast to the clear influence of SO_2 and $\text{SO}_2 + \text{O}_3$ on conifer wood increment, ozone alone has no effect on wood growth or structure (HOLLAND *et al.* 1995).

In contrast to the many studies demonstrating links between wood production and long-term environmental pollution (MOHRING 1983), other studies have failed to reveal such clear correlations (SCHWEINGRUBBER *et al.* 1986). A lack of pollutant effects may be explained by site fertility, the physical and chemical properties of the soils, and by environmental factors favoring plant growth or compensating for the negative influences of the pollutant. Population or individual genetic differences, as well as tree growth conditions, may also be important factors mitigating the effects of environmental pollutants (KRAMER 1986).

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15. WOOD PROPERTIES AND USES

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As a raw material (*Picea abies*), Norway spruce wood, has wide application as a building material and in industry, especially in northern European countries. The wood of Norway spruce is an important natural resource in Germany, Austria, Slovakia, the Czech Republic, Romania, as well as the Scandinavian countries. In addition to its wood, Norway spruce is highly valued for its tannin-rich bark and resins.

15.1. WOOD

15.1.1. *Important anatomical features*

The wood of Norway spruce is nearly white in color, sometimes with a light-yellow tint, and characterized by a subtle gloss. The annual rings of spruce wood are clearly visible in all planes, but especially in the transverse and the tangential planes. The borders of the annual rings are very distinct owing to differences in the composition of earlywood and latewood. Resin canals are generally not numerous and indistinct (KOKOCIŃSKI 2002). The presence of resin in spruce wood results in the pleasant resinous scent of green wood (GALEWSKI and KORZENIOWSKI 1958; GROSSER and TEETZ 1987). Owing to the poor self-pruning of branches in Norway spruce, the wood contains numerous knots, distributed in whorls. The knots appear darker than the surrounding wood, sometimes nearly black in color. The knots are typically hard and tend to loosen and fall out after drying. Some knots are friable and are termed “punk knots”.

15.1.2. *Chemical composition of wood*

The chemical composition of Norway spruce wood became a matter of interest as early as the 19th century, when in addition to fir (*Abies alba*), it was the raw material for the developing pulp and paper industry. The excellent pulping properties are largely due to the length of the tracheids, which in Norway

spruce exceed 2.9 mm. The tracheids are easily de-fiberized during the mechanical beating process. Consequently, Norway spruce not only produces pulp suitable for quality paper products with high mechanical strength, but also high quality pulp for further chemical processing. The large geographic distribution of Norway spruce led to many investigations that aimed to determine geographic and genetic differences in the wood chemical composition of the species (Table 15.1, 15.2).

Norway spruce wood has been used in numerous model studies, often of great theoretical importance, especially in pulping of wood. Research on lignin isolated from Norway spruce wood allowed FORSS (1968) to advance

Table 15.1. Chemical composition of Norway spruce wood of different geographic regions

Region	Mineral sub- stances	Extract			Cellu- lose Kürschn er- Hoffer	Pento- sans	Lignin
		Water	alcohol	ether			
[%]							
Karelia (2)	0.20	4.1	–	3.1	45.2	9.5	29.0
Petersburg (2)	0.26	1.4	–	1.5	59.1*	10.0	28.1
Germany (1)	0.77	–	1.5	0.7	57.8	11.3	28.3
Romania (3)	0.19	1.7	1.2**	–	51.1	7.3	28.7

(1) – HÄGGLUND 1951, (2) – NIKITIN 1962, (3) – TOCAN *et al.* 1963

* cellulose obtained by the CROSS-BEVAN method, ** alcohol-benzene mixture 1:1

Table 15.2. Chemical composition of Norway spruce wood of Polish origin (PROSIŃSKI 1984)

Range	Age	Percentage content of chemical compounds in wood									
		Min- eral sub- stanc es	Soluble substances				Alco- hol + ben- zene	Cellu- lose	Alpha cellu- lose	Pento- sans	Lignin
			cold water	hot water	1% NaO H	10% KOH					
Northern	38	0.18	0.35	0.97	8.13	13.15	3.27	60.08	64.55	11.31	24.20
	75	0.14	0.56	1.18	7.70	11.46	2.52	57.04	70.17	10.99	27.17
Southern	38	0.23	0.63	0.80	13.12	24.57	2.98	55.26	70.08	12.87	27.89
	75	0.29	0.24	0.98	7.00	21.61	4.17	53.11	75.34	11.71	25.25

our understanding of the polymer structure and binding properties of lignin. Structural differences were noted in comparisons of the chemical composition of normal and compression wood in Norway spruce (Table 15.3). In addition to differences in anatomy, compression wood also contains significantly lower amounts of cellulose, a somewhat higher content of hemicellulose, and higher amounts of lignin (KIN 1971; BLAŽEJ and KOŠIK 1985; FENGEL and WEGENER 1989).

Spruce wood also contains small amounts of resin, consisting mainly of resin acids (e.g. α -levo-pimaric acid, palustric acid, and abietic acid), resin oxyacids, and a certain amount of acetic acid, propionic acid, butyric acid, and valeric acid (SIŁA and SEKULSKI 1961; BARDYŠEV *et al.* 1965; KIMLAND and NORIN 1967; VOLS'KIY and SCHMIDT 1970). The resin also consists of a number of terpenes of the following contents: α -pinene 15–20%, bipentene

Table 15.3. Chemical composition of normal and compression wood of Norway spruce of Swedish origin (STOCKMAN and HÄGGLUND 1948)

Chemical composition of wood	Normal wood	Compression wood
	[%]	
Cellulose	41.5	27.3
Hemicellulose		
1. Hardly hydrolysing	8.3	9.4
Mannan	2.9	2.1
Xylan	2.2	2.4
Fructan	1.2	0.9
Glycan	2.0	4.0
2. Easily hydrolysing	16.0	19.9
Mannan	7.4	4.0
Arabinan	0.5	5.2
Xylan	5.4	–
Galactan	1.9	9.5
Glycan	0.8	1.2
Lignin	28.0	38.0
Acetyl groups	1.4	0.8
Resin, mineral substances, proteins and undetermined substances	4.8	4.6
Total	100.0	100.0

Table 15.4. Components of Norway spruce turpentine (SANDERMANN 1960; SCHMIDT-VOGT 1986)

Terpene	Content %
α -pinene	18.6–23.2
Camphene	0.9–2.3
β -pinene	15.3–36.8
3 Carene	0.5
Limonene, β -phellandrene	6.8–26.4

25–30%, lariciresinol 15–20% (HÄGGLUND 1951). Lignans are represented by pinoresinol and lariciresinol and their derivatives (WEINGES 1960). Resin substances, particularly the resin acids and others, result in spruce wood pH values of ca 5.04, whereas the pH in pine is ca 4.00 (ZENKTELER and WOŹNIAK 1965). Spruce resin may be obtained from damaged trees or from resin blazes, created by intentionally scoring the trunk. Distillation of spruce resin is used to produce turpentine (Table 15.4) and rosin having properties similar to pine resin (VODZINSKIY 1969; SURMIŃSKI 1994).

Terpene-like substances are also present in spruce needles and their content is ca 0.15–0.25%. They form oils, consisting of santalol, α -pinene, β -phellandrene, bipentene, β -bornyl acetate, and cadinene. Small quantities of Norway spruce oil are produced in Austria, Germany, and the former Yugoslavia and used in the perfume and pharmaceutical industries (KLIMEK 1959; KIMLAND and NORIN 1967).

15.1.3. Physical and mechanical properties of wood

Depending on geographic region and climatic conditions, Norway spruce wood exhibits variation in the width of the annual growth rings. Consequently, variation in physical and mechanical wood properties is expected. Differences in wood properties also occur among morphological variants of Norway spruce, although differences may not be strictly correlated with a specific morphological form (SIEK 1970).

Density is a basic physical property that may be used to characterize wood quality (TRENDELENBURG and MAYER-WEGELIN 1955; LVOV and KLIMOV 1971). The density of spruce wood depends primary on site quality and ranges from 300 to 680 kg/m³. Wood from rich sites has a density of ca 400 kg/m³, whereas in wood from medium and poor sites, the density increases to ca 450 kg/m³. Other physical and mechanical properties of Norway spruce wood are shown in Tables 15.5, 15.6, 15.7.

Norway spruce wood is light, soft, and easily split. Sanding and finishing is more difficult in Norway spruce than Scots pine (*Pinus sylvestris*) due to its

*Table 15.5. Density of Norway spruce wood
(TRENDELENBURG and MAYER-WEGELIN 1955)*

<i>Density [kg/m³]</i>	<i>Geographic region</i>	<i>Altitude above sea level [m]</i>
370–390	Alps	1100–1900
	Hungary	250–700
400–420	Alps	1100–1700
	Norway	over 700
430–450	Bavaria	920
	Harz Mountains, Thüringen	400–1200
460–480	Swiss Alps	900–1200
	Silesia	140–250

softness (GALEWSKI and KORZENIOWSKI 1958), although its low resin content facilitates the use of finishes and application of adhesives (GRABOWSKI and NIWIŃSKI 1957). In comparison to Scots pine, Norway spruce is characterized by a more uniform light color and does not darken when exposed to sunlight. The mechanical processing of spruce wood is problematic owing to the presence of numerous hard and dark-colored knots (often termed horn knots). Occasionally, spruce wood contains friable knots, which give rise to holes in sawn lumber. In the pulping process, knots are the cause of impurities (and spots) in paper products.

An essential and key feature of Norway spruce wood is the low permeability of the heartwood, resulting from the presence of closed pits. However, spruce wood impregnation is possible using mixtures of appropriate salts, such as acid ammonium phosphate. Oil-based preservatives do not deeply pene-

*Table 15.6. Physical properties of Norway spruce wood
(KOLLMANN 1951, KOKOCIŃSKI 2004)*

<i>Property</i>	<i>Value</i>
Oven-dry density, ρ_0 (kg/m ³)	300–430–640
Density at a moisture content, ρ_{12} (kg/m ³)	340–470–680
Porosity (average), C (%)	71.3
Longitudinal shrinkage, β_L (%)	0.3
Radial shrinkage, β_R (%)	3.6
Tangential shrinkage, β_T (%)	7.8
Volumetric shrinkage, β_V (%)	12.0

* – moisture content of 10%

Table 15.7. Mechanical properties of Norway spruce wood (KOKOCIŃSKI 2004)

Property	Value
Static bending strength, R_g (MPa)	49–78–136
Modulus of elasticity in static bending, E (MPa)	7300–1100–21400
Compression strength, R_{cl} (MPa)	33–50–79
Tensile strength along fibers, R_{tl} (MPa)	21–90–245
Tensile strength across fibers, R_r (MPa)	1.5–2.7–4.0
Impact strength, U (J/cm ²)	1.0–4.6–11.0
Shear strength, R_{sl} (MPa)	4.0–6.7–12.0
Janka hardness in tranverse plane, HJ (MPa)	26

trate spruce wood (WYTWER 1970) and high-pressure application of preservatives may cause damage to wood (BOSSHARD 1968). Some tests have used a brief initial exposure of wood to the action of fungi to enhance permeability by degrading cell walls, especially around the toruses of bordered pits (TRYANINA and KONSTANTNAYA 1965).

Spruce wood dries relatively quickly with minimal shrinkage, but is prone to cracking. Under excessive loads, the sound of cracking Norway spruce wood is an important warning signal, especially in the case of mine timbers. Norway spruce harvested and debarked in summer tends to crack quickly. Freshly debarked wood is very susceptible to fungi, and should be stored in stacks to ensure good ventilation (SPLAWA-NEYMAN and OW CZARZAK 1993).

Norway spruce wood is durable and may persistence for long periods of time. In comparison to contemporary wood, archaeological samples of spruce wood are characterized by lower carbohydrate contents and higher contents of lignin and mineral substances (FENGEL 1971; LIESE *et al.* 1975). The natural durability of properly dried Norway spruce wood varies from 120 to 900 years, whereas for wood exposed to weathering, durability ranges from 40 to 70 years. However, the durability of non-impregnated footers is ca 5 years (WANIN 1953). Spruce wood easily undergoes storage decay caused by *Lanzites abietina* – *Gleophyllum abietinum*. However, in contrast to other species, especially pine, Norway spruce wood is highly susceptible to stain fungi (MAŃKA 1998). Norway spruce wood floated in water turns yellow, similar to other resinous softwood species, but the tint disappears after drying.

15.1.4. Resonant wood

The physical and mechanical properties of Norway spruce wood make it a prized source of resonant wood used in construction of musical instruments.

The main purpose of resonant wood used in musical instruments is to amplify the emitted tones. In a stringed instrument such as a violin, the vibration of a string alone is too weak to project sound at a desirable volume. The transmission of the vibrations into a resonance box or sounding board constructed of the right wood and correct shape propagates vibrations into the air (GONET 1966).

In amplifying tones, resonance characteristics depend on the resistance of the wood to sound wave propagation as well as internal friction. A portion of the absorbed sound energy causes internal vibrations in the wood, while the major portion is emitted. The damping of vibrations through emission depends on the sound velocity in the wood and wood density. Internal friction attenuates the vibration wave propagated in the wood, resulting in heat production and decreased sound intensity.

The best resonance properties are found in wood that converts the smallest portion of sound energy into heat via friction and simultaneously converts the largest portion of the energy into emitted vibrations. The resonance properties of wood are often expressed as a dimensionless number termed the music constant (K) and defined according to the formula:

$$K = \sqrt{\frac{E}{\rho^3}}$$

where E is the modulus of elasticity in static bending in kg/cm² and ρ^3 is wood density in g/cm³ (KRZYSIK 1978).

The music constant is typically above 1000 for resonant wood or lower in some cases (HOLZ 1967; HOLZ and SCHMIDT 1968). For instance, resonant wood of Norway spruce of Polish origin has a music constant varying from 931 to 2172 with an average value of 1472. By comparison, wood of Romanian origin exhibits musical constants varying from 1233 to 3006 with the average value of 1873. Resonance properties improve with increasing values of the music constant (BIELCZYK and BOBROWICZ 1960; BLOSSFELD *et al.* 1962).

In the case of Norway spruce, resonant wood starts to form at the age of ca 45 years, when the crown tends to stabilize (GRAPINI 1967). Resonant wood is obtained from stems of trees over 100-years old from closed and dense stands of high mountain forests at altitudes of 800 to 1400 m above sea level. Presently, such wood is usually found in the Alps or the Romanian Carpathians. In Poland, resonant wood largely originates from stands in the Sudety and western Beskidy Mts (BOBROWICZ 1959; BLOSSFELD *et al.* 1962) as well as the Mazurian lake region (GONET 1965, 1966).

Norway spruce resonant wood should have a density varying from 0.40 to 0.45 g/cm³ and be white in color with a satin gloss. Thus, it will easily split due to a high content of wood rays. Resonant wood also has uniform annual rings of a thickness varying from 0.5 to 2.0 mm or from 2.0 to 4.0 mm. Narrow-ringed wood resonates higher tones optimally, whereas wider-ringed wood optimally

resonates lower tones. The content of latewood in individual annual rings should equal ca 25%. A characteristic anatomic feature of spruce resonance wood is visible in the transverse plane as a somewhat wavy run of annual rings.

Resonant wood is cut only from the heartwood of spruce logs at a minimum thickness of 28 cm. Such wood is sawn radially (HOLZ 1967). The distance from the resonance zone to the wood surface should not exceed 4.0 cm. The wood has to meet high strength requirements and therefore cannot contain compression wood, which markedly decreases resonance properties and promotes warping. The wood should be free of any knots, resin canals, and stain (MAKAREVA 1968; GHELMEZIU and BELDIE 1970; VOL'SKIY and SCHMIDT 1970). Resonant wood should be air dried to a final moisture content of 11–13%. Kiln drying negatively impacts resonance properties, but if necessary, temperatures should not exceed 80–100°C (ILLE 1968; SHITOVA 1969).

Norway spruce wood, which was formerly used by famous Italian violin makers for building instruments, was probably subjected to long-term soaking in limewater. This process decreased the hygroscopic properties of the wood and increased its acoustic characteristics. In addition to selection and initial processing, a key step is forming the wood into the correct shape and thickness for use in musical instruments. The proper shape and thickness of elements are critical (HARAJDA and POLISZKO 1971). The historic violins made by Italian masters, such as AMATI, GUARNERI and STRADIVARIUS are unequalled examples of musical instruments built with wood. In addition to their beautiful tone, these instruments are characterized by a 30% higher acoustic effect in comparison to contemporary violins. Their sound is audible at a radius of 1000 m in open areas (GONET 1966).

15.1.5 Products derived from chemical processing

Norway spruce wood containing low amounts of resin may be processed using sulfite or alkaline methods. Sulfite processing of wood results in the release of pollutant sulfur oxides. Therefore, the method is not presently used in Poland, where pulp is produced using the alkaline method, which is more efficient and safer for the environment (KIN 1971; SUREWICZ 1971). Moreover, spruce pulpwood may be processed together with pine pulpwood. Norway spruce pulp is primarily used to produce a variety of paper products, including printing paper, cardboard, writing paper, blotting paper, various packing papers, and parchment. Norway spruce pulp free of impurities is used to produce nitrocellulose lacquer and explosives.

Other uses of Norway spruce include the production of fiberboard and particle board (SCHMIDT-VOGT 1986; GROSSER and TEETZ 1987; SPŁAWA-NEYMAN and OW CZARZAK 1993). Norway spruce was formerly used to produce charcoal for iron ore smelting, especially in Scandinavia. According to KLASON, Norway spruce charcoal contains 82.5% elemental carbon and 4.1%

Table 15.8. Distillation products of Norway spruce wood (KLASON *et al.* 1907, 1908)

<i>Distillation products</i>	<i>Content [%]</i>
Charcoal	37.81
Gas products:	
carbon dioxide	10.30
Ethylene	0.20
carbon monoxide	3.78
Methane	0.62
Liquid products:	
methyl alcohol	0.96
Acetone	0.20
acetic aldehyde	0.02
acetic acid	3.19
other organic acids	7.75
Tar	8.08
Acid water	25.70
Losses	2.39
Total	100.00

hydrogen. Its lower heating value is 7695 cal/g (HÄGGLUND 1951). In addition, distillation processes are used to obtain numerous chemical products from Norway spruce wood (see Table 15.8).

15.2. BARK

The bark content of a Norway spruce log is ca 12% of the total stem volume (calculated with bark). Bark has an average density of ca 340 kg/m³ and tannin content of 8.5%. Spruce bark is one of the most important and least expensive sources of tanning compounds for leather production. The bark is primarily used in northern and eastern European countries for tanning Russian leather. Until recently, spruce bark was used in a number of Polish tanneries (JANICKI *et al.* 1951). At present, tannin extracts are obtained from oak wood and imported mimosa bark (*Acacia catechu*) and Norway spruce bark is not used in industrial applications (MUSZYŃSKI and MC NATT 1984). The tannin content of spruce bark ranges from 6–15%. The highest contents are found in bark of 30–60 year-old trees. Tannin content depends mainly on site conditions. In

Table 15.9. Chemical composition of Norway spruce bark (SCHMIDT-VOGT 1986)

<i>Chemical component</i>	<i>Content %</i>
Lignin	10
Holocellulose	28
Extracts	62
ether	7
ethanol	18
hot water	13
1% NaOH	24

Norway spruce, bark originating from the south-eastern Alps is considered a highly valued tannin source (SURMIŃSKI 1996).

In addition to tannins, Norway spruce bark contains ca 7.5% of non-tannin compounds, consisting primary of monosaccharides, and up to 65% of insoluble substances. The water content of bark is typically 15–18% (KRZYSWICKI 1949; LIIRI 1967; SEMENOVA 1971). Norway spruce bark also contains trace amounts of fungistat substances, such as piceatannol, resveratrol, quercetin, taxipholin, catechin, and leukocyanidine (Table 15.9). The majority of these substances occur in glycoside forms (ALCUBILLA 1970). Spruce bark is used in some countries, e.g. Austria and Finland, for composting with the use of decomposing bacteria (ZNAIMER and WAZDA 1967).

15.3. OTHER USES OF WOOD AND BARK

Spruce wood is a choice material for woodworking and furniture making. Its texture, weight, and bright uniform color are highly valued. The low resin content in Norway spruce wood facilitates its use in the production of barrels and wooden boxes, pallets, and other packaging materials for the food-processing industry. Spruce wood is also a suitable material for plywood production, and has been used in the aircraft industry, especially for the gliders and parts for sport aircraft (GOŁAWSKI 1956). Historically, Norway spruce wood had numerous applications as a building material, including bridges, mining timbers, and ship masts. As discussed earlier, spruce wood is highly valued for its resonant properties in constructing violins and other music instruments.

The bark of Norway spruce contains tannins and other past uses include roofing shingles and tannin production in small tanneries.

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REFERENCES

- ABATUROV YU. D., ZVORYKINA K. V., ORLOV A. YA., PIS'MEROVA A. V. 1988. Tipy lesa. In: UTKIN A. I., ORLOV A. YA. (eds.). Korennye temnokhvoynye lesa yuzhnoy taygi. Nauka, Moskva. pp: 48–129.
- ABRAHAMSEN G. 1984. Effects of acidic deposition on forest soil and vegetation. Phil. Trans. R. Soc. London 305: 369–382.
- ABRAZHKO M. A. 1989. K kharakteristike rosta podrosta eli v subklimaksovykh soobshchestvakh. Bot. Zh. 74: 885–890.
- ABRAZHKO M. A. 1985. O vliyaniy azotnykh udobreniy na raspredelenie i fraktsionnyy sostav korney *Picea abies* (Pinaceae). Bot. Zh. 70 (2): 250–254.
- ADAMOVIĆ L. 1909. Vegetationsverhältnisse der Balkanländer. Verlag Wilhelm Engelmann, Leipzig, 567 pp.
- AFELE J. C., SENARATNA T., MCKERSIE B. D., SAXENA P. K. 1992. Somatic embryogenesis and plant regeneration from zygotic embryo culture in blue spruce (*Picea pungens* ENGELMAN.). Plant Cell Rep. 11: 299–303.
- AGERER R. (1987–1995) Colour atlas of ectomycorrhizae. Einhorn-Verlag Eduard Dietenberger, Schwäbisch Gmünd, Germany.
- AGERER R. 1989. Impacts of artificial acid rain and liming on fruitbody production of ectomycorrhizal fungi. Agric. Ecosyst. Environ. 28: 3–8.
- AGERER R., KLOSTERMEYER D., STEGLICH W., FRANZ F., ACKER G. 1996. Ectomycorrhizae of *Albatrellus ovinus* (Scutigeraceae) on Norway spruce with some remarks on the systematic position of the family. Mycotaxon 59: 289–307.
- AGERER R., TAYLOR A. F. S., TREU R. 1998. Effects of acid irrigation and liming on the production of fruitbodies by ectomycorrhizal fungi. Plant and Soil 199: 83–89.
- AL ABRAS K., BILGER I., MARTIN F., LE TACON F., LAPEYRIE F. 1988. Morphological and physiological changes in ectomycorrhizas of spruce [*Picea excelsa* (LAM.) LINK] associated with ageing. New Phytol. 110: 535–540.
- ALCUBILLA M. 1970. Z. Pflernähr Bodenkunde 127 (1): 65–74.
- ALDEN B. 1987. Taxonomy and geography of the genus *Picea*. Int. Dendrol. Soc. Yearb. 1986: 85–96.
- ALEKSANDROV A. H. 1976. Radioustoychivost na potomstvoto ot sm'rchovite populatsii v B'lgarija. Gorskostopanska Nauka 13 (6): 3–10.
- ALEKSANDROV A. H. 1985. Otbor i ocenka na najperspektivnite sortpopulatsii pri sm'rcha (*Picea abies* (L.) KARST.) ot mesteni chuzhdproizkhod. Gorskostopanska Nauka 22 (4): 3–10.
- ALEKSANDROV A. H. 1993. Genetic and tree-breeding peculiarities of some of the southernmost populations of Norway spruce on the Balkan peninsula. Norway spruce provenances and breeding. Proc. of IUFRO (S2.2–11). Symposium, Riga, Latvia: 1–5.
- ALEXANDER I. J., 1983. The significance of ectomycorrhizas in the nitrogen cycle. In: LEE J. A., MCNEILL S., RORISON I. H. (eds.). Nitrogen as an Ecological Factor (eds.). Blackwell, Oxford, UK. pp. 69–94.
- ALEXANDER I. J., FAIRLEY R. I. 1983. Effects of N fertilization on populations of fine roots and mycorrhizas in spruce humus. Plant and Soil 71: 49–53.
- ALTUKHOV Y. P., KRUTOVSKII K. V., GAFAROV N. I., DUKHAREV V. A., MOROZOV G. P. 1986. Allozyme variability in natural population of Norway spruce (*Picea abies* (L.) KARST. I. Polymorphism systems and mechanisms of their genetic control. (in Russian). Genetika 22: 2135–2151.
- ALVA A. K., EDWARDS D. G., ASHER C. J., BLAMEY F. P. C. 1986. Relationship between root length of soybean and calculated activities of aluminium monomers in nutrient solution. Soil. Sci. Soc. Am. J. 50: 959–962.

- AMIET R., EGLI S. 1991. Die Ektomykorrhiza des Grubigen Milchlins [*Lactarius scrobiculatus* (SCOP: FR.) FR.] an Fichte (*Picea abies* KARST.). Schweiz. Z. Forstwes., 142: 53–60.
- ANDERS S. 1974. Untersuchungen zur Klärung ökologischer Möglichkeiten und Grenzen der Fichtennaturverjüngung in den sächsisch-thüringischen Mittelgebirgen mit Hilfe von Pfadkoeffizienten. Ph.D. thesis, Tharandt.
- ANDERS S. 1976. Klärung multikollinearer ökologischer Beziehungen mit Hilft von Pfadkoeffizienten, dargestellt am Beispiel der Fichtennaturverjüngung. Wissensch. Zeitschr. Techn. Univ. Dresden 25 (4): 1009–1018.
- ANDERSEN CH. P., RYGIEWICZ P. T. 1991. Stress interactions and mycorrhizal plant response: Understanding carbon allocation priorities. Environm. Poll. 73: 217–244.
- ANDERSSON E. 1954. Några data om pollenvariationen och pollenfertiliteten hos gran och tall. Svensk Papp. Tid. 57 (7): 242–255; ibidem 57 (18): 654–676.
- ANDERSSON E. 1965. Cone and Seed Studies in Norway Spruce (*Picea abies* L. KARST.). Stud. For-est. Suec. 23.
- ANDERSSON E. 1980. Temperature-conditioned irregularities in pollen mother cells of *Picea abies* (L.) KARST. Hereditas 92: 27–35.
- ANDERSSON E., EKBERG I., ERIKSSON G. 1969. A summary of meiotic investigations in conifers. Stud. Forest. Suec. 70: 1–20.
- ANDERSSON E., JANSSON R., LINDGREN D. 1974. Some results from second generation crossing involving inbreeding in Norway spruce (*Picea abies*). Silvae Genet. 23 (1–3): 34–43.
- ANDERSSON S., SÖDERSTRÖM B. 1995. Effects of lime (CaCO₃) on ecto-mycorrhizal colonization of *Picea abies* (L.) KARST. seedlings planted in a spruce forest. Scand. J. For. Res. 10: 149–154.
- ANONIM 1971. Tree species and hybrids in nurseries and arboreta. Tree Breeding Unit, Research Branch, Ont. Dept. Lands and Forests. Maple.
- ANONIM 1981. Polnisch-Deutscher-Fichtenprovenienzversuch. Hessische Forstliche Versuchsanstalt, Jahresbericht 1980, Han. Münden: 7–8.
- ANONIM 1999. AFOCEL. Memento. Nangis 29 pp.
- ANONIM 2001. Leśnictwo. Główny Urząd Statystyczny, Warszawa.
- ANONIM 1994. Kwarantannowe Agrofagi Europy (zb.) Inspektorat Kwarantanny Roślin, Warszawa. 1069 pp.
- ANTOINE J. 1974. Unterschiede im Kronenaufbau bei Klonen und Herkünften der Fichte (*Picea abies* (L.) KARST.). Silvae Genet. 23 (5): 156–159.
- ANTONOV E. I. 1988. Gruppovoy sposob vosstanovleniya eli na vyrubkakh. Les. Khoz. 10: 22–25.
- ARMON K. A., FUNG M., BUNTING W. R. 1980. Operational rooting of black spruce cuttings. J. For. 87 (6): 341–343.
- ARNOLD S. von, HAKMAN I. 1988. Regulation of somatic embryo development in *Picea abies* by abscisic acid. J. Plant Physiol. 132: 164–169.
- ARNOLDS E. 1991. Decline of ectomycorrhizal fungi in Europe. Agric. Ecosyst. Environ. 35: 209–244.
- ARONSSON A. 1983. Growth disturbances caused by boron deficiency in some fertilized pine and spruce stands on mineral soils. Comm. Inst. For. Fenn. 116: 116–122.
- AROVARA H., ILESNIEMI H. 1990. Effects of soluble inorganic aluminium on the growth and nutrient concentrations of *Pinus sylvestris* and *Picea abies* seedlings. Scand. J. For. Res. 5: 49–57.
- ASP H., BENGTSSON B., JENSÉN P. 1988. Growth and cation uptake in spruce (*Picea abies* Karst.) grown in sand culture with various aluminium contents. Plant and Soil 111 (1): 127–133.
- ASSMANN E. 1961. Waldertragskunde. München – Basel – Wien.
- ASSMANN E. 1968. Nauka o produktywności lasu. [Science of forest productivity] PWRiL, Warszawa. (in Polish).
- ASTROLOGOVA L. 1990. Vozobnovlenie eli pod pologom sosnyaka chernichnogo svezhego. Les. Zh. (1990)5: 13–16.
- ATHARI S. 1984. Jahrringausfall, ein meist unbeachtetes Problem bei Zuwachsuntersuchungen in rauchgeschädigten und gesunden Fichtenbeständen. JUFRO Working Party S2. 09–10. Methods of Forest Mensuration in Diagnosis and Evaluation: Increment Problems in Air Pollution Research. Mitt. Forstl. Bund., Vienna 139: 7–27.

- ATTENBERGER J. 1954. Mischwald im Vorland der Alpen. B. z. Forstw. Ztb. 3. Hamburg u. Berlin.
- ATTREE S. M., MOORE D., SAWHNEY V. K., FOWKE L. C. 1991. Enhanced maturation and desiccation tolerance of white spruce (*Picea glauca* (MOENCH.) VOSS.) somatic embryos: effects of a non-plasmolysing water stress and abscisic acid. *Ann. Bot.* 68: 519–525.
- ATTREE S. M., POMEROY M. K., FOWKE L. C. 1994. Production of vigorous, desiccation tolerant white spruce (*Picea glauca* (MOENCH.) VOSS.) synthetic seeds in a bioreactor. *Plant Cell Rep.* 13: 601–606.
- ATTREE S. M., TAUTORUS T. E., DUNSTAN D. I., FOWKE L. C. 1990. Somatic embryo maturation, germination and soil establishment of plants of black and white spruce (*Picea mariana* and *Picea glauca*). *Can. J. Bot.* 68: 2583–2589.
- AWZAN L., KASPROWICZ M., WĘGLARSKI K. 1986/87. Zmienność górnoregłowego boru karpackiego oraz morfologia świerka przy górnej granicy lasu na północnych zboczach Babiej Góry. *Rocz. Dendrol.* 37: 5–24.
- AYALA F. J. 1976. Molecular evolution. Sunderland (Massachusetts): Sinauer Assoc. Publishers.
- BÄCK J., HUTTUNEN S. 1992. Effects of long-term exposure to simulated acid rain on conifer needle ultrastructure and hardening status. *For. Ecol. Managm.* 95–103.
- BÄCK J., NEUVONEN S., HUTTUNEN S. 1994. Pine needle growth and fine structure after prolonged acid rain treatment in the subarctic. *Plant Cell Environ.* 17: 1009–1021.
- BAGNI N., BIONDI S. 1987. Polyamines. W: BONGA J. M., DURZAN DON J. (red.) *Cell and Tissue Culture in Forestry*, vol.1: 113–123. Martinus Nijhoff Publishers, Dordrecht.
- BAILLON F., DALSCHAERT X., GRASSI S., GEISS F. 1988. Spruce photosynthesis: possibility of early damage diagnosis due to exposure to magnesium or potassium deficiency. *Trees* 2 (3): 173–179.
- BAKER E. A. 1982. Chemistry and morphology of plant epicuticular waxes. In: CUTLER, D. F.; ALVIN, K. L.; PRICE, C. E. (eds.). *The plant cuticle*. Academic Press. pp.: 139–165.
- BALAŻY S. 1965. Obserwacje nad występowaniem w Polsce owadziarek (*Terebrantia*, Hym.) pasożytujących na kornikach (*Scolytidae*, Col.). *Folia Forest. Polonica*, Ser. A 11: 301–331.
- BALAŻY S. 1966. Organizmy żywe jako regulatory liczebności populacji korników w drzewostanach świerkowych ze szczególnym uwzględnieniem owadobójczych grzybów. I. PTPN, Prace Komisji Nauk Rolniczych i Komisji Nauk Leśnych 21 (1): 3–50.
- BALAŻY S. 1968. Analysis of beetle bark mortality in spruce forests in Poland. *Ekologia Polska*, Ser. A. 16 (33): 657–687.
- BALAŻY S., BARGIELSKI J., ZIÓLKOWSKI G., CZERWIŃSKA C. 1967. Śmiertelność dorosłych chrząszczy kornika drukarza – *Ips typographus* (L.) (Col., *Scolytidae*) w żerowiskach i jej przyczyny. *Polskie Pismo Entomolog.* 38: 201–205.
- BALAŻY S., MICHAŁSKI J. 1960. Materiały do znajomości chrząszczy (*Coleoptera*) występujących w chodnikach korników (*Scolytidae*). *Polskie Pismo Entomolog.* 30 (9): 133–144.
- BALAŻY S., MICHAŁSKI J. 1962. Pasożyty korników (*Coleoptera*, *Scolytidae*) z rzędu błonkówek (*Hymenoptera*) występujące w Polsce. PTPN, Prace Komisji Nauk Rolniczych i Komisji Nauk Leśnych 13 (1): 71–141.
- BALAŻY S., MICHAŁSKI J. 1977. Badania nad fauną ksylofagów Wielkopolskiego Parku Narodowego. II. *Bad. Fizjogr. Pol. Zach.*, Ser. C 30: 99–107.
- BALAŻY S., MICHAŁSKI J. 1982. Badania nad fauną ksylofagów Wielkopolskiego Parku Narodowego. IV. *Bad. Fizjogr. Pol. Zach.*, Ser. C 33: 139–145.
- BALAŻY S., MICHAŁSKI J. 1983. Wstępna charakterystyka entomofauny drewna i środowiska podkorowego drzew w Wielkopolskim Parku narodowym. *Folia Forest. Polonica*, Ser. A 25: 163–184.
- BALAŻY S., WIŚNIEWSKI J. 1986. Two new species of *Hirsutella* infecting mites in Poland. *Trans. Brit. Mycol. Soc.* 86: 629–635.
- BALAŻY S., WIŚNIEWSKI J. 1987. Functional aspects of communities of mites (*Acarina*) in the feeding sites of cambio- and xylophagous insects. IV Symposium of the Protection of Forest Ecosystems. SGGW-AR: 143–151.
- BALCAR V. 1996. Acute air pollution injury of ten coniferous species in the Trutnov region. *Lesnictví* 42: 460–472.
- BALDWIN H. I. 1967. Comparative results of the 1938 provenance test of *Picea abies*. *Papers XIV IUFRO Congress, Munchen, III*: 783–786.

- BALDWIN H. I., ELIASON E. J., CARLSON D. E. 1973. IUFRO Norway spruce provenance tests in New Hampshire and New York. *Silvae Genet.* 22 (4): 93–114.
- BALSBERG-PÅHLSSON A.-M. 1989. Effects of heavy-metal and SO₂ pollution on the concentration of carbohydrates and nitrogen in tree leaves. *Can. J. Bot.* 67: 2106–2113.
- BALUT S. 1984. Kształtowanie się wzrostu wysokości polskich pochodzeń świerka pospolitego (*Picea abies* KARST.) objętych doświadczeniem IPTNS-IUFRO 64/68 na powierzchni w LZD w Krynicy. *Acta Agr. Silv.* 23: 19–35.
- BALUT S., SABOR J. 1984. Odporność świerka pospolitego pochodzeń doświadczenia IPTNS-IUFRO 1964/68 w Krynicy na ochojnika zielonego (*Sacchiphantes viridis* RATZ.). *Acta Agr. Silv.* 23: 37–51.
- BALUT S., SABOR J. 1993. Current state of investigation in the international provenance test of Norway spruce – IUFRO 1964/68 in Krynica (site no. 19, Poland). Norway spruce provenances and breeding. *Proc. of IUFRO (S2.2–11)*. Symposium, Riga, Latvia: 6–33.
- BANNAN M. W. 1963. Cambial behavior with reference to cell length and ring width in *Picea*. *Can. J. Bot.* 41: 811–822.
- BARABIN A. J. 1967. Morfologicheskije razlichija v stroeni i raspolozheni generativnykh i vegetativnykh pochetk u eli. *Lesn. Zh.* 10 (2): 160–161.
- BARABIN A. J. 1969. Ssravnitel'nyj analiz urozhaya semyan eli semennogo i malourozhainogo goda v uchebno-opytnom leskhozie ALTI. *Lesn. Zh.* 3 (12): 137–138.
- BARDYSHEV I. I. *et al.* 1965. Kolichestvennyj sostav smolyarnykh kislot zhyvitsy sony i yeli. *Gidrolesokhim. Prom.* 18 (2): 10–11.
- BARKLUND P., AXELSSON G., UNESTAM T. 1984. *Gremmeniella abietina* in Norway spruce, latent infection, sudden outbreaks, acid rain, predisposition. In: MANION P. D. (ed.). *Scleroderris* canker of conifers. Proceedings of an international symposium on scleroderris canker of conifers, held in Syracuse, USA, June 21–24, 1983. Martinus Nijhoff/Dr W. Junk Publishers, The Hague. pp.: 111–113.
- BARLOW C. Y., WOODHOUSE J. 1990. Bordered pits in spruce from old Italian violins. *J. of Microscopy* 160 (2): 203–211.
- BARNES J. D., BROWN K. A. 1990. The influence of ozone and acid mist on the amount and wettability of the surface waxes in Norway spruce (*Picea abies* (L.) KARST.). *New Phytol.* 114 (3): 531–535.
- BARNES J. D., DAVISON A. W., BOTH T. A. 1988. Ozone accelerates structural degradation of epicuticular wax on Norway spruce needles. *New Phytol.* 110 (3): 309–318.
- BÄRTELS A. 1982. Rozmnażanie drzew i krzewów ozdobnych. PWRiL, Warszawa.
- BARTELS H. 1971. Genetic control of multiple esterases from needles and macrogametophytes of *Picea abies*. *Planta* 99: 283–299.
- BARZDAJN W. 1982. Przyrostowa i morfologiczna charakterystyka krajowych populacji świerka pospolitego (*Picea abies* (L.) KARST.) na uprawie porównawczej w Nadleśnictwie Doświadczalnym Laski. *Roczn. AR Poznań* 140: 17–49.
- BARZDAJN W. 1996. Ocena wartości diagnostycznej morfologicznych cech szyszek świerka pospolitego [*Picea abies* (L.) KARSTEN] dla wyróżniania jego proveniencji. [Estimation of the diagnostic value of the morphological characters of Norway spruce [*Picea abies* (L.) KARSTEN] cones for provenance distinguishig.] *Sylwan* 140 (9): 59–72.
- BARZDAJN W. 1997. Dwudziestoletnie doświadczenie proveniencyjne ze świerkiem (*Picea abies* [L.] KARSTEN) serii IUFRO 1972 w Leśnym Zakładzie Doświadczalnym Siemianice. V. Próba syntezy. *Sylwan* 141 (8): 11–17.
- BARZDAJN W., MODRZYŃSKI J. 1981. Analiza wzrostu jednorocznych siewek świerkowych wyrosłych z nasion zebranych w Karkonoskich drzewostanach nieznanego pochodzenia. *Roczn. AR Poznań* 132: 3–16.
- BARZDAJN W., URBĄŃSKI K., WESOŁY W. 1990. Wzrost polskich pochodzeń świerka pospolitego (*Picea abies* (L.) KARST.) w doświadczeniu proveniencyjnym z 1972 r. w Nadleśnictwie Doświadczalnym Laski. *Sylwan* 134 (2): 33–43.

- BASTIDE J. G. A. LA, VREDENBURCH C. L. M. VAN. 1970. The influence of weather conditions on the seed production of some forest trees in Netherlands. Meded. Bosbouwproefst. Wageningen, 102 pp.
- BAUCH J., GÖTTSCHE-KÜHN H., RADEMACHER P. 1986. Anatomische Untersuchungen am Holz von gesunden und kranken Bäumen aus Waldschadensgebieten. *Holzforschung* 40: 281–288.
- BAUCH J., KLEIN P., FRÜHWALD A., BRILL H. 1979. Alterations of wood characteristics in *Abies alba* Mill. due to “fir-dying” and considerations concerning its origin. *Eur. J. For. Path.* 9: 321–331.
- BAUER G., SCHULZE E.-D., MUND M. 1997. Nutrient contents and concentrations in relation to growth of *Picea abies* and *Fagus sylvatica* along a European transect. *Tree Physiol.* 17 (12): 777–786.
- BAULE H., FRICKER C. 1973. Nawożenie drzew leśnych. PWRiL, Warszawa.
- BAUMBUSCH L. O., EIBLMEIER M., SCHNITZLER J. P., HELLER W., SANDERMANN H. JR., POLLE A. 1998. Interactive effects of ozone and low UV-B radiation on antioxidants in spruce (*Picea abies*) and pine (*Pinus sylvestris*) needles. *Physiol. Plant.* 104: 248–254.
- BAUMGARTNER A. 1970. Sauerstoffumsätze von Bäumen und Wäldern. *Allg. Forst-Ztschr.* 25: 482–483.
- BAUMGARTNER A. 1982. Wald und Biosphäre. *Allg. Forst-Ztschr.* 37: 615–621.
- BAUR M., LAUCHERT U., WILD A., PAOLETTI E. 1998. Biochemical indicators for novel forest decline in spruce. *Chemosphere* 36: 865–870.
- BEASON R. C., JR., PROBSTING W. M. 1988. Scion Water Relations during Development in Colorado Blue spruce Grafts. *J. Amer. Soc. Hort. Sci.* 113 (3): 427–431.
- BECKER M., LÉVY G. 1983. Influence d'un dessèchement du sol sur la nutrition minérale de jeunes plants de résineux. *Ann. Sci. For.* 40 (4): 325–335.
- BEDA G. 1988. Konstanz Abhängigkeit und Wirkungen der Johanistriebbildung bei der Fichte. *Schweiz. Z. Forstwes.* 139 (10): 851–868. [FA. 51: 7804.]
- BEDNAROVÁ E. 1999. Epicuticular waxes of spruce *Picea abies* (L.) KARST. needles as indicators of air pollution in the Ore Mts. *J. For. Sci.* 45: 186–191.
- BEHRENS V. 1987. Kühlagerung von unbewurzelten Koniferenstecklingen III. Zusammenhang Reservestoffgehalte und Bewurzelung. *Gartenbauwissenschaft* 52 (4): 161–165.
- BEISSNER L. 1909. *Handbuch der Nadelholzkunde*. Paul Pary, Berlin.
- BELDIE Al. 1967. Flora si vegetatia Muntilor Bucegi. *Acad. Repub. Soc. România, București*. 578 pp.
- BELDIE Al. 1972. *Plantele din Munii Bucetgi*. Acad. Repub. Soc. România, București. 409 pp.
- BELL A. A. 1981. Biochemical mechanisms of disease resistance, *Ann. Rev. Plant Physiol.* 32: 21–81.
- BELLAROSA R., MO L.H., von ARNOLD S. 1992. The influence of auxin and cytokinin on proliferation and morphology of somatic embryos of *Picea abies* (L.) KARST. *Ann. Bot.* 70: 199–206.
- BENEDIKZ P. 1974. Kvæmistilraunir með barrtré. *Ársrit Skógræktarfélags Íslands*: 46–53.
- BENNETT J. P., BUCHEN M. J. 1995. BIOLEFF three databases on air pollution effects on vegetation. *Environm. Poll.* 88: 261–265.
- BENTZER B. 1985. Operational cutting production of Norway spruce *Picea abies* (L.) KARST. IUFRO join meeting of working parties S2.04 – 05 and S2.03 – 14. Grosshansdorf 25–28 Jun 1985: 134–141.
- BENTZER B. 1988. Rooting and early shoot characteristics of *Picea abies* (L.) KARST. cuttings originating from shoots with enforced vertical growth. *Scand. J. For. Res.* 3: 482–491.
- BERAN F. 1993. The oldest IUFRO international provenance experiment with Norway spruce (*Picea abies* (L.) KARST.) in the Czech Republic. *Norway spruce Provenances and Breeding. Proc. of IUFRO (S2.2–11)*. Symposium, Riga, Latvia: 34–37.
- BERDEN M., NILSSON S. I., NYMAN P. 1997. Ion leaching before and after clear cutting in a Norway spruce stand – effects of long-term application of ammonium nitrate and superphosphate. *Water, Air, Soil Poll.* 93 (1–4): 1–26.
- BERGMANN F. 1965. (Moving spruce provenances in central Norrland) *Arsb. Foren. Skogstradsforadl Stockholm* 1964: 85–103. [FA. 27, 3738]

- BERGMANN F. 1971. Genetische Untersuchungen bei *Picea abies* mit Hilfe der Isoenzym-Identifizierung. I. Möglichkeiten für genetische Zertifizierung von Forstsaatgut. Allg. Forst- Jagdztg. 142: 278–230.
- BERGMANN F. 1973. Genetische Untersuchungen bei *Picea abies* mit Hilfe der Isoenzyme-Identifizierung. III Geographische Variation an 2 Esterase und 2 Leucinaminopeptidase Loci in der schwedischen Fichten population. Silvae Genet. 22 (3): 63–66.
- BERGMANN F. 1974. The genetics of some isoenzyme systems in spruce endosperm (*Picea abies*) Genetica 6: 353–360.
- BERGMANN F. 1978. The allelic distribution at an acid phosphatase locus in Norway spruce (*Picea abies*) along similar climatic gradients. Theor. Appl. Genet. 52: 57–64.
- BERGMANN F., HOSIUS B. 1996. Effects of heavy-metal polluted soils on the genetic structure of Norway spruce seedling population. Water, Air, Soil Poll. 89: 363–373.
- BERGMANN F., SCHOLZ F. 1987. The impact of air pollution on the genetic structure of Norway spruce. Silvae Genet. 36: 80–83.
- BERGMANN F., SCHOLZ F. 1989. Selection effects of air pollution in Norway spruce (*Picea abies*) populations. Ed. F. Scholz, H.R.Gregorius, D.Rudin, Genetic effects of air pollutions in forest tree populations. Springer-Verlag Berlin Heidelberg:143–160.
- BERGMANN W. 1983. Ernährungsstörungen bei Kulturpflanzen: Entstehung und Diagnose. Gustav Fischer Verlag, Jena.
- BERMADINGER E., GRILL D., GOLOB P. 1987. Einfluss von Magnesitstauben auf Fichtennadelwachse. Phytion (Austria) 27 (1): 15–29.
- BERMADINGER., GRILL D., GOLOB P. 1988. Influence of different air pollutants on the structure of needle wax of spruce (*Picea abies* (L.) KARSTEN). GeoJournal 17: 289–293.
- BEUKER E. 1994a. Adaptation to climatic changes of the timing of bud burst in populations of *Pinus sylvestris* L. and *Picea abies* (L.) KARST. Tree Physiol. 14: 961–970.
- BEUKER E. 1994b. Long-term effects of temperature on the wood production of *Pinus sylvestris* L. and *Picea abies* (L.) KARST. in old provenance experiments. Scand. J. For. Res. 9: 34–45.
- BEUKER E. 1996. Implications of climate adaptability in provenance trials with Scots pine and Norway spruce in Finland for the possible effects of climate warming. Ph.D. Thesis. Univ. Joensuu, Fac. For.
- BEVILACQUA B., VIDA KOVIĆ M. 1963. Effect of gamma rays on the chromosome of the somatic cells in *Picea abies* KARST. Silvae Genet. 12 (2): 41–46.
- BIAŁECKA K. 1982. Rośliny naczyniowe grupy Pilska w Beskidzie Żywieckim. Zesz. Nauk UJ. 168, Prace Bot. 10. 149 pp.
- BIAŁOBOK S., BARTKOWIAK E. 1967. Analiza kariotypu i zmienność cech morfologicznych *Picea abies* (L.) KARST. z Beskidu Cieszyńskiego. Materiały z Konferencji nad świerkiem pospolitym, Kórnik: 23–37.
- BIAŁOBOK S., OLEKSYN J., RACHWAŁ L. 1984. Selection of trees and shrubs for forest restructuring in industrial regions. In: GRODZIŃSKI W., WEINER J., MAYCOCK P. F. (eds.). Forest Ecosystems in Industrial Regions, Springer-Verlag, Berlin – Heidelberg – New York – Tokyo. Ecol. Stud. 49: 239–244.
- BIELCZYK S., BOBROWICZ E. 1960. Badania niektórych własności świerkowego drewna rezonansowego pochodzenia polskiego i rumuńskiego. Prace Inst. Technol. Drewna 7 (2): 3–25.
- BIRKS H. J. B. 1986. Late-Quaternary biotic changes in terrestrial and lacustrine environments, with particular reference to north-west Europe. W: BERGLUND B. E. (red.). Handbook of Holocene palaeoecology and palaeohydrology. John Wiley & Sons Ltd. pp. 3–65.
- BJÖRKMAN E. 1942. Über die Bedingungen der Mykorrhizabildung bei Kiefer und Fichte. Symb. Bot. Upsal. 112: 1–190.
- BJÖRKMAN E. 1949. The ecological significance of the ectotrophic mycorrhizal association in forest trees. Svensk Bot. Tidskr. 43: 223–262.
- BJÖRKMAN E. 1956. Über die Nature der Mykorrhizabildung unter besonderer Berücksichtigung der Waldbaum die Anwendung in der Forstlichen Praxis. Forstw. Cbl. 75: 265–286.
- BLASCHKE H. 1986a. Einfluß von saurer Berebnung und Kalkung auf Biomasse und Mykorrhizierung der Feinwurzeln von Fichten. Forstw. Cbl. 105: 324–329.

- BLASCHKE H. 1986b. Vergleichende Untersuchungen über die Entwicklung mykorrhizierter Feinwurzeln van Fichten in Waldschadensgebieten. Forstw. Cbl. 105: 477–487.
- BLASCHKE H. 1990. Mycorrhizal populations and fine root development on Norway spruce exposed to controlled doses of gaseous pollutants and simulated acidic rain treatments. Environ. Poll. 68: 409–418.
- BLASCHKE H., BREHMER U., SCHWARZ H. 1985. Wurzelschäden und Waldsterben: Zur Bestimmung morphometrischer Kenngrößen von Feinwurzelsystemen mit dem IBAS – erste Ergebnisse. Forstw. Cbl. 104: 199–205.
- BLASCHKE H., WEISS M. 1990. Impact of ozone, acid mist and soil characteristics on growth and development of fine roots and ectomycorrhiza of young clonal Norway spruce. Environ. Poll. 64: 255–263.
- BLASIUS D., FEIL W., KOTTKE I., OBERWINKLER F. 1986. HARTIG net structure and formation in fully ensheathed ectomycorrhizas. Nord. J. Bot., Sect. Mycol. 6: 837–842.
- BLAŽEJ A., KOŠIK M. 1985. Fytomasa ako chemická surovina. Veda, Bratislava. 150 pp.
- BLEYMÜLLER H. 1976. Investigations on the dependence of flowering in spruce (*Picea abies* (L.) KARST.) upon age and hormone treatment. Silvae Genet. 25 (2): 83–85.
- BLEYMÜLLER H. 1978. Flower induction by hormone treatment in grafts of Norway spruce. Silvae Genet. 27: 117–122.
- BLOSSFELD O., HAASEMANN W., HALLER K. 1962. Resonanz-holz und ihre Eigentum. Sozial. Forstw., Berlin 12 (5): 140–144.
- BLOUIN D., BEAULIEU J., DAOUST G., POLIQUIN J. 1994. Wood quality of Norway spruce grown in plantations in Quebec. Wood and Fibre Science 26 (3): 342–353. [FA. 55, 8838.]
- BOBROV E. G. 1970. Generis *Picea* historia et systematica. Novitates Systematicae Plantarum Vascularum 7: 5–40.
- BOBROV E. G. 1978. Lesobrazuyushchie khvojnye SSSR. Nauka, Leningrad. 186 pp.
- BOBROWICZ E. 1959. Ustalenie baz surowcowych świerkowego i jodłowego drewna rezonansowego w Polsce. Sylwan 103 (9): 61–72.
- BODNER J. 1987. Holzanatomische und densitometrische Untersuchungen an Fichten im Umfeld eines Emittenten. Holzforschung und Holzverwertung 39 (3): 57–61.
- BOHDANECKI J. 1880. Erziehung junger Fichtenbestände. Forstw. Ctbl. 130
- BOLLMARK M., CHEN H.-J., MORITZ T., ELIASSON L. 1995. Relations between cytokinin level, bud development and apical control in Norway spruce, *Picea abies*. Physiol. Plant. 95: 563–568.
- BOLLMARK M., ELIASSON L. 1990a. Ethylene accelerates the breakdown of cytokinins and thereby stimulates rooting in Norway spruce hypocotyl cuttings. Physiol. Plant. 80: 534–540.
- BOLLMARK M., ELIASSON L. 1990b. A rooting inhibitor present in Norway spruce seedlings grown at high irradiance – a putative cytokinin. Physiol. Plant. 80: 527–533.
- BOLSTAD P. V., GOWER S. T. 1990. Estimation of leaf area index in fourteen southern Wisconsin forest stands using a portable radiometer. Tree Physiol. 7 (1–4): 115–124.
- BONNET-MASIMBERT M. 1987. Preliminary results on gibberellin induction of flowering of seedlings and cuttings of Norway spruce indicate some carry-over effect. For. Ecol. Managm. 19: 163–171.
- BONNET-MASIMBERT M. 1989. Field experiment on the effect of girdling and gibberellin application on flowering induction of 12 yr old seedlings of Douglas fir and Norway spruce. Ann. Sci. For. 46, suppl.: 47–50.
- BORATYŃSKA K. 1998. Rozmieszczenie geograficzne. W: BORATYŃSKI A., BUGAŁA W (ed.) Biologia świerka pospolitego. Instytut Dendrologii PAN, Bogucki Wydawnictwo Naukowe. Pp. 63–79.
- BORATYŃSKA K., BORATYŃSKI A., HANTZ J. 1980. Świerk pospolity – *Picea abies* (L.) KARSTEN. In: BROWICZ K. (ed.). Atlas of distribution of Trees and Shrubs in Poland 30: 5–15 + map. PWN, Warszawa – Poznań.
- BORATYŃSKI A. 1991. Chorologiczna analiza flory drzew i krzewów Sudetów Zachodnich. Instytut Dendrologii PAN, Kórnik, 323 pp.

- BORATYŃSKI A. 1998. O dysjunkcjach w zasięgu świerka. [About disjunctions in the Norway spruce range]. In: BORATYŃSKI A., BUGAŁA W. (eds.). *Biologia świerka pospolitego* [Biology of Norway spruce]. Instytut Dendrologii, Bogucki Wydawnictwo Naukowe, Poznań, pp. 80–90.
- BORATYŃSKI A., BROWICZ K., ZIELIŃSKI J. 1992. *Chorology of Trees and Shrubs in Greece*. Sorus, Poznań–Kórnik. 286 pp.
- BORATYŃSKI A., BUGAŁA W. (eds.) 1998. *Biologia świerka pospolitego*. Bogucki Wyd. Naukowe, Poznań.
- BORATYŃSKI A., KONCA B., ZIENTARSKI J. 1987. Sudeckie bory górnoreglowe, *Plagiothecio-Piceetum hercynicum* – warunki występowania, struktura, zagrożenie przez zanieczyszczenia środowiska. *Arbor. Kórnickie* 32: 163–205.
- BORNMAN J. F., TERAMURA A. H. 1993. Effects of Ultraviolet-B radiation on Terrestrial Plants. In: YOUNG A. R., BJÖRN L. O., MOAN J., NULTSCH W. (eds.). *Environmental UV photobiology*. Plenum Press, New York and London pp.: 427–471.
- BÖRTITZ S., VOGL M. 1972. Gaswechselsphysiologische Untersuchungen im oberen Erzgebirge zur individuellen Rauchhärte der Fichte. *Biol. Cbl.* 9 (4): 437–441.
- BORYSIK J. 1986. Zespół jarzębiny *Athyrio-Sorbetum* ass. nova w strefie górnej granicy lasu masywu Babiej Góry (Beskid Zachodni). *Bad. Fizjogr. Pol. Zach. Ser. B.* 36: 115–133.
- BOSCH C., PFANNKUCH E., REHFUESS K. E., RUNKEL K. H., SCHRAMPEL P., SENSER M. 1986. Forst-Härte, Ernährungszustand und Biomasseproduktion junger Fichten (*Picea abies* [L.] Karst.). *Forstw. Cbl.* 105 (4): 218–229.
- BOSEL F. 1983. Tests comparatifs de provenances vaudoises d'épicéa. Résultats et conséquences pour le forestier. *Schweiz. Z. Forstwes.* 134 (5): 339–360.
- BOSSHARD H. H. 1968. Impregnierung vor Fichtenholz. *Holz. Roh Werkstoff* 12: 462–469.
- BOTTON B., CHALOT M. 1995. Nitrogen assimilation: enzymology in ectomycorrhizas. In: VARMA A., HOCK B. (eds.). *Mycorrhizas. Structure, Function, Molecular Biology and Biotechnology*. Springer-Verlag, Berlin, Germany. pp. 325–363.
- BOURIQUET R., TSOOGAS M., BLASELLE A. 1985. Essais de rajeunissement de *Iepicea* par les cytokinines. *Ann. Rech. Sylvic., AFOCEL* 173–185.
- BOUVAREL P. 1961. Observations sur la date de l'aûtement de quelques provenances françaises d'épicéa. *Ann. Ec. Eaux For. Nancy* 18 (1): 96–129. [FA. 23, 121]
- BOUVAREL P. 1962. (The influence of spruce seed source on growth in the nursery, early flushing and frequency of Lammas shoots). *Ann. Ec. Eaux For. Nancy* 19 (3): 419–439. [FA. 24, 3239.]
- BOUVAREL P. 1974. L'adaptation écologique des arbres forestiers. Application à la sélection. In: PESSON P. (ed.). *Ecologie forestiere*. Gautther-Villars, Paris. pp.: 155–173.
- BOUVAREL P., LEMOINE M. 1957. L'expérience internationale sur les provenances d'épicéa (*Picea excelsa* LINK.) *Silvae Genet.* 6: 91–97.
- BOYCE J.S. 1961. *Forest pathology*. 3 ed., McGraw Hall Book company Inc. New York.
- BOYER J. S. 1980. Physiological adaptations to water stress. W: TURNER N. C., KRAMER P. J. (eds.). *Adaptation of plants to water and high temperature stress*. John Wiley and Sons, New York - Toronto. pp.: 443–444.
- BOZHOKOV P. V., LEBEDENKO L. A., SHIRYAEVA G. A. 1992. A pronounced synergistic effect of abscisic acid and 6-benzyladenine on Norway spruce (*Picea abies* L. KARST.) somatic embryo maturation. *Plant Cell Rep.* 11: 386–389.
- BRADSHAW R., HANNON G. 1992. The disturbance dynamics of Swedish boreal forest. In: TELLER A., MATHY P., JEFFERS J. (eds.). *Responses of forest ecosystems to environmental changes*. Elsevier Sci. Publ., London. pp.: 528–535.
- BRÆKKE F. H. 1979. Boron deficiency in forest plantations on peatland in Norway. *Medd. Norsk Inst. Skogforskning* 35 (3): 213–236.
- BRÆKKE F. H. 1983. Micronutrients – prophylactic use and cure of forest growth disturbances. *Comm. Inst. For. Fenn.* 116: 159–169.
- BRANDES B., GODBOLD D. L., KUHN A. J., JENTSCHKE G. 1998. Nitrogen and phosphorus acquisition by the mycelium of the ectomycorrhizal fungus *Paxillus involutus* and its effect on host nutrition. *New Phytol.* 140 (4): 735–743.

- BRANDRUD T. E. 1995. The effects of experimental nitrogen addition on the ectomycorrhizal fungus flora in an oligotrophic spruce forest at Gårdsjön, Sweden. *For. Ecol. Managm.* 71: 111–122.
- BRANDRUD T. E., TIMMERMAN V. 1998. Ectomycorrhizal fungi in the NITREX site at Gårdsjön, Sweden; below and above-ground responses to experimentally-changed nitrogen inputs 1990–95. *For. Ecol. Managm.* 101: 207–214.
- BRAUN H. J., SAUTER J. J. 1983. Unterschiedliche Symptome des “Waldsterbens” im Schwarzwald – mögliche Kausalketten und Basis- Ursachen. *Allg. Forstztg.* 38: 656–660.
- BRAUN H., WEISS M., KOHLSTOCK N. 1983. Der Anbau von Fichtenherkunftssorten – ein Beitrag zur Erhöhung der Stabilität der Waldbestände. *Socialistische Forstwirtschaft* 33 (3): 88–89.
- BRECHT E., SCHULZ H. 1989. Early physiological responses of conifers to sulphur dioxide as studied by optical spectroscopy of chlorophyll. *Photosynthetica* 23 (2): 181–188.
- BRODA J. 1998. Świerk w czasach historycznych. [Norway spruce in the historical times]. In: BORATYŃSKI A., BUGAŁA W. (eds.). *Biologia świerka pospolitego [Biology of Norway spruce]. Instytut Dendrologii, Bogucki Wydawnictwo Naukowe, Poznań*, pp. 25–40. (in Polish).
- BRODOWICZ J. 1888. Słowo o urządzeniu gospodarstwa lasowego ze szczególnem uwzględnieniem stosunków krajowych. *Sylwan* 6: 73–84, 113–123.
- BRØNDBO P. 1969. Induction of flowering by high temperature treatment in grafts of Norway spruce (*Picea abies* (L.) KARST.). *Medd. Norske Skogforsøk.* 27 (98): 298–311.
- BRØNDBO P. 1970. The effect of meteorological factors on the flowering intensity and cone crop of *Picea abies* in Southeastern Norway. *Proc. IUFRO Mtg. on Sexual Reproduction of Forest Trees*. Varparanta, Finland: I/2.
- BROWICZ K. 1982. *Chorology of Trees and Shrubs in South-West Asia and Adjacent Regions*. Polish Sci. Publ. Warszawa. 172 pp.
- BROWN A. D. H. 1979. Enzyme polymorphism in plant populations. *Theor. Pop. Biol.* 15: 1–42.
- BRUNNER I. 1991. Comparative studies on ectomycorrhizae synthesized with various in vitro techniques using *Picea abies* and two *Hebeloma* species. *Trees* 5: 90–94.
- BUCHER-WALIN I. K., BERNHORD L., BUCHER J. B. 1979. Einfluss niedriger SO₂-Konzentrationen auf die Aktivität einiger Glykosidasen der Assimilationsorgane verklonter Waldbäume. *Eur. J. For. Path.* 9 (1): 6–15.
- BUJAKIEWICZ A. 1981. Grzyby Babiej Góry. II. Wartość wskaźnikowa *Macromycetes* w zespołach leśnych. *Acta Mycol.* 17 (1–2): 63–125.
- BURCZYK W., ZAKRZEWSKI J. 1990. Fizjologiczne aspekty procesu rizogenezy w pędach drzew i krzewów. *Wiad. Bot.* 34 (1): 3–12.
- BURCZYK J., GIERTYCH M. 1991. Response of Norway spruce (*Picea abies* (L.) KARST.) annual increments to drought for various provenances and locations. *Silvae Genet.* 40 (3/4): 146–152.
- BURGER H. 1953. Fichten im gleichalterigen Hochwald. *Mitt. Schw. Anst. Forstl. Versuchsw.* 29 (1): 38–130.
- BURKOT-KLONOWA L. 1971. O występowaniu grzyba *Discula brunneotingens* E. I. MEYER w sękach sosny zwyczajnej. *Prace Kom. Nauk Roln. i Kom. Nauk Leśn.* PTPN 31: 3–8.
- BUSCOT F., MUNCH J. C., CHARCOSSET J. Y., GARDES M., NEHLS U., HAMPP R. 2000. Recent advances in exploring physiology and biodiversity of ectomycorrhizas highlight the functioning of these symbioses in ecosystems. *FEMS Microbiol. Rev.* 24: 601–614.
- BUSH R. M., SMOUSE P. E. 1992. Evidence for the adaptive significance of allozymes in forest trees. *New For.* 6: 179–196.
- BUSH S. M., BROKS J., PELSE B. 1970. Vliyanie sostava pitatel'nogo rastvora na molodye rasteniya sosny i eli pri razlichnykh substratakh vyrashchivaniya. *Pitanie drevesnykh rasteniy*. Riga: 3–17.
- BUTIN H. 1989. *Krankheiten der Wald- und Parkbaume*. Georg Thieme, Stuttgart. 216 pp.
- BUYAK A. Z. 1975. Prirost drevesiny eli obyknovennoy v zavisimosti ot intensivnosti semyanosheniya. *Lesoved.* 5: 58–62.
- CAIRNEY J. W. G., MEHARG A. A. (1999). Influences of anthropogenic pollution on mycorrhizal fungal communities. *Environ. Poll.* 106: 169–182.
- CAPE J. N., FREER-SMITH P. H., PATERSON I. S., PARKINSON J. A., WOLFENDEN J. 1990. The nutritional status of *Picea abies* (L.) KARST. across Europe, and implications for 'forest decline'. *Trees* 4 (4): 211–224.

- CAPE J. N., PATERSON J. S., WOLFENDEN J. 1989. Regional variation in surface properties of Norway spruce and Scots pine needles in relation to forest decline. *Environ. Poll.* 58 (4): 325–342.
- CAPECKI Z. 1967. Drwalnik paskowany – *Trypodendron lineatum* OL. (Scolytidae, Coleoptera) na terenie Polski. *Prace IBL, Warszawa* 314: 3–80.
- CAPECKI Z. 1978. Badania nad owadami kambio- i ksylofagicznymi rozwijającymi się w górskich lasach świerkowych uszkodzonych przez wiatr i okiść. *Prace IBL, Warszawa* 563: 37–117.
- CAPECKI Z. 1983. Czynniki gospodarcze i naturalne powodujące zagrożenie lasów górskich. *Las Polski* (9): 9–11.
- CAPECKI Z. 1986a. Gradacja zagrożenia lasów górskich i możliwości ich ochrony. *Sylwan* 130 (2–3): 13–22.
- CAPECKI Z. 1986b. Zagrożenie lasów sudeckich przez szkodniki na tle szkód spowodowanych przez huragany i okiść. *Sylwan* 130 (2–3): 57–64.
- CAPECKI Z. 1993. Stan sanitarny lasów górskich a gradacje szkodników wtórnych. *Sylwan* 137 (9): 61–68.
- CAPECKI Z., GRODZKI W. 1998. Owady jako przyczyny, wskaźniki i następstwa zmian w ekosystemach leśnych Sudetów Zachodnich. In: SAROSIEK J., STURSA J. (eds.): *Geoekologiczne problemy Karkonoszy*. Acarus, Poznań. 2: 85–92.
- CARLETON T. J. 1982. The pattern of invasion and establishment of *Picea mariana* into the subcanopy layer of *Pinus banksiana* dominated stands. *Can. J. For. Res.* 12: 973–984.
- CARLSSON C. E. 1980. Kraft mill gases damage Douglas-fir in western Montana. *Eur. J. For. Path.* 10: 145–151.
- CECICH R. A. 1985. White spruce (*Picea glauca*) flowering in response to spray application of gibberellin A4/7. *Can. J. For. Res.* 15: 875–879.
- CEITEL J. 1994a. Naturalne formy regeneracji lasu w wylesionych obszarach Gór Izerskich. [Natural forms of forest regeneration in deforested areas of the Izerskie Mts]. *Prace IBL, Warszawa, Ser B* 121: 257–271.
- CEITEL J. 1994b. Wpływ więzby sadzenia świerka pospolitego (*Picea abies* L. KARST.) na wzrost i procesy rozwojowe w I klasie wieku. [Influence of planting spacing of Norway spruce (*Picea abies* L. KARST.) on the growth and development processes in age class I]. *Mater. Sesji Naukowej "Nauka – Doświadczałnictwo – Praktyka Leśna,, Rogów*.
- CEITEL J., SZYMAŃSKI S., ZIENTARSKI J. 1989. Zmiany cech drzewostanowych w naturalnej świerczynie górnoregłowej w rezerwacie "Pilsko" w okresie 10 lat. In: Stav, vyvoj, produkčné schopnosti a funkčné využívanie lesov v oblasti Babieĥ Hory a Pilska. *Zwolen. pp.*: 10–27.
- CEITEL J., SZYMAŃSKI S., ZIENTARSKI J. 1992, 1993, 1994. Zmiany w budowie i strukturze górnoregłowego boru świerkowego w rezerwacie Pilsko 1–3. *Roczn. AR Poznań* 241: 3–15; *ibidem* 255: 23–33; *ibidem* 263: 49–57.
- CELIŃSKI F., WOJTERSKI T. 1961. Mapa zbiorowisk roślinnych Babiogórskiego Parku Narodowego. *Kom. Biol. PTPN, Poznań*.
- CELIŃSKI F., WOJTERSKI T. 1978. Zespoły leśne masywu Babiej Góry. *Kom. Biol. PTPN* 48: 1–62.
- CHALLINOR D. 1968. Alteration of surface soil characteristics by four tree species. *Ecology* 49 (2): 286–290.
- CHALOT M., BRUN A. 1998. Physiology of organic nitrogen aquisition by mycorrhizal fungi and ectomycorrhizas. *FEMS Microbiol. Rev.* 22:21–44.
- CHALOT M., JAVELLE A., BLAUDEZ D., LAMBILLIOTE R., COOKE R., SENTENAC H., WIPF D., BOTTON B. 2002. An update on nutrient transport process in ectomycorrhizas. *Plant and Soil* 244: 165–175.
- CHALUPA V. 1987. Somatic embryogenesis and plant regeneration in *Picea*, *Quercus*, *Betula*, *Tilia*, *Robinia*, *Fagus* and *Aesculus*. *Comm. Inst. Forest. Czech.* 15: 133–148.
- CHALUPKA W. 1972. Obrządzanie szyszek w roku 1971 a wiek drzew i drzewostanów świerka *Picea abies* (L.) KARST. *Sylwan* 116 (4): 73–77.
- CHALUPKA W. 1975b. Badania nad obfitością kwitnienia świerka pospolitego (*Picea abies* (L.) KARST.) w zależności od warunków siedliskowych. *Ph.D. thesis, Kórnik*.
- CHALUPKA W. 1975a. Wpływ czynników klimatycznych na urodzaj szyszek u świerka pospolitego (*Picea abies* (L.) KARST.) w Polsce. *Arbor. Kórnickie* 20: 213–225.

- CHALUPKA W. 1976. Effect of mineral fertilization on the content of reproductive organs in the litter dropped by a Norway spruce (*Picea abies* (L.) KARST.) canopy. Arbor. Kórnickie 21: 333–359.
- CHALUPKA W. 1979. Effect of growth regulators on flowering of Norway spruce (*Picea abies* (L.) KARST.) grafts. Silvae Genet. 28 (4): 125–127.
- CHALUPKA W. 1981. Influence of growth regulators and polythene covers on flowering of Scots pine and Norway spruce grafts. Silvae Genet. 30 (4–5): 142–146.
- CHALUPKA W. 1985. Regulacja kwitnienia na plantacjach nasiennych sosny zwyczajnej (*Pinus sylvestris* L.) i świerka pospolitego (*Picea abies* (L.) KARST.). Instytut Dendrologii PAN, Kórnik: pp.146.
- CHALUPKA W. 1988. Kwitnienie i zamieranie szczepów na modelowej plantacji nasiennej świerka pospolitego (*Picea abies* (L.) KARST.) w Kórniku. Arbor. Kórnickie 23: 127–157.
- CHALUPKA W. 1997. Carry-over effect of gibberellins (GA_{4/7}) and ringing on female flowering in Norway spruce (*Picea abies* (L.) KARST.) seedlings. Ann. Sci. For. 54: 237–241.
- CHALUPKA W., CECICH R. A. 1997. Control of the first flowering in forest trees. Scand. J. For. Res. 12: 102–111.
- CHALUPKA W., GIERTYCH M. 1973. Seed years in *Picea abies* (L.) KARST. Arbor. Kórnickie 18: 183–186.
- CHALUPKA W., GIERTYCH M. 1977. The effect of polythene covers on the flowering of Norway spruce (*Picea abies* (L.) KARST.) grafts. Arbor. Kórnickie 22: 185–192.
- CHALUPKA W., GIERTYCH M. 1979. Możliwości wykorzystania światłowodów w badaniu fizjologii rozwoju pąków roślin drzewiastych. Materiały II Krajowego Sympozjum “Światłowodowy i ich zastosowania”, Jabłonna, 13–15 luty 1979: 109–111.
- CHALUPKA W., GIERTYCH M., KOPCEWICZ J. 1982. Effect of polythene covers, a flower inducing treatment, on the content of endogenous gibberellins-like substances in grafts of Norway spruce. Physiol. Plant. 54: 79–82.
- CHALUPKA W., GIERTYCH M., KRÓLIKOWSKI Z. 1975a. The effect of growth on cone crops in Norway spruce (*Picea abies* (L.) KARST.). Arbor. Kórnickie 20: 193–200.
- CHALUPKA W., GIERTYCH M., KRÓLIKOWSKI Z. 1975b. The effect of cone crops on growth in Norway spruce (*Picea abies* (L.) KARST.). Arbor. Kórnickie 20: 201–212.
- CHALUPKA W., GIERTYCH M., KRÓLIKOWSKI Z. 1977. Relation between specific gravity of wood in Norway spruce (*Picea abies* (L.) KARST.), some growth parameters and cone yield. Arbor. Kórnickie 22: 205–212.
- CHALUPKA W., ROŻKOWSKI R. 1995. Kwitnienie i zamieranie szczepów świerkowych (*Picea abies* (L.) KARST.) w 1993 roku na modelowej plantacji nasiennej w Kórniku. Arbor. Kórnickie 40: 107–115.
- CHANTRE G., GOUMA R. 1994. Influence du genotype, de l'age et de la station sur relation entre l'infradensité du bois et la vigueur chez l'épicéa commun (*Picea abies* KARTS.). Ann.Rech. Sylvic., AFOCEL 1993/94: 61–89.
- CHAPIN F. S. 1991. Integrated response of plants to stress. BioScience 41 (1): 29–36.
- CHELIAK W. M., PITEL J. A. 1985. Inheritance and linkage of allozymes in *Larix laricina*. Silvae Genet. 34: 142–148.
- CHEN H. J., BOLLMARK M., ELIASSON. L. 1996. Evidence that cytokinin controls bud size and branch form in Norway spruce. Physiol. Plant. 98: 612–618.
- CHEN Y. M., WELLBURN A. R. 1989. Enhanced ethylene emission from red and Norway spruce exposed to acid mist. Plant Physiol. 91: 357–361.
- CHENG W. C., FU L. K., CHENHG C. Y. 1975. Species Novae in Gymnospermae sinicae. Acta Phytotax. Sin. 13 (4): 56–90.
- CHLEPKO V., TOMKOVÁ E. 1990. Výskum autovegetatívneho množenia smreka obyčajného (*Picea abies* (L.) KARST.) pre imisné oblasti. Lesnictví 36 (7): 541–551.
- CHMELÍKOVÁ E., CUDLÍN P. 1990. Stimulace zakořeňování řízku smrku ztepilého (*Picea abies* (L.) KARST.) pomocí ektomykorhizních hub. Lesnictví 36 (12): 985–992.
- CHOPIK V. I. 1976. Visokogirna flora Ukrain'skikh Karpat. Naukova Dumka, Kiyev, 267 pp.
- CHRISTERSSON L. 1985. Frost damage during the growing season. Plant Production In The North – Proceedings From “Plant Adaptation ...”: 191–198.

- CHRISTERSSON L., FIRCKS H. 1990. Frost and winter desiccation as stress factors. *Aquilo*, Ser. Bot. 29: 13–19.
- CHRISTIANSEN H. 1972. On the development of pollen and fertilization mechanism of *Picea abies* (L.) KARST. *Silvae Genet.* 21: 51–61.
- CHROUST L. 1980. Erziehung von Fichtenbeständen in durch Schnee und Wind gefährdeten Lagen. *Schrift. Forstl. Fakultät Univer. Göttingen Niedersächsischen Forstl. Versuchsanstalt.* 67: 206–213.
- CHYLARECKI H., GIERTYCH M. 1969. Variability of *Picea abies* (L.) KARST. cones in Poland. *Arbor. Kórnickie* 14: 39–71.
- CHZHAN SHI-TSYUI 1969. Vavivoranie chisla semyaddei i vskhodov eli v svyazi s ee geograficheskim proiskhozhdeniem i formovym raznoobraziem. *Lesoved.* (2): 79–81.
- ĚIŽKOVA R. 1988. Srovnání anatomických znaků asimilačních orgánů vybraných jehličnanů. *Lesnictví* 34 (11): 961–972.
- CLAIR J. B. ST., KLEINSCHMIT J., SVOLBA J. 1985. Juvenility and serial vegetative propagation of Norway spruce clones (*Picea abies* KARST.). *Silvae Genet.* 34 (1): 42–48.
- CLEGG M. T. 1980. Measuring plant mating systems. *Bioscience* 30: 814–818.
- CLEMENSSON-LINDELL A., ASP H. 1995. Fine root morphology and uptake of ^{32}P and ^{35}S in a Norway spruce (*Picea abies* [L.] KARST.) stand subjected to various nutrient and water supplies. *Plant and Soil* 173 (1): 147–155.
- CLEMENT A. 1977. Comparison between the mineral nutrition of *Pinus nigra nigricans* and *Picea excelsa* in very calcareous, calcareous and non-calcareous soils; effects of mineral and organic anions on metabolism. *Ann. Sci. For.* 34 (4): 293–309. [FA. 39, 1858]
- CLINE M. L., FRANCE R. C., REID C. P. P. 1987. Intraspecific and interspecific growth variation of ectomycorrhizal fungi at different temperatures. *Can. J. Bot.* 65: 869–875.
- COLLEAU C. 1968. Anatomie comparée des feuilles de *Picea*. *La cellule* 67 (2): 185–253.
- CONKLE M. T. 1981. Isozyme variation and linkage in six conifer species. *Proc. Symposium Isozymes of North American Forest Trees and Forest Insects.* Berkeley: 11–17.
- COODE M. J. E., CULLEN J. 1965. *Picea* DIETR. W: DAVIS P. H. (ed.): *Flora of Turkey*, 1: 70–71. Edinburgh.
- COOLEY D. R., MANNING W. J. 1987. The impact of ozone on assimilate partitioning in plants: A review. *Environ. Poll.* 47: 95–113.
- CORNIC G., JARVIS P. G. 1972. Effects of oxygen on CO_2 exchange and stomatal resistance in sitka spruce and maize at low irradiances. *Photosynthetica* 6: 225–238.
- CORRIVEAU A., BEAULIEU J., DAOUST G. 1989. Phenotypic stability and productivity of Central European Norway spruce provenances in Quebec, Canada. *Inst. Forest Improvement, Uppsala.* Rep. 11 “Norway spruce; provenances, breeding and genetic conservation” Ed. STEINER L.-G., WERNER M.: 28–51.
- COUTTS M. P., NICOLL B. C. 1990. Waterlogging tolerance of Sitka spruce clones and of strands from *Thelephora terrestris* mycorrhizas. *Can. J. For. Res.* 20 (12): 1894–1899.
- CROMACK K. JR., TODD R. L., MONK C. D. 1975. Patterns of basidiomycete nutrient accumulation in conifer and deciduous forest litter. *Soil Biol. Biochem.* 7: 265–268.
- CUMMING J. R., ECKERT R. T., EVANS L. S. 1985. Effect of aluminum on ^{32}P uptake and translocation by red spruce seedlings. *Can. J. For. Res.* 16 (4): 864–867.
- CUTLER D. F., RUDALL P. J., GASSON P. E., GALE R. M. O. 1987. Root identification manual of trees and shrubs. Chapman and Hall, London.
- CZAJA A. T. 1962. Über das Problem der Zementstaubwirkung auf Pflanzen. *Staub* 22: 228–232.
- CZECH I. 1993. Zmienność proveniencyjna i rodowa świerka pospolitego (*Picea abies* (L.) KARST.) z Beskidu Śląskiego i Żywieckiego na powierzchni doświadczalnej w Kórniku. *MSc. Thesis, Wydział Biologii, UMK Toruń* pp.: 1–117.
- CZERWIŃSKI A. 1966. Les forêts d'épicéas des marécages du voïvodat de Białystok. *Bull. Soc. Amis Sci. Lettr., Poznań, Ser. D* 7: 15–36.
- CZERWIŃSKI A. 1967. The variation and development of stands within the association *Peucedano-Pinetum typicum* in Augustów and Knyszyn Forests. *Ekol. Pol., Ser. A* 15 (32): 617–640.

- CZERWIŃSKI A. 1973. Lasy dębowo-świerkowe Działu Północnego. In: CZECZUGA B. (ed.) Przyroda Białostockizny i jej ochrona. Prace Białostockiego Tow. Nauk. 19: 135–203.
- CZERWIŃSKI A. 1974. Lasy dębowo-świerkowe Działu Północnego. In: CZECZUGA B. (ed.) Przyroda Białostockizny i jej ochrona. Prace Białostockiego Tow. Nauk. 19: 135–203.
- CZERWIŃSKI A. 1977. Świerczyny niżowe północno-wschodniej Polski. In: BIAŁOBOK S. (ed.) Świerk pospolity, *Picea abies* (L.) KARST. Nasze drzewa leśne. PWN, Warszawa-Poznań. 5: 372–404.
- CZERWIŃSKI A. 1978. Zbiorowiska leśne północno-wschodniej Polski. Zesz. Nauk. Polit. Białostockiej 27: 1–326.
- CZERWIŃSKI A. 1983. Bory i lasy mieszane bagienne w Mazursko-Podlaskiej Krainie Przyrodniczo-Leśnej. Sylwan 127 (3): 19–30.
- CZERWIŃSKI A. 1995. Geobotanika w ochronie Środowiska lasów Podlasia i Mazur. Wyd. Politechniki Białostockiej, Białystok. 345 pp.
- DAHLBERG A. 1991. Ectomycorrhiza in coniferous forest: structure and dynamics of populations and communities. Ph.D. thesis, Department of Forest Mycology and Pathology, Swedish University of Agricultural Sciences, Uppsala, Sweden.
- DAHLBERG A., JONSSON L., NYLUND J.-E., 1997. Species diversity and distribution of biomass above and belowground among ectomycorrhizal fungi in an old Norway spruce forest in south Sweden. Can. J. Bot. 75: 1323–1335.
- DAKEV T. 1969. V'rchu rasteža na sm'rkovi fidanki ot različna nadmorska visočina otgleždani v razsadnici s različna nadmorska visočina. Gorskostopanska Nauka 6 (3): 19–25.
- DANIELEWICZ W., PAWLACZYK P. 1998. Rola świerka w strukturze i funkcjonowaniu fitocenoz. In: BORATYŃSKI A., BUGAŁA W. (eds.). Biologia świerka pospolitego. Bogucki Wyd. Nauk., Poznań. pp.: 359–426.
- DANIELSON R. M., PRUDEN M. 1989. The ectomycorrhizal status of urban spruce. Mycologia 81: 335–341.
- DANILOV D. N. 1953. Vliyanie plodonosheniya na strukturu godichnogo sloya u eli (*Picea excelsa* LINK.). Bot. Zh. 38 (3): 367–377.
- DANUSEVICIUS J. 1993. Growth peculiarities of Norway spruce provenances and families in Lithuania. Norway spruce provenances and breeding. Proc. of IUFRO (S2.2–11). Symposium, Riga, Latvia: 38–43.
- DARVILL A. G., ALBERSHEIM P. 1984. Phytoalexins and their elicitors – A defense against microbial infection in plants. Ann. Rev. Plant Physiol. 35: 243–275.
- DÄSSLER, H.-G., RANFT H., REHN K.-H. 1972. Zur Widerstandsfähigkeit von Gehölzen gegenüber Fluorbindungen und Schwefeldioxid. Flora 161: 289–302.
- DAVISON A. W., BARNES J. B., RENNER C. J. 1988. Interactions between air pollutants and cold stress. In: SCHULTE-HOSTEDE S., DARRALL N. M., BLANK L. W., WELLBURN A. R. (eds.). Air pollution and plant metabolism. International Symposium on Air Pollution and Plant Metabolism (2nd; 1987; Munich, Germany). Elsevier Applied Sci. London and New York. pp.: 307–328.
- DAY W. R., PEACE T. R. 1946. Spring frosts with special reference to frosts of May 1935. For. Comm. Bull. 18. [FA. 8, 2073.]
- DÉBAZAC E. F. 1965. Morphogénèse et sexualité chez les Pinacées. Bull. Acad. Soc. Lorraines Sci. 5 (4): 212–228.
- DÉBAZAC E. F. 1977. Manuel des Conifères. Imprimerie Louis-Jean GAP. Nancy, 172 pp.
- DEKKER-ROBERTSON D. L., KLEINSCHMIT J. 1991. Serial Propagation in Norway Spruce (*Picea abies* (L.) KARST.): Results from Later Propagation cycles. Silvae Genet. 40 (5/6): 202–214.
- DEMIDENKO V. P., ALEKSEEV Yu. B., URUSOV V. M. 1984. Geografičeskie kul'tury sosny i eli na jуге zapadnoj Sibiri. Les. Khoz. (3): 40–42.
- DENGLER A. 1913. Die Wälder des Harzes einst und jetzt. Ztschr. Forst- Jagdw. 3.
- DENGLER A. 1943. Waldbau auf ökologischer Grundlage. Berlin.
- DENNIS J. J. 1985. Effect of pH and temperature in *in vitro* growth of ectomycorrhizal fungi. Information Report BC-X-273 Pacific Forestry Centre, Canadian Forestry Service. pp.: 1–19.
- DEUBER C. G., FARRAR J. L. 1940. Vegetative propagation of Norway spruce. J. For. 38: 578–585.
- DICKSON R. E. 1989. Carbon allocation in trees. Ann. Sci. For. 46: 631–647.

- DIECKERT H. 1964. Einige Untersuchungen zur selbststerilität und Inzucht bei Fichte und Lärche. *Silvae Genet.* 13: 77–86.
- DIETRICH A. 1824. *Flora der Gegend um Berlin*, 2. Berlin.
- DIETRICHSON J. 1961. Breeding for frost resistance. *Silvae Genet.* 10: 172–179.
- DIETRICHSON J. 1963. Some results from an anatomic investigation of Norway spruce provenances in four international spruce tests of 1938 in Sweden and Norway. (FAO/FORGEN 63) – 1: 3/7.
- DIETRICHSON J. 1964. Proveniensproblemat belyst ved studier av vekstrytme og klima. *Medd. Norsk. Inst. Skosforsk.* 19 (5), 71: 499–656.
- DIETRICHSON J. 1967a. Klimaskader, vekstrytme og høydeutvikling. Resultater fra et 12 år gammelt granproveniensforsøk på Rødser i Åremark. *Medd. Norsk. Inst. Skosforsk.* 88 (21): 141–158.
- DIETRICHSON J. 1967b. Broad sense heritability estimates of growth rhythm and height growth of Norway spruce (*Picea abies* (L.) KARST.), seedlings of southern Norwegian origin. *Medd. Norsk. Inst. Skosforsk.* 239 (85): 201–221.
- DIETRICHSON J. 1969a. The geographic variation of spring frost resistance and growth cessation in Norway spruce (*Picea abies* (L.) KARST.). *Medd. Norsk. Inst. Skosforsk.* 96, 27 (1): 91–106.
- DIETRICHSON J. 1969b. Growth rhythm and yield as related to provenance progeny and environment. 2nd World Consult. on For. Tree Breeding, FO – FTB – 69 (2/3): 1–15.
- DIETRICHSON J. 1979. Norway spruce provenance trials in Nordic countries. Proc. IUFRO Joint Meet. WPs Norway spruce provenances and breeding. Bucharest: 3–14.
- DIETRICHSON J. 1986. Genetic variation and fitness: the key to successful breeding at high latitudes. Provenances and Forest Tree Breeding for High Latitudes. Proc. “Frans Kempe” Symposium. Umeå, Sweden, Report 6: 11–20.
- DIETRICHSON J. 1989. Norway spruce (*Picea abies* L. Karst.) seed production in orchards. Experiences from Norway. Proc. IUFRO WP S2.02.–11. Mtg. on Norway Spruce Provenances, Breeding and Genetic Conservation, Sweden 1988. Eds. L.G. Stener and M. Werner, Inst. för Skogsförbättring, Uppsala, Rap. 11: 167–188.
- DIETRICHSON J. 1993. Climatic change and Norway spruce breeding. Norway spruce provenances and breeding. Proc. of IUFRO (S2.2–11). Symposium, Riga, Latvia: 157–170.
- DIETRICHSON J., KIERULF C. 1982. Selection of eight-year-old Norway spruce (*Picea abies* (L.) KARST.) plants in a progeny trial and mass production by cuttings. *Medd. Norsk. Inst. Skosforsk.* 38 (1): 1–28.
- DIETRICHSON J., ROGNERUD P. A., HAVERAEN O., SKRØPPA T. 1985. Stem cracks in Norway spruce (*Picea abies* (L.) KARST.). *Medd. Norsk. Inst. Skosforsk.* 38 (21): 1–32.
- DIETRICHSON J., TUTTUREN R. 1978. Meget got frøproduksjon 6–10 år etter podning. *Norsk. Skogbruk* 24 (6–7): 21–24. [FA. 40, 1254]
- DIGHTON J., JANSEN A. E. 1991. Atmospheric pollutants and ectomycorrhizae: more questions than answers? *Environ. Poll.* 73: 179–204.
- DIMITRI L., FRÖHLICH H. J. 1971. Einige Frage zur Resistenzforschung bei der durch *Fomes annosus* (FR.) Cooke verursachten Rotfäule der Fichte. *Silvae Genet.* 20 (6): 184–191.
- DOGRA P. D. 1970. Gymnosperm embryology in India. *Plant Sci.* 2: 1–16.
- DOHMEN G. P., KÖPPERS A., LANGEBARTELS C. 1990. Biochemical responses of Norway spruce (*Picea abies* (L.) KARST.) towards 14-month exposure to ozone and acid mist: Effects on amino acid, glutathione and polyamine titers. *Environ. Poll.* 64: 375–383.
- DOHRENBUSCH A., JAEHNE S. 1998. Die Variation der Elementkonzentrationen in einem Fichtenaltbestand. *Forstarchiv* 69 (5): 199–208.
- DOLGOSHOV V. 1958. Nekotorye osobennosti plodonosheniya eli obyknovennoi. *Les. Khoz.* 11 (10): 77–78.
- DOLUKHANOV A. G., SKHIRELI V. S. 1959. *Picea* Dietrich. In: GULISASHVILI V. Z. (ed.) *Dendroflora Kavkaza*, vol. 1: 85–115. Tbilisi.
- DOMINIK J., STARZYK J. 1989. *Owady niszczące drewno*. Wyd. 2. PWRiL, Warszawa. 524 pp.
- DOMINIK T. 1961. Studium nad mikotrofizmem świerka pospolitego – *Picea excelsa* (LAM.) LK. w Polsce. *Prace IBL, Warszawa* 209: 59–102.

- DORMLING I. 1963. Anatomical and histological examinations of the union of scion and stock in grafts of Scots pine (*Pinus silvestris* L.) and Norway spruce (*Picea abies* (L.) KARST.) Stud. Forest. Suec. 13: 1–136.
- DORMLING I. 1970. Studies on flower production in connection with topophysis test in *Picea abies* (L.) KARST. Proc. IUFRO Mtg. on Sexual Reproduction of Forest Trees. Varparanta, Finland: I/5.
- DORMLING I. 1973. Photoperiodic control of growth cessation in Norway spruce seedlings. Proc. IUFRO Symp. Dormancy in Trees, Kórnik: 1–16.
- DORMLING I. 1976. Studier over kritisk nattlängd för knoppsättningen hos gran. Breeding Norway spruce. Proc. Conf. In Bogenesund, January 1976: P 3–4.
- DORMLING I. 1977. Critical night length for bud-set in *Picea abies* L. KARST. Influence of light intensity and temperature. Experimental Genecology, Dept of Forest Genetics, Sweden, Res. Not. 27: 18–25.
- DORMLING I. 1979. Influence of light intensity and temperature on photoperiodic response of Norway spruce provenances. Proc. IUFRO Joint Meet. WPs Norway spruce provenances and breeding. Bucharest: 398–408.
- DORMLING I., ERICSSON R., PERSSON S. 1977. Vegetativ förökning. Forskningsverksamheten 1977. Dept. of Forest Genetics, Swedish University of Agricultural Sciences, Res. Not. 26: 37–40.
- DORMLING I., GUSTAFSSON A., WETTSTEIN D. VON. 1968. The experimental control of the life cycle in *Picea abies* (L.) KARST. I. Some basic experiments on the vegetative cycle. Silvae Genet. 17 (2–3): 44–64.
- DORMLING I., KELLERSTAM H. 1981. Rooting and rejuvenation in propagating old Norway spruce by cuttings. Proc. Symposium on clonal forestry, Uppsala, Sweden, April 8–9, 1981: 65–72.
- DOSTAL J. 1989. Nová Květena ČSSR, 1. Československá akademie věd. Praha, 87 pp.
- DRAXLER G., RUPPERT W. 1989. Anatomische Studien an geschädigten Fichtennadeln aus dem Höhenprofil 'Zillertal'. Phytion-Horn. 29 (3): 133–145.
- DREYER E., FICHTER J., BONNEAU M. 1994. Nutrient content and photosynthesis of young yellowing Norway spruce trees (*Picea abies* L. KARST.) following calcium and magnesium fertilisation. Plant and Soil 160 (1): 67–78.
- DRIESSCHE R., van den LANGEBAEELS C. 1994. Foliar symptoms ethylene biosynthesis and water use of young Norway spruce (*Picea abies* (L.) KARST.) exposed to drought and ozone. Water, Air, Soil Poll. 78: 153–168.
- DULLINGER S., DIRNBÖCK T., GRABHERR G. 2003. Patterns of shrub invasion into high mountain grasslands of the Northern calcareous Alps, Austria. Arctic, Antarctic Alpine Res. 35 (4): 434–441.
- DULLINGER S., DIRNBÖCK T., GRABHERR G. 2004. Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. J. Ecol. 92: 241–252.
- DUNBERG A. 1973. Gibberellin-like substances from Norway spruce (*Picea abies*). Physiol. Plant. 28: 358–360.
- DUNBERG A. 1974. Occurrence of gibberellin-like substances in Norway spruce (*Picea abies* (L.) KARST.) and their possible relation to growth and flowering. Stud. Forest. Suec. 111: 62.
- DUNBERG A. 1976. Changes in gibberellin-like substances and indole-3-acetic acid in *Picea abies* during the period of shoot elongation. Physiol. Plant. 38: 186–190.
- DUNBERG A. 1979. Flower induction in Norway spruce. Proc. of the IUFRO Mtg. Working Party on Norway Spruce Provenances and Norway Spruce Breeding. Lower Saxony Forest Research Institute, Escherode, Federal Republic of Germany: 139–157.
- DUNBERG A. 1980. Stimulation of flowering in *Picea abies* by gibberellins. Silvae Genet. 29 (2): 51–53.
- DUNBERG A., MALMBERG G., SASSA T., PHARIS R. P. 1983. Metabolism of tritiated gibberellins A₄ and A₅ in Norway spruce, *Picea abies* (L.) KARST. Effects of a cultural treatment known to enhance flowering. Plant Physiol. 71: 257–262.
- DÜNISCH O., BAUCH J. 1994. Influence of mineral elements on wood formation of old growth spruce (*Picea abies* [L.] KARST.). Holzforschung 48 (Suppl.).
- DURSIN A. 1976. Geograficheske posadki eli obyknovennoj. Les. Khoz. (6): 38–39.

- DUTKIEWICZ W. 1968. Variation in seed weight in relation to boundaries of two ranges of Norway Spruce in Poland. In: TYSZKIEWICZ S (ed). Population studies of Norway Spruce in Poland. pp. 45–52. Instytut Badawczy Lesnictwa, Warszawa.
- DUTKIEWICZ W. 1979. Response to shading conditions in two progenies of Norway spruce from Białowieża Forest. Proc. IUFRO Joint Meet. WPs Norway spruce provenances and breeding. Bucharest: 409–416.
- DYAKOWSKA J. 1959. Podręcznik palynologii. Wyd. Geolog., Warszawa.
- DYAKOWSKA J. 1964. The variability of the pollen grains of *Picea excelsa* Link. Acta Soc. Bot. Pol. 33 (4): 729–748.
- DYESIUS M., JONSSON B. G. 1991. Dating uprooted trees: comparison and application of eight methods in a boreal forest. Can. J. For. Res. 21: 655–665.
- DZIUBATOWSKI S. 1928. Etude phytosociologique du Massif de S-te Croix. I. Les forêts de la partie centrale de la chaîne principale et des montagnes “Stawiana” et “Miejska”. Acta Soc. Bot. Pol. 5 (5): 1–43.
- DZWONKO Z. 1986. Klasyfikacja numeryczna zbiorowisk polskich Karpat. Fragn. Flor. Geobot. 30 (2): 93–167.
- EBEL B., ROSENKRANZ J., SCHIFFENS A., LUTZ C. 1990. Cytological observations on spruce needles after prolonged treatment with ozone and acid mist. In: BLANCK L. W., LUTZ C. (eds.). Tree exposure experiment in closed chambers. Environ. Poll. 64 (3–4): 323–335.
- EDWARDS M. V. 1955. Norway spruce provenance experiments. Rep. For. Comm., London 1953/54: 114–126.
- EFIMOV Y. 1993. Seed crop of Norway spruce in seed orchards of the central forest-steppe of Russia. Proc. IUFRO Symp. on Norway Spruce Provenances and Breeding. Riga (Latvia) 1993: 254–258.
- EFIMOV Y. P. ISAKOV Y. N., MASHKINA O. S., SHEVERNOZHUK A. M., SHIRNIN V. K., SHOUTIAYEV A. M. 2000. Genetics and Breeding of Forest Trees. In: TEISSIER DU CROSS E. (ed.). Proceeding of the First Brain Storming Meeting, INRA, Orléans, France. Janvier 2000. 49–51.
- EGLI S., AMIET R., ZOLLINGER M., SCHNEIDER B. 1993. Characterization of *Picea abies* ectomycorrhizas: discrepancy between classification according to macroscopic versus microscopic features. Trees 7: 123–129.
- EGLI S., KÄLIN I. 1991. The root window – a technique for observing mycorrhizae on living trees. Agric. Ecosyst. Environ. 28: 107–110.
- EICHRODT R. 1969. Über die Bedeutung von Moderholz für die natürliche Verjüngung im subalpinen Fichtenwald. Diss. Nr. 4261, Böhleer Buchdruck, Zürich. 123 pp.
- EIFLER I. 1955. Künstliche Polyloide = Erzeugung bei *Picea abies* und *Betula verrucosa*. Z. Forstgenetik 4: 162–166.
- EIKELAND H., BLINGSMO K. R. 1991. Produksjon hos ulike granprovenienser i fire forsøk i Ringsaker, Hedmark. Rap. Norsk Institutt Skogsforsk. 1. 1–28. [FA. 54, 1607.]
- EK H., ANDERSSON S., ARNEBRANT K., SÖDERSTRÖM B. 1994. Growth and assimilation of NH_4^+ and NO_3^- by *Paxillus involutus* in association with *Betula pendula* and *Picea abies* as affected by substrate pH. New Phytol. 128: 629–637.
- EKBERG I., ERIKSSON G., DORMLING I. 1979. Photoperiodic reactions in conifer species. Holarctic Ecol., Copenhagen 2: 255–263.
- EKLUND B. 1954. Variation in the widths of the annual rings in pine and spruce due to climatic conditions in northern Sweden during the years 1900–1944. Medd. Statens Skogsforskningsinstitut 44 (8).
- EKLUND B. 1957. The annual ring variations in spruce in the centre of northern Sweden and their relation to the climatic conditions. Medd. Statens Skogsforskningsinstitut 47 (1).
- EKLUND L. 1993. Movement and possible metabolism of ethylene in dormant *Picea abies*. Plant Growth Reg. 12: 37–41.
- EKLUND L., CIENCIALA E., HILGREN J. E. 1992. No relation between drought stress and ethylene production in Norway spruce. Physiol. Plant. 86: 297–300.
- EKLUND L., SÄLL H., LINDER S. 2003. Enhanced growth and ethylene increase spiral grain formation in *Picea abies* and *Abies balsamea* trees. Trees 17: 81–86. 72

- EKLUND L., TILTU A. 1999. Cambial activity in normal spruce *Picea abies* (L.) KARST. and snake spruce *Picea abies* (L.) KARST. f. *virgata* (JACQ.) REHD. in response to ethylene. J. Exp. Bot. 50: 1489–1493.
- EL FARES L. 1974. Contribution à l'étude des mycorhizes de l'*Epicea*. Méthodes expérimentales et influence des sols et des litières. Ph.D. thesis, Nancy.
- ELDHUSET T., GORANSSON A., INGESTAD T. 1987. Aluminium toxicity in forest tree seedlings. In: HUTCHINSON T. C., MEEMA K. M. (red.) Effects of atmospheric pollutants on forest, wetlands, and agricultural ecosystems. Springer – Verlag, New York. pp.: 401–409.
- ELERŠEK L., JERMAN I. 1988. Pomen selekcije in vegetativnega razmnoževanja pri vzgoji hitrorastočih smrek. Zbornik Gozdarstva i Lesarstva 31: 27–37. [FA. 54, 542.]
- ELIASON E.J., CARLSON D. E. 1968. Variability of flower and cone production in Norway spruce. Proc. 11th Mtg Comm. For. Tree Breeding in Canada, Part 2: 273–280.
- ELLENBERG H. 1978. Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht. Verlag Eugen Ulmer, Stuttgart.
- ELSTNER E. F., OSWALD W. 1984. Fichtensterben in "Reinluftgebieten": Strukturreisistenzverlust. Naturw. Rundschau 37: 52–61.
- ELTROP L., MARSCHNER H. 1996. Growth and mineral nutrition of non-mycorrhizal and mycorrhizal Norway spruce (*Picea abies*) seedlings grown in semi-hydroponic sand culture. New Phytol. 133: 469–478.
- ENDLER J. A. 1977. Geographic variation speciation and clines. Princeton University Press, New Jersey. 246 pp.
- ENDLER Z. 1979. Analiza geobotaniczna borów Wzniesień Piłackich. Fragm. Flor. Geobot. 25 (4): 509–562.
- ENDLER Z. 1987. Charakterystyka i stanowisko systematyczne zbiorowisk świerkowych Mazur Garbanych. Acta Acad. Agricult. Tech., Olsztyn 44 suppl. B: 3–84.
- ENDLER Z. 1991. Charakterystyka fitosocjologiczna zespołów świerkowych Puszczy Boreckiej. Fragm. Flor. Geobot. 35 (1/2): 295–303.
- ENESCU V., CONTESCU L., NEAMȚU 1979. Testarea îri faza de pepinieră a valorii genetice a unor populatii de molid rezervatiî de seminte. Ministerul Economiei Forestiere se Materialelor de Constructii. Institutul de Cercetari si amenajari silvice. Seria a II-a: 1–37.
- ENESCU V., DURAN V., COJOCARU I., VARGA D. 1973. Cercetări privind stimularea fructificăpiei în rezervapiile de seminþe. I. Molid (*Picea abies* (L.) KARST.). Inst. cercetări proiectări si documentare silvică. Buletin de informare 8: 107–114.
- ENGELMARK O. 1987. Fire history correlations to forest type and topography in northern Sweden. Ann. Bot. Fenn. 24: 317–324.
- ENGELMARK O. 1993. Early post-fire tree regeneration in a *Picea-Vaccinium* forest in northern Sweden. J. Veg. Sci. 4: 791–794.
- EREMIN V. M. 1977. Osobennosti anatomicheskogo stroenya kory razlichnykh form *Picea excelsa* LINK. Lesn. Zh. 1977 (5): 510.
- EREMIN V. M. 1982. Osobennosti anatomicheskogo stroenija nekotorykh sosnowykh v sviazi s uslovijami proizrastaniya. Lesn. Zh. 3: 14–19.
- ERIKSSON G., ANDERSSON S., SCHELANDER B. 1975. Lovande tillväxt hos introducerade granprovenienser on kombinerad klon-och fröplantsplantage in norra Uppland. Sveriges Skog. Förb. Tidskr. 73 (3): 277–286.
- ERIKSSON G., EKBERG I., DORMLING I., MATÉRN B. 1978. Inheritance of bud-set and bud-flushing in *Picea abies* (L.) KARST. Theor. Appl. Genet. 52: 3–19.
- ERIKSSON G., EKBERG I., JONSSON A. 1970. Meiotic investigations in pollen mother cells of Norway spruce cultivated in a plastic green house. Hereditas 66: 1–20.
- ERIKSSON G., JONSSON A., LINDGREN D. 1973. Flowering in a clone trial of *Picea abies* Karst. Stud. For. Suec. 110.
- ERIKSSON G., LINDGREN D. 1975. Några genetiska reflexioner kraing plantsortering. Sveriges Skog. Förb. Tidskr. 2: 615–621.
- ERIKSSON G., SCHELANDER B., ÅKEBRAND V. 1973. Inbreeding depression in an old experimental plantation of *Picea abies*. Hereditas 73 (2): 185–194.

- ERIKSSON H. M., BERDEN M., ROSEN K., NILSSON S. I. 1996. Nutrient distribution in a Norway spruce stand after long-term application of ammonium nitrate and superphosphate. *Water, Air, and Soil Poll.* 92 (3–4): 451–467.
- ERLAND S., JONSSON L., MAHMOOD T., FINLAY R. 1999. Below-ground ectomycorrhizal community structure in two *Picea abies* forests in southern Sweden. *Scand. J. For. Res.* 14: 209–217.
- ERLAND S., TAYLOR A. F. F. 2002. Diversity of ecto-mycorrhizal fungal communities in relation to the abiotic environment. In: VAN DER HEIJDEN M. G. A., SANDERS I. (eds.). *Mycorrhizal Ecology*, pp. 163–199, Springer, Berlin-Heidelberg.
- ERNST W. 1976. Physiological and biochemical aspects of metal tolerance. W: T. A. MANSFIELD (red.), *Effects of Air Pollutants on Plants*, Cambridge University Press, New York.
- ESAU K. 1969. The phloem. *Handb. der Pflanzenanatomie* 5, 2. Gebrüder Borntraeger, Berlin.
- ESAU K. 1977. *Anatomy of seed plants*. J. Wiley & Sons, New York/Santa Barbara.
- ESCH A., MENGEL K. 1998. Combined effects of acid mist and frost drought on the water status of young spruce trees (*Picea abies*). *Environ. Exp. Bot.* 39: 57–65.
- ESCHRICH W., BLECHSCHMIDT-SCHNEIDER S. 1992. Extrinsic and intrinsic influences on tree growth anatomical analysis of spruce branches. *Trees* 6: 179–185.
- ETVERK I. 1970. Geograafilise päritolu mõjust kuuseokaste morfoloogiale. *Metsandusl. uurivuused* 8, Tallin, "Valgus": 5–8.
- ETVERK I., HAINLA V. 1972. Emapunde mõjust hariliku kuuse istikute Kasvule. *Metsanduslikud Uurimused IX Tallin*: 14–46.
- EVERS F. H. 1963. Die Wirkung von Ammonium- und Nitratstickstoff auf Wachstum und Mineralstoffhaushalt von *Picea* und *Populus*. *Ztschr. Bot.*, Stuttgart 51 (1): 61–79.
- EVERS F. H. 1967a. Die Kennzeichnung der Ernährungssituation von Waldbeständen durch kohlenstoffbezogene Nährelementwerte (C/N, C/P, C/K und C/Ca). *Proc. 14th Congr. IUFRO*, Munich 1967 Pt. IV, Sec. 23: 171–187.
- EVERS F. H. 1967b. Zur Frage der Zusammenhänge zwischen Standort, Bestandestyp, Wachstum und Nährstoffverhältnissen des Bodens. *Proc. 14th Congr. IUFRO*, Munich 1967 Pt. II, Sect. 21: 187–193.
- EVERS F. H. 1967c. Carbon/Nutrient ratios (C/N, C/P, C/K, C/Ca) as indicators of the nutrient status of forest soils. *Mitt. Ver. Forstl. Standortskunde Forstpflzücht.* No. 17: 69–76. [FA. 29, 1760]
- EVERS F. H. 1972. Die Ernährungskundliche Auswertung der Standortskartierung in Baden-Württemberg. *Allg. Forst- Jagdztg.* 143 (1): 6–12.
- EVERS F. H. 1983. Ein Versuch zur Aluminium – Toxizität bei Fichte-Ergebnisse eines Gefasskulturversuchs mit bewurzelten Fichtenstecklingen. *Forst. Holzwirt.* 38: 305–313.
- EWALD D., PUTENIKHIN V., MATSCHKE J. 1991. Mikropropfung adulter Koniferen. *Allg. Forstztg.* 17: 878–880.
- EWALD D., SCHACHLER G. 1990. Bessere Bewurzelung bei der Stecklingsvermehrung adulter Fichtenklone. *Allg. Forst-Ztschr.* (37–38): 961–963.
- FABIAN P. 1991. Klima und Wald – Perspektiven für die Zukunft. *Forstw. Cbl.* 110: 286–304.
- FABIANOWSKI J., JAWORSKI A., MUSIEL W. 1974. Wykorzystanie niektórych cech morfologicznych jodły (*Abies alba* MILL.) i świerka (*Picea excelsa* LINK.) dla oceny potrzeb świetlnych i jakości podrostów. *Acta Agr. Silv.* 22.
- FABISZEWSKI J. 1968. Porosty Śnieżnika Kłodzkiego i Gór Bialskich. *Monogr. Bot.* 26: 1–116.
- FACKLER U., HUBER W., HOCK B. 1986a. Einfluss von Mineralstoffernahrung, Ozon und saurem Nebel auf Indolessigsäure und Abscisinsäure in Nadeln von *Picea abies* (L.) KARST. *Forstw. Cbl.* 105: 254–259.
- FACKLER U., REICH J., HOCK B. 1986b. Auxin distribution in spruce needles. *J. Plant Physiol.* 126: 163–172.
- FALIŃSKI J. B. 1976. Windwürfe als Faktor der Differenzierung und der Vernderung des Urwaldbiotopes im Licht der Forschungen auf Dauerflächen. *Phytocoenosis* 5 (2): 85–108.
- FALIŃSKI J. B. 1977. Research on vegetation and plant population dynamics conducted by Białowieża Geobotanical Station of the Warsaw University in the Białowieża Forest and in the environ (1952–1977). *Phytocoenosis* 6(1–2): 1–132.

- FALIŃSKI J. B. 1978. Uprooted trees, their distribution and influence in the primeval forest biotope. *Vegetatio* 38 (3): 175–183.
- FALIŃSKI J. B. 1986. Vegetation dynamics in temperate lowland primeval forests. Dr Junk, Dordrecht. 572 pp.
- FALIŃSKI J. B. 1988. Succession, regeneration and fluctuation in the Białowieża Forest (NE Poland). *Vegetatio* 77: 115–128.
- FAN S., BLAKE T. J. 1994. Absciscic acid induced electrolyte leakage in woody species with contrasting ecological requirements. *Physiol. Plant.* 90: 414–419.
- FANTA J. 1974. Morphologische Variabilität der Fichte und Grundzüge der genetischen Rekonstruktion der Gebirgsfichtenwälder im Krkonoše Nationalspark (ČSSR). *Arch. Naturschutz u. Landschaftsforsch.* 3: 179–200.
- FARJON A. 1990. Pinaceae: Drawings and description of the genera *Abies*, *Cedrus*, *Pseudolarix*, *Keteleeria*, *Nothotsuga*, *Tsuga*, *Cathaya*, *Pseudotsuga*, *Larix* and *Picea*. Koelz Sci. Books, Königsstein, Germany.
- FARJON A. 2001. World checklist and bibliography of Conifers, ed. 2. The Royal Botanic Gardens, Kew. 309 pp.
- FARRIS M. A., MITTON J. B. 1984. Population density, outcrossing rate, and heterozygote superiority in ponderosa pine. *Evolution* 38: 1151–1154.
- FAULKNER R., FLETCHER A. M., LONGMAN K. A., JOHNSTONE R. C. B. 1970. Forest Genetics. Rep. For. Comm., London 1969/70: 106–113.
- FEGER K. H., RASPE S., SCHMID M., ZÖTTL H. W. 1991. Verteilung der Elementvorräte in einem schlechtwüchsigen 100jährigen Fichtenbestand auf Buntsandstein. *Forstw. Cbl.* 110 (4): 248–262.
- FEHLEN N., PICARD J. F. 1994. Influence de la fertilisation sur la végétation spontanée et la croissance radiale de l'épicéa commun (*Picea abies* [L.] KARST.) dans une plantation adulte des Ardennes françaises. *Ann Sci For* 51 (6): 569–580.
- FEIL W., KOTTKE I., OBERWINKLER F. 1988. The effect of drought on mycorrhizal production and very fine root system development of Norway spruce under natural and experimental conditions. *Plant and Soil* 108: 221–231.
- FEILER S. 1985. Einflüsse von Schwefeldioxid auf die Membranpermeabilität und Folgen für die Frostempfindlichkeit der Fichte (*Picea abies* (L.) KARST.). *Flora* 177: 217–226.
- FEILER S., TESCHE M., MICHAEL G., RANFT H., BELLMANN C. 1989. Physiologische Reaktionen der Fichte (*Picea abies*) auf komplexen SO₂- und Trockenstress. Teil 3. Reaktionen Schwefeldioxid-belasteter Fichten auf nachfolgende Trockenheit. *Eur. J. For. Path.* 19: 414–422.
- FELIKSIK E. 1972. Studia dendroklimatologiczne nad świerkiem (*Picea excelsa* L.). Część I. Badania nad świerkiem z Lasu Gąsienicowego w Tatrach. *Acta Agr. Silv., Ser. Silv.* 12: 39–70.
- FELLNER R. 1989. Mycorrhiza-forming fungi as bioindicators of air pollution. *Agric. Ecosyst. Environ.* 28: 115–120.
- FENAROLI L., GAMBI G. 1976. Alberi. Museo Tridentino di Science Naturali, Trento. 717 pp.
- FENGEL D. 1971. Chemical and electron microscopic study of a fossil Spruce wood. *Holz. Roh Werkstoff* 29 (8): 305–314.
- FENGEL D., WEGENER G. 1989. Wood, Chemistry, Ultrastructure, Reactions. Gruyter, Berlin – New York.
- FERLUGA R., POLDINI L. 1978. Indagine floristica delle Dolomiti Pesarine. *Boll. Soc. Adriatica Sci.* 62: 1–95.
- FERRIER R. C., ALEXANDER I. J. 1985. Persistence under field conditions of excised fine roots and mycorrhizas of spruce. In: FITTER A. H. (ed.). *Ecological Interactions in Soil*. Special Publications, British Ecological Society, Blackwell Scientific Publications, Oxford. pp.: 175–179.
- FIEDLER H. J. 1975. Abhängigkeit des Ernährungszustandes der Baumart Fichte von Boden und Klima. *Beitr. Forstwirtschaft* 9 (3): 118–122.
- FIEDLER H. J. 1979. Relationships between soil types, forest stand and edaphon in ecosystems of spruce forests. In: KLIMO Ě. (ed.) *Stability of spruce forest ecosystems*, sponsored by the Czechoslovak MAB nat. comm. and the 1st Division of IUFRO, 12 mon, 81/863.

- FIEDLER H. J., HÖHNE H. 1987. Ratios of the basic nutrients in Norway spruce needles and their dependence on biological factors. *Beitr. Forstwirtschaft* 21 (1): 17–21. [FA. 51, 2833]
- FIEDLER H. J., HUNGER W., PALME K. 1965. Über den Ernährungszustand optimalwüchsiger älterer Fichten auf terrestrischen Böden unterschiedlicher Trophie. *Arch. Forstw.* 14 (9): 987–1001.
- FIEDLER H. J., ILGEN G., GETAHUN G. B. A. 1990. Pot experiments on the zinc nutrition of spruce seedlings in relation to the new kind of forest decline. *Fertilizer Res.* 26 (1–3): 237–242.
- FIEDLER H. J., KATZSCHNER W. 1990. Verlauf des Ernährungszustandes junger ungedüngter und gedüngter Koniferenbestände des Tharandter Waldes. *Beitr. Forstwirtschaft* 24 (1): 26–31.
- FIEDLER H. J., NEBE W. 1963. Über die Beurteilung der Düngebedürftigkeit von Mittelgebirgsstandorten durch Bodenanalysen. *Arch. Forstw.* 12 (9): 963–991.
- FIEDLER H. J., NEBE W., HOFFMANN F. 1973. *Forstliche Pflanzenernährung und Düngung*. Gustav Fischer Verlag, Jena.
- FIEDLER H. J., NEBE W., HOFMANN W., KRÜGER P., DREGER K., RÖLLIG H. 1981. Beziehungen zwischen Standort und Fichtenwachstum im ostseennahen Bereich. *Arch. Acker- Pflanzenbau Bodenkd.* 25 (4): 245–255.
- FIEDLER H. J., NEBE W., LEHMANN E., ZEHLER H. 1977. Untersuchungen zur Höhe und jahresweisen Verteilung von Kalkammonsalpetergaben bei der Düngung älterer Fichtenbestände. *Beitr. Forstwirtschaft* 11 (3): 144–146.
- FIND. J. I. 1997. Changes in endogenous ABA levels in developing somatic embryos of Norway spruce (*Picea abies* (L.) KARST.) in relation to maturation medium, desiccation and germination. *Plant Sci.* 128: 75–83.
- FINÉR L. 1989. Biomass and nutrient cycle in fertilized and unfertilized pine, mixed birch and pine and spruce stands on a drained mire. *Acta For. Fenn.* 208: 1–63.
- FINK S. 1983. Histologische und histochemische Untersuchungen an Nadeln erkrankter Tannen und Fichten im Südschwarzwald. *Allg. Forstztg.* 38: 660–663.
- FINK S. 1989. Pathological anatomy of conifer needles subjected to gaseous air pollutants or mineral deficiencies. *Aquilo, Ser. Bot.* 27: 1–6.
- FINK S. 1991. Structural changes in conifer needles due to Mg and K deficiency. *Fertilizer Res.* 27 (1): 23–27. [FA. 52, 7900].
- FINKELDEY R. 1995. Homogeneity of pollen allele frequencies of single seed trees in *Picea abies* (L.) KARST. *Heredity* 74: 451–463.
- FINLAY R. D., FROSTEGARD A., SONNERFELDT A. N. 1992. Utilization of organic and inorganic nitrogen sources by ectomycorrhizal fungi in pure culture and in symbiosis with *Pinus contorta* DOUGL EX LOUD. *New Phytol.* 120: 105–116.
- FISCHBACH R. J., ZIMMER I., STEINBRECHER R., PFICHNER A., SCHNITZLER J. P. 2000. Monoterpene synthase activities in leaves of *Picea abies* (L.) KARST. and *Quercus ilex* L. *Phytochem.* 54: 257–265.
- FISCHER A. 1992. Long term vegetation development in Baranian mountain forest ecosystems following natural destruction. *Vegetatio* 103: 93–104.
- FISCHER A., ABS G., LENZ F. 1990. Natürliche Entwicklung von Waldbeständen nach Windwurf. Ansätze einer „Urwaldforschung“ in der Bundesrepublik. *Forstw. Cbl.* 109: 309–326.
- FISCHER F. 1949. Ergebnisse von Anbauversuchen mit verschiedenen Fichtenherkünften (*Picea abies* (L.) KARST.). *Mitt. Schw. Anst. Forstl. Versuchsw.* 26 (1): 155–200. [FA. 13, 219]
- FITSCHEN J. 1930. *Handbuch der Nadelholzkunde*. Paul Parey, Berlin.
- FLINN B. S., ROBERTS D. R., NEWTON C. H., CYR D. R., WEBSTER F. B., TAYLOR I. E. P. 1993. Storage protein gene expression in zygotic and somatic embryos of interior spruce. *Physiol. Plant.* 89: 719–730.
- FOBER H. 1974. Wpływ poziomu potasu, magnezu i wapnia w pożywce na cechy wzrostowe i rozwojowe oraz na zawartość składników mineralnych w siewkach świerka pospolitego (*Picea abies* (L.) KARST.). *Arbor. Kórnickie* 19: 135–179.
- FOBER H. 1976. Distribution of mineral elements within the crown of Scots pine (*Pinus silvestris* L.) and Norway spruce (*Picea abies* (L.) KARST.). *Arbor. Kórnickie* 21: 323–331.
- FOBER H. 1977. Concentration of mineral elements in Norway spruce (*Picea abies* (L.) KARST.) wood. *Arbor. Kórnickie* 22: 213–218.

- FOBER H. 1978. Wpływ poziomu związków toksycznych w pożywce mineralnej na cechy wzrostowe i rozwojowe siewek świerka pospolitego (*Picea abies* (L.) KARST.). Materiały z sympozjum nt.: "Reakcje biologiczne drzew na emisje przemysłowe." Kórnik: 6–7.
- FOBER H. 1979. Tolerance differences between polish Norway spruce (*Picea abies* (L.) KARST.) provenances in susceptibility to soil pollution. Proc. IUFRO Meeting on Norway Spruce Provenances and Norway Spruce Breeding. Bucharest: 417–422.
- FOBER H. 1986. Genetic differences in the level of macroelements in spruce (*Picea abies* [L.] KARST.) needles of several clones. Arbor. Kórnickie 31: 195–204.
- FOBER H. 1990. Wpływ zróżnicowanego poziomu fosforu w pożywce mineralnej na wzrost siewek świerka pospolitego (*Picea abies* (L.) KARST.) różnych rodów i proveniencji. Arbor. Kórnickie 35: 105–118.
- FOBER H. 2004. Genetic reactivity of Norway spruce (*Picea abies* (L.) KARST. to soil fertility. Dendrobiology 51, suppl.: 57–63.
- FOBER H., GIERTYCH M. 1968. Zróżnicowanie siewek świerka polskich proveniencji w zależności od stężenia azotu w pożywce i stopnia konkurencji z trawą. Arbor. Kórnickie 13: 217–260.
- FOBER H., GIERTYCH M. 1970a. Phosphorus uptake by Spruce (*Picea abies* (L.) KARST.) seedlings of various provenance. Arbor. Kórnickie 15: 99–115.
- FOBER H., GIERTYCH M. 1970b. The uptake of ^{32}P by spruce seedlings (*Picea abies* (L.) KARST.) growing in competition with grass. Acta Soc. Bot. Pol. 39 (1): 115–121.
- FOBER H., GIERTYCH M. 1971. Variation among Norway spruce of Polish provenances in seedling growth and mineral requirements. Arbor. Kórnickie 16: 107–120.
- FOGAL W. H., JOBIN G., SCHOOLEY H. O., COLEMAN S. J., WOLYNETZ M. S. 1996. Stem incorporation of gibberellins to promote sexual development of white spruce, Norway spruce and jack pine. Can. J. For. Res. 26: 186–195.
- FORNES R. H., BERGLUND J. V., LEAF A. L. 1970. A comparison of the growth and nutrition of *Picea abies* (L.) KARST. and *Pinus resinosa* AIT. on a K-deficient site subjected to K fertilization. Plant and Soil 33 (2): 345–360.
- FORSCHNER W., SCHMITT V., WILD A. 1989. Investigations on the starch content and ultrastructure of spruce needles relative to the occurrence of novel forest decline. Bot. Acta 102 (3): 208–221.
- FORSS K. 1968. Fichtenlignin. Holzforschung 22 (3): 66–68.
- FOSTER G. S., LAMBETH C. C., GREENWOOD M. S. 1987. Growth of loblolly pine rooted cuttings compared with seedlings. Can. J. For. Res. 17: 157–164.
- FOTTLAND H., SKRØPPA T. 1989. The IUFRO 1964–68 provenance experiment with Norway spruce (*Picea abies*) in Norway. Variation in mortality and height growth. Medd. Norsk. Inst. Skosforsk. 43 (1): 1–30.
- FOURRE J.-L. 1992. Mise en évidence d'un chromosome supernuméraire chez un plant de *Picea abies* (L.) KARST. produit par embryogenèse somatique. Mass production technology for genetically improved fast growing forest tree species. Actes AFOCEL/IUFRO Symposium, Bordeaux: 485–487.
- FOWELLS H. A. 1965. Silvics of Forest Trees of the United States. Agricul. Handb. Washington. 271 pp.
- FOWLER D. P. 1979. Norway spruce provenance experiments in North America. Proc. IUFRO Joint Meet. WPs Norway spruce provenances and breeding. Bucharest: 28–40.
- FRANCO J. AMARAL 1964. *Picea* A. DIETR. W. TUTIN T. G. i in. (red.). Flora Europaea 1: 31. Cambridge University Press, Cambridge.
- FRANK A. B. 1885. Über die auf Wurzelsymbiose beruhenden Ernährung gewisser Bäume durch unterirdische Pilze. Ber. Dtsch. Bot. Ges. 3: 128–145.
- FRANK A. B. 1894. Die Bedeutung der Mykorrhiza-pilze für die gemeine Kiefer. Forstw. Cbl. 16: 185–190.
- FRANSSON P. M. A., TAYLOR A. F. S., FINLAY R. D. 2000. Effects of continuous optimal fertilization on belowground ectomycorrhizal community structure in a Norway spruce forest. Tree Physiol. 20: 599–606.
- FRANSSON P. M. A., TAYLOR A. F. S., FINLAY R. D. 2001. Elevated atmospheric CO_2 alters root symbiont community structure in forest trees. New Phytol. 152: 431–442.

- FRANZ F. 1983. Auswirkungen der Waldkrankheiten auf Struktur und Wuchsleistung von Fichtenbeständen. Forstw. Cbl. 102: 186–200.
- FREER-SMITH P. H., DOBSON M. C. 1989. Ozone flux to *Picea sitchensis* (BONG) CARR. and *Picea abies* (L.) KARST. during short episodes and the effects on these on transpiration and photosynthesis. Environ. Poll. 59: 161–176.
- FREIJ J. 1986. [Criteria of when to collect spruce cuttings in the autumn – direct rooting or storage]. Institutionen för skogsskötsel, Sveriges Lantbruksuniversitet, Umeå.
- FRIEND R. B., WILFORD B. H. 1933. The spruce gall aphid as a forest pest. J. For. 31: 355–368.
- FRITZE H., NIINI S., MIKKOLA K., MÄKINEN A. 1989. Soil microbial effects of a Cu-Ni smelter in southwestern Finland. Biol. Fertil. Soils 8: 87–94.
- FRÖHLICH H. J. 1960. Untersuchung über Benadelungsverhältnisse verschiedener Fichten Provenienzen. Abstr. in Silvae Genet. 9 (5): 138.
- FRÖHLICH H. J. 1961. Untersuchungen über das physiologische und morphologische Verhalten von Vegetativvermehrungen verschiedener Laub- und Nadelbaumarten. Allg. Forst- Jagdztg. 132: 39–58.
- FRÖHLICH H. J. 1966. Sonderherkünfte und Forstpflanzenzüchtung dargestellt am Beispiel der Fichte. Mitt. Hess Landesforstverwaltung 4: 36–56.
- FRÖHLICH H.-J. 1988. Bodenschutz und Forstwirtschaft. Allg. Forst-Ztschr. 43: 1162–1163.
- FROSTERGÅRD A., TUNLID A., BÄÄTH E. 1993. Phospholipid fatty acid composition, biomass and activity of microbial communities from two soil types experimentally exposed to different heavy metals. Appl. Environ. Microbiol. 59: 3605–3617.
- FRÜHWALD A., BAUCH J., GÖTTSCHE-KÜHN H. 1984. Über die Holzeigenschaften von Fichten aus Waldschadensgebieten. Teil 1: Untersuchungen an frisch gefälltem Holz. Holz Roh Werkst. 42: 441–449.
- FÜHRER G., PAYER H. D., PFLANZ H. 1993. Effects of air pollutants on the photosynthetic capacity of young Norway spruce trees. Response of single needle age classes during and after different treatments with O₃, SO₂, or NO₂. Trees 8: 85–92.
- FUKAREK P. 1981. Ein Beitrag über ergebnisse der vegetationskartierung von Bosnien-Herzegovina. Angewandte Pflanzensoziol. 26: 51–57.
- GADD G. M. 1993. Interactions of fungi with toxic metals. New Phytol. 124: 25–60.
- GADD G. M., DE ROME L. 1988. Biosorption of cooper by fungal melanin. Appl. Microbiol. Biotechnol. 29: 610–617.
- GABRILAVICHYUS R. B. 1972. Karyological investigation of *Picea abies* in Lithuania. Lesoved. 2: 76–78.
- GAGOV V. 2000. Genetics and Breeding of Forest Trees. In: TEISSIER DU CROSS E. (ed.). Proceeding of the First Brain Storming Meeting, INRA, Orléans, France. Janvier 2000. 15–16.
- GAILIS A. 1993. Norway spruce provenances in Latvia. Norway Spruce Provenances and Breeding. Proc. of IUFRO (S2.2–11). Symposium, Riga, Latvia: 44–49.
- GALEWSKI W., KORZENIOWSKI A. 1958. Atlas najważniejszych gatunków drewna. PWRiL, Warszawa. pp.: 25–29.
- GALSTON A. W., KAUR-SAWHNEY R. 1987. Polyamines as endogenous growth regulators. In: DAVIES P. J. (ed.) Plant Hormones and their Role in Plant Growth and Development.: 280–295. Martinus Nijhoff Publishers, Dordrecht.
- GANCHEV P., CVETKOVA P. 1977. Radiochuvstvitelnostlia na sm'rca (*Picea excelsa* LINK.) s proizhd ot razlichna nadmorska visochina. Gorskostopanska Nauka. 14 (3): 19–26.
- GARBAYE J. 2000. The role of ectomycorrhizal symbiosis in the resistance of forests to water stress. Outlook Agricult. 29: 63–69.
- GARDES M., BRUNS T. 1996. Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: above- and below-ground view. Can. J. Bot. 74: 1572–1583.
- GÄRTNER E. 1975. Untersuchungen zur Beurteilung der Jungendentwicklung vom Fichtenprovenienzen. Tag der mündlichen Prüfung 11: 1–133.
- GÄRTNER E. J. 1980. Beiträge zur Beurteilung der Jungendentwicklung von Fichtenprovenienzen. Mitt. Hess. Landesforstverwaltung 15: 1–114.

- GAŚIENICA-BYRCYN W., KOT M. 1987. Przyziemna cyrkulacja powietrza a żywotność drzew powyżej górnej granicy lasu w dolinie Kasprowej w Tatrach. Parki Narod. Rez. Przyr. 8 (1): 55–64.
- GATHY P. 1957. Recherches Belges sur la variabilité génétique des espèces forestières. *Silvae Genetica* 6: 32–38.
- GATHY P. 1960a. L'origine des graines d'épicéa commun (*Picea abies*) KARST.). Resultats en Belgique. Stat. Rech. Eaux Forêts, Groenendaal – Hoeilaart, Belg. Trav. Ser. B 24.
- GATHY P. 1960b. L'expérience internationale sur l'origine des graines d'épicéa (*Picea abies* KARST.). Resultats en Belgique. Stat. Rech. Eaux Forêts, Groenendaal-Hoeilaart, Belg. Trav. Ser. B 24.
- GÄUMANN E. 1964. Die Pilze. Birkhauser Verlag, Basel und Stuttgart.
- GÄUMANN E., ROTH C., ANLIKIER J. 1934. Über die Biologie der *Herpotrichia nigra*. Ztschr. Pflanzenkr. Pflanzenschutz. 44: 99–116.
- GAUSSEN H. 1966. Les Gymnospermes actuelles et fossiles. Fasc. VIII. Toulouse.
- GEBUREK T. 1998. Genetic variation of Norway spruce (*Picea abies* (L.) KARST.) populations in Austria I. Digenic disequilibrium and microspatial patterns derived from allozymes. *For. Genet.* 5 (4): 221–230.
- GEBUREK T. 1999. Genetic variation of Norway spruce (*Picea abies* (L.) KARST.) populations in Austria. III. Macrospace patterns of high elevation populations. *For. Genet.* 6: 201–211.
- GEBUREK T., SCHOLZ F. 1992. Response of *Picea abies* (L.) KARST. provenances to sulphur dioxide and aluminum: a pilot study. *Water, Air, and Soil Poll.* 62 (3–4): 227–232. [FA. 54, 7741]
- GEBUREK T., VON WUEHLISCH G. 1989. Linkage analysis of isozyme gene loci in *Picea abies* (L.) KARST. *Heredity* 62: 185–191.
- GEHRHARDT E. 1924. Stammzahlenhaltung in jungen Fichtenbeständen. *Allg. Forst- u. Jgdtz.*
- GEMMEL P., ÖRLANDER G., HÖGBERG K. A. 1991. Norway Spruce Cuttings Perform Better than Seedlings of the Same Genetic Origin. *Silvae Genet.* 40 (5/6): 198–202.
- GENYS J. B. 1969. Intraspecific variation among 200 strains of two-year-old Norway spruce. *Proc. 16th NE For. Tree. Improv. Conf. Quebec* 1968: 61.
- GENYS J. B. 1979. Intraspecific variation in Norway spruce (*Picea abies*) from 74 different seed sources studied in Maryland. First North Central Tree Improvement Conference, Madison, Wisc.: 33–43.
- GEORGE E., STOBER C., SEITH B. 1999. The use of different soil nitrogen sources by young Norway spruce plants. *Trees* 13 (4): 199–205.
- GERARD et al. 2001.
- GHELMEZIU N., BELDIE I. P. 1970. The characteristics of resonance wood of *Picea abies*. *Bull. Inst. Politehnic, Braşov, Ser. B* 12: 315–325.
- GIA T. D. 1927. Beitrag zur Kenntnis der Schattenfestigkeit verschiedener Holzarten im 1. Lebensjahre. *Forstw. Cbl.* (1927): 386–397, 425–435, 468–482.
- GIANNINI R. 1990. Effects of pollution on the genetic structure of forest tree populations. *Proc. of the Meet. Rome, April 3.* 1990. Consiglio Nazionale Ricerche: 95.
- GIANNINI R., MORGANTE M., VENDRAMIN G. G. 1991. Allozyme variation in Italian populations of *Picea abies* (L.) KARST. *Silvae Genet.* 40: 160–166.
- GIERTYCH M. 1969. Heritability of some growth parameters in spruce (*Picea abies* (L.) KARST.) *Genet. Polonica* 10: 138–140.
- GIERTYCH M. 1970. Doświadczenie proveniencyjne nad świerkiem pospolitym (*Picea abies* (L.) KARST.) założone w roku 1969. *Arbor. Kórnickie* 15: 263–276.
- GIERTYCH M. 1972. Provenance differences in the time of spruce (*Picea abies* (L.) KARST.) flushing in Poland. *Arbor. Kórnickie* 17: 169–183.
- GIERTYCH M. 1973. Przyczynek do dyskusji o zasięgach i pochodzeniu świerka w Polsce. *Sylvan* 117 (10): 14–25.
- GIERTYCH M. 1976a. Summary results of the IUFRO 1938 Norway spruce (*Picea abies* (L.) KARST.) provenance experiment. Height growth. *Silvae Genet.* 25 (5–6): 154–164.
- GIERTYCH M. 1976b. Zmienność genetyczna polskich ras świerka (*Picea abies* (L.) KARST.). *Arbor. Kórnickie* 21: 189–211.
- GIERTYCH M. 1976c. Sexual expression in Pines in relation to their ontogenetic development. *Acta Hort.* 56: 99–104.

- GIERTYCH M. 1977. Genetyka [Genetics]. In: BIAŁOBOK S. (ed.). Świerk pospolity *Picea abies* (L.) KARST. PWN, Warszawa – Poznań. Nasze drzewa leśne 5: 287–331.
- GIERTYCH M. 1979. Norway spruce (*Picea abies* (L.) KARST.) provenance experiments in Eastern Europe. Proc. IUFRO Joint Meet. WPs Norway spruce provenances and breeding. Bucharest: 15–28.
- GIERTYCH M. 1984. Report on the IUFRO 1938 and 1939 provenance experiments on Norway spruce (*Picea abies* (L.) KARST.). ID PAN Kórnik: 1–179.
- GIERTYCH M. 1988. Produktivność różnych polskich proveniencji świerka (*Picea abies* (L.) KARST.) w zależności od lokalizacji i wieku drzew. Arbor. Kórnickie 33: 171–179.
- GIERTYCH M. 1989. Effect of age and environment on the results of Norway spruce (*Picea abies* (L.) KARST.) provenance experiments. Inst. Forest Improvement. Uppsala, Rep. 11 “Norway spruce provenances, breeding and genetic conservation”. Red. L-G. Steiner, M. Werner: 66–73.
- GIERTYCH M. 1992. Dziedziczenie cytoplazmatyczne cechy wyróżniającej *Picea abies* f. *deflexa* TYSZK. Sylwan 136 (3): 43–48.
- GIERTYCH M. 1993. Breeding Norway spruce in Poland: From provenance tests to seed orchards. Norway spruce provenances and breeding. Proc. of IUFRO (S2.2–11). Symposium, Riga, Latvia: 193–199.
- GIERTYCH M. 1996. Effects of thinnings on the evaluations of provenance experiments as exemplified by a Norway spruce (*Picea abies* (L.) KARST.) trial. Forest genetics and tree breeding: perspectives and challenges. IUFRO World Series 6: 93–101.
- GIERTYCH M. 1997. Przemieszczanie polskich populacji świerka (*Picea abies* (L.) KARST.) a ich wartość hodowlana. Sylwan 141 (4): 59–67.
- GIERTYCH M. 1998. Zmienność proveniencyjna i dziedziczenie. In: BORATYŃSKI A., BUGAŁA W. (eds). Biologia świerka pospolitego. Bogucki Wydawnictwo Naukowe. pp. 213–255.
- GIERTYCH M., KRUPSKI P. 1996. Analiza produktywności polskich proveniencji świerka pospolitego (*Picea abies* (L.) KARST.) na czterech krajowych powierzchniach doświadczalnych. Arbor. Kórnickie 41: 59–74.
- GIERTYCH M., PRZYBYLSKI T. 1965. Badania nad metodami szczepienia sosny i świerka. Arbor. Kórnickie 10: 184–192.
- GIESECKE T., BENNETT K. D. 2004. The Holocene spread of *Picea abies* (L.) KARST. in Fennoscandia and adjacent areas. J. Biogeogr. 31 (9): 1523–1548.
- GIROUARD R. M. 1974. Propagation of spruce by stem cuttings. N. Z. J. For. Sci. 4 (2): 140–149.
- GIROUARD R. M. 1975. Seasonal rooting response of Norway spruce stem cuttings. The Plant Propag. 21: 9–10.
- GLADUNOV I. M. 1966. Ritmichnost' pogloshcheniya kaliya i natriya kornyami prorostkov khvojnykh. Termodinamika zhivyykh sistem. Trudy LTA, 104: 65–73.
- GLATZEL G. 1970. Ein Versuch zur Frage der Mineralstoffernährung von Fichte auf Kalk-Rendzina Böden. Cbl. Ges. Forstw. 87 (3): 127–144.
- GLATZEL G. 1971. Mineral nutrition of Spruce plantations at high altitudes. Cbl. Ges. Forstw. 88 (4): 195–223.
- GLATZEL G. 1985. Heavy metal damage to forests in the vicinity of a smelter in Brixlegy, Austrian Tyrol. Part 2. Growth and mineral nutrition of Norway spruce (*Picea abies*) on litter polluted with heavy metals. Cbl. Ges. Forstw. 102 (1): 41–51. [FA.46, 4091]
- GLATZEL G., PUXBAUM H. 1983. Untersuchungen der Zusammensetzung von sauren Stammabläufen. VDI-Bericht, Düsseldorf: VDI-Verlag. 500: 187–194.
- GÖBL F. 1986. Effects of simulated acid rain on soils and young Norway spruce plants in a pot experiment. Part 3: Studies on mycorrhizas. Cbl. Ges. Forstw. 103: 89–107.
- GÖBL F., HOLZER K. 1976. Die Beeinflussung der Kulturkammertestung van Fichte durch Applikation von Bodenpilzen. Cbl. Ges. Forstw. 93 (4): 191–204.
- GÖBL F., MUTSCH F. 1985. Heavy metal damage to forests in the vicinity of a smelter in Brixlegg, Austrian Tyrol. Part 1. Studies on mycorrhiza and humus. Cbl. Ges. Forstw. 102: 28–40.
- GODBOLD D. L. 1991. Aluminium decreases root growth and calcium and magnesium uptake in *Picea abies* seedlings. In: WRIGHT R. J., BALIGAR V. C., MURMMANN R. P. (eds.). Plant-soil interactions at low pH. Kluwer, Dordrecht. pp.: 747–753.

- GODBOLD D. L., DICTUS K., HÜTTERMANN A. 1988. Influence of aluminium and nitrate on root growth and mineral nutrition of Norway spruce (*Picea abies*) seedlings. *Can. J. For. Res.* 18 (9): 1167–1171.
- GODBOLD D. L., SCHLEGEL H. I., HÜTTERMANN A. 1985a. Toxicity of heavy metals to spruce seedlings. In: LEKKAS T. D. (ed.) *Heavy Metals in the Environment*, Athens, 1: 500–502.
- GODBOLD D. L., SCHLEGEL H., HÜTTERMANN A. 1985b. Heavy metals – a possible factor in spruce decline. In *Forest dieback: influencing factors and their evaluation. Proceedings of a symposium held at Goslar, W. Germany, 18–20 June, 1985*. VDI Berichte 560: 703–716.
- GODBOLD D. L., TISCHNER R., HÜTTERMANN A. 1987. Effects of heavy metals and aluminium on the root physiology of spruce (*Picea abies* KARST.) seedlings. In: HUTCHINSON T. C., MEEMA K. M. (eds.). *Effects of pollutants of forests, wetlands and agricultural ecosystems*. Springer, Berlin. pp.: 387–400.
- GODZIK S., KNABE W. 1973. Vergleichende elektronenmikroskopische Untersuchungen von Chloroplasten einiger Pinus-Arten aus den Industriegebieten an Ruhr und in Oberschlesien. *Proc. 3rd Int. Clean Air Congr.*, A164–170: 1–7.
- GØHRN V. 1966. Proveniensenforsøg med gran (*Picea abies* (L.) KARST.). *Det. Forst. Forsøgsv. Danmark* 29 (4): 309–437.
- GOŁAWSKI S. 1956. Fizyczne i mechaniczne własności drewna świerkowego jako surowca zastępczego dla sosny lotniczej. *Biul. Inst. Techn. Drewna* 3 (4): 64–80.
- GOLUBETS M. A. 1972. Areal jalini evropejs'koj [(*Picea abies* (L.) KARST.) v Evropi. *Ukr. Bot. Zh.* 29 (4): 439–445.
- GOLUBETS M. A., POLOVNIKOV L. I. 1973. Produktivnist' jalinovich derevostaniv zalezno vid pochodzhenija j sistemachnoy prinalezhnosti jalinii (*Picea abies* (L.) KARST.). *Ukr. Bot. Zh.* 30 (4): 433–438.
- GÖMÖRY D. 1992. Effect of stand origin on the genetic diversity of Norway spruce (*Picea abies* (L.) KARST.) populations. *For. Ecol. Managm.* 54: 215–223.
- GONCHARENKO G. G., PADUTOV V. E., SILIN A. E. 1994. Construction of genetic maps for some Eurasian coniferous species using allozyme genes. *Biochem. Genet.* 32: 223–236.
- GONCHARENKO G. G., ZADEIKA I. V., BIRGELIS J. J. 1995. Genetic structure, diversity and differentiation of Norway spruce (*Picea abies* (L.) KARST.) in natural populations of Latvia. *For. Ecol. Managm.* 72: 31–38.
- GONCHARENKO G., KRIVKO V. G., POTENKO V. V. 1991. Endospermy *Picea abies* kak test-sistema dla opredeleniya tempov mutirovaniya v rajonakh s radioaktivnym zagraznieniem. *Doklady Akademii Nauk BSSR.* 35 (4): 365–369.
- GONET B. 1965. Zagadnienie drewna rezonansowego w Polsce. *Przemysł Drzewny* 11: 401–403.
- GONET B. 1966. Wstępne badania drewna rezonansowego krajowego pochodzenia. *Sylvan* 100 (3): 47–55.
- GOODWIN T. W., MERCER E. I. 1983. *Introduction to plant biochemistry*. Pergamon Press. Oxford. pp.: 18–54.
- GÖRANSSON A., ELDHUSET T. D. 1991. Effects of aluminium on growth and nutrient uptake of small *Picea abies* and *Pinus sylvestris* plants. *Trees* 5: 136–142.
- GORCHAKOVSKIY P. L. 1958. Novoe v metodike issledovaniya dinamiki semenosheniya khvoynykh. *Bot. Zh.* 43 (10): 1445–1459.
- GRABAROVA S., MARTINKOVA M. 2001. Changes in mineral nutrition of Norway spruce (*Picea abies* [L.] KARST.) under the impact of drought. *Ecologia, Bratislava* 20: 46–60.
- GRABOWSKI J., NIWIŃSKI T. 1957. Produkcja celulozy z drewna. WPLiS, Warszawa. pp.: 95–99.
- GRAPINI V. 1967. Spruce producing resonanse wood. *Rev. Padurilor* 82 (7): 343–344.
- GREGORIUS H. R. 1991. Limitations of gene markers as applied to the characterization of plant mating systems. In: *Biochemical Markers in the Population Genetics of Forest Trees*. In: FINESCHI S., MALVOLTI M. E., CANNATA F., HATTEMER H. H. (eds.). *Acad. Publ. The Hague, The Netherlands*. Pp.: 129–142.
- GREGORY R. A. 1971. Cambial activity in Alaskan spruce. *Amer. J. Bot.* 58 (2): 160–171.
- GREGORY R. A., ROMBERGER J. A. 1972. The shoot apical ontogeny of the *Picea abies* seedling. I. Anatomy, apical dome diameter, and plastochron duration. *Amer. J. Bot.* 59 (6): 587–597.

- GREMMEN J. 1972. Our present-day knowledge of Scleroderma canker control. Eur. J. For. Pathol. 2 (1): 40–43.
- GREUTER W. (ed.) 1994. International Code of Botanical Nomenclature (Tokyo Code). Regnum Vegetabile 131: 1–389. Koelz Sci. Books, Königsstein, Germany.
- GRIERSON A. J. C., LONG D. G. 1983. Flora of Bhutan, 1, 1. Royal Bot. Gard. Edinburgh. 186 pp.
- GRILL D. 1973a. Rasterelektronenmikroskopische Untersuchungen an Wachststrukturen der Nadeln von *Picea abies* (L.) KARSTEN. Micron. 4: 146–154.
- GRILL D. 1973b. Rasterelektronenmikroskopische Untersuchungen an Fichtennadel-Spaltöffnungen. Microscop. Acta 75: 136–141.
- GRILL D. 1973c. Rasterelektronenmikroskopische Untersuchungen an SO₂-belasteten Fichtennadeln. Phytopath. Z. 79: 75–80.
- GRILL D., PFEIFHOFFER H., HALBWACHS G., WALTINGER H. 1987. Investigations on epicuticular waxes of differently damaged spruce needles. Eur. J. For. Path. 17: 4–5.
- GRILL D., ZELLNIG G., BERMADINGER-STABENTHEINER E., MÜLLER M. 1992. Strukturelle Veränderungen in Abhängigkeit verschiedener Luftschadstoffe. Forstw. Cbl. 112: 1–11.
- GRIME J. P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, Chichester. 221 pp.
- GRODZKI W. 1997a. Możliwości kontroli liczebności populacji kornika zroszowanego *Ips duplicatus* C.R.Sahlb. na południu Polski. Sylwan 141 (11): 25–36.
- GRODZKI W. 1997b. Parazytoidy, drapieżce i komensale kambiofagów świerka w warunkach zubożenia różnorodności biologicznej ekosystemów leśnych Sudetów. Prace IBL, Warszawa, Ser. A 841: 193–213.
- GRODZKI W. 1997c. *Pityogenes chalcographus* – an indicator of man-made changes in Norway spruce stands. Biologia, Bratislava 52 (2): 217–220.
- GRODZKI W. 1998. Wybrane objawy stresu w świerczynach Sudetów Zachodnich w aspekcie oddziaływania czynników abiotycznych i skutków masowego pojawu wskaźnicy modrzewianeczki *Zeraphera griseana* Hb. (Lepidoptera: Tortricidae). Prace IBL, Warszawa, Ser. A 848: 127–155.
- GRODZKI W. 2003. Zasięg występowania kornika zroszowanego *Ips duplicatus* C.R.Sahlb. (Col.: Scolytidae) w obszarach górskich południowej Polski. Sylwan 147 (8): 29–36.
- GRODZKI W. 2004. Zagrożenie górskich drzewostanach świerkowych w zachodniej części Beskidów ze strony szkodników owadzych. Leśne Prace Badawcze 2: 35–47.
- GRODZKI W., JACHYM M. 2004. Developing a Central European database and map on major forest pests: towards the wider look on forest protection problems. Proceedings from the IUFRO WP 7.03.10 Workshop “Biotic damage in forests”, Matrafured, Hungary, 12–16 September 2004.
- GRODZKI W., JAKUŠ R., GAZDA M. 2003. Patterns of bark beetle occurrence in Norway spruce stands of national parks in Tatra Mts. in Poland and Slovakia. J. Pest Sci. 76 (3): 78–82.
- GRODZKI W., MCMANUS M., KNÍŽEK M., MESHKOVA V., MIHALCIUC V., NOVOTNY J., TURČANI M., SLOBODYAN Y. 2004. Occurrence of spruce bark beetles in forest stands at different levels of air pollution stress. Environ. Poll. 130 (1): 73–83.
- GRONBACH E., AGERER R. 1986. Charakterisierung und Inventur der Fichten-Mykorrhizen in Högwald und deren Reaktion auf saure Beregnung. Forstw. Cbl. 105: 329–335.
- GROB H. 1934. Die Fichte (*Picea excelsa* Lk.) in Ostpreußen. Ztschr. Forst- Jagdw. 65: 421–436.
- GROSSER D. 1986. On the occurrence of trabeculae with special consideration of diseased trees. IAWA Bulletin 7 (4): 319–341.
- GROSSER D., TEETZ 1987. CMA – Centrale Marketinggesellschaft der Deutschen. Agrarwirtschaft m.b.H. Arbeitsgemeinschaft Holz e. V. Düsseldorf.
- GUDERIAN R. 1977. Air pollution. Berlin/Heidelberg/New York: Springer Verlag. pp.: 127.
- GUDERIAN R., KUPPERS K., SIX R. A. D. 1985. Wirkungen von Ozon, Schwefeldioxid und Stickstoffdioxid auf Fichte und Pappel bei unterschiedlicher Versorgung mit Magnesium und Kalzium sowie auf die Blattflechte *Hypogymnia physodes*. In: Forest dieback: influencing factors and their evaluation. Proc. Symposium at Goslar, W. Germany, 18–20 June, 1985. VDI-Berichte 560: 657–701.

- GUDERIAN R., VOGELS K., MASUCH G. 1986. Comparative physiological and histological studies on Norway spruce (*Picea abies* L. KARST.) using climatic chamber experiments and field studies in damaged forest stands. Proc. 7th Int. Clean Air Congr. 1986. Sydney. pp.: 148–57.
- GULDEN G., HOILAND K., BENDIKSEN K., BRANDRUD T. E., FOSS B. S., JENSSEN H. B. 1992. Macromycetes and air pollution: mycocoenological studies in oligotrophic spruce forests in Europe. Bibl. Mycol. 144.
- GUNIA S., ŻYBURA H. 1987. Height of half-sib Norway spruce (*Picea abies* (L.) KARST.) families of Polish lowland and mountain provenances during first years in plantation. Ann. Warsaw Agric. Univ., For. Wood Technol. 36: 79–87.
- GÜNTHARDT M. S., WANNER H. 1982a. Die Menge des cuticulären Wachses auf Nadeln von *Pinus cembra* L. und *Picea abies* (L.) KARSTEN in Abhängigkeit vom Nadelalter und Standort. Flora 172: 125–137.
- GÜNTHARDT M. S., WANNER H. 1982b. Veränderungen der Spaltöffnungen und der Wachsstruktur mit zunehmendem Nadelalter bei *Pinus cembra* L. und *Picea abies* (L.) KARSTEN an der Waldgrenze. Bot. Helvetica 92: 47–60.
- GÜNTHARDT-GEORG M. S., KELLER T. 1987. Some effects of long-term ozone fumigation on Norway spruce. II Epicuticular wax and stomata. Trees 1 (3): 145–150.
- GÜNTHARDT-GOERG M. S., KELLER T., MATYSSEK R., SCHEIDEGGER C. 1994. Environmental effects on Norway spruce needle wax. Eur. J. For. Path. 24 (2): 92–111.
- GÜNZL L. 1969. Ergebnisse aus der Fichten – Provenienz-forschung. Allg. Forstztg. 80 (3): 53–55.
- GÜNZL L. 1979a. Internationale Fichten-Provenienzversuche der IUFRO 1938 und 1964–68 sowie Versuche mit österreichischen Herkunft. Allg. Forstztg. 90 (7): 1–11.
- GÜNZL L. 1979b. International IUFRO Norway spruce provenance experiments of 1938 and 1964–68 and additional Austrian provenance experiments. Proc. IUFRO Joint Meet. WPs Norway spruce provenances and breeding. Bucharest: 51–56.
- GUSEV I. I., JAROSLAVTSEV S. V. 1988. Struktura el'nikov kraynego Severa. Lesn. Zh. 6: 111–113.
- GUSSONE H. A., ZÖTTL H. W. 1975. Die Wirkung jahreszeitlich verschiedener Düngung auf junge Fichten. Forstw. Cbl. 94 (6): 334–343.
- GUZICKA M. 2001. Changes in starch distribution within an embryonic shoot of Norway spruce [*Picea abies* (L.) KARST.] before resumption of mitotic activity. Dendrobiology 46: 27–31.
- GUZICKA M., WOŻNY A. 2003. Mid-winter ultrastructural changes in the vegetative embryonic shoot of Norway spruce [*Picea abies* (L.) KARST.]. Ann. Sci. For. 60: 461–466.
- HAAG C., STOBER F., LICHTENTHALER H. K. 1992. Pigment content, chlorophyll fluorescence and photosynthetic activity of spruce clones under normal and limited mineral nutrition. Photosynthetica 27 (3): 385–400.
- HACKIEWICZ-DUBOWSKA M. 1936. Roślinność gnijących pni puszczy Białowieskiej. Sprawozd. Tow. Nauk. Warsz. Wyd. IV, Nauk Biol. 29 (7–9): 189–222.
- HAEUPLER H., SCHÖNFELDER P. 1989. Atlas der Farn- und Blütenpflanzen der Bundesrepublik Deutschland. Ulmer, Stuttgart. 768 pp.
- HAFNER I. 1986. Zur Feinstruktur der geschädigten Kiefernadel. Allg. Forstztg. 45: 1119–1121.
- HAFSTEN U. 1985. The immigration and spread of spruce (*Picea abies* (L.) KARST.) in Norway, traced by pollen analysis and radiocarbon datings. A. preliminary report. Ecol. Medit. 11: 83–89.
- HÄGGLUND E. 1951. Chemistry of wood. New York.
- HAGMAN M. 1971. Mellaneuropeisk gran i försök på Åland. Skogsbruket 41 (10): 224–227.
- HAGMAN M. 1973. Differences in resistance to voles in provenances of Norway spruce (*Picea abies* (L.) KARST.). Proc. IUFRO WP S2.02.11 Meet., Biri. Norway: 40.
- HAGMAN M. 1979. Experiments with Norway spruce provenances in Finland. Proc. IUFRO Joint Meet. WPs Norway spruce provenances and breeding. Bucharest: 422–434.
- HAGNER S. 1955. Iakttagelser över granens kottproduktion i norrländska höjdlägen kottåret 1954. Norrl. Skogsv. Förb. Tidskr.: 181–206. [FA 17: 319]
- HAGNER S. 1958. On the production of cones and seeds in Swedish coniferous forests. Medd. Statens Skogsforskningsinstitut 47 (8).
- HAGNER S. 1965. Cone crop fluctuations in Scots pine and Norway spruce. Stud. Forest. Suec. 33.

- HAHN G., MARSCHNER H. 1998. Effect of acid irrigation and timing on root growth of Norway spruce. *Plant and Soil* 199 (1): 11–22.
- HAIN P. F. 1987. Interactions of insects, trees and air pollutants. *Tree Physiol.* 3: 93–107.
- HÅKANSSON A. 1956. Seed development of *Picea abies* and *Pinus silvestris*. *Medd. Statens Skogsforskningsinstitut* 46 (2): 1–23.
- HAKMAN I. 1993. Embryology in Norway spruce (*Picea abies*). An analysis of the composition of storage reserves during seed development and somatic embryogenesis. *Physiol. Plant.* 87: 148–159.
- HAKMAN I., STABEL P., ENGSTROM P., ERIKSSON T. 1990. Storage protein accumulation during zygotic and somatic embryo development in *Picea abies* (Norway spruce). *Physiol. Plant.* 80: 441–445.
- HALLINGBÄCK T. 1994. The macrofungi of Sweden. Uppsala: Swedish Threatened Species Unit, Swedish University of Agricultural Sciences. SNV Report 4313.
- HAMPP R., SCHAFER C., WALLEND T., STULTEN C., JOHAN P., EINIG W. 1995. Changes in carbon partitioning or allocation due to ectomycorrhiza formation: biochemical evidence. *Can. J. Bot.* 73, Suppl. 1: 548–556.
- HAMPP R., WIESE J., MIKOLAJEWSKI S., NEHLS U. 1999. Biochemical and molecular aspects of C/N interaction in ectomycorrhizal plants: an update. *Plant and Soil* 215: 103–113.
- HAMRICK J. L., LINHART Y. B., MITTON J. B. 1979. Relationship between life history characteristics and electrophoretically detectable genetics variation in plants. *Ann. Rev. Ecol. Syst.* 10: 173–200.
- HAN Y. C., LEE K. Y., CHOI S. K., SHIM S. Y. 1984. Provenance test in Korea of Norway spruce (*Picea abies* (L.) KARST.) introduced from Romania and West Germany at age of 7 and 8. *Res. Rep. Inst. For. Genet. Korea* 20: 82–89.
- HAN Y. C., LEE K. Y., SHIM S. Y., RYU K. O., CHANG S. O. 1987 Growth performance of 14 provenances of Norway spruce in Korea. *Res. Rep. Inst. For. Genet. Korea* 23: 91–95.
- HANNERZ M. 1994. Predicting the risk of frost occurrence after bud burst of Norway spruce in Sweden. *Silva Fenn.* 28 (4): 243–249.
- HANTGE A. 1992. Eignung der Isozymmuster von Peroxidase, Superoxid-Dismutase und saurer Phosphatase aus Nadeln der Fichte (*Picea abies* (L.) KARST.) zur Indikation von Schadstoffeffluessen. *Forstl. Forschungsber., München.* 118, 177 pp.
- HARAJDA H., POLISZKO S. 1971. *Folia Forest. Polonica*, Ser. B 10: 19–34.
- HARLEY J. L., SMITH S. E. 1983. *Mycorrhizal Symbiosis*. Academic Press, London, New York.
- HARLOW W. M., HARRAR E. S. 1950. *Textbook of Dendrology*, wyd. 3. New York, Toronto-London. 555 pp.
- HARRISON S. G., DALLIMORE E. A. 1966. *Handbook of Coniferae and Ginkgoaceae*. E. Arnold, London.
- HARTIG M. 1986. Praktische Erfahrungen bei der autovegetativen Anzucht von Fichten. *Soz. Forstwirtschaft* 36 (6): 177–181.
- HARTIG R. 1874. *Wichtige Krankheiten der Waldbäume*. Berlin.
- HARTMANN G., NIENHAUS F., BUTIN H. 1988. Barwny atlas uszkodzeń drzew leśnych. *Diagnozowanie chorób drzew*. IBL, Warszawa.
- HARTMUT E. 1976. Descripcion de la vegetacion Montañesa en los Estados Mexicanos de Puebla y Tlaxcala. *Willdenowia* 10: 30–31.
- HASEMANN G., JUNG G., WILD A. 1990. The loss of structural integrity in damaged spruce needles from locations exposed to air pollution. II. Epidermis and stomata (dermal tissue). *J. Phytopath.* 128 (1): 33–45.
- HASEMANN G., WILD A. 1990. The loss of structural integrity in damaged spruce needles from locations exposed to air pollution. I Mesophyll and central cylinder. *J. Phytopath.* 128: 15–32.
- HATTEMER H. H. 1978. Bedeutung der genetischen Vielfalt der Waldbäume für die Forstwirtschaft. *Forstarchiv* 49 (12): 249–256.
- HATTENSCHWILER S., KORNER C. 1998. Biomass allocation and canopy development in spruce model ecosystems under elevated CO₂ and increased N deposition. *Oecologia* 113 (1): 104–114.
- HAUCK O. 1987. Vliv původu smrkových řízků na jejich zakořeňování. *Lesnictví* 33 (6): 533–540.

- HAUCK O., VOLNÁ M. 1990. Vliv místa odbíru řízků z osmiletého smrku ztepilého (*Picea abies* (L.) KARST.) na jejich zakořeňování. Lesnictví 36 (7): 571–578.
- HAUG I., KOTTKE I., OBERWINKLER F. 1986. Licht- und elektronenmikroskopische Untersuchungen von Mykorrhizen der Fichte (*Picea abies* L. (KARST.)) in Vertikalprofilen. Ztschr. Mykolog. 52: 373–391.
- HAUG I., OBERWINKLER F. 1987. Some distinctive types of spruce mycorrhizae. Trees 1: 172–188.
- HAUSSER K. 1971. Düngungsversuche zu 45- bis 90-jährigen Fichten- und Fichten-Tannen-beständen auf oberem und mittlerem Buntsandstein des Württembergischen Schwarzwalds. Allg. Forst- Jagdztg 142 (1): 4–11, (3): 69–85.
- HAVERAAN O. 1978. Liming and fertilization of peat soil in pot experiment with spruce. Meldinger Norges Landbrukshoegskole 57 (44): 1–22. [FA. 41, 4041]
- HAVMÖLLER P. 1981. Rooting success and growth of two cutting types. Proc. Symposium on clonal forestry, Uppsala, Sweden, April 8–9, 1981: 81–84.
- HAVRANEK W. M., PFEIFHOFFER H., GRILL D. 1990. Pigmentgehalte und Gaswechsel von Tief- und Hochlagenfichten nach chronischer Ozonbelastung. Forstw. Cbl. 109 (4): 200–209.
- HAYEK A. 1931. Prodromus Florae peninsulae Balcanicae. Repert. Spec. Nov. Regni Veget. 30, 1: 39–40. Berlin-Dahlem.
- HEBER U., WAGNER U., KAISER W., NEIMANIS S., BAILEY K., WALKER D. 1994. Fast cytoplasmic pH regulation in acid-stressed leaves. Plant Cell Physiol. 35: 479–488.
- HECHT-BUCHHOLZ C., JORNS C. A., KEIL P. 1987. Effect of excess aluminium and manganese on Norway spruce seedlings as related to magnesium nutrition. J. Plant Nutr. 10 (9–16): 1103–1110. [FA. 49, 6611]
- HEIDE O. M. 1986. Effects of ABA application on cessation of shoot elongation in long-day grown Norway spruce seedlings. Tree Physiol. 1: 79–83.
- HEIKKINEN O., OBRĘBSKA-STARKEL B., TUHKANEN S. 1995. Introduction: the timberline – a changing battlefield. Zesz. Nauk. UJ, Prace Geogr. 98: 7–16.
- HEIKINHEIMO O. 1954. Taimitarhan maantieteellinen sijainti, siemenen alkuperä ja istutuskaudet. Acta For. Ferm. 61(9): 1–28.
- HEIKINHEIMO O. 1956/58. Metsäututkimuslaitoksen kokeiluelueita 2 Ruotsinkylä. Helsinki 1956–58. (Ex Gøhrn 1966).
- HEINS DORF D., KRAUSS H. H., HIPPEL P. 1988. Ernährungs- und bodenkundliche Untersuchungen in Fichtenbeständen des mittleren Thüringer Waldes unter Berücksichtigung der in den letzten Jahren aufgetretenen Umweltbelastungen. Beitr. Forstwirtschaft 22 (4): 160–167.
- HEINS DORF D., KRAUSS H. H., HIPPEL P., BEHM R. 1990. Bericht über boden- und nadelanalytische Untersuchungen nach “Revitalisierungsdüngungen” in immissionsgeschädigten Fichtenbeständen der Kamm- und oberen Berglagen des Thüringer Waldes. Beitr. Forstwirtschaft 24 (2): 74–85.
- HEJNOWICZ A. 1969. Badania nad zmiennością cech anatomicznych drewna *Picea abies* (L.) KARST. Arbor. Kórnickie 14: 89–132.
- HEJNOWICZ A., OBARSKA E. 1995. Structure and development of vegetative buds, from the lower crown of *Picea abies*. Ann. Sci. For. 52: 433–447.
- HELLMERS H., GENTHE M. K., RONCO F. 1970. Temperature affects growth and development of Engelmann spruce. For. Sci. 16: 447–452.
- HENSEL W. 1980. Polska starożytna. Wyd. 2, Ossolineum, Wrocław, Warszawa, Kraków, Gdańsk. 640 pp.
- HENTSCH E., GODBOLD D. L., MARSCHNER P., SCHLEGEL H., JENTSCHKE G. 1993. The effect of *Paxillus involutus* Fr. on aluminium sensitivity of Norway spruce seedlings. Tree Physiol. 12: 379–390.
- HÉOIS B. 1992. Le programme des vergers à graines forestiers de l'état. Mass production technology for genetically improved fast growing forest tree species. Proc. IUFRO Symp. Bordeaux: 465.
- HÉOIS B., VAN DE SYPE H. 1991. Variabilité génétique de quinze provenances roumaines d'épicéa commun (*Picea abies* (L.) KARST. Premiers résultats. Ann. Sci. For. 48 (2): 179–192.
- HERBICH F. 1860. Pflanzengeographische Bemerkungen über die Wälder Galiziens. Verhandl. k. k. zool.-bot. Gesellschaft Wien 10: 359–366 + 1 map.

- HERBICH J. 1982. Zróżnicowanie i antropogeniczne przemiany roślinności Wysoczyzny Staniszewskiej na Pojezierzu Kaszubskim. Monogr. Bot. 63: 1–162.
- HESMER H., FELDMANN A. 1953. Der Oberflächenabfluß auf bewaldeten und unbewaldeten Hangflächen des südlichen Sauerlandes. Forstarchiv (24) 11/12: 245–256.
- HESS H. E., LANDOLT E., HIRZEL R. 1967. Flora der Schweiz, 1. Birkhäuser Verlag, Basel und Stuttgart, 858 pp.
- HINTIKKA V. 1988. High aluminium tolerance among ectomycorrhizal fungi. Karstenia 28: 41–44.
- HO R. H. 1991. Timing of gibberellin A4/7 application for cone production in potted black spruce grafts. Can. J. For. Res. 21: 1137–1140.
- HODSON M. J., WILKINS D. A. 1991. Localization of aluminium in the roots of Norway spruce [*Picea abies* (L.) KARST.] inoculated with *Paxillus involutus* Fr. New Phytol. 118: 271–278.
- HOFFMANN K., SCHEUMANN W. 1967. Anthocyanverfärbung und Wuchsleistung von Fichtenkeimlingen. Arch. Forstw. 16 (6/9): 683–688.
- HOFGAARD A. 1993a. Structure and regeneration patterns in a virgin *Picea abies* forest in northern Sweden. J. Veg. Sci. 4: 601–608.
- HOFGAARD A. 1993b. 50 years of change in a Swedish boreal old-growth *Picea abies* forest. J. Veg. Sci. 4: 773–782.
- HOFFMANN D. 1985. Arthybrdisierung bei Fichte – ein möglicher Beitrag zur Resisenzzüchtung. Forst- Holzwirt. 40 (17): 450–454.
- HÖGBERG K. A., ERIKSSON U. 1994. Effects of root pruning and stem injection with gibberellin A_{4/7} on flowering and cone harvest in three *Picea abies* seed orchards. Scan. J. For. Res. 9: 323–328.
- HÖGBERG P., HÖGBOM L., SCHINKEL H. 1998. Nitrogen-related root variables of trees along an N-deposition gradient in Europe. Tree Physiol. 18: 823–828.
- HÖGBERG P., TAMM C.-O., HÖGBERG M. 1992. Variations in ¹⁵N abundance in a forest fertilization trial: critical loads of N, N saturation, contamination and effects of revitalization fertilization. Plant and Soil 142 (2): 211–219.
- HOHENDORFF U., VOGELS K. 1990. Einfluss von Immissionen auf die Ethenproduktion und den Primärstoffwechsel von Fichten (*Picea abies* (L.) KARST.). Eur. J. For. Path. 20 (4): 219–230.
- HÖHNE H. 1963. Blattanalytische Untersuchungen an jüngeren Fichtenbeständen. Arch. Forstw. 12 (4): 341–360.
- HOLDHEIDE W. 1951. Anatomie mitteleuropäischer Gehölzrinden. In: FREUND H.: Handbuch der Mikroskopie in der Technik 5/1, Frankfurt a. M., Umschau: 193–367.
- HOLEKSA J. 1998. Rozpad drzewostanu i odnowienie świerka a struktura i dynamika karpackiego boru górnoregłowego. Monogr. Bot. 82: 1–209.
- HOLEKSA J., CIAPAŁA S. 1998. Usuwanie martwych drzew a naturalne odnowienie świerka w górno-regłowych borach świerkowych Beskidu Wysokiego. In: Struktura i dynamika górskich borów świerkowych. Zesz. Nauk AR, Kraków 332: 161–175.
- HOLEKSA J., KARCZMARSKI J., WILCZEK Z., CIAPAŁA S. 1996. Rezerwat “Romanka w Beskidzie Żywieckim” jako przykład niewłaściwej ochrony ekosystemu leśnego. Ochr. Przyr. 53: 19–35.
- HÖLL W. 1985. Seasonal fluctuation of reserve materials in the trunkwood of spruce (*Picea abies* (L.) KARST.). J. Plant Physiol. 117: 355–362.
- HOLLAND M. R., MÜLLER P. W., RÜTTER A. J., SHAW P. J. A. 1995. Growth of coniferous trees exposed to SO₂ and O₃ using an open-air fumigation system. Plant Cell Environ. 18 (3): 227–236.
- HOLMSGAARD E. 1955. Åringsanalyser af danske skovtræer. Forstl. Forsøgsv. Danmark 22 (1): 1–246.
- HOLOPAINEN T., ANTTONEN S., PALOMAKI V., KAINULAINEN P., HOLOPAINEN J. K. 1996. Needle ultrastructure and starch content in Scots pine and Norway spruce after ozone fumigation. Can. J. Bot. 74: 67–76.
- HOLOPAINEN T., NYGREN P. 1989. Effects of potassium deficiency and simulated acid rain, alone and in combination, on the ultrastructure of Scots pine needles. Can. J. For. Res. 19: 1402–1411.
- HOLOPAINEN T., RANTANEN L. 1992. Effects of open field fumigation on the development of Scots pine and Norway spruce mycorrhizas. In: TESCHE M., FEILER S. (eds.), Air Pollution and Interactions between Organisms in Forest Ecosystems. Proc. 15th Internat. Meeting Specialists Air Poll. Effects Forest Ecosystems, Tharandt/Dresden September 9–11, 1992. pp.: 223–227.

- HOLST M. J. 1955. Breeding for weevil resistance in Norway spruce Z. Forstgenetik 4: 33–37.
- HOLST M. 1963. Growth of Norway spruce (*Picea abies* KARST.) provenances in Eastern North America. (FAO/FORGEN 63), 1: 3/3.
- HOLSTENER-JØRGENSEN H., BRYNDUM H. 1970. Tre gødningsforsøg i ældre rødgran på jysk sandjord. Dansk Skovforen. Tidsskr. 55 (4): 330–333.
- HOLSTENER-JØRGENSEN H., GREEN B. 1971. Et gødningsforsøg i en rødgrankultur i Hønning plantage. Forstl. Forsøgsv. Danmark. 32 (4): 359–365.
- HOLSTENER-JØRGENSEN H., HOLMSGAARD E. 1993. Fertilization and irrigation of Norway spruce on sandy soil. For. Landscape Res. 1 (1): 1–8.
- HOLUBČÍK M. 1969a. Velkost' a tvar šišek smreka obyčajneho na Slovensku. Lesn. Stud., Zvolen 1: 1–122.
- HOLUBČÍK M. 1969b. The investigation of the variability of Norway Spruce (*Picea abies* Karst.) in the region of its natural distribution in Slovakia. Kongr. IUFRO 7/10, Washington.
- HOLUBČÍK M. 1971. Variability in cones of the Norway Spruce (*Picea abies* KARST.) from the Tatra mountain region. Zborník TANAP 13: 5–47.
- HOLUBČÍK M. 1972. Dedivost rastových a niektorých ďalších znakov smreka obyčajného (*Picea abies* KARST.). Acta Mus. Silesiae, Dendrologia (1): 17–39.
- HOLUBČÍK M. 1973. Fenológia smreka obyčajneho (*Picea abies* KARST.). Ved. Prace Vys. Úst. Lesn. Hosp., Zvolen 14: 67–110.
- HOLUBČÍK M. 1980. Vplyv prostredia na výškový rast domácich a poľských proveniencií smreka obyčajného (*Picea abies* KARST.). Folia Dendrol. 7: 35.
- HOLUBČÍK M. 1984. Wachstum und Qualität von Provenienzen der Gemeinen Fichte (*Picea abies* KARST.) in trockeneren und wärmeren Regionen der Slowakei. Folia Dendrol. 11: 263–287.
- HOLZ D. 1967. Untersuchungen an Resonanzholz. Holztechnologie 8 (4): 221–224.
- HOLZ D., SCHMIDT J. 1968. Untersuchungen an Resonanzholz. Hochttechnologie 9 (2): 225–228.
- HOLZER K. 1960. Ergebnisse einer Fichtensämlingstestung in der Kulturkammer. Silvae Genet. 9 (5): 137–138.
- HOLZER K. 1963. Physiological investigations on *Picea abies* (L.) KARST. in view of genetics (FAO/FORGEN 63) 1: 5/3.
- HOLZER K. 1964. Die Seehöhengliederung der Fichtentypen in den österreichischen Alpen. In: Forstsamengewinnung und Pflanzenzucht für das Hochgebirge. BLV, München–Basel–Vien. pp.: 66–73.
- HOLZER K. 1966. Die Vererbung von physiologischen und morphologischen Eigenschaften der Fichte. I. Sämlingsuntersuchungen. Mitt. Forstl. Bundes-Versuchsanstalt, Mariabrunn. 71, Österreichischer Agrarverlag, Wien. 185 pp.
- HOLZER K. 1967a. Das Wachstum des Baumes in seiner Anpassung an zunehmende Seehöhe. Ökologie der Alpenen Waldgrenze. Mitt. Forst. Budn. Wien 75: 427–456.
- HOLZER K. 1967b. Die Augusttriebblüfung als Höhenagentest bei der Fichte (*Picea abies* (L.) KARST.) Papers XIV IUFRO Kongress, München III: 602–620.
- HOLZER K. 1968. Vererbungsverhältnisse in einer Halbgeschwister familie von *Picea abies* (L.) KARST. f. *virgata* (Jacques) Rehd. Silvae Genet. 17 (2/3): 64–68.
- HOLZER K. 1969a. A late frost injury in an alpine Norway spruce (*Picea abies* L. KARST.) provenance test. Proc. 2nd World Conf. For. Tree Breeding, Washington, FO-FTB–69–6/10.
- HOLZER K. 1969b. Cold resistance in spruce. Proc. 2nd World Conf. For. Tree Breeding, Washington, FO-FTB–69–6/2.
- HOLZER K. 1975. Zur Identifizierung von Fichtenherkünften (*Picea abies* (L.) KARST.). Silvae Genet. 24 (5–6): 169–175.
- HOLZER K. 1978. Die Kulturkammertestung zur Erkennung des Erbwertes bei Fichte (*Picea abies* (L.) KARST.). 2. Merkmale des Vegetationsablaufes. Cbl. Ges. Forstw. 95 (1): 30–51.
- HOLZER K. 1979. Die Kulturkammertestung zur Erkennung des Erbwertes bei Fichte (*Picea abies* (L.) KARSTEN) 3. Quantitative Merkmale. Cbl. Ges. Forstw. 96 (3): 129–144.
- HOLZER K. 1981a. Genetische Zusammenhänge der Fichtenverbreitung in den Alpen. Forstztg. 12: 421–424.

- HOLZER K. 1981b. Die Kulturkammertestung zur Erkennung des Erbwertes bei Fichte (*Picea abies* (L.) KARST.). 4. Qualitative Merkmale. Cbl. Ges. Forstw. 2: 65–87.
- HOLZER K. 1985. Die Bedeutung der Genetik für den Hochlagenwaldbau. Proc. 3rd IUFRO Workshop P1.07–00, 1984, Eidg. Anst. forstl. Versuchswes., Ber. 270: 225–232.
- HOLZER K. 1988. Die Vegetationszeitlänge bei Fichtensämlingen, ihre Bedeutung und Beeinflussbarkeit durch Umweltfaktoren. Forum Genetik-Wald-Forstwirtschaft, Innsbruck 1987. FBVA Berichte 28: 73–86.
- HOLZER K. 1993. The evolution of Alpine Norway spruce during immigration into high altitudes and its consequences. Norway spruce provenances and breeding. Proc. of IUFRO (S2.2–11). Symposium, Riga, Latvia.: 68–78.
- HOLZER K., OHENE-COFFIE F., SCHULTZE U. 1991. Vegetative Vermehrung von Fichte für Hochlagenaufforstungen. Forstl. Bundesversuchsanstalt Berichte, Wien 59: 1–73. [FA. 54, 5275]
- HOLZER K., SCHULTZE U. 1988. Die Bedeutung von Herkunft und Austrieb bei einem Fichtenblattwespenbefall. Cbl. Ges. Forstw. 105 (4): 207–216. [FA. 52, 4085]
- HORIKAWA Y. 1976. Atlas of the Japanese Flora. Publ. by Gakken Co. Tokyo, 500 pp.
- HORN R., ZECH W., HANTSCHER R., KAUPENJOHANN M., SCHNEIDER B. U. 1987. Relations between soil properties and forest dieback. Allg. Forst-Ztschr. 12: 300–302. [FA. 51, 5556]
- HÖRNBERG G., OHLSON M., ZACKRISSON O. 1995. Stand dynamics, regeneration patterns and long-term continuity in boreal old-growth *Picea abies* swamp forests. J. Veg. Sci. 6: 291–298.
- HORNTVEDT R., ROBAK H. 1975. Relative susceptibility of eleven conifer species to fluoride air pollution. Reports of The Norwegian Forest Research Institute 32.5, Ås Norway: 187–206.
- HRYNKIEWICZ-SUDNIK J., SĘKOWSKI B., WILCZKIEWICZ M. 1991. Rozmnażanie drzew i krzewów nagozalążkowych. PWN, Warszawa.
- HULTÉN E. 1949. On the races in the Scandinavian flora. Svensk Bot. Tidskr. 43: 383–406.
- HULTÉN E. 1971. Atlas över växternas utbredning i Norden. Generalstabens Litografiska Anstalts Förlag. Stockholm, 531 pp.
- HUMPHREYS F. R., TRUMAN R. 1964. Aluminum and phosphorus requirements of *Pinus radiata*. Plant and Soil 20: 131–134.
- HUNGER W. 1985. Zum Einfluss der Bodenbehandlung auf das Wachstum einer Fichtenplantage. Sozial. Forstw. 35 (12): 371–372.
- HUNGER W. 1986. Growth of *Larix decidua* and Norway spruce in stands on similar sites. Beitr. Forstwirtschaft 20 (3): 101–107. [FA. 49, 148]
- HUNGER W., FIEDLER H. J. 1965. Düngungsdiagnosen für ältere Fichtenbestände des Erzgebirges und Vogtlandes. I. Standortverhältnisse. II. Wachstum und Ernährung der Fichte. Arch. Forstw. 14 (9): 933–986.
- HUNGER W., MARSCHNER W. 1987. Zum Ernährungszustand der Fichte (*Picea abies* (L.) KARST.) auf Naßstandorten im Lausitzer Tiefland. Arch. Naturschutz Landschaftsforsch. 27 (3): 195–204.
- HUNGER W., NEBE W. 1964. Zur Ernährung der Fichte im Mittelgebirge in Abhängigkeit von den Standortverhältnissen. Albrecht Thaer Arch., Berlin 8 (4/5): 293–312.
- HUNTLEY B. 1988. Glacial and holocene vegetation history. Europe. In: HUNTLEY B., WEBB T. III (ed.). Vegetation history. Handbook of vegetation science 7: 341–383. Kluwer Academic Publishers. Dordrecht / Boston / London.
- HUNTLEY B., BIRKS H. J. B. 1983. An atlas of past and present pollen maps for Europe: 0–13 000 years ago. Cambridge University Press, Cambridge, London.
- HÜSER R. 1979. Wald und Wasserqualität. Deutscher Verband für Wasserwirtschaft und Kulturbau. Schriftenreihe DVWK 41: 89–107.
- HUSTED L., LAVENDER D. P. 1989. Effect of soil temperature upon the root growth and mycorrhizal formation of white spruce (*Picea glauca* (MOENCH) VOSS) seedlings grown in controlled environments. Ann. Sci. For. 46 (suppl.): 750–753.
- HUTCHINSON T. C., BOZIC L., MUNOZ-VEGA G. 1986. Responses of five species of conifer seedlings to aluminum stress. Water, Air Soil Poll. 31: 283–294.
- HÜTTERMANN A. 1985. The effects of acid deposition on the physiology of the forest ecosystem. Experientia 41: 584–590.

- HÜTTERMANN A., ULRICH B. 1984. Solid phase-solution-root interactions in soils subjected to acid deposition. Phil. Trans. R. Soc. London, B 305: 353–368.
- HÜTTL R. F., FINK S. 1988. Diagnostische Düngungsversuche zur Revitalisierung geschädigter Fichtenbestände (*Picea abies* L. KARST.) in Südwestdeutschland. Forstw. Cbl. 107: 173–83.
- HÜTTL R. F., ORLOVIUS K., SCHENK B. V. 1990. Messung elektrischer Widerstände im Kambialbereich gedüngter und ungedüngter Fichten. Forstw. Cbl. 109 (4): 190–199.
- HUTTUNEN S. 1978. The effects of air pollution on provenances of Scots pine and Norway spruce in northern Finland. Silva Fenn. 12 (1): 1–16.
- HUTTUNEN S. 1984. Interactions of disease and other stress factors with atmospheric pollution. In: TRESHOW, M. (ed.). Air pollution and plant life. John Wiley & Sons Ltd. pp.: 321–356.
- HUTTUNEN S., HAVAS P., LAINE K. 1981. Effects of air pollutants on the wintertime water economy of the Scots pine, *Pinus sylvestris*. Holarctic Ecol., Copenhagen 4: 94–101.
- HUTTUNEN S., LAINE K. 1983. Effects of air-borne pollutants on the surface wax structure of *Pinus sylvestris* needles. Ann. Bot. Fenn. 20: 79–86.
- HUTTUNEN S., SOIKKELI S. 1984. Effects of various gaseous pollutants on plant cell ultrastructure. In: Koziol M., Whatley F. R. (eds.). Gaseous air pollutants and plant metabolism. Butterworth. pp.: 117–127.
- HÜVE K., DITTRICH A., KINDERMANN G., SLOVIK S., HEBER U. 1995. Detoxification of SO₂ in conifers differing in SO₂-tolerance. A comparison of *Picea abies*, *Picea pungens* and *Pinus sylvestris*. Planta 195: 578–585.
- HWANG J. W., HYUN S. K. 1979. Growth performances of Norway spruce of some aged stands and nursery stock of different provenances of Europe in Korea. Proc. IUFRO Joint Meet. WPs Norway spruce provenances and breeding. Bucharest: 100–116.
- HYTTENBORN H., PACKHAM J. R., VERWIJST T. 1987. Tree population dynamics, stand structure and species composition in the montane virgin forest of Vallibacken, northern Sweden. Vegetatio 72: 3–19.
- ILLE R. 1968. Ozvučné dřevo smrku. Sborník Ved. Les. Ust. Vysoké Školy Zemed. 11: 67–90.
- ILLIES Z. M. 1951/1952. Auslese und künstliche Herstellung Polyploider bei *Larix* und *Picea*. Z. Forstgenetik Forstplanzenzüchtung 1: 58.
- ILLIES Z. M. 1958. Polysomatie im Meristem von Einzelbaumabsäaten bei *Picea abies* Silvae Genet. 7: 94–97.
- ILLIES Z. M. 1959. Weitere Mehrlingsuntersuchungen bei *Picea abies* L. KARST. Silvae Genet. 8: 111–113.
- ILSTEDT B., ERIKSSON G. 1982. Fröproduktion i nordiska fröplantager. 1. Orsaker till skillnader i fröproduktion mellan plantager och ar. Sveriges Lantbruksuniversitet, Inst. Skogsgenetik, Rapporter 33: 1–83.
- IMBAULT N., TARDIEU I., JOSEPH C., ZAERR J. B., BONNET-MASIMBERT M. 1988. Possible role isopentenyladenine and isopentenyladenosine in flowering of *Pseudotsuga menziensis*: endogenous variations and exogenous applications. Plant Physiol. Biochem. 26: 289–295.
- INGEMARSSON B. S. M. 1995. Ethylene effects on peroxidases and cell growth patterns in *Picea abies* hypocotyl cuttings. Physiol. Plant. 94: 212–218.
- INGEMARSSON S. B. M., EKLUND L., ELIASSON L. 1991. Ethylene effects on cambial activity and cell wall formation in hypocotyls of *Picea abies* seedlings. Physiol. Plant. 82: 219–224.
- INGERSLEV M. 1999. Above ground biomass and nutrient distribution in a limed and fertilized Norway spruce (*Picea abies*) plantation. Part I. Nutrient concentrations. Forest Ecol. Managm. 119 (1–3): 13–20.
- INGERSLEV M., HALLBACKEN L. 1999. Above ground biomass and nutrient distribution in a limed and fertilized Norway spruce (*Picea abies*) plantation. Part II. Accumulation of biomass and nutrients. Forest Ecol. Managm. 119 (1–3): 21–38.
- INGESTAD T. 1959. Studies on the nutrition of forest tree seedlings. II. Mineral nutrition of Spruce. Physiol. Plant. 12 (3): 568–593.
- INGESTAD T. 1963. Effects of fertilization on growth and type of forest tree seedlings in nurseries. Rapp. Uppsats. Instn. Skogskol. Skogshogsk., Stockholm 2: 1–27. [FA. 26, 508]

- INGESTAD T. 1967. Methods for uniform optimum fertilization of forest tree plants. Proc. 14th Congr. IUFRO, Munich Pt. III, Sec. 22: 265–269.
- INGESTAD T. 1979. Mineral nutrition requirements of *Pinus silvestris* and *Picea abies* seedlings. *Physiol. Plant.* 45 (4): 373–380.
- INGESTAD T., ELDHUSE T., GÖRANSSON A. 1985. Effects of Al^{3+} on seedling growth of Norway spruce, Scots pine and birch at steady state nutrition. In: ANDERSSON F., KELLY J. M. (eds.). Aluminum toxicity to trees. Proc. of an International Workshop in Uppsala, Sweden. 14–17 May 1984. Swedish Univ. of Agric. Sci., Uppsala, Sweden. pp.: 45–48.
- INGESTAD T., KÄHR M. 1985. Nutrition and growth coniferous seedlings at varied relative nitrogen addition rate. *Physiol. Plant.* 65: 109–116.
- INGLEBY K., MASON P. A., LAST F. T., FLEMING L. V. 1990. Identification of Ectomycorrhizas. Institute of Terrestrial Ecology Research Publication 5, HMSO, London, UK.
- INNES J. L. 1994. The occurrence of flowering and fruiting on individual trees over 3 years and their effects on subsequent crown condition. *Trees* 8: 139–150.
- ISIK K., KLEINSCHMIT J., SVOLBA J. 1995. Survival, growth trends and genetic gains in 17-year old *Picea abies* clones at seven test sites. *Silvae Genet.* 44 (2–3): 116–128.
- IVONIS I. Yu. 1988. Vliyanie aktivnosti prirodnykh regulatorov rosta na zalozhenie strobilov ieli evropeyskoy. *Lesoved.* (4): 68–73.
- IVONIS I. Yu., KYALINA L. V., LITVINOVA V. B., KHOKHLINA E. V. 1981. Annual dynamics of gibberellin-like substances in needles of Norway spruce clones of different sexes. *Sov. Plant Physiol.* 28: 915–920.
- IVONIS I. Yu., KYALINA L. V., LITVINOVA V. B., KHOKHLINA E. V. 1983. Prirodnye regulatory rosta v khvoje prvytykh dererien ieli obyknovennoy. *Lesoved.* (1): 35–40.
- Yachewskiy A. A. 1933. Osnovy mikologii. Gos. Izd. Kolkh. Sowkh. Lit., Moskwa–Leningrad. 1036 pp.
- JACKSON D. I., SWEET G. B. 1972. Flower initiation in temperate woody plants. A review based largely on the literature of conifers and deciduous fruit trees. *Hort. Abs.* 42: 9–24.
- JACKSON G. E., IRVINE J., GRACE J., KHAIL A. A. M. 1995. Abscissic acid concentrations and fluxes in droughted conifer saplings. *Plant Cell Environ.* 18: 13–22.
- JÄGER H.-J. 1976. S-Lokalisation in SO_2 -begasten Fichtennadeln. *Eur. J. For. Path.* 6 (1): 25–29.
- JAIN S. M., NEWTON R. J., SOLTES E. J. 1988. Enhancement of somatic embryogenesis in Norway spruce (*Picea abies* L.). *Theor. Appl. Genet.* 76: 501–506.
- JAKUBOWSKA-GABARA J. 1985. Zespoły leśne Wysoczyzny Rawskiej i ich antropogeniczne przekształcenia. *Monogr. Bot.* 65: 1–148.
- JAKUBOWSKA-GABARA J., PRZEMYSKI A., BEDNORZ L. 1991. Relacje między sosną i świerkiem w borze świeżym (*Peucedano-Pinetum*) w Białowieckim Parku Narodowym. *Phytocoenosis N.S., Semin. Geobot.* 1: 151–160.
- JALAS J., SUOMINEN J. 1973. *Atlas Florae Europaeae*, 2: 13–15. Helsinki.
- JAŃCZYK-KOPIKOWA Z. 1991. Problemy palinostratygrafii glacialnego plejstocenu Polski z uwzględnieniem wyników analizy pyłkowej osadów interglacialnych z Besiekierza (Środkowa Polska). *Ann. UMCS* 46, Supl. 1: 1–26.
- JANDL R. 1996. Gefäßversuche mit Magnesiumdüngern. *Cbl. Ges. Forstw.* 113 (3–4): 115–130.
- JANICKI J., ŻURAKOWSKI M., FILIPEK Z. 1951. *Garbniki roślinne*. Warszawa. pp.: 45–93.
- JANSON L. 1968. Observations on the growth of spruce seedlings of certain proveniences taken in vegetation hall and nursery. In: TYSZKIEWICZ S. (ed.). *Population studies of Norway spruce in Poland*. IBL, Warszawa. pp.: 52–65.
- JANSON L. 1990. Rozmnażanie starych drzew świerka (*Picea excelsa* LINK.) przez zrzesy. *Prace IBL, Warszawa* 720.
- JAROSLAVTSEV S. V. 1986. Vozrastnoe stroenie el'nikov Kraynego Severa. *Les. Zh.* (1986) 3: 9–13.
- JASIČOVA M. 1966. *Picea* A. DIETR. In: FUTÁK J. (red.). *Flora Slovenska*, 2: 269–273.
- JASIEWICZ A. 1965. Rośliny naczyniowe Bieszczadów Zachodnich. *Monogr. Bot.* 20: 1–332.
- JAWORSKI A. 1998. Budowa, struktura i dynamika górnoreglowych borów świerkowych w Karpatach a metody postępowania hodowlanego. In: *Struktura i dynamika górskich borów świerkowych*. Zesz. Nauk. AR, Kraków 332: 37–67.

- JAWORSKI A., KARCZMARSKI J. 1989. Budowa, struktura i dynamika górnoreglowych borów świerkowych w Babiogórskim Parku Narodowym. In: Stav, vyvoj, produkčné schopnosti a funkčné využívanie lesov v oblasti Babie Hory a Pilska. Zvolen – Poznań – Kraków. pp.: 122–247.
- JAWORSKI A., ZARZYCKI K. 1983. Ekologia. In: BIAŁOBOK S. (ed.). Jodła pospolita *Abies alba* MILL. Nasze drzewa leśne 4. PWN, Warszawa–Poznań. pp.: 317–430.
- JEDLIŃSKI W. 1922. O granicach zasięgu buka, jodły, świerka i innych drzew na Wyżnach Małopolskiej i Lubelskiej oraz o ich znaczeniu dla gospodarstwa leśnego. Z 6 mapami i 8 tabelami. Zamość. Przedruk w: JEDLIŃSKI W. 1953. Prace wybrane. PWRiL, Warszawa. pp.: 9–92.
- JEDLIŃSKI W. 1926. O pasie bezświerkowym na ziemiach Polski i jego znaczeniu hodowlanem. Las Polski (1926), 1–2. Reprint in: JEDLIŃSKI W. 1953. Prace wybrane. PWRiL, Warszawa. pp.: 90–101.
- JEDLIŃSKI W. 1927. Wyniki dalszych badań tak zwanego pasa bezświerkowego w Polsce. Las Polski 3. Reprint in: JEDLIŃSKI W. 1953. Prace wybrane. PWRiL, Warszawa. pp.: 103–112.
- JEDLIŃSKI W. 1928. O naturalnym zasięgu świerka w środkowej Polsce i jego znaczeniu gospodarczym. Sylwan 46 (1): 1–33.
- JEFFERS R. M. 1971. Research at the Institute of Forest Genetics USDA For. Ser. Res. Pap. NC–67.
- JEFFREE C. E., BAKER E. A., HOLLOWAY P. J. 1975. Ultrastructure and recrystallization of plant epicuticular waxes. New Phytol. 75: 539–549.
- JEFFREE C. E., JOHNSON R. P., JARVIS P. G. 1971. Epicuticular wax in the stomatal antechamber of sitka spruce and its effects on the diffusion of water vapour and carbon dioxide. Planta 98: 1–10.
- JENSEN K. F., KOZŁOWSKI T. T. 1975. Absorption and translocation of sulfur dioxide by seedlings of four forest tree species. J. Environ. Qual. 4: 379–382.
- JENTSCHKE G., BRANDES B., KUHN A. J., SCHRÖDER W. H., BECKER J. S., GODBOLD D. L. 2000. The mycorrhizal fungus *Paxillus involutus* transports magnesium to Norway spruce seedlings. Evidence from stable isotope labeling. Plant and Soil 220 (1–2): 243–246.
- JENTSCHKE G., BRANDES B., KUHN A. J., SCHRÖDER W. H., GODBOLD D. L. 2001a. Interdependence of phosphorus, nitrogen, potassium and magnesium translocation by the ectomycorrhizal fungus *Paxillus involutus*. New Phytol. 149: 327–338.
- JENTSCHKE G., GODBOLD D. L., BRANDES B. 2001b. Nitrogen limitation in mycorrhizal Norway spruce (*Picea abies*) seedlings induced mycelial foraging for ammonium: implications for Ca and Mg uptake. Plant and Soil 234: 109–117.
- JENTSCHKE G., GODBOLD D. L., HÜTTERMANN A. 1991. Culture of mycorrhizal tree seedlings under controlled conditions: Effects of nitrogen and aluminium. Physiol. Plant. 81: 408–416.
- JEREB O. 1977. Összehasonlító vizsgálat hazai és svéd lucfenyo származékok között. ERDO 26 (6): 268–272. [Ref. Zh. 4.56.106]
- JESTAEDT M. 1980. Die autovegetative Vermehrung von Forstpflanzen. Allg. Forstztg. 35: 691–693.
- JESTAEDT M., RAPP H.-J. 1977. Versuche zur Lagerung von Fichtenstecklingen. Forstarchiv 48 (1): 10–13.
- JOHNSEN Ø. 1985. Successive bulk propagation of juvenile plants from full-sib families of Norway spruce. Forest Ecol. Managm. 11: 271–282.
- JOHNSEN Ø. 1986. Rooting of Juvenile Succulent Cuttings from Half-sib Families of *Picea abies*. Scand. J. For. Res. 1: 27–36.
- JOHNSEN Ø. 1988. After-effects on progenies from orchard clones moved to non-native environments. Proc. 10th N. Amer. For. Biol. Workshop: 1–11.
- JOHNSEN Ø., DÆHLEN O. G., HAUG G., GRØNSTAD B. S., ROGNSTAD A. T. 1994a. Seed cone abortion and full seed production in an indoor seed orchard with potted grafts of *Picea abies*. Scand. J. For. Res. 9: 329–332.
- JOHNSEN Ø., HAUG G., DÆHLEN O. G., GRØNSTAD B. S., ROGNSTAD A. T. 1994b. Effects of heat treatment, timing of heat treatment, and gibberellin A₁₇ on flowering in potted *Picea abies* grafts. Scand. J. For. Res. 9: 333–340.
- JOHNSON L. P. V. 1939. A descriptive list of natural and artificial interspecific hybrids in N. American Forest tree Genera. Can. J. For. Res. 17, Ser. C (12): 411–444.

- JONEBORG S. 1945. Monströs kottebildning hos granen. Vegetativt skott eller kotte? Svenska Skogs Fören. Tidskr. 43: 453–462.
- JONES H. G. 1978. How plants respond to stress. *Nature* 271: 610.
- JONES H. G. 1992. Plants and microclimate. A quantitative approach to environmental plant physiology. Cambridge University Press, Cambridge. 428. pp.
- JONSSON A. 1973. Meiotic investigations on embryo sac mother cells of normal and desynaptic Norway spruce. *Stud. Forest. Suec.* 105: 1–46.
- JONSSON B. 1969. Studies of variations in the widths of annual rings in Scots pine and Norway spruce due to weather conditions in Sweden. *Inst. Skogsprod. Skogshögsk., Rapporter och uppsatser* 16: 1–297.
- JONSSON B. G., DYNESIUS M. 1993. Uprooting in boreal spruce forests: long term variation in disturbance rate. *Can. J. For. Res.* 23: 2383–2388.
- JONSSON L., DAHLBERG A., BRANDRUD T. E. 2000. Spatiotemporal distribution of an ectomycorrhizal community in an oligotrophic Swedish *Picea abies* forest subjected to experimental nitrogen addition: above- and below-ground views. *For. Ecol. Managm.* 132: 143–156.
- JONSSON L., DAHLBERG A., NILSSON M. C., ZACKRISSON O., KÄREN O. 1999. Ectomycorrhizal fungal communities in late-successional Swedish boreal forests and composition following wildfire. *Mol. Ecol.* 8: 205–215.
- JORDAN H. W. 1986. Saltzote Baume als Indicatoren von Bodenverunreinigungen. *Holz Zentralblatt* 112: 87–88.
- JORNS A., HECHT-BUCHHOLZ C. 1985. Aluminium-induzierter Magnesium- und Calciummangel im Laborversuch bei Fichtensämlingen. *Allg. Forstztg.* 46: 1248–1252.
- JORUS A. C. 1987. Presence and function of the casparian band in roots of Norway spruce [*Picea abies* (L.) KARST.]. *J. Plant Physiol.* 129: 493–496.
- JOSIFOVIĆ M. 1970. Flora de la Republ. Societiste de Serbie, 1: 135–140. Beograd.
- JOSLIN J. D., WOLFE M. H. 1988. Responses of red spruce seedlings to changes in soil aluminum in six amended forest soil horizons. *Can. J. For. Res.* 18: 1614–1623.
- JUNG G., WILD A. 1988. Electron microscopic studies of spruce needles in connection with the occurrence of novel forest decline. I. Investigations of the mesophyll. *J. Phytopath.* 122: 1–12.
- JUNG J., RIEHLE G. 1966. Foliar and needle analysis evaluations in long-term fertilization studies with forest plants in pots. *Forstw. Cbl.* 85 (9/10): 295–305. [FA. 28, 1911]
- JUNGHANS H. 1967. Die Intensität der direkten Sonnenstrahlung auf geneigten Flächen. *Ztschr. Angew. Meteorol., Sonderdruck* 5 (7–8): 217–221.
- JUNIPER B. E., COX G. C. 1973. The anatomy of the leaf surface: The first line of defence. *Pestic. Sci.* 4: 543–561.
- JUNIPER B. E., JEFFREE C. E. 1983. Plant surfaces. Edward Arnolds, London.
- JURKEVICH I. D., GOLOD D. S. 1966. Sezonnoe razvitie eli obyknovennoy. *Nauka i Tekhnika*, Minsk.
- JURKEVICH J. D., PARFENOV V. I. 1967. K voprosu o sistematike *Picea abies* KARST. *Byull. Glavn. Bot. Sada.* 64: 41–55.
- JURKIEWICZ J., PARFIENOW W. 1966. Świerkowe lasy Polesia. *Sylvan* 110 (3): 1–30.
- KACZMAREK S., MICHALSKI J., RATAJCZAK G. 1992. Zgrupowania roztoczy (*Acari*, *Gamasida*) zasiedlające żerowiska niektórych korników. *Sylvan* 136 (5): 51–59.
- KACZMAREK S., MICHALSKI J. 1995a. Żerowiska korników środowiskiem bytowania roztoczy (*Acari*, *Mesostigmata*). Konferencja naukowa Szkodniki wtórne, ich rola oraz znaczenie w lesie. *Poznań. pp.*: 37–42.
- KACZMAREK S., MICHALSKI J. 1995b. Roztocze *Acari*, *Gamasida* w żerowiskach korników *Coleoptera*, *Scolytidae* z rodzaju *Ips* na terenie wybranych parków narodowych. *Parki Narod. Rez. Przyr.* 13 (1) (Suppl.): 35–42.
- KAISER G., MARTINOIA E., SCHRÖPPEL-MEIER G., HEBER U. 1989. Active transport of sulphate into the vacuole of plant cells provides halotolerance and can detoxify SO_2 . *Plant Physiol.* 133: 756–763.
- KALELA E. K. 1951. Mönnikäiden ja kuusikoiden juurisuiteista. *Acta For. Fenn.* 57 (2).

- KAMALITINOV G. Sh., LIBRECHT L. I. 1984. Osobennosti rosta geograficheskikh kul'tur eli v zasukhlivom 1981 godu v Tatarskoj ASSP. Lesovosstanovl. v Sred. Povolzh'e. Rukopis CBNTI 331, 1984: 55–62. [Ref. Zh. 2.56.87]
- KANNENBERG N., GROSS K. 1999. Allozymic variation in some Norway spruce populations of the international IUFRO provenance-testing programme of 1964/1968. *Silvae Genet.* 48: 209–217.
- KANTOROWICZ W. 2000. Half a century of seed years in major tree species of Poland. *Silvae Genet.* 49 (6): 245–249.
- KARAS M. 1995. Naturalne biogrupy świerkowe a problem restytucji lasu w reglu górnym Gór Izer-skich. *Prace IBL, Warszawa*, B 25: 235–250.
- KÅREN O., NYLUND J. E. 1996. Effects of N-free fertilization on ectomycorrhiza community struc-ture in Norway spruce stands in Southern Sweden. *Plant and Soil* 181: 295–305.
- KÅREN O., NYLUND J. E. 1997. Effects of ammonium sulphate on the community structure and bio-mass of ectomycorrhizal fungi in a Norway spruce stand in South West Sweden. *Can. J. Bot.* 75: 1628–1642.
- KÄRENLAMP L., HOUPIS J. L. J. 1986. Structural conditions of mesophyll cells of *Pinus ponderosa* var. *scopulorum* after SO₂ fumigation. *Can. J. For. Res.* 16: 1381–1385.
- KARHU M., HUTTUNEN S. 1986. Erosion effects of air pollution on needle surface. *Water, Air, Soil Poll.* 31: 417–423.
- KAROLEWSKI P., SIEPAK J., GRAMOWSKA H. 2000. Response of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and Douglas fir (*Pseudotsuga menziesii*) needles to environmental pollution with fluorine compounds. *Dendrobiology* 45: 41–46.
- KARPIŃSKI J. 1935. Przyczyny ograniczające rozmnażanie się korników drukarzy (*Ips typographus* L. i *I. duplicatus* SAHLB.) w lesie pierwotnym. *Prace IBL, Warszawa*, Ser. A 15: 86.
- KARPIŃSKI J., STRAWIŃSKI K. 1948. Korniki ziem Polski. *Annales UMCS, Suppl.* 4, Ser. C. 239 pp. + 28 tabl.
- KARPOV V. G. (ed.). 1983. Faktory regulacji ekosistem elovyykh lesov. Nauka, Leningrad. 316 pp.
- KARTUSCH B., KARTUSCH R., WEILGONY P. 1991. Site-specific differences in calcium oxalate con-tent of the secondary phloem of spruce (*Picea abies* KARST.). *Flora* 185: 377–384.
- KASPROWICZ M. 1996. Zróżnicowanie roślinności pięter reglowych masywu Babiej Góry (Karpaty Zachodnie). *Idee Ekol.* 9 (3): 1–215.
- KATO J., PURVES W., PHINNEY B. O. 1962. Gibberellin-like substances in plants. *Nature* 196: 687–688.
- KATZENSTEINER K., GLATZEL G., KAZDA M., STERBA H. 1992. Effects of air pollutants on mineral nutrition of Norway spruce and revitalization of declining stands in Austria. *Water, Air, Soil Poll.* 61 (3/4): 309–322.
- KAUNISTO S., SARJALA T. 1997. Critical needle potassium concentrations indicated by diamine putrescine in Norway spruce growing on peat soils. *Silva Fenn.* 31: 383–390.
- KAWECKA A. 1975. Owłosienie pędów świerka pospolitego (*Picea abies* (L.) KARST.) na terenie Pol-ski. *Sylvan* 119 (1): 33–40.
- KAWECKA A. 1977. Różnice w budowie igieł świerka pospolitego (*Picea abies* (L.) Karst.) w różnych poziomach korony. *Rocz. Dendrol.* 30: 67–73.
- KAWECKA A. 1991. Zmiany roślinności i odnowienia naturalne w drzewostanach Puszczy Białowie-skiej uszkodzonych przez huragany. *Parki Narod. Rez. Przyr.* 10 (3/4): 45–67.
- KAWECKA A., GUTOWSKI J. 1988. Skutki huraganowych wiatrów z zimy 1982/83 w Puszczy Białowie-skiej. *Prace IBL, Warszawa* 677: 125–144.
- KELLER H. M. 1968. Der heutige Stand der Forschung über den Einfluß des Waldes auf den Wasser-haushalt. *Schweiz. Z. Forstwes.* 119: 364–379.
- KELLER T. 1976. Histologische und physiologische Untersuchungen an Forstpflanzen in einem Flu-rschadensgebiet. *Eidg. Anst. Forstl. Versuchs.* 154, Ber., Diss. Univ. Basel: 82pp.
- KELLER T. 1977a. The effect of long duration low SO₂ concentrations upon photosynthesis of conif-ers. The fourth international clean air congress 1977, IUAPPA, Tokyo, Proceedings: 81–83.
- KELLER T. 1977b. Der Einfluss von Fluorimmissionen auf die Nettoassimilation von Waldbäumar-ten. *Mitt. Eidg. Anst. Forstl. Versuchs.* 53 (4): 163–198.

- KELLER T. 1978a. Begriff und Bedeutung der latenten Immissionsschädigung. Allg. Forst- Jagdztg. 148: 115–20.
- KELLER T. 1978b. Der Einfluss einer SO₂-Belastung zu verschiedenen Jahreszeiten auf CO₂-Aufnahme und Jahrringbau der Fichte. Schweiz. Z. Forstwes. 129: 381–393.
- KELLER T. 1980. The effect of a continuous springtime fumigation with SO₂ on CO₂ uptake and structure of the annual ring in spruce. Can. J. For. Res. 10: 1–6.
- KELLER T. 1982. Physiological bioindications of an effect of air pollution on plants. In: STEUBING L., JÄGER H.-J. (eds.). Monitoring of air pollutants by plants. Dr W. Jank Publishers, The Hague. pp.: 99–107.
- KELLER T. 1989. Oberirdische Wirkung von Luftschadstoffen auf Bäume und Pflanzenteile. Neuere Ergebnisse. W: SCHMIDT-VOGT H. 1989. Die Fichte. II/2. Parey, Hamburg u. Berlin. pp.: 280–314.
- KELLEY A. P. 1950. Mycotrophy in plants. Chronica Botanica Co. 1–223.
- KEMPF K., ALLWINE E., WESTBERG H., CLAIBORN C., LAMB B. 1996. Hydrocarbon emissions from spruce using environmental chamber and branch enclosure methods. Atmospheric Environ. 30: 1381–1389.
- KENK G., UNFRIED P., EVERS F. H., HILDEBRAND E. E. 1984. Zur längerfristigen Wirkung von Düngungen auf Zuwachs, Ernährung und Gesundheitszustand in einem Fichten Bestand des Buntsandstein Odenwaldes. Mitt. Forstl. Versuchs- Forschungsanstalt Baden-Württemberg, Freiburg. 114: 1–42.
- KENNEDY R. 1966. Intra-increment variation and heritability of specific gravity, parallel-to-grain tensile strength, stiffness and tracheid length, in clonal Norway spruce. Tappi 49 (7): 292–296.
- KEPPLER L. D., BAKER C. J., ATKINSON M. M. 1989. Active oxygen production during a bacteria-induced hypersensitive reaction in tobacco suspension cells. Phytopathology 79: 974–978.
- KETNER P. 1966. Variability of recent and subfossil cones of *Picea excelsa* LK. in Southern Poland. A biometric study. Fragm. Flor. Geobot. 12: 373–386.
- KIELISZEWSKA-ROKICKA B., RUDAWSKA M., LESKI T. 1996. Wpływ glinu na wzrost grzybni i aktywność kwasnej fosfatazy ektomikoryzowych symbiontów sosny. In: SIWECKI R. (ed.). Reakcje biologiczne drzew na zanieczyszczenia przemysłowe, Materiały III Krajowego Sympozjum, Kórnik 1994. pp. 471–479.
- KIELISZEWSKA-ROKICKA B., RUDAWSKA M., STASZEWSKI T., KURCZYŃSKA E., KARLIŃSKI L., KUBIESA P. 2003. Ectomycorrhizal associations in Norway spruce stands influenced by long lasting air pollution (Silesian Beskid Mountains, Poland). Ekologia (Bratislava 22, Suppl. 1: 108–118).
- KIELLANDER C. L. 1950. Poliploidy in *Picea abies*, Hereditas 36 (4): 513–516. FA. 13 1951/52: 76]
- KIELLANDER C. L. 1951. Sortskillnader i 10-åriga fältförsök med svensk och mellaneuropeisk gran. Årsberätt. Fören. Växtförädl. Skogsträd 1950: 30–49. [FA. 13: 1121]
- KIELLANDER C. L. 1966. (Late-flushing spruce provenances in some Swedish provenance trials). Sveriges Skogs. Förb. Tidskr. 64 (8): 735–748. [FA. 28, 3655]
- KIELLANDER C. L. 1970a. Studies on populations in *Picea abies* (L.) KARST. with special regard to growth and frost resistance. Lund 1970, C. Bloms Boktryckeri A. – B.: 1–31.
- KIELLANDER C. L. 1970b. Frosthärdigheten i ett proveniensmaterial av gran. Sveriges Skog. Förb. Tidskr. 68 (1): 3–72.
- KIELLANDER C. L., NILSSON E. 1967. Skillnader i höstfrosthärdighet i ett proveniensmaterial av gran. Sveriges Skog. Förb. Tidskr. 65 (6): 625–631.
- KIELCZEWSKI B., BAŁAZY S. 1966. Zagadnienie drapieżnictwa roztoczy (*Acarina*) na jajach korników (*Scolytidae*, *Coleoptera*). Ekol. Pol., Ser. B 12 (2): 161–163.
- KIELCZEWSKI B., BAŁAZY S., SENICZAK S. 1973. Rola drapieżnych roztoczy w ograniczaniu liczebności szkodników w lesie. Zesz. Probl. Post. Nauk Roln. 144: 131–138.
- KIELCZEWSKI B., MICHALSKI J. 1962. Wpływ roztoczy (*Acarina*) na gęstość populacji ogłódków (*Scolytidae*). Zesz. Probl. Post. Nauk Roln. 35: 133–135.
- KIELCZEWSKI B., WIŚNIEWSKI J. 1983. Bark beetle acarofauna in different types of forest habitat. Part I and II. Introduction and *Mesostigmata*. Folia Forest. Polonica, Ser. A 25: 129–162.

- KIENAST F. 1982. Jahrringanalytische Untersuchungen in immissionsgefährdeten Waldschadensgebieten des Walliser Rhonentales. *Geogr. Helvetica* 3: 143–148.
- KIM Y. S. 1985. REM Beobachtungen immissionsgeschädigter Fichtennadeln. *Cbl. Ges. Forstw.* 102: 96–105.
- KIM Y. S., LEE J. K. 1990. Chemical and structural characteristics of conifer needles exposed to ambient air pollution. *Eur. J. For. Path.* 20 (4): 193–200.
- KIMLAND B., NORIN T. 1967. The oleoresin of Norwegian Spruce. *Acta Chem. Scand.* 21 (3): 825–826.
- KIN Z. 1971. Lignina – chemia i wykorzystanie. Warszawa.
- KINELSKI S., SZUJECKI A. 1959. Materiały do poznania chrząszczy (*Coleoptera*) fauny krajowej. *Polskie Pismo Entomol.* 29: 215–250.
- KING J. N., DANCİK B. P. 1983. Inheritance and linkage of isozymes in white spruce (*Picea glauca*). *Can. J. Genet. Cytol.* 25: 430–436.
- KING J., RUDOLF P. O. 1969. Development of white and Norway spruce trees from several seed sources 29 years after planting. *N. C. For. Exp. Sta., For. Ser. USDA, Res. Note NC – 70*.
- KINRAIDE T. B., PARKER D. R. 1989. Assessing the phytotoxicity of mononuclear hydroxy-aluminum. *Plant Cell Environ.* 12: 479–487.
- KLAHEHN F. U., WHEELER W. P. 1961. X-Ray study of artificial crosses in *Picea abies* (L.) KARST. and *Picea glauca* (Moench) Voss. *Silvae Genet.* 10: 71–77.
- KLAP J. M., VOSHAAR J. H. O., DE VRIES W., ERISMAN J. W. 2000. Effects of environmental stress on forest crown condition in Europe. IV: Statistical analysis of relationship. *Water, Air, Soil Poll.* 119: 387–420.
- KLASON P., HEIDENSTAM G. VON, NORLIN E. 1907, 1908. *Arkiv Kemi. Mineral Geol.* 1 (10).
- KLEIN J. I. 1977. Survival and growth of Norway spruce populations in Manitoba 14 years after planting. Information Report, Northern Forest Res. Centre, Canada, nr. NOR-X-179, 1–8. [FA. 39, 5086]
- KLEIN R. M. 1985. Effect of acidity and metal ions on water movement through red spruce. In: ADAMS D. D., PAGE W. P. (eds.). *Acid Deposition*. Plenum Publishing Corporation. pp.: 302–322.
- KLEINSCHMIT J. 1972a. Einfluß von Bodenheizung und Stecksubstrat auf die Bewurzelung von Fichten- und Douglasienstecklingen. *Forstarchiv* 43 (12): 250–255.
- KLEINSCHMIT J. 1972b. Möglichkeiten der Stecklingsvermehrung bei Nadelbaumarten. *Forstpfl. Forstsaamen* 12: 1–7.
- KLEINSCHMIT J. 1974. A programme for large scale cutting propagation of Norway spruce. *N.Z.J. For. Sci.* 4 (2): 359–366.
- KLEINSCHMIT J. 1982. Variation in mineral nutrient content between young plants of Norway spruce provenances and clones. *Silvae Genet.* 31 (2–3): 77–80.
- KLEINSCHMIT J. 1992. Use of spruce cuttings in plantations. *For. Comm. Bull.* 103: 1–10.
- KLEINSCHMIT J. 2000. Topics for cooperation with other European countries. In: TEISSIER DU CROSS E. (ed.). *Proceeding of the First Brain Storming Meeting, INRA, Orléans, France. Janvier 2000*. pp.: 33–34.
- KLEINSCHMIT J., KNIGGE W. 1967. Durch Umwelt und Erbanlagen bedingte Variation der Trocken-substanzerzeugung. Struktur und Rohdichte junger Fichten (*Picea abies* KARST.). *Papers XIV IUFRO Kongress, München III*. Pp.: 557–580.
- KLEINSCHMIT J., MÜLLER W., SCHMIDT J., RACZ J. 1973. Entwicklung der Stecklingsvermehrung von Fichte (*Picea abies* KARST.) zur Praxisreife. *Silvae Genet.* 22 (1–2): 4–13.
- KLEINSCHMIT J., SCHMIDT J. 1977. Experiences with *Picea abies* cuttings propagation in Germany and problems connected with large scale application. *Silvae Genet.* 26: 197–203.
- KLEINSCHMIT J., SVOLBA J. 1991. Variation im Wachstum von Fichtenstecklingen (*Picea abies* (L.) KARST.) in Niedersachsen. *Allg. Forst- Jagdztg.* 162 (1): 7–12. [FA. 54, 2107]
- KLEM G. G. 1956. Dyrkingsverdien av norsk og mellaneuropeisk gran. *Norsk Skogbr.* 2 (6): 181. [FA. 17, 3834]
- KLEM G. G. 1957. Kvalitetsundersøkelser av norsk og tysk gran. *Medd. Norsk. Inst. Skogforsk.* 14 (48): 285–314. [FA. 19, 1126]

- KLÍMA S. 1990. Porovnání růstu řízkovanců a stromů semenného původu druhu *Picea abies* (L.) KARST. Lesnictví 36: 531–540.
- KLIMEK R. 1959. Olejki roślinne. Warszawa.
- KLIMETZEK D., VITĚ P. 1989. Tierische Schädlinge. In: SCHMIDT-VOGT H. Die Fichte. II/2 – Krankheiten. Schäden. Fichtensterben. Verlag Paul Parey, Hamburg i Berlin. pp.: 40–133.
- KLUCZYŃSKI B. 1975. Wpływ związków fluoru na stan zdrowotny drzew i krzewów przy Hucie Aluminum “Konin”. Arbor. Kórnickie 20: 317–343.
- KLUK K. 1808. Dykcyonarz roślinny, 2. Drukarnia Xięży Piarów, Warszawa. 256 ss. Reprint: Wyd. Artystyczne i Filmowe, Warszawa 1985.
- KLUMPP G., GUDERIAN R., KÜPPERS K. 1989. Peroxidase- und Superoxiddismutase-Aktivität sowie Prolingehalte von Fichtennadeln nach Belastung mit O₃, SO₂ und NO₂. Eur. J. For. Path. 19: 84–97.
- KNABE W. 1976. Effects of sulfur dioxide on terrestrial vegetation. Ambio 5: 213–218.
- KNIGGE W., ASZMUTAT H., WEISS W. 1985. Verändern die Immissionsbelastungen die Holzeigenschaften unserer Wälder? Forstarchiv 56: 65–70.
- KNOWLES P., FURNIER G. R., ALEKSIUK M. A., PERRY D. J. 1987. Significant level of self-fertilization in natural populations of tamarack. Can. J. Bot. 65: 1087–1091.
- KNUDSEN M. V. 1956. A comparative study of some technological properties of Norway spruce in a provenance test. IUFRO 12th Congress. Oxford, Papers 4, sect. 41: 219–228.
- KOBAYASHI O., FUNADA R., FUKAZAWA K., OHTANI J. 1997. Abrupt growth changes in Norway spruce and Yezo spruce near an industrial district in Hokkaido, Japan. Trees 11: 183–189.
- KOBENDZA R. 1922. O wegetatywnym rozmnażaniu świerka (*Picea excelsa*) w Puszczy Białowiejskiej. Białowieża 2: 1–33.
- KOBLIHA J. 1993. Study of crossability within the genus *Picea* in Czechia with special respects on combination with Norway spruce. Norway spruce provenances and breeding. Proc. of IUFRO (S2.2–11). Symposium, Riga, Latvia: 219–223.
- KOCH H. G. 1958. Der Holzzuwachs der Waldbäume in verschiedenen Höhenlagen Thüringens in Abhängigkeit von Niederschlag und Temperatur. Arch. Forstwes. 7: 27–49.
- KOCH W., MAIER-MAERCKER U. 1986. Changes in the humidity response characteristics of *Picea abies* (L.) KARST. produced by fumigation with SO₂. Eur. J. For. Pathol. 16: 329–341.
- KOCOUREK R., BYSTRČAN A. 1989. Fine root and mycorrhizal biomass in Norway spruce (*Picea abies* (L.) KARSTEN) forest stands under different pollution stress. Agric. Ecosyst. Environ. 28: 235–242.
- KOCZAŃSKA J. 1970. Badania porównawcze anatomicznej budowy drewna świerkowego rezonansowego i nierezonansowego. Zesz. Nauk. WSR, Kraków, Leśnictwo 57 (5): 85–104.
- KOHNERT H. 1991. Neue Möglichkeiten bei der heterovegetativen Vermehrung von Waldbäumen durch die Chip-Veredlung. Die Holzzucht 45 (3 – 4): 30–32.
- KOKOCIŃSKI W. 2002. Anatomia drewna. Prodrak, Poznań, 162 pp.
- KOKOCIŃSKI W. 2004. Drewno – pomiary właściwości fizycznych i mechanicznych. Prodrak, Poznań. 201 pp.
- KOLLMANN F. 1951. Technologie des Holzes u. Holzwerkstoffe. Vol. 1, Tabl. V/2, V/4.
- KOMAROV V. L. 1934. *Gymnospermae*. W: KOMAROV V. I. (ed.). Flora URSS 1: 129–195. Nauka, Leningrad.
- KOMLENOVIĆ N., MARTINOVIĆ J., MILKOVIĆ S. 1969. Kloroza obične smreke u mladim kulturama na području vriština. Šum. List 93 (3/4): 92–103.
- KONDRATYUK E. N. 1986. Chorologiya flory Ukrainy. Naukova Dumka, Kiev. 272 pp.
- KÖNIG A. 1976. Some comments to the German Norway spruce trials IUFRO 1964/68 (no.13,14 and 15). Kongres IUFRO, Oslo, 1–2.
- KÖNIG A. 1981. Einige Ergebnisse aus dem IUFRO-Fichtenprovenienzversuch von 1964/68 in der Bundesrepublik Deutschland. Allg. Forstztg. (8).
- KÖNIG A. 1989. Correlations between growth data in the IUFRO 1964/68 Norway spruce provenance experiment. Inst. Forest Improvement, Uppsala. Rep. 11: 249–254.
- KONIGSHOFER H. 1989. Seasonal changes in polyamine content in different parts of juvenile spruce trees (*Picea abies* (L.) KARST.). J. Plant Physiol. 134: 736–740.

- KONIGSHOFER H. 1991. Distribution and seasonal variation of polyamines in shoot-axes spruce (*Picea abies* (L.) KARST.). J. Plant Physiol. 137: 607–612.
- KONNERT M. 1994. Überprüfung der Anzucht von Pflanzgut mit Hilfe der Isoenzymanalyse. Allg. Forst-Ztschr. 49 (5): 225–227.
- KONNERT M., FRANKE A. 1991. Die Fichte (*Picea abies* (L.) KARST.) im Schwarzwald: genetische Differenzierung von Beständen. Allg. Forst- Jagdztg. 162 (5–6): 100–106.
- KONŮPKA J., ŠIMAK M. 1990. Rast a statické vlastnosti výškových proveniencií smreka obyčajného na trvalých výskumných plochách v SR. Lesníctví 36 (10): 825–842.
- KOOP H. 1989. Forest dynamics. SILVI-STAR: a comprehensive monitoring system. Springer, Berlin. 229 pp.
- KÖPPEN T. 1889. Geographische Verbreitung der Holzgewächse des Europäischen Russlands und des Kaukasus, 2. Buchdruckerei der Kaiserlichen Akademie der Wissenschaften, St. Petersburg.
- KORABLEV V. N., FEDOTOVA L. T., SHABUROV V. I., SHIMKEVICH V. A. 1975. Rost eli razlichnogo geograficheskogo proischoydeniya v sedmiletnikh kul'turach v Permskom leskhoze. Trudy Inst. Ekol. Rast. Zhivot. 94: 132–144.
- KORABLEV V. N., KUPCHINSKIY V. L., ZHUK L. T., ZHUK M. I. 1976. Geograficheskie kul'tury eli evropejskoy v Sverdlovskoy oblasti. Lesa Urala i chvozhaystvo v nich 9: 172–176. [Ref. Zh. 12, 105]
- KORHONEN K. 1978a. Intersterility and clonal size in the *Armillariella mellea* complex. Karstenia 18: 31–42.
- KORHONEN K. 1978b. Intersterility groups of *Heterobasidion annosum*. Comm. Inst. For. Fenn. 94 (6): 1–25.
- KORNAŠ J. 1957. Rośliny naczyniowe Gorców. Monogr. Bot. 5: 3–258.
- KOROBKO P. V., SEVERSKAYA V. L., BEREZYUK L. I. 1983. Srovnitel'naya ocenka rosta sejanecv raznykh vidov eli v geograficheskikh posevach v Zailiyskom Alatau. Vsesoyuznoe soveshchanie po lesnoj genetike, selektsii i semenovodstvu 1–4. XI. 1983, Petrozavodsk 1: 150–152.
- KORPEL Š. 1981. Štruktúra, produkcia a regenerácia smrekových porastov v závislosti od nadmorskej výšky a vyvojovej fázy v SPR Pilsko. In: Prirodne pomery a charakteristika smrecin v komplexie Pilska. Zvolen. pp.: 63–93.
- KORPEL Š. 1989a. Pralesy Slovenska. Veda, Vyd. Slov. Akad. Ved, Bratislava, 329 pp.
- KORPEL Š. 1989b. Štruktúra, vyvoj, regenerácia, produkčné a funkčné schopnosti smrekových prírodných lesov na Babej Hore. In: Stav, vyvoj, produkčné schopnosti a funkčné využívanie lesov v oblasti Babej Hory a Pilska. Zvolen. pp.: 78–121.
- KORZENIEWSKI L. 1953. Wstęp do zagadnień zmienności świerka. Monogr. Bot. 1: 1–86.
- KOSIŃSKI G., GIERTYCH M. 1982. Light conditions inside developing buds affect floral induction. Planta 155: 91–94.
- KOSKI V. 1970. A study of pollen as a mechanism of gene flow in conifers. Comm. Inst. For. Fenn. 70 (4): 1–78.
- KOSKI V. 1971. Embryonic lethals of *Picea abies* and *Pinus sylvestris*. Comm. Inst. For. Fenn. 75.3.
- KOSKI V. 1983. Adaptation of trees to the variation in the length of the growing season. Plant production in the north. Proceed. f. Plant adaptation workshop. pp.: 267–276.
- KÖSTLER J. N., BRÜCKNER E., BIBELRIETHER H. 1968. Die Wurzeln der Waldbäume. Verlag P. Parey, Hamburg Berlin. pp.: 107–114.
- KÖSTLER N., MAYER H. 1970. Waldgrenzen im Berchtesgadener Land. Jahrb. Ver. Schutze Alpenfl. Tiere 35: 1–33.
- KOŠULIČ M. 1984. Autovegetativní množení smrku ztepilého (*Picea abies* KARST.) ve vegetačních obalech. Lesníctví 30 (11): 983–992.
- KOTTKE I. 1991. Electron energy loss spectroscopy and imaging techniques for subcellular localization of elements in mycorrhizas. Method. Microbiol. 23: 369–382.
- KOTTKE I., OBERWINKLER F. 1986. Mycorrhiza of forest trees. Structure and function. Trees 1: 1–24.
- KOTTKE I., OBERWINKLER F. 1987. The cellular structure and function of the HARTIG net: coenocytic and transfer cell-like organization. Nord. J. Bot., Sect. Mycol. 7: 85–95.
- KOTTKE I., WEBER R., RITTER T., OBERWINKLER F. 1993. Vitality of mycorrhizas and health status of trees in diverse forest stands in Western Germany. In: HÜTTL R. F., MUELLER-DOMBOIS D.

- (eds.). Forest Decline in the Atlantic and Pacific Region, 189–201. Springer Verlag, Berlin, Heidelberg.
- KOWALSKI M., WŁOCZEWSKI T. 1972a. Wzrost potomstwa różnych pochodzeń sosny i świerka na obcych stanowiskach. Sylwan 116 (8): 33–41.
- KOWALSKI M., WŁOCZEWSKI T. 1972b. Przebieg wzrostu wysokości potomstwa świerków pochodzących z różnych dzielnic Polski. Zesz. Nauk. SGGW, Leśnictwo 17: 7–29.
- KOZIOŁ C., KRUPSKI P. 1994. Niezwykła deformacja szyszki świerka pospolitego (*Picea abies* (L.) KARST. Rocz. Dendrol. 42: 129–130.
- KOZLOVSKAYA I. V., PARFENOV V. I. 1972. Chorologiya flory Belorussii. Nauka i Technika, Minsk. 310 pp.
- KOZLOWSKI T. T., CONSTANTINIDOU H. A. 1986. Environmental pollution and tree growth. Part. II. Factors affecting responses to pollution and alleviation of pollution effects. For. Abstr. 47: 105–132.
- KOZLOWSKI T., KRAMER P. J., PALLARDY G. 1991. The physiological ecology of woody plants. Academic Press Inc., San Diego ... Toronto. 657 pp.
- KOZUBOV G. M. 1974. Biologiya plodonosheniya khvoynykh na severe. Nauka, Leningrad.
- KOZUBOV G. M., RONIS E. J., IVONIS I. J., KONDRATEVA V. P., SAMUELSON K. P., ERIKSSON G., DUNBERG A. 1981. Biologicheskie osnovy tsveteniya i stimulirovaniya plodonosheniya eli. Izd. Kareliya, Petrozavodsk.
- KRAIGHER H. 1999. Diversity of types of ectomycorrhizae on Norway spruce in Slovenia. Phytos 39: 199–202.
- KRAIGHER H., HANKE D. E. 1996. Cytokinins in Norway spruce seedlings and forest pollution. Phytos 36: 57–60.
- KRAIGHER H., AGERER R., JAVORNIK B. 1995. Ectomycorrhizae of *Lactarius lignyotus* on Norway spruce, characterized by anatomical and molecular tools. Mycorrhiza 5: 175–180.
- KRAL F. 1961. Untersuchungen über den Nährstoffhaushalt von auf gleichem Standort erwachsenen Fichtenjungpflanzen in Abhängigkeit von ihrer Wuchsenenergie und Herkunft. Cbl. Ges. Forstw. 78 (1): 18–38.
- KRAL F. 1963. Über Reaktionsweisen von Fichten- und Lärchenherkünften auf Änderung des Lichtfaktors. Cbl. Ges. Forstw. 80 (4): 217–232.
- KRAMER H. 1986. Relation between crown parameters and volume increment of *Picea abies* stands damaged by environmental pollution. Scand. J. For. Res. 1 (2): 251–263.
- KRAMER P. J., KOZLOWSKI T. 1979. Physiology of woody plants. Academic Press Inc., Orlando ... Tokyo. 811 pp.
- KRAMER W., ULRICH B. 1985. A lime augmentation trial in the Syke Forest District. Forst-Holzwirt. 40 (6): 147–150, 152–154. [FA. 49, 3767]
- KRAPFENBAUER A., BODNER J., KNOLL T. 1985. Anomalien bei der immissionsgeschädigten Fichten. Cbl. Ges. Forstw. 102 (3): 150–160.
- KRAUSE C. R., HOUSTON D. B. 1983. Morphological variation in epicuticular wax of SO₂-sensitive and -tolerant eastern white pine clones. Phytopathology 73: 1266–1269.
- KREBB K. 1979. Ekofizjologia roślin. PWN, Warszawa. 213 pp.
- KREUTZER K. 1981. Der Einfluss der Düngung auf die forstliche Produktion und die dadurch entstehenden Umweltprobleme. Allg. Forst-Ztschr. 32: 816–821.
- KREUTZER K., HÜSER R. 1978. Der Einfluß der Waldbewirtschaftung auf die Wasserspende und die Wasserqualität. Forstw. Cbl. 97: 80–92.
- KRIEBITZSCH W. U., SCHOLZ F., PFADENHAUER J. 1996. Zur Wirkung erhöhter SO₂-konzentration auf den Gaswechsel von Fichtenklonen (*Picea abies* (L.) KARST.) aus dem Fichtelgebirge. Verh. Ges. Okol. 26: 121–126.
- KRIEK W. 1975. Fijnsparherkomstenonderzoek in Nederland. Uitvoerig Verslag 13 (2): 3–19.
- KROPAČEK K., KRISTINOVÁ M., CHMELIKOVÁ E., CUDLIN P. 1989. The mycorrhizal inoculation potential of forest soils exposed to different pollution stress. Agric. Ecosyst. Environ. 28: 271–277.
- KRÓL S., MICHALSKI J. 1961. Zaobserwowane szkodniki owadzie *Pinus contorta* var. *latifolia* Engelm. w Polsce i ich niektóre pasożyty. Folia Forest. Polonica, Ser. A 6: 127–140.

- KRUEGER K. W., RUTH R. H. 1969. Comparative photosynthesis of red alder, Douglas-fir, sitka spruce, and western hemlock seedlings. *Can. J. Bot.* 47: 519–527.
- KRUPIŃSKI K. 1995. Stratygrafia pyłkowa i sukcesja roślinności interglacjału mazowieckiego. *Acta Geogr. Lodziensia* 70: 1–200.
- KRUPSKI P., GIERTYCH M. 1995. Zmienność proveniencyjna i rodowa świerka pospolitego (*Picea abies* (L.) KARST.) z Polski północno-wschodniej na powierzchni doświadczalnej w Kórniku. *Arbor. Kórnickie* 40: 71–85.
- KRUPSKI P., GIERTYCH M. 1997. Analiza produktywności proveniencji i rodów świerka pospolitego (*Picea abies* (L.) KARST.) z niżu południowej Polski. *Arbor. Kórnickie* 42: 185–198.
- KRUPSKI P., GIERTYCH M., CZECH I. 1996. Interakcje genotypu ze środowiskiem świerka pospolitego (*Picea abies* (L.) KARST.) z Beskidu Śląskiego, Żywieckiego i Orawy. *Sylvan* 140 (9): 33–45.
- KRÜSSMANN G. 1972. *Handbuch der Nadelgehlze*. Paul Parey, Berlin, Hamburg.
- KRÜSSMANN G. 1964. *Die Baumschule*. Paul Parey, Berlin u. Hamburg.
- KRUTZSCH P. 1973. First results of the IPTNS in South Sweden. Preliminary report. IUFRO W. P. S2.02.11, Meet. Oslo, Norway, Aug. 73.
- KRUTZSCH P. 1974. The IUFRO 1964/68 Provenance Test with Norway Spruce (*Picea abies* (L.) KARST.). *Silvae Genet.* 23 (1–3): 58–62.
- KRUTZSCH P. 1975. Die Pflanzenschulenergebnisse eines inventierenden Fichtenherkunftsversuches (*Picea abies* KARST. und *Picea obovata* LEDEB.). *Skogshogskolan, Skogsgenetik. Res. Not.* 14: 1–64.
- KRUTZSCH P. 1986. An investigation on bud set in Norway spruce (*Picea abies*). Provenances and Forest Tree Breeding for High Latitudes. *Proc. Frans Kempe Symposium. Umeå, Sweden, Report.* 6: 21–31.
- KRZYSIK F. 1978. *Nauka o drewnie*. Warszawa.
- KRZYWICKI T. 1949. *Garbarstwo roślinne*. Warszawa.
- KUBIN E. 1977. The effect of clear cutting upon the nutrient status of a spruce forest in northern Finland. *Acta For. Fenn.* 155: 1–40.
- KUBISKE M. E., GODBOLD D. L. 2001. Influence of CO₂ on the growth and function of roots and root systems. In: KARNOSKY D. F., CEULEMANS R., SCARASCIA-MUGNOZZA G. E., INNES J. L. (eds.). *The Impact of Carbon Dioxide and Other Greenhouse Gases on Forest Ecosystems*, IUFRO Research Series 8, CABI Publishing. pp 147–191.
- KUCZYŃSKA I. 1972. Zbiorowiska leśne Gór Opawskich. *Acta Univ. Wratislav.* 149, *Prace Bot.* 14: 1–60.
- KUHN A. J., BAUCH J., SCHRÖDER W. H. 1995. Monitoring uptake and contents of Mg, Ca and K in Norway spruce as influenced by pH and Al, using microprobe analysis and stable isotope labeling. *Plant and Soil* 168–169: 135–150.
- KUKIER M. 1992. Wkraczanie świerka pospolitego (*Picea abies* (L.) KARST.) na torfowiska wysokie w Puszczy Białowieskiej. MSc. Thesis, Białowieska Stacja Geobotaniczna UW, Warszawa – Białowieża.
- KUKKOLA M. 1978. Lannoituksen vaikutus eri latvuskerrosten puiden kasvuun mustikkatypin kuusikossa. *Folia Forest. Inst. For. Fenn.* 362: 1–15.
- KULCZYŃSKI S. 1928. Zespoły roślin w Pieninach. *Bull. Acad. Pol. Sci. Lett., Cl. Sci. Math. Nat., Ser. B., Suppl.* 2: 57–203.
- KULCZYŃSKI S., WIERDAK S. 1928. Mapa zasięgu świerka. In: SZYMKIEWICZ D. *Botanika*. Jakubowski, Lwów. 912 pp.
- KULIG L. 1955. Zagospodarowanie zlewni potoków i dorzeczy rzek górskich pod kątem regulacji spływu wód. *Sylvan* 99 (3): 215–224.
- KUNDLER P. 1963. Einfluß verschiedenartiger Waldbestände auf die Bodenentwicklung. *Archiv Forstw.* 12 (7): 659–675.
- KÜNSTLE E. 1962. Das Höhenwachstum von Fichte, Tanne und Kiefer in Mischbeständen des östlichen Schwarzwaldes.
- KUOCH R., AMIET R. 1970. Die Verjüngung im Bereich der oberen Waldgrenze der Alpen mit Berücksichtigung von Vegetation und Ablegerbildung. *Mitt. Schw. Anst. Forstl. Versuchsw.* 46: 159–328.

- KUPCHINSKIY V. L., GORBUNOVA G. A., POPOV P. P. 1980. Geograficheskoe kul'tury eli obyknovnoy v sverdlovskoy oblasti. Les. Khoz. (3): 35–37.
- KÜPPERS K., KLUMPP G. 1987. Effects of ozone, sulfur dioxide, and nitrogen dioxide on gas exchange and starch economy in Norway spruce (*Picea abies* L. KARST.). Proc. 14th Int. Bot. Congr. 1987. Berlin.
- KURAKIN B. N. 1990. Izmenchivost' chisla semyadoley u prorostkov eli raznogo geograficheskogo proiskhozhdeniya. Les. Khoz. (11): 39–40. [Ref. Zh. 4.56.112]
- KURATA S. 1964. Illustrated Important Forest Trees of Japan, 22–26. Tokyo.
- KURATA S., HAMAYA T. 1971. Distribution maps of Japanese trees and shrubs, 1: 217–221. Tokyo.
- KURATA S., HAMAYA T. 1974. Distribution maps of Japanese trees and shrubs, 2: 165–166. Tokyo.
- KURDIANI S. Z. 1908. O sravnitel'noy sposobnosti nashikh lesnykh derev'ev k estestvennomu razmnozheniu pri pomoshchi cherenkov. Lesn. Zh. 38 (3): 306–315; ibidem 38 (5): 602–615.
- KWIATKOWSKI W. 1986. Roślinność leśna Puszczy Rominckiej i jej uwarunkowania środowiskowe. Ph.D. thesis, UAM, Poznań.
- LAATSCH W., ZECH W. 1967. Die Bedeutung der Beschattung fuer unzureichend ernaehrte nadelbaeume. Anal. Edafol. Agrobiol. 26: 691–702.
- LACASSAGNE M. 1934. Etude morphologique, anatomique et systematique du genre *Picea*. Toulouse.
- LACAZE J. F. 1968. Un épicéa tardif. Rev. For. Franc. 6: 401–406.
- LACAZE J. F. 1969a. Étude de la variabilité infraspécifique de l'épicéa (*Picea abies* KARST.) provenances françaises et polonaises résultats au stade juvénile. Ann. Sci. For. 26 (3): 345–396.
- LACAZE J. F. 1969b. Héritabilité du caractère debourrement végétatif dans une population d'épicéa du 2e plateau du Jura. Proc. 2nd World Consult. on For. Tree Breeding, Washington Fo-FTB 69 6/13.
- LACAZE J. F. 1970. Analyse d'une expérience multi-stationnelle de provenances d'épicéa (*Picea abies* KARST.). Ann. Sci. For. 27 (1): 5–37.
- LACAZE J. F., POLGE H. 1970. Relations phénotypiques au stade juvénile entre la densité du bois et divers caractères phénologiques et de vigueur chez *Picea abies* KARST. Ann. Sci. For. 27 (3): 231–242.
- LACAZE J. F., ARBEZ M. 1971. Variabilité intra-spécifique de l'épicéa (*Picea abies* KARST. partie septentrionale, de l'aire française). Héritabilité et corrélations génétiques de quelques caractères au stade juvénile. Ann. Sci. For. 28 (2): 141–183.
- LACAZE J. F., KOCIĘCKI S. 1979. Zmienność populacyjna świerka z Polski na powierzchniach we Francji i w Polsce. Sylwan 123 (6): 1–21.
- LADEFOGED K. 1958. The periodicity of wood formation. Biol. Skr. Kong. 7 (3): 1–98.
- LAFLAMME G. 1993. Symptoms of *Gremmeniella* spp. on pine, spruce, fir and larch. In: BARKLUND P., LIVSEY S., KARLMAN M., STEPHAN. R. (eds.). Shoot diseases of conifers Proc. IUFRO W.P. S2.06.02. 1993: 25–29. Proceedings of an International Symposium Garpenberg, Sweden, 10–15 June 1991. Meeting of the IUFRO Working Party S2.06.02. Canker and shoot blight of conifers. Uppsala 1993.
- LAGERBERG T. 1933. *Ascochyta parasitica* (HARTIG), en skadsevanppa Granplantor. Svenska Skogsv. Foren. Tidskr. 30: 1–10.
- LAGERCRANTZ U., RYMAN N. 1990. Genetic structure of Norway spruce (*Picea abies*): concordance of morphological and allozymic variation. Evolution 44: 38–53.
- LAGERCRANTZ U., RYMAN N., STÅHL G. 1988. Protein loci in diploid tissue of Norway spruce (*Picea abies* K.); description and interpretation of electrophoretic variability patterns. Hereditas 108: 149–158.
- LAIHO O. 1970. *Paxillus involutus* as a mycorrhizal symbiont of forest trees. Acta For. Fenn. 196: 1–72.
- ŁAKOMY P. 2001. The first record of *Armillaria mellea* sensu stricto in a forest ecosystem in Poland. Phytopathol. Pol. 21: 155–163.
- LALK I., HARTMANN A., DÖRFFLING K. 1992. Wirkung kurzzeitiger Schadgas-Expositionen (SO₂, NO₂, O₃) auf geklonte Jungfichten im Simulationsexperiment. In: MICHAELIS W., BAUCH J.

- (eds.). Luftverunreinigungen und Waldschäden am Standort "Postturm", Forstamt Farchau/Ratzeburg GKSS-Forschungszentrum Geesthacht GmbH, GKSS 92/E/100: 309–340.
- LANCHERT U., WILD A. 1995. Studies on the correlation of putrescine and potassium content in the needles of spruce trees. *J. Plant Physiol.* 147: 267–269.
- LANDOLT W., BUHLMANN U., BLEULER P., BUCHER J. B., FÜHRER J. 2000. Ozone exposure-response relationships for biomass and root/shoot ratio of beech (*Fagus sylvatica*) ash (*Fraxinus excelsior*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). *Environ. Poll.* 109: 473–478.
- LANG G. 1994. Quartäre Vegetationsgeschichte Europas. Gustav Fischer, Jena, Stuttgart, New York.
- LANGLET O. 1940 Om utvecklingen av granar ur frö efter självbefruktning och efter fri vindpollinering. *Medd. Skogsförsöksanst.*, Stockholm 32 (1): 1–22.
- LANGLET O. 1960. Mellaneuropeiska granprovenienser i svenskt skogsbruk. *Kungl. Skogs-Lantbruksakad. Tidskr.* 99 (5–6): 259–329.
- LANGLET O. 1963. Practical results and current problems in provenance research in Sweden (FAO/FORGEN 63), 1 (3/1): 1–10.
- LANGLET O. 1964. Proveniensiualets betydelse för produktion och skogsträdsförädling av gran. *Svenska Skogsv. Fören. Tidskr.* 62 (2): 145–155.
- LANGLET O. 1971. Two hundred years genecology. *Taxon* 20 (5/6): 653–752.
- LANGNER W. 1953. Eine Mendelspaltung bei *Aurea*-Formen von *Picea abies* (L.) KARST. als Mittel zur Klärung der Befruchtungsverhältnisse im Walde. *Z. Forstgenetik* 2: 49–51.
- LANGNER W., STERN K. 1964. Untersuchungen über den Austriebstermin von Fichten und dessen Beziehungen zu anderen Merkmalen. *Allg. Forst- Jagdztg.* 135: 53–60.
- LÄRCHER W. 1969. The effect of environmental and physiological variation on the carbon dioxide gas exchange of trees. *Photosynthetica* 3: 167–198.
- LÄRCHER W. 1994. Ökophysiologie der Pflanzen. Verlag Eugen Ulmer, Stuttgart.
- LÄRCHER W. 1995. Physiological plant ecology. Springer Verlag, Berlin-Tokyo. 506 pp.
- LARSEN C. M. 1946. Experiments with soft-wood cuttings of forest trees. *Forstl. Forsøgsv. Danmark* 17 (2): 289–443.
- LARSON P. R. 1964. Contribution of different-aged needles to growth and wood formation of young red pines. *For. Sci.* 10: 224–238.
- LAVRICHENKO V. M. 1968. Opredelenie potrebnosti lesa v udobrenii. *Les. Khoz.* (8): 41–43.
- LAWRENCE W. T., OECHEL W. C. 1983a. Effects of soil temperature on the carbon exchange of taiga seedlings. I. Root respiration. *Can. J. For. Res.* 13: 840–849.
- LAWRENCE W. T., OECHEL W. C. 1983b. Effects of soil temperature on the carbon exchange of taiga seedlings. II. Photosynthesis, respiration and conductance. *Can. J. For. Res.* 13: 850–859.
- LĂZĂRESCU C. 1966. Comportarea puieților de molid (*Picea abies* KARST.) în culturi comparative în funcție de condiție fizico – geografice ale stațiunilor de proveniență. *Rev. Padurilor* 81 (9): 487–492.
- LĂZĂRESCU C., BENEĂ V. 1973. New data regarding the international Norway spruce (*Picea abies* (L.) Karst.) provenances trial (1938) from Predeal – Romania. *Proc. IUFRO WP. S.2.02.11. Meet., Biri, Norway*: 15.
- LĂZĂRESCU C., CARNIAȚCHI A. 1963. Rezultatele experimentarii internationale de provenientie 1937 la molid în România. *Stud. Cerc. Inst. Cerc. For. București* 23 B: 49–58.
- LE TACON F., BOUCHARD D., PERRIN R. 1986. Effects of soil fumigation and inoculation with pure culture of *Hebeloma cylindrosporum* on survival, growth and ectomycorrhizal development of Norway spruce and Douglas fir seedlings. *Eur. J. For. Path.* 16: 257–265.
- LEAF A. L. 1970. America's oldest intensive forest fertilization experiments. *Adv. Front. Pl. Sci.* 24: 1–39.
- LEAL I., MISRA S., ATTREE S. M., FOWKE J. C. 1995. Effect of abscisic acid, osmoticum and desiccation on 11S storage protein gene expression in somatic embryos of white spruce. *Plant Sci. Lim.* 106: 121–128.
- LEANDERSON O. 1970. An unusual type of *Picea abies* found in S. Västergöthland. *Svensk Bot. Tidskr.* 64 (2): 196–197. [FA. 32, 2051]

- LECHNER F., HOLZER K., TRANQUILLINI W. 1977. Über Austrieb und Zuwachs von Fichtenklonen in verschiedener Seehöhe. *Silvae Genet.* 26 (1): 33–40.
- LEDIG F. T. 1986. Heterozygosity, heterosis, and fitness in outbreeding plants. In: SOULE M. E. (ed.) *Conservation Biology: The Science Scarcity and Diversity*. Sinauer, Sunderland, MA: 77–104.
- LEE S. CH. 1935. *Forest Botany of China*. Shanghai, 990 pp.
- LEEMANS R. 1991. Canopy gaps and establishment patterns of spruce (*Picea abies* (L.) KARST.) in two old-growth coniferous forests in central Sweden. *Vegetatio* 93: 157–165.
- LEEMANS R., PRENTICE I. C. 1987. Description and simulation of tree-layer composition and size distribution in a primaeval *Picea-Pinus* forest. *Vegetatio* 69: 147–156.
- LEHTO T., MÄLKÖNEN E. 1994. Effects of liming and boron fertilization on boron uptake of *Picea abies*. *Plant and Soil* 163 (1): 55–64.
- LEI J., DEXHEIMER J. 1988. Ultrastructural localization of ATPase activity in the *Pinus sylvestris* / *Laccaria laccata* ectomycorrhizal associations. *New Phytol.* 108: 329–334.
- LEIKOLA M., RAULO J., PUKKALA T. 1982. Männyn ja kuusen siemensadin vaihteluiden ennustaminen. *Folia Forest. Inst. For. Fenn.* 537: 1–43.
- LELU M. A. 1988. Variations morphologiques et génétiques chez *Picea abies* obtenus après embryogenèse somatique. *Ann. AFOCEL* 1987: 35–47.
- LEONARDI S., RADDI S., BORGHETTI M. 1996. Spatial autocorrelation of allozyme traits in a Norway spruce (*Picea abies*) population. *Can. J. For. Res.* 26: 63–71.
- LEPISTÖ M. 1974. Successful propagation by cuttings of *Picea abies* in Finland. *N. Z. J. For. Sci.* 4 (2): 367–370.
- LEPŠOVÁ A., MEJSTŘÍK V. 1989. Trace elements in fruit bodies of fungi under different pollution stress. *Agric. Ecosyst. Environ.* 28: 305–312.
- LESKI T., RUDAWSKA M., KIELISZEWSKA-ROKICKA B. 1995. Intraspecific aluminium response in *Suillus luteus* (L.) S. F. GRAY., an ectomycorrhizal symbiont of Scots pine. *Acta Soc. Bot. Pol.* 64 (1): 97–105.
- LETHO T. 1994. Effects of liming and boron fertilization on mycorrhizas of *Picea abies*. *Plant and Soil* 163: 65–68.
- LEVITT J. 1980. *Responses of Plants to Environmental Stresses*. 2nd ed., Academic Press, New York. 2 Vol.
- LEWANDOWSKI A., BURCZYK J. 2002. Allozyme variation of *Picea abies* in Poland. *Scand. J. For. Res.* 17: 487–494.
- LEWANDOWSKI A., BURCZYK J., CHALUPKA W. 1997. Preliminary results on allozyme diversity and differentiation on Norway spruce (*Picea abies* (L.) KARST.) in Poland based on plus tree investigations. *Acta Soc. Bot. Pol.* 66: 197–200.
- LEWANDOWSKI A., MEJNARTOWICZ L. 1994. Detection of close linkage between glutamate and isocitrate dehydrogenase allozyme loci in *Picea abies*. *Hereditas* 120: 281–282.
- LEWICKI I. 1985. Zmienność morfologiczna świerka *Picea abies* Karst. i jego drzewostanów przy górnej granicy lasu w Tatrzańskim Parku Narodowym. Ph.D. thesis, Forest Faculty, Poznań.
- LEWONTIN R. C. 1974. *The genetic basis of evolutionary change*. Columbia University Press. New York.
- LI H.-L. 1975. *Pinaceae*. In: *Flora of Taiwan*. Printed in Taiwan, 518 pp.
- LICHTENTHALER H. K., BUSCHMANN C. 1984. Beziehungen zwischen Photosynthese und Baumsterben. *Allg. Forstztg.* 39: 12–16.
- LIESE W., SCHNEIDER M., ECKSTEIN D. 1975. Histometrische Untersuchungen am Holz einer rauchgeschädigten Fichte. *Eur. J. For. Path.* 5: 152–161.
- LIHNEL D. 1942. Cenococcum graniforme als Hykorrhizabildungner von Waldbäumen. *Synab. Bof. Uppsäl.* 5: 1–18.
- LIIRI O. 1967. Spruce bark as raw material for practice board. *Teecl. Valt. Tekn. Tutkimusl* (seria 1 – Puu).
- LINDER S. 1972. Seasonal variation of pigments in needles. A study of Scots pine and Norway spruce seedlings grown under different nursery conditions. *Stud. Forest. Suec.* 100: 1–37.
- LINDER S. 1995. Foliar analysis for detecting and correcting nutrient imbalances in Norway spruce. *Ecol. Bull.* 44: 178–190.

- LINDGREN D., ERIKSSON G. 1976. Plantskoleförsök. Granförädlig. Breeding Norway spruce, Konf. Bogesund, Inst. f. skogsgenetik, Skogshögskolan, Stockholm: 1–15.
- LINDGREN K., EKBERG I., ERIKSSON G. 1977. External factors influencing female flowering in *Picea abies* (L.) Karst. Stud. Forest. Suec. 142.
- LINDQUIST B. 1939. Die Fichtenmykorrhiza im Lichte der modern Wuchstoffsorschung. Bot. Not.: 315–356.
- LINDQUIST B. 1948. The main varieties of *Picea abies* (L.) Karst. in Europe, with a contribution to the theory of a forest vegetation in Scandinavia during the last Pleistocene glaciation. Acta Horti Bergiani 14 (7): 249–342.
- LINDQUIST E. E. 1964. Mites parasiting eggs of bark beetles of the genus *Ips*. Can. Ent. 96: 125–126.
- LINDQUIST E. E. 1967. Mites and the regulation of bark beetle populations. Proc. Intern. Congres Acarol. 1967: 389–399.
- LINDQUIST E. E. 1969. Review of Holarctic tarsonemid mites (*Acarina: Prostigmata*) parasitizing eggs of ipine bark beetles. Mem. Ent. Soc. Canada, 60: 11 pp.
- LINDQUIST E. E. 1970. Relationship between mites and insects in forest habitats. Can. Ent. 102 (8): 978–984.
- LINES R. 1960. Studies of the indumentum of young shoots of Norway spruce in some Scottish provenance experiments. Rep. on For. Res. 1959. For. Comm.: 170–178.
- LINES R. 1973a. Inventory provenance test with Norway spruce in Britain: First results. For. Comm. Res. Develop. Paper 99: 1–11.
- LINES R. 1973b. International Norway spruce experiment at the Bin Huntley Forest Aberdeenshire. Results up to twenty-five years. For. Comm. Res. Develop. Paper 98: 1–5.
- LINES R. 1974. Summary report on the IUFRO 1938 Provenance experiments with Norway spruce, *Picea abies*, Karsten. For. Comm. Res. Develop. Paper 105: 1–12.
- LINES R. 1979. Results of the IUFRO 1964/68 experiments with *Picea abies* in Scotland after 11 years. Proc. IUFRO Joint Meet. WPs Norway spruce provenances and breeding. Bucharest: 41–50.
- LIPECKI J., DENNIS F. 1970. Kofaktory ukorzeniania się sadzonek. Wiad. Bot. 14 (2): 141–147.
- LISS B., BLASCHKE H., SCHÜTT P. 1984. Vergleichende Feinwurzeluntersuchungen an gesunden und erkrankten Aitfichten auf zwei Standorten in Bayern – ein Beitrag zur Waldsterbensforschung. Eur. J. For. Path. 14: 340–356.
- LITTLE E. 1971. Coniferales and Important Hardwoods. Atlas of U.S. Trees 3. Washington.
- LIU J. C., TRÜBY P. 1989. Bodenanalytische Diagnose von K- und Mg Mangel in Fichtenbeständen (*Picea abies* Karst.). Ztschr. Pflanzenernährung Bodenkunde 152 (4): 307–311.
- LIU T. S. 1982. A New Proposal for the Classification of the Genus *Picea*. Acta Phytotax. Sin. 33: 227–244.
- LO BUGLIO K.F. 1999. *Cenococcum*. In: CAIRNEY J. W. G., CHAMBERS S. M. (eds.). Ecto-mycorrhizal Fungi: key genera in profile. Springer, Berlin–Heidelberg–New York. pp.: 2887–309.
- LOBANOV N. W. 1960. Mikotrofnost' dreviesnykh rasteniy. Lesn. Promyshl., Moskwa 1971. 216 pp.
- LOCH J. 1991. Regeneracja drzewostanu górnoregłowego boru świerkowego zniszczonego przez zasnę wysokogórską *Cephalcia falleni* (DALM.) na przykładzie Mostownicy w Gorczańskim Parku Narodowym. Prądnik 4: 49–56.
- LOCH J. 1992. Regeneracja drzewostanu górnoregłowego boru świerkowego *Piceetum tatricum sub-normale* zniszczonego przez zasnę wysokogórską *Cephalcia falleni* DALM. w Gorczańskim Parku Narodowym. Parki Narod. Rez. Przyr. 11 (4): 39–49.
- LOCH J. 1998. Strategia życiowa jarzębu pospolitego – *Sorbus aucuparia* L. subsp. *aucuparia* L. – a dynamika drzewostanów świerczyny górnoregłowej. Zesz. Nauk AR, Kraków 332: 197–212.
- LOCHELET S. 1994. Bestimmung genetischer Merkmale von Fichten (*Picea abies* [L.] KARST.) mit unterschiedlich ausgeprägten Schadsymptomen auf baden-württembergischen Dauerbeobachtungsflächen. Allg. Forst- Jagdztg. 165 (2): 21–27.
- LOEWE A., EINIG W., HAMPP R. 1996. Coarse and fine control and annual changes of sucrose-phosphate synthase in Norway spruce (*Picea abies* (L.) KARST.) needles. Plant Physiol. 112: 641–649.

- LOEWE A., EINIG W., SHI L., DIZENGREMEL P., HAMPP R. 2000. Mycorrhization and elevated CO₂ both increase the capacity for sucrose synthesis in source leaves of spruce and aspen. *New Phytol.* 145: 565–574.
- LOKVENEC T. 1959/1960. Vegetativní rozmnožování smrku (*Picea excelsa* LINK) v Krkonoších. *Acta Dendrol. Českoslov.* 2: 71–82.
- LONGAUER R., GÖMÖRY D., PAULE L., KARNOSKY D. G., MANKOVSKA B., MÜLLER-STARCK G., PERCY K., SZARO R. 2001. Selection effects of air pollution on gene pools of Norway spruce, European silver fir and European beech. *Environ. Poll.* 115 (3): 405–411.
- LONGMAN K. A. 1989. *Picea*. In: HALEVY. A. H. (ed.). *CRC Handbook of Flowering*. CRC Press, Inc. Boca Raton, Florida, 6: 522–537.
- LÖSEL D. M. 1988. Fungal lipids. In: RATLEDGE C., WILKINSON S. G. (eds.). *Microbial lipids*, 1: 699–806. Academic Press, London.
- LOVELESS M. D., HAMRICK J. L. 1984. Ecological determinants of genetic structure in plant populations. *Ann. Rev. Ecol. Syst.* 15: 65–95.
- LUBLINERÓWNA K. 1934. Analizy pyłkowe torfowisk pasa bezświerkowego. *Inst. Bad. Lasów Państwowych, Ser A* 5: 1–40.
- LUCAS P. W., DIGGLE P. J. 1997. The use of longitudinal data analysis to study the multi-seasonal growth response of Norway and Sitka spruce to summer exposure to ozone: implications for the determination of critical levels. *New Phytol.* 137: 315–323.
- LÜDEMANN G. 1978. Die Rolle der deutschen Forstbaumschulen bei der Herkunftssicherung forstlichen Saat- und Pflanzgutes. *Allg. Forstztg.* 37: 32–35.
- LUMME I., SOMOLANDER A. 1996. Effect of nitrogen deposition level on nitrogen uptake and bud burst in Norway spruce (*Picea abies* KARST.) seedlings and N uptake by soil microflora. *For. Ecol. Managm.* 89: 197–204.
- LUNDKVIST K. 1974. Analysis of linkage in *Picea abies* by means of isozyme analysis. *Proc. Of the IUFRO joint meeting of working parties on population and ecological genetics, breeding, theory and progeny testing*. Stockholm.
- LUNDKVIST K. 1979. Allozyme frequency distributions in four Swedish populations of Norway spruce (*Picea abies* K.) I. Estimations of genetic variation within and among populations, genetic linkage and a mating system parameter. *Hereditas* 90: 127–143.
- LÜTZ C., HEINZMANN U., GULZ P. G. 1990. Surface and epicuticular wax composition of spruce needles after long-term treatment with ozone and acid mist. In: BLANK L. W., LUTZ C. (eds.). *Tree exposure experiments in closed chambers*. *Environ. Poll.* 64 (3–4): 313–322.
- LÜTZ C., STEIGER A., GODDE D. 1992. Influence of air pollutants and nutrient on D-1 protein content and photosynthesis in young spruce trees. *Physiol. Plant.* 85 (4): 611–617.
- LUUKKANEN O. 1979. Hormonal treatment increases flowering of Norway spruce grafts grown in a plastic greenhouse. *Ann. Rep. Found. Forest Tree Breeding, Finland*: 20–26.
- LUUKKANEN O., RÄSÄNEN P. K., YLI-VAKKURI P. 1971. Neulasten väri myöhemmän kasvun ja lannoitusvaikutuksen ilmaisijana. *Silva Fenn.* 5 (4): 297–313.
- LVOV P. N., KLIMOV R. N. 1971. O kachestve drevesiny eli i listvennicy kraynego severo-vostoka Komi ASSR. *Lesn. Zh.* 14 (4): 124–125.
- MADRONICH S. 1993. The atmosphere and UV-B radiation at ground level. In: YOUNG A. R., BJÖRN L. O., MOAN J., NULTSCH W. (eds.) *Environmental UV photobiology*. Plenum Press, New York and London. pp.: 1–39.
- MADSEN S. F. 1989. Afkom af danske rødgranbevoksninger. *Det forstlige forsøgsvæsen i Danmark*. *Rep.* 42 (3): 151–213.
- MAERCKER U. 1965. Zur Kenntnis der Transpiration der Schließzellen. *Protoplasma* 60: 61–78.
- MAGEL E., ZIEGLER H. 1986. Einflu von Ozon und saurem Nebel auf die Struktur der stomatären Wachsprossen in den Nadeln von *Picea abies* (L.) KARSTEN. *Forstw. Cbl.* 105: 234–238.
- MAGNESEN S. 1969. Experimental – økologiske undersøkelser over vekstavslutningen hos frøplanter av gran (*Picea abies* (L.) KARST.) 1. Virkning av daglengde og vekstsesongens varmekold. *Medd. Vestland. Forstl. Forsøksst.* 48: 1–50.
- MAGNESEN S. 1971. Experimental – økologiske undersøkelser over vekstavslutningen hos frøplanter av gran (*Picea abies* (L.) KARST.) 2. Virkning av daglengde og vekstsesongens

- varmeforkold om høsten og perioder med lav natt-temperatur. Medd. Vestland. Forstl. Forsøksst. 51: 223–269.
- MAGNESEN S. 1972. Experimental – økologiske undersøkelser over vekstavlutningen hos frøplanter av gran (*Picea abies* (L.) KARST.). Medd. Vestland. Forst. Forsøksst. 52: 271–317.
- MAGNESEN S. 1977. Growth chamber experiments used in provenance research. Experimental Genetics. Dept. For. Genet. Res. Not. 27: 11–17.
- MAGNESEN 1996.
- MAHMOOD S., FINLAY R. D., ERLAND S. 1999. Effects of repeated harvesting of forest residues on the ectomycorrhizal community in a Swedish spruce forest. New Phytol. 142: 577–585.
- MAI D. H. 1995. Tertiäre Vegetationsgeschichte Europas. Gustav Fischer, Jena, Stuttgart, New York.
- MAIER-MAERCKER U. 1983. The role of peristomatal transpiration in the mechanism of stomatal movement. Plant Cell Environ. 6: 369–380.
- MAIER-MAERCKER U. 1986. Histological studies on the bundle sheath in needles of *Picea abies* (L.) KARST. diseased or fumigated with SO₂. Eur. J. For. Pathol. 16: 352–359.
- MAIER-MAERCKER U. 1989. Delignification of subsidiary and guard cell walls of *Picea abies* (L.) KARST. by fumigation with ozone. Trees 3: 57–64.
- MAIER-MAERCKER U., KOCH W. 1986. Delignification of subsidiary and guard cell walls by SO₂ and probable implication on the humidity response of *Picea abies* (L.) KARST. Eur. J. For. Pathol. 16: 342–351.
- MAIER-MAERCKER U., KOCH W. 1992. The effect of air pollution on the mechanism of stomatal control. Trees 7 (1): 12–25.
- MAKAREVA T. A. 1968. Vliyaniye razlichnykh faktorov na znachenie akusticheskoy konstanty rezonansovoy drevesiny. Drevo Obrabot. Promyshl. 17 (10): 14–15.
- MAKKONEN-SPIECKER K. 1985. Auswirkung des Aluminiums auf junge Fichten (*Picea abies* KARST.) verschiedener Provenienzen. Forstw. Cbl. 104: 341–353.
- MALHOTRA S. S., KHAN A. A. 1980. Effects of sulphur dioxide and other air pollutants on acid phosphatase activity in pine seedlings. Biochem. Physiol. Pflanzen. 175: 228–236.
- MÄLKÖNEN E. 1971. Fertilizer treatment and seed crop of *Picea abies*. Comm. Inst. For. Fenn. 73.4.
- MAMAEV S. A., TISHECHKIN A. N., KUPCHINSKIY V. L. 1982. Rost geograficheskikh kul'tur eli na Srednem Urale. Lesoved. (6): 55–62.
- MAMAKOWA K. 1989. Late middle Polish glaciation, Eemian and Early Vistulian vegetation at Imbramowice near Wrocław and the pollen stratigraphy of this part of the Pleistocene in Poland. Acta Paleobot. 29 (1): 11–176.
- MANDRE M. 2002. Relationships between lignin and nutrients in *Picea abies* L. under alkaline air pollution. Water, Air, Soil Poll. 133: 361–377.
- MANDRE M., KLOSEIKO J., OTS K. 2000. The effect of cement dust on the growth, content of nutrients and carbohydrates in various organs of five conifer species. Baltic For. 6: 16–23.
- MANDRE M., OTS K. 1999. Growth and biomass partitioning of 6-year-old spruce under alkaline dust impact. Water, Air, Soil Poll. 114: 13–25.
- MANDRE M., TUULMETS L. 1997. Pigment changes in Norway spruce induced by dust pollution. Water, Air, Soil Poll. 91: 247–258.
- MANGALIS I. 1969. Izucheniye vliyaniya udobreniy na rost sazhencev eli. Voprosy lesnoj selektsii i semenovodstva v Latvishskoy SSR, Riga: 229–239.
- MANNINEN S., HUTTUNEN S. 2000. Response of needle sulphur and nitrogen concentrations of Scots pine versus Norway spruce to SO₂ and NO₂. Environ. Poll. 107: 421–436.
- MANSFIELD T. A. 1998. Stomata and plant water relations: does air pollution create problems?. Environ. Poll. 101: 1–11.
- MAŃKA K. 1953. Badania terenowe i laboratoryjne nad opieńką miodową – *Armillaria mellea* (VAHL.) QUEL. Prace IBL, Warszawa 94: 1–96.
- MAŃKA K. 1961. Rozwój opieńki miodowej (*Armillaria mellea* [VAHL.] QUEL.) na tle biotycznych właściwości mikoflory korzeniowej świerka (*Picea excelsa* L.). Roczn. WSR, Poznań 10: 21–74.

- MAŃKA K. 1986. Trzebieże jako zabiegi przeciwdziałające występowaniu huby korzeni (*Heterobasidion annosum* [FR.] BREF.) i zamieraniu pędów sosny (*Gremmeniella abietina* [LAGERB.] MORELET). Sylwan 130 (7): 1–8.
- MAŃKA K. 1990. Saprofityczna mikoflora środowiska glebowego a zdrowotność roślin. Phytopath. Pol. 11: 122–134.
- MAŃKA K. 1995. Fitopatologia leśna. 5 ed., PWRiL, Warszawa. 367 pp.
- MAŃKA K., DYSPOŁSKA W., MAŃKA M., SZURKOWSKI L. 1974. Wpływ szerokości słoików drewna pniakowego i siedliska leśnego na porażenie pniaków sosny zwyczajnej przez grzyb *Fomes annosus* (FR.) CKE. Roczn. Nauk Roln., Ser. E 4 (2): 97–107.
- MAŃKA K., KWAŚNA H., BABKIEWICZ M., KAZIMIERCZAK T. 1991. Biotic resistance of soil to plant pathogens. In: Biotic interactions and soil-borne diseases. Developments in agricultural and managed forest ecology. 23: 311–315.
- MAŃKA K., MAŃKA M. 1993. Choroby drzew i krzewów leśnych. Wydawnictwo Świat, Warszawa. 86 pp.
- MAŃKA K., MAŃKA M., KWAŚNA H., ŁAKOMY P., BABKIEWICZ M. 1993b. Zagrożenie sadzonek drzew leśnych przez patogeny korzeni a zbiorowiska grzybów ryzosferowych. Materiały z IV Konferencji Sekcji Biologicznych Metod Ochrony Roślin przed Chorobami PTFit., Skierniewice 22–23 kwietnia 1993: 7–13.
- MAŃKA K., PRZEBÓRSKI A. 1972. Wpływ korowania pniaków sosny zwyczajnej na ich zakażenie przez grzyb *Fomes annosus*. Prace Kom. Nauk Rol. i Kom. Nauk Leśn. PTPN 34: 127–131.
- MAŃKA K., PRZEBÓRSKI A. 1974. *Fomes annosus* (FR.) COOKE and *Peniophora gigantea* (FR.) and other fungi colonising stumps of *Pinus sylvestris* L. Proceedings of the Fourth International Conference on *Fomes annosus*, Athens–Georgia, September 17–22, 1973, IUFRO-Section 24: 251–259.
- MAŃKA K., PRZEBÓRSKI A., PUKACKI P. 1972. Okresy zagrożenia i braku zagrożenia pniaków sosny zwyczajnej przez grzyb *Fomes annosus*. Prace Kom. Nauk Rol. i Kom. Nauk Leśn. PTPN 34: 133–140.
- MAŃKA K., ŁAKOMY P. 1995. Effect of thinning in Scots pine (*Pinus sylvestris* L.) stand growing on former arable land, on suppressiveness of soil to *Heterobasidion annosum* (FR.) BREF. and *Armillaria obscura* (SCHAEFF.) HERINK. Phytopath. Pol. 9 (21): 45–51.
- MAŃKA M., ŁAKOMY P., MAĆKOWIAK Sz. 1993a. Effect of thinning in Scots pine (*Pinus sylvestris* L.) stand growing on forest land, on suppressiveness of soil to *Heterobasidion annosum* (FR.) BREF. and *Armillaria obscura* (SCHAEFF.) HERINK. Phytopath. Pol. 6 (18): 55–60.
- MARCO H. F. 1939. The anatomy of spruce needles. J. Agric. Res. 58: 357–368.
- MAREK M., LOMSKÝ B. 1987. Vliv odlišných forem hnojení amonným dusíkem na fotosyntetickou produktivitu různých proveniencí smrku ztepilého (*Picea abies* (L.) KARST.). Lesnictví 33 (2): 109–120.
- MARKS G. C., FOSTER R. C. 1972. Structure, morphogenesis and ultrastructure of ectomycorrhiza. In: MARKS G. C., KOZLOWSKI T. T. (eds.). Ectomycorrhizae, pp. 2–35, Academic Press, London.
- MARKS G. C., FOSTER R. C. 1973. Structure, Morphogenesis, and Ultrastructure of Ectomycorrhizae. In: MARKS G. C., KOZLOWSKI T. T. (eds.). Ectomycorrhizae, their ecology and physiology. Academic Press, New York, London. pp.: 79–105.
- MARQUARD R. D., HANOVER J. W. 1984. Relationship between gibberellin A4/7 concentration, time of treatment and crown position on flowering *Picea glauca*. Can. J. For. Res. 14: 547–553.
- MARSCHNER H., HÄUSSLING M., GEORGE E. 1991. Ammonium and nitrate uptake rates and rhizosphere pH in non-mycorrhizal roots of Norway spruce [*Picea abies* (L.) KARST.]. Trees 5 (1): 14–21.
- MARSCHNER P., HENTSCHEL E., KLAM A., JENTSCHKE G., GODBOLD D. L. 1992. Einfluß von Aluminium und Blei auf Mykorrhizapilze und mykorrhizierte Fichtenkeimlinge. Proceedings of IUFRO Congress on Air Pollution and Interactions between Organisms in Forest Ecosystems. Sept. 9–11. 1992. pp. 228–237.
- MARTIN F., RUBINI P., COTE R., KOTTKE I. 1994. Aluminium polyphosphate complexes in the mycorrhizal basidiomycete *Laccaria bicolor*: A ²⁷Al-nuclear magnetic resonance study. Planta 194: 241–246.

- MARX D. H. 1977. Tree host range and world distribution of the ectomycorrhizal fungus *Pisolithus tinctorius*. Can. J. Microbiol. 23: 217–223.
- MARX D. H., CORDELL C. E., KENNEDY D. S., MEXAL J. G., ARTMAN S. D., RIFFLE J. W., MOLINA R. J. 1984. Commercial vegetative inoculum of *Pisolithus tinctorius* and inoculation techniques for development of ectomycorrhizae on bare-root seedlings. Forest Sci. Monograph 25.
- MASCHNING E., LANGNER W. 1971. Ergebnisse einer 13-jährigen Nachkommenschaftsprüfung bei Fichte. Allg. Forst-Ztschr. 26 (39): 793–794.
- MASSEY C. L. 1974. Biology and taxonomy of nematode parasites and associates of bark beetles in the United States. U. S. Forest Service, Agricult. Handbook 446.
- MATERNA J. 1960. Príspevek k otázke výživy smrku na šumavský rašelinistič. Sborn. Čsl. Akad. Zemid. (Lesn.) 6 (6): 495–504.
- MATERNA J. 1962. Kupfer-, Zink- und Mangangehalte in Fichtenbeständen. Dt. Akad. Landwirtsch.-Wiss. Berlin, Tag.-Ber. 50: 45–52.
- MATERNA J. 1989. Mineral nutrition of Norway spruce stands in the western part of Czechoslovakia. Lesnictvi 35 (11): 975–982.
- MATHE P. 1985. Mitwirkung von Epibiosen in belasteten Waldökosystemen. Allg. Forstztg. 27: 674–675.
- MATRAS J. 1993. Growth of Norway spruce in IUFRO 1972 experiment. Norway spruce provenances and breeding. Proc. of IUFRO S2.2.11 Symposium, Riga, Latvia: 100–104.
- MATSCHKE J., SCHACHLER G., NÖHRING E. 1991. Ein Beitrag zur Rejuvenilisierung bei *Picea abies*. Die Holzzucht 45 (1/2): 1–5.
- MATUSZKIEWICZ J. 1977. Przegląd fitosocjologiczny zbiorowisk leśnych Polski. Cz. 4. Bory świerkowe i jodłowe. Phytocoenosis 6 (3): 149–227.
- MATUSZKIEWICZ J. M. 1988. Przegląd fitosocjologiczny zbiorowisk leśnych Polski. Bory mieszane i acidofilne dąbrowy. Fragm. Flor. Geobot. 33 (1–2): 107–190.
- MATUSZKIEWICZ J. M. 2001. Zespoły leśne Polski. Wyd. Nauk. PWN, Warszawa. 358 pp.
- MATUSZKIEWICZ W. 2001. Przewodnik do oznaczania zbiorowisk roślinnych Polski. Wyd. Nauk PWN, Warszawa. 537 pp.
- MATUSZKIEWICZ W., FAŁIŃSKI J. B., KOSTROWICKI A. S., MATUSZKIEWICZ J. M., OLACZEK R., WOJTERSKI T. (ed.). 1995. Potencjalna roślinność naturalna Polski. Mapa przeglądowa 1:300 000. WZKart., Warszawa. 12 map.
- MATUSZKIEWICZ W., MATUSZKIEWICZ A. 1960. Pflanzensociologische Untersuchungen der Waldgesellschaften des Reisengebirges. Acta Soc. Bot. Pol. 29 (3): 499–530.
- MATUSZKIEWICZ W., MATUSZKIEWICZ J. M. 1996. Przegląd fitosocjologiczny zbiorowisk leśnych Polski. Phytocoenosis 8, NS, Sem. Geobot. 3: 3–79.
- MATUSZKIEWICZ W., MATUSZKIEWICZ A. 1975. Mapa zbiorowisk roślinnych Karkonoskiego Parku Narodowego. Ochr. Przyr. 40: 45–112.
- MATUSZKIEWICZ W., MATUSZKIEWICZ A. 1967. Zespoły roślinne Karkonoskiego Parku Narodowego. Cz. 1. Zbiorowiska leśne. Prace Wrocł. Tow. Nauk., Ser. B 135: 1–99.
- MATZNER E. 1985. Auswirkungen von Düngung und Kalkung auf den Elementumsatz und die Elementverteilung in zwei Waldökosystemen im Solling. Allg. Forst-Ztschr. 43: 1143–1147.
- MATZNER E., MURACH D., FORTMANN H. 1986. Soil acidity and its relationship to growth in declining forest stands in Germany. Water, Air, Soil Poll. 31: 273–282.
- MAUER O., PALATKOVA E. 1989. Minimalizace mechanomorfoz korenoveho systemu krytokorenneho sadebniho materialu smrku ztepileho (*Picea abies* L. KARSTEN) aplikaci rustovych latek. Acta Univ. Agric., Fac. Silv. 58: 25–45.
- MAUER O., PALÁTKOVÁ E. 1994. Vývoj kořenového systému řízkovanců smrku obecného [*Picea abies* (L.) KARST.] do dvaceti pítí let po výsadbě. Lesnictví 40: 298–306.
- MAYER H. 1969. Zur waldbaulichen Beurteilung der Fichte in den Ostalpen. Allg. Forst- Jagdztg. 140: 204–209, 226–231.
- MAYER H. 1976. Gebirgswaldbau, Schutzwaldpflege. Gustav Fischer, Stuttgart.
- MAYER H. 1984. Wälder Europas. G. Fischer, Stuttgart–New York. 691 pp.
- MAYER-KRAPOLL H. 1964. Die Düngung im Walde, Auswertung langjähriger Versuche und Erfahrungen. Düsseldorf.

- MAYER-KRAPOLL H. 1968. Empfehlungen für die Walddüngung. Eine Auswertung langjähriger Versuche. 2. erweiterte Auflage. Düsseldorf.
- MAYR H. 1906. Fremdländische Wald- und Parkbäume für Europa. Paul Parey, Berlin.
- MAZUR A. 1996. Drapieżcy i pasożyty kornika drukarza (*Ips typographus* L.) i cetyńca większego (*Tomicus piniperda* L.). Mscr. Dyrekcja Generalna Lasów Państwowych, Warszawa. pp. 68–74.
- MAZZARINO M. J., HEINRICH S., FÖLSTER H. 1983. Holocene versus accelerated actual proton consumption in German forest soil. In: ULRICH B., PANKRATH W. (eds.). Effects of Accumulation of Air Pollutants in Forest Ecosystems. Reidel Publishing Company, Dordrecht. pp.: 113–123.
- MCCORMICK L. H., STEINER K. C. 1978. Variation in aluminum tolerance among six genera of trees. For. Sci. 24: 565–568.
- MCCREIGHT J. D., SCHROEDER D. B. 1982. Inhibition of growth of nine ectomycorrhizal fungi by cadmium, lead and nickel *in vitro*. Environ. Exp. Bot. 22: 1–7.
- MEAD D. J., TAMM C. O. 1988. Growth and stem form changes in *Picea abies* as affected by stand nutrition. Scand. J. For. Res. 3 (4): 505–513.
- MEĐEDOVIĆ S. 1987. Ožiljavanje reznica smrče u cilju razvijanja tehnologije masovne proizvodnje sadnica. Šumarstvo i prerada drveta, Sarajevo 41 (1–3): 27–33.
- MEDWECKA-KORNAŚ A. 1955. Zespoły leśne Gorców. Ochr. Przyr. 23: 1–111.
- MEDWECKA-KORNAŚ A. 1977. Zespoły leśne i zaroślowe. In: SZAFER W., ZARZYCKI K. (eds.). Szata roślinna Polski PWN, Warszawa. pp.: 383–441.
- MEHMANN B., EGLI S., BRAUS G. H., BRUMMER I. 1995. Coincidence between molecularly or morphologically classified ectomycorrhizal morphotypes and fruitbodies in a spruce forest. In: Stocchi V. (ed.). Biotechnology of Ectomycorrhizae. Plenum Press, New York. pp.: 41–52.
- MEHNE B. 1990. Propfersuche mit Reiseren grüner und vergilbter Fichten (*Picea abies* [L.] KARST.) aus Waldschadengebieten. Allg. Forst- Jagdztg. (5): 96–103, ibidem (6/7): 129–136.
- MEHUS H. 1986. Fruit body production of macrofungi in some Norwegian forest types. Nord. J. Bot. 6: 679–701.
- MEIER S., GRAND L. F., SCHOENEBERGER M. M., REINERT R. A., BRUCK R. I. 1990. Growth, ectomycorrhizae and nonstructural carbohydrates of loblolly pine seedlings exposed to ozone and soil water deficit. Environ. Poll. 64: 11–27.
- MEIER S., ROBARGE W. P., BRUCK R. I., GRAND L. F. 1989. Effects of simulated rain acidity on ectomycorrhizae of red spruce seedlings potted in natural soil. Environ. Poll. 59: 315–324.
- MEJNARTOWICZ L. 1983. Changes in genetic structure of Scots pine (*Pinus sylvestris* L.) population affected by industrial emission of fluoride and sulphur dioxide. Genet. Polonica 24: 41–50.
- MEJNARTOWICZ L. 1984. Enzymatic investigations on tolerance in forest trees. In: KOZIOŁ M. J., WHITLY F. R. (eds.). Gaseous Air Pollutants and Plant Metabolism. London–N.Y.: 381–398.
- MEJNARTOWICZ L. 1986. Genotypes of Scots pine trees differing in resistance to the action of fluoride and sulphur dioxide described on the basis of glutamatic-oxalacetic-transaminase isoenzymes. Acta Univ. Lodziensis, Folia Physiol. Cytol. Genet. 1: 139–146.
- MEJNARTOWICZ L., PALOWSKI B. 1989. Studies of Scots pine populations in polluted and clear areas. In: Genetic Effects of Air Pollutants in Forest Tree Populations.: 115–125. Eds. F. SCHOLZ, H. R. GREGORIUS, D. RUDIN. Springer Verlag, Berlin, New York, London, Tokyo.
- MEJSTRÍK V., KOCOUREK R. 1992. Fine and mycorrhizal root biomass of *Picea abies* growing in different emission conditions. In: TESCHE M., FEILER S. (eds.). Air Pollution and Interactions between Organisms in Forest Ecosystems. Proceedings of 15th International Meeting of Specialists in Air Pollution Effects on Forest Ecosystems, Tharandt/Dresden, September 9–11, 1992. pp.: 211–222.
- MEL'NYK V. I. 1993. Ostřivni jalinniki Ukrains'kogo Polissya [The island Norway spruce forests in the Ukrainian Polissya]. Naukova Dumka, Kijiv. 104 pp. (in Ukrainian).
- MELCHIOR G. H. 1987. Increase in flowering of Norway spruce (*Picea abies*) by known rootstocks and planting grafts in southern sites. For. Ecol. Managm. 19: 23–33.
- MELIN E. 1922. On the mycorrhizas of *Pinus sylvestris* and *Picea abies*. A preliminary note. J. Ecol. 9: 254–257.

- MELIN E. 1923. Experimentelle Untersuchungen über die Konstitution und ökologie der Mykorrhizen von *Pinus sylvestris* L. und *Picea abies* (L.) KARST. Mykolog. Unters. Berichte 2: 73–331.
- MELIN E. 1924. Über den Einfluss der Wasserstoffionenkonzentration auf die Virulenz der Wurzelpilze von Kiefer und Fichte. Bot. Not.: 38–48.
- MELIN E. 1925. Untersuchungen über die Bedeutung der Baummykorrhiza. Eine ökologische-physiologische Studie. Gustav Fischer Verlag, Jena. 125 pp.
- MELIN E. 1963. Some effects of forest tree roots on mycorrhizal *Basidiomycetes*. Symposia of the Society for General Microbiology 13: 125–146.
- MELZER E. W. 1980. Ergebnisse einer Nachdüngung auf einem im Kulturstadium technisch-biologisch meliorierten Standort. Arch. Acker- Pflanzenbau Bodenkd. 24 (5): 317–322.
- MELZER E. W., KARGE A. 1991. Langzeitwirkungen von Adaptationen in Fichtenjungpflanzen. Forstarchiv 62 (2): 70–73. [FA. 54, 1863]
- MELZER E. W., LUCKE E. 1984. Wirkung von Mineraldüngung, Lupineneinsaat und Baumartenmischung auf den Zuwachs der Fichte (*Picea abies* (L.) Link) in der Jugendphase. Arch. Acker- u. Pflanzenbau u. Bodenkd. 28 (12): 763–768.
- MERGEN F. 1960. Variation and heritability of physiological and morphological traits in Norway spruce. Vth World Forestry Congress, Seattle [ex HATTEMER 1963 (FAO/FORGEN 63) 2a (3)]
- MERGEN F., BURLEY J., YEATMAN C. W. 1964. Variation in growth characteristics and wood properties of Norway spruce. Tappi 47: 499–504.
- MESSER H. 1956. Untersuchungen über das Fruchten der Fichte (*Picea abies* Karst.). W: Fortschritte des forstlichen Saatgutwesens. J. D. Sauerländer's Verlag, Frankfurt a/M. [FA. 20, 1705]
- METZLER B., OBERWINKLER F. 1986. Charakteristische Meristemschäden in Fichtenwurzeln durch niedrigen pH-Wert und Aluminium Ionen. Allg. Forstztg. 42: 649–651.
- MEYBERG M., LOCKHAUSEN J., KRISTEN U. 1987. Ultrastrukturelle Veränderungen in Fichtennadeln durch organische Luftschadstoffe. VDI Berichte 609: 501–506.
- MEYBERG M., LOCKHAUSEN J., KRISTEN U. 1988. Ultrastructural changes in mesophyll cells of spruce needles from a declining forest in northern Germany. Eur. J. For. Path. 18: 169–175.
- MEYER E. I. 1953. Opriedielitil drevookrashivayushchich gribov. Moskwa–Leningrad.
- MEYER F. H. 1973. Distribution of Ectomycorrhizae in Native and Man-Made Forests. In: MARKS G. C., KOZLOWSKI T. T. (eds.). Ectomycorrhizae, their Ecology and Physiology. Academic Press, New York, London. Pp.: 79–105.
- MEYER F. H. 1987a. Das Wurzelsystem geschädigter Waldbestände. Allg. Forst-Ztschr. 27–29: 754–257.
- MEYER F. H. 1987b. Extreme sites and ectomycorrhiza (particularly *Cenococcum geophilum*). Angewandte Bot. 61: 39–46.
- MEZERA A. 1939. O rozšíření šiškových forem smrku v ČSR. Lesn. Práce 18: 35–60.
- MICHALIK S. 1990. Sukcesja roślinności na polanie reglowej w Gorczańskim Parku Narodowym w okresie 20 lat w wyniku zaprzestania wypasu. Prądnik 2: 137–149.
- MICHALSKI J. 1982. Studies on the pathogenic microorganisms of the *Tomicus piniperda* and *T. minor* (Coleoptera, Scolytidae). Final Report FG-PO. Chair of Forest Entomology, Academy of Agriculture, Poznań. 126 pp.
- MICHALSKI J. 1984. Możliwość wykorzystania niektórych nicieni (*Nematoda*) w biologicznym zwalczaniu cetyńca większego *Tomicus piniperda* L. (Coleoptera: Scolytidae). Roczniki AR, Poznań 42: 35–40.
- MICHALSKI J. 1988. On the occurrence and significance of Nematodes (*Nematoda*) in the galleries of *Tomicus piniperda* (L.) (Coleoptera: Scolytidae). Bull. Soc. Amis. Sci. Lettr. Poznań, Ser. D 26: 129–137.
- MICHALSKI J. 1989. Wstępne badania porównawcze składu gatunkowego szkodników wtórnych i fauny pasożytniczej występującej w drzewostanach objętych i nie objętych zwalczaniem chemicznym przeciwko brudnicy mniszce (*Ocneria monacha* L.). In: Proc. Seminarium naukowego pt. Wpływ gospodarki leśnej na środowisko. Wyd. SGGW-AR, Warszawa. pp.: 176–181.
- MICHALSKI J. 1996. Korniki (Coleoptera: Scolytidae) na terenie Parku Narodowego Gór Stołowych. Sympozjum Środowisko Przyrodnicze Parku Narodowego Gór Stołowych. Szczeliniec: 189–195.

- MICHALSKI J. 1998. Gradacje kornikowe w ostatnim 50-leciu w drzewostanach świerkowych Polski. In: BORATYŃSKI A., BUGAŁA W. (eds.). *Biologia świerka pospolitego*. Bogucki Wyd. Naukowe. pp. 468–508.
- MICHALSKI J., BANASZAK J. 1994. Muchówki z rodzaju *Medetera* FISCHER (*Diptera, Dolichopodiidae*) występujące w niektórych żerowiskach korników. *Prace Komisji Nauk Rolniczych i Komisji Nauk Leśnych PTPN* 78: 131–134.
- MICHALSKI J., RATAJCZAK E. 1989. Korniki (*Coleoptera, Scolytidae*) wraz z towarzyszącą im fauną w Górach Świętokrzyskich. *Fragm. Faunist.* 32: 279–318.
- MICHALSKI J., RATAJCZAK E. 1994. Korniki (*Coleoptera, Scolytidae*) wraz z towarzyszącą im fauną w Roztoczańskim Parku Narodowym. *Fragm. Faunist.* 37: 291–313.
- MICHALSKI J., STARZYK J.R., KOLK A., GRODZKI W. 2004. Zagrożenie świerka przez kornika druzkarza – *Ips typographus* (L.) w drzewostanach Leśnego Kompleksu Promocyjnego Puszcza Białowieża w latach 2000–2002. *Leśne Prace Badawcze* 2004 (3): 5–30.
- MICHALSKI J., TOMALAK M. 1984. Zniekształcenia niektórych narządów wewnętrznych *Tomicus piniperda* L. (*Coleoptera: Scolytidae*) wywołane przez nicienie (*Nematoda*). *Roczniki AR, Poznań* 42: 43–49.
- MICHNIEWICZ M. 1969. Znaczenie endogennych, fizjologicznie czynnych substancji w procesie ukończenia. *Post. Nauk Roln.* 2 (116): 3–16.
- MIEHLICH G. 1971. Einfluß des Fichtenanbaus auf Grobporenverteilung, pH-Wert, Humus und Nährelementgehalte eines Lößlehm-Pseudogleys. *Forstw. Cbl.* 90: 301–318.
- MIKKELSEN T. N., DODELL B., LÜTZ C. 1995. Changes in pigment concentration and composition in Norway spruce induced by long-term exposure to low levels of ozone. *Environ. Poll.* 87: 197–205.
- MIKKELSEN T. N., RO-POULSEN H. 1994. Exposure of Norway spruce to ozone increases the sensitivity of current year needles to photoinhibition and desiccation. *New Phytol.* 128: 153–163.
- MIKKOLA L. 1969. Observations on interspecific sterility in *Picea*. *Ann. Bot. Fenn.* 6 (4): 285–339.
- MIKKOLA L. 1970. Kuusilajien risteytyvyydestä. *Silva Fenn.* 4 (4): 291–300.
- MIKOLA J. 1989. Age-to-age correlations for growth among families and provenances of Norway spruce. *Inst. Forest Improvement. Uppsala, Rep.* 11 “Norway spruce provenances, breeding and genetic conservation”. Eds. L.-G. Steiner, M. Werner: 113–123.
- MIKOLA P. 1950. On variations in tree growth and their significance to growth studies. *Comm. Inst. For. Fenn.* 38.5.
- MIKUŁOWSKI M. 1995a. Koncepcja nowych form odnawiania lasu na obszarze kłęski ekologicznej w Sudetach. In: SAROSIEK J. (ed.). *Geoekologiczne problemy Karkonoszy*. pp.: 107–110.
- MIKUŁOWSKI M. 1995b. Nowe formy odnawiania lasu w Sudetach Zachodnich. *Prace IBL, Warszawa, Ser. B* 25: 251–264.
- MININA E.T. 1960. Opredelenie pola u lesnykh drevesnykh rastenii. *Trudy Inst. Lesa AN SSSR* 47 (2): 76–163.
- MIREK Z., PIĘKOŚ-MIREK H., ZAJĄC A., ZAJĄC M. 2002. Flowering plants and Pteridophytes of Poland. *Inst. Botaniki PAN, Kraków*. 442 pp.
- MITSCHERLICH G. 1971. Wald, Wachstum und Umwelt. Eine Einführung in die ökologischen Grundlagen des Waldwachstums. II. Waldklima und Wasserhaushalt. Sauerländer's Verlag, Frankfurt am Main. 365 pp.
- MIYAKE K. 1903. On the development of sexual organs and fertilization in *Picea excelsa*. *Ann. Bot.* 17 (56): 351–372.
- MO L. H., VON ARNOLD S., LAGERCRANTZ U. 1989. Morphogenic and genic stability in long term embryogenic cultures and somatic embryos of Norway spruce (*Picea abies* L. KARST.). *Plant Cell Rep.* 8: 375–378.
- MODESS O. 1939. Experimentelle Untersuchungen über Hymenomyceten und Gasteromyceten als Mykorrhizabildner bei Kiefer und Fichte. *Svensk Bot. Tidskr.* 33: 91–93.
- MODESS O. 1941. Zur Kenntniss der Mykorrhizenbildner von Kiefer und Fichte. *Symb. Bot. Upsal.* 5: 3–147.

- MODRZYŃSKI J. 1978. Stan naturalnego odnowienia świerka (*Picea abies* (L.) KARST.) w Karkonoskim Parku Narodowym na tle warunków przyrodniczo-leśnych. Prace Komisji Nauk Rolniczych i Komisji Nauk Leśnych PTPN 46: 101–116.
- MODRZYŃSKI J. 1979. Dynamika naturalnego odnowienia świerka (*Picea abies* (L.) KARST.) w drzewostanach położonych na różnych wysokościach nad poziomem morza w Karkonoskim Parku Narodowym. Prace Komisji Nauk Rolniczych i Komisji Nauk Leśnych PTPN 48: 113–132.
- MODRZYŃSKI J. 1988a. Nieprawidłowe zależności między udziałem drewna późnego i przyrostem grubości drzewostanów świerkowych (*Picea abies* (L.) KARST.) w Karkonoskim Parku Narodowym a wzniesieniem nad poziom morza. Roczn. AR, Poznań 190: 103–123.
- MODRZYŃSKI J. 1988b. Próba wyjaśnienia zakłóceń w rytmie zawiązywania pąków szczytowych u proveniencji świerka (*Picea abies* (L.) KARST.) z różnych wysokości nad poziomem morza. Roczn. AR, Poznań 193: 61–77.
- MODRZYŃSKI J. 1989. Środowiskowe przystosowanie i pochodzenie świerka pospolitego (*Picea abies* (L.) KARST.) w Karkonoskim Parku Narodowym. Roczn. AR, Poznań, Rozpr. Nauk. 192: 1–103.
- MODRZYŃSKI J. 1991. Pochodzenie i ekologiczna adaptacja świerka w Sudetach i Karpatach. In: Zagospodarowanie Lasów Górskich. Synteza wyników badań. CPBR 10.20. Kraków: 56–65.
- MODRZYŃSKI J. 1993. The question of foreign origin of Norway spruce (*Picea abies* (L.) KARST.) in the Sudetic Mts. Norway spruce provenances and breeding. Proc. of IUFRO (S2.2–11). Symposium, Riga, Latvia: 105–110.
- MODRZYŃSKI J. 1995. Altitudinal adaptation of Norway spruce (*Picea abies* (L.) KARST.) progenies indicates small role of introduced populations in the Karkonosze Mountains. Silvae Genet. 44 (2–3): 70–75.
- MODRZYŃSKI J. 1996. Ocena defoliacji wybranych drzewostanów świerkowych w Sudetach i Karpatach. In: SIWECKI R. (ed.) Reakcje biologiczne drzew na zanieczyszczenia przemysłowe. III Krajowe Symp. 23–26.05.1994, Poznań–Kórnik. pp.: 281–286.
- MODRZYŃSKI J. 1999. Potencjalny naturalny zasięg świerka uzasadnia jego hodowlę na Pomorzu Zachodnim. Sylwan 143 (7): 63–67.
- MODRZYŃSKI J. 2003. Defoliation of older Norway spruce (*Picea abies*/L./Karst.) stands in the Polish Sudety and Carpathian mountains. Forest Ecology and Management, 181: 289–299.
- MODRZYŃSKI J., ERIKSSON G. 2002. Response of *Picea abies* populations from elevational transects in the Polish Sudety and Carpathian mountains to simulated drought stress. For. Ecol. Mangm. 165 (1–3): 101–112.
- MODRZYŃSKI J., PRUS-GŁOWACKI W. 1998. Isoenzymatic variability in some of the Polish populations of Norway spruce (*Picea abies*) in the IUFRO – 1972 provenance trial. Acta Soc. Bot. Pol. 67: 75–82.
- MOHRING K. 1983. Wurzel, Holz und Kronenschaden sowie Vitalitätsschwund bei alterer Fichte in einen nordwestdeutschen Mittelgebirgsrevier. Forstarchiv 54 (1): 8–13.
- MOILANEN M., PENTTILÄ T., ISSAKAINEN J. 1996. Lannoituksen vaikutus kuusikoiden kasvuun ja ravinnetilaan ojitetuilla turvemailla Pohjois-Suomessa. Suo 47 (3): 85–94.
- MOKRZECKI Z. 1933. Rabusie i pasożyty kornika drukarza *Ips typographus* L. na ziemiach polskich. Polskie Pismo Enomol. 12 (1–4): 275–289 + tabl. XVI and XVII.
- MOLCHANOV A. A. 1950. Plodonoshenie eli v svyazi s tipami lesa. Byull. Mosk. Obshch. Isp. Prir. (Otd. Biol.) 55 (4).
- MOLCHANOV A. A. 1967. Geografiya plodonosheniya glavneyshikh drevesnykh porod v SSSR. Nauka, Moskva.
- MOLINA R., MASSICOTTE H., TRAPPE J. M. 1992. Specificity phenomena in mycorrhizal symbiosis: community-ecological consequences and practical implications. In: ALLEN M. F. (ed.). Mycorrhizal functioning an integrative plant-fungal process. Capman & Hall, New York. pp.: 357–423.
- MOOI J. 1982. Beschadigingen door luchtverontreiniging. In: Bosbeschering. Pudoc. Wageningen 1982: 350–368.
- MORGANTE M., VENDRAMIN G. G., GIANNINI R. 1989. Genetics of 6PGD and SKDH in Norway spruce (*Picea abies* (L.) KARST.). J. Genet. Breed. 43: 67–71.

- MORGANTE M., VENDRAMIN G. G., ROSSI P. 1991. Effects of stand density on outcrossing rate in two Norway spruce (*Picea abies*) populations. Can. J. Bot. 69: 2704–2708.
- MORITZ T., ODÉN P. C. 1990. Metabolism of tritiated and deuterated gibberellin A₃ in Norway spruce (*Picea abies*) shoots during the period of cone-bud differentiation. Physiol. Plant. 79: 242–249.
- MORSELT A. F. W., SMITS W. T. M., LIMONARD T. 1986. Histochemical demonstration of heavy metal tolerance in ectomycorrhizal fungi. Plant and Soil 96: 417–420.
- MOSER M. 1958. Der Einfluss tiefer Temperaturen auf das Wachstum und die Lebenstätigkeit höherer Pilze mit spezieller Berücksichtigung von Mykorrhizapilzen. Sydowia 12: 386–399.
- MOSER O. 1965. Untersuchungen über die Abhängigkeit der natürlichen Vejüngung der Fichte von Standort. Cbl. Ges. Forstw. 82 (1): 18–55.
- MOSKOVICH A. M. 1992. Proembriogeneza i rannij embriogeneza u eli obyknovennyj *Picea abies* (L.) KARST. Bul. Acad. Științe Rep. Moldova. Științe Biologice și Chimice 4 (259): 8–14.
- MOULALIS D. 1973. (Flushing behaviour of Norway spruce in Bavaria and breeding for resistance to late frost). Forstw. Cbl. 92 (1): 24–47. [FA. 34, 6195]
- MÜLLER F. 1988. Entwicklung von Fichtensämlingen in Abhängigkeit von Ernährung und seehöhenangepasster Wachstumsdauer im Versuchsgarten Mariabrunn. Mitteil. Forstl. Bundes-Versuchsanstalt, Wien 160: 1–252.
- MÜLLER G. 1977. Investigations on the degree of natural self-fertilization in stands of Norway spruce (*Picea abies* (L.) KARST.) and Scots pine (*Pinus sylvestris* L.). Silvae Genet. 26: 207–217.
- MÜLLER M., GRILL D., GUTTENBERGER H. 1994. The effects of interactions between ozone and CO₂ on the chromosomes of Norway spruce root meristems. Phytom (Austria) 34: 321–335.
- MÜLLER-STARCK G., 1995. Genetic variation in high elevated populations of Norway spruce (*Picea abies* [L.] KARST.) in Switzerland. Silvae Genet. 44: 356–362.
- MÜLLER-STARCK G., BARADAT P., BERGMANN F. 1992. Genetic variation within European tree species. New For. 6: 23–47.
- MÜLLER-STARCK G., SCHUBERT R. 2001. Genetic Response of Forest Systems to Changing Environmental Conditions. Forest Sciences 70. Kluwer Academic Publishers. Dordrecht–Boston–London.
- MÜNZENBERGER B., HEILEMANN J., STRACK D., KOTTKE I., OBERWINKLER F. 1990. Phenolics of mycorrhizas and non-mycorrhizal roots of Norway spruce. Planta 182: 142–148.
- MÜNZENBERGER B., KOTTKE I., OBERWINKLER F. 1995. Reduction of phenolics in mycorrhizas of *Larix decidua* MILL. Tree Physiol. 15: 191–196.
- MUONA O., PAULE L., SZMIDT A. E., KARKKAINEN K. 1990. Mating system analysis in a Central and Northern European population of *Picea abies*. Scand. J. For. Res. 5: 97–102.
- MUONA O., YAZDANI R., LINDQVIST G. 1987. Analysis of linkage in *Picea abies*. Hereditas 106: 31–36.
- MURACH D. 1984. Die Reaktion der Feinwurzeln von Fichten (*Picea abies* KARST.) auf zunehmende Bodenversauerung. Gött. Bodenkd. Ber. 77: 1–126.
- MURACH D., SCHÜNEMANN E. 1985. Reaktion der Feinwurzeln von Fichten auf Kalkungsmassnahmen. Allg. Forstztg. 43: 1151–1154.
- MUSZYŃSKI Z., MC NATT J. D. 1984. Investigations on the use of the Spruce bark in the manufacture of practice board in Poland. Forest Product 34: 28–35.
- MYCZKOWSKI S. 1955. Ekologia zespołów leśnych Tatr Polskich ze szczególnym uwzględnieniem jej związków z pokrywą śnieżną. Ochr. Przyr. 23: 112–203.
- MYCZKOWSKI S. 1964. Struktura i ekologia zespołu świerka *Picea tatrae* u górnej granicy zasięgu w Tatrzańskim Parku Narodowym w dolinach Stawów Gąsienicowych i Pańszczycy. Ochr. Przyr. 30: 51–105.
- MYCZKOWSKI S. 1977. Świerczyny gór i wyżyn w Polsce. In: BIAŁOBOK S. (ed.). Świerk pospolity, *Picea abies* (L.) KARST. Nasze drzewa leśne. PWN, Warszawa–Poznań 5: 405–460.
- MYCZKOWSKI S., FELIKSIK E., SŁODYCZKA S. 1975. Świerk *Picea excelsa* LINK. Stud. Ośrodka Dok. Fizjogr. 4: 195–220.
- MYCZKOWSKI S., LESIŃSKI J. 1974. Rozsiedlenie rodzimych gatunków drzew tatrzańskich. In: MYCZKOWSKI S. (ed.). Rodzime drzewa Tatr. Cz. 1. Stud. Ośrodka Dok. Fizjogr. 3: 13–70.

- NAGEL J., SABOROWSKI J., KRAMER H. 1985. Beziehungen zwischen unterschiedlichen Schadklassen und dem Holzzuwachse bei Fichte. *Allg. Forstztg.* 35: 1399–1401.
- NANSON A. 1964. Données complémentaires au sujet de l'Expérience internationale sur l'Origine des Graines d'Epicéa en Belgique. *Stat. de Rech. Eaux et Forêts, Groenendaal – Hoeilaart. Belgique. Trav. Sér. B*, 28.
- NANSON A. 1971. Tests de descendance d'Epicéa commun. *Stat. de Rech. Eaux et Forêts, Groenendaal – Hoeilaart. Belgique. Trav. Sér. E*, 4.
- NANSON A. 1972. Provenances recommandables pour la sylviculture en Belgique. *Bull. Soc. Roy. For. Belgique* 79 (8–9): 417–458.
- NANSON A. 1974. Tests précoces de provenances d'Epicéa commun. *Stat. de Rech. Eaux et Forêts, Groenendaal – Hoeilaart. Belgique. Trav. Sér. E*, 6: 1–38.
- NANSON A. 1981. Comment accroître la production, la qualité et la santé de nos forêts par la génétique forestière? *Bull. Soc. Roy. For. Belgique* 88 (2): 49–66.
- NANSON A., SACRÉ E., FRAIPONT L. 1975. Test précoces de la qualité du bois de provenances d'épicéa commun. *Bull. Rech. Agron. Gembloux* 10 (4): 527–558.
- NAPOLA M. L. 1989. Kuusen kaukoristeymät kasvanvat hyvin. Provenienciissihybridien menestyminen Etelä-Suomen koeviljelyksissä. *Metsänjalostussäätiö Tiedote* 1/1989.
- NAPOLA M. L. 1993. Experience with Norway spruce provenance hybrids in southern Finland. Norway spruce provenances and breeding. *Proc. of IUFRO (S2.2–11). Symposium, Riga, Latvia*: 111–112.
- NATSVLISHVILI K. D. 1981. Intensivnost' rosta geograficheskikh kul'tur eli v Gruzii. *Trudy Inst. Gorn. Lesovod. Minleschoza GSSR* 29: 68–79.
- NEBE W. 1968. Über Beziehungen zwischen Klima und Wachstum der Fichte (*Picea abies* L.) in ihrem europäischen Verbreitungsgebiet. *Arch. Forstw.* 17: 1219–1238.
- NEBE W. 1970. Die Düngung von Fichtenbeständen. VEB Chemiehandel Düngemittel, Berlin.
- NEBE W. 1974. Zur Düngung von älteren Fichtenbeständen auf Quarzporphyrstandorten. *Arch. Acker- Pflanzenbau Bodenk.* 18 (12): 917–929.
- NEBE W. 1991. Veränderung der Stickstoff- und Magnesiumversorgung immissionsbelasteter älterer Fichtenbestände in ostdeutschen Mittelgebirgen. *Forstw. Cbl.* 110 (1): 4–12.
- NEHLS U., MIKOLAJEWSKI S., ECKE M., HAMPP R. 1999. Identification and expression analysis of two fungal cDNAs regulated by ectomycorrhiza and fruit body formation. *New Phytol.* 144: 195–202.
- NEHLS U., WIESE J., GUTTENBERGER M., HAMPP R. 1998. Carbon allocation in ectomycorrhizas: identification and expression analysis of an *Amanita muscaria* monosaccharide transporter. *Mol. Plant. Microbe Interact.* 11: 167–176.
- NEHLS U., WIESE J., HAMPP R. 2000. Exchange of carbohydrates between symbionts in ectomycorrhiza. In: HOCK B. (ed.) *Mycota*, Vol. IX. Springer.
- NEHLS U., MIKOLAJEWSKI S., MAGEL E., HAMPP R. 2001. Carbohydrate metabolism in ectomycorrhizas: gene expression, monosaccharide transport and metabolic control. *New Phytol.* 150: 533–541.
- NEI M. 1975. *Molecular population genetics and evolution*. North-Holland Publ. Co., Amsterdam–Oxford.
- NESTEROVICH N. D., DERYUGINA T. F., LUCHKOV A. I. 1986. Strukturnye osobennosti listev khvojnykh. *Nauka i Tekhnika*, Minsk.
- NEUHAUSL R. 1975. *Hochmoore am Teich Velke Darko*. Academia, Praha. 267 pp.
- NICKLE W. 1967. On the classification of the insect parasitic nematodes of the *Sphaerularidae* Lubbock, 1861 (*Tylenchoidea: Nematoda*). *Proc. Helminthol. Soc. Washington* 34 (1): 72–94.
- NIEDERER M., PANKOW W., WIEMKEN A. 1988. Trehalose synthesis in mycorrhiza of Norway spruce: an indicator of vitality. *Eur. J. For. Path.* 19 (1): 14–20.
- NIEDERER M., PANKOW W., WIEMKEN A. 1989. Trehalose synthesis in mycorrhiza of Norway spruce: an indicator of vitality. *Eur. J. For. Path.* 19: 14–20.
- NIEDERER M., PANKOW W., WIEMKEN A. 1992. Seasonal change of soluble carbohydrates in mycorrhizas of Norway spruce and changes induced by exposure to frost and desiccation. *Eur. J. For. Path.* 22: 291–299.

- NIENSTAEDT H. 1959. The Effect of Rootstock Activity on the Success of Fall Grafting of Spruce. J. For. 57: 828–832.
- NIHLGARD B. 1971. Pedological influence of spruce planted on former beech forest soils in Scania, South Sweden. Oikos 22: 302–314.
- NIKITIN N. I. 1962. Khimiya drevesiny i cellyulozy. Moskva-Leningrad.
- NIKKANEN T. 2001. Reproductive phenology in a Norway spruce seed orchard. Silva Fenn. 35 (1): 39–53.
- NIKKANEN T., RUOTSALAINEN S. 2000. Variation in flowering abundance and its impact on the genetic diversity of the seed crop in a Norway spruce seed orchard. Silva Fenn. 34 (3): 205–222.
- NILSEN P. 1995. Effect of nitrogen on drought strain and nutrient uptake in Norway spruce (*Picea abies* (L.) Karst.) trees. Plant and Soil 172 (1): 73–85.
- NILSEN P., BØRJA I., KNUTSEN H., BREAN R. 1998. Nitrogen and drought effects on ectomycorrhizae of Norway spruce [*Picea abies* (L.) KARST.]. Plant and Soil 198: 179–184.
- NILSSON B. 1958. Studier av 3-åriga aukommar efter korsning svensk-gran x kontinentgran. Svensk. SkogsFören. Tidskr. 56(2): 225–250. [FA. 20, 380].
- NILSSON B. 1963a. Intraspecific hybridization and heterosis within *Picea abies* (FAO/FORGEN 63) 1: 2b/6.
- NILSSON B. 1963b. Wood density in progenies after hybridization within *Picea abies* (FAO/FORGEN 63) 2: 7/8.
- NILSSON B. 1967. Genetisk varians och kombinationsförmåga hos tall och gran. Årsb. Föreningen Skogsträdsförädl. 1966: 136–153.
- NILSSON B., ANDERSSON E. 1969. Spruce and pine racial hybrid variations in northern Europe. Silvae Genet. 18 (5–6): 196–197.
- NILSSON B., ANDERSSON E. 1970. Spruce and pine racial hybrid variations in northern Europe. Proc 2nd Meet. W. G. Quant. Gen. Sec. 22, IUFRO, Raleigh, N.C. USA, For. Ser. USDA, New Orleans: 118–128.
- NILSSON B., WIMAN S. 1967. Cone setting of plus trees and grafts in Norway spruce (*Picea abies*). Årsb. Fören. Skogsträdsförädl.: 59–68.
- NILSSON L. O., WIKLUND K. 1992. Influence of nutrient and water stress on Norway spruce production in south Sweden – the role of air pollutants. Plant and Soil 147 (2): 251–265.
- NILSSON L. O., WIKLUND K. 1994. Nitrogen uptake in a Norway spruce stand following ammonium sulphate application, fertigation, irrigation, drought and nitrogen-free-fertilization. Plant and Soil 164 (2): 221–229.
- NILSSON L. O., WIKLUND K., HÜTTL R. F., JOHANSSON U. T. 1995. Nutrient balance and P, K, Ca, Mg, S and B accumulation in a Norway spruce stand following ammonium sulphate application, fertigation, irrigation, drought and N-free-fertilisation. Plant and Soil 168–169: 437–446.
- NIȚU C. 1974. Aspecte privind variabilitatea genetică a unor proveniente de molid. Stud. Cerc. Silvicult. 31: 49–58.
- NIȚU C. 1979. Cercetări referitoare la proveniențe de molid din țară i străinătate. Dept. Silvicult. Inst. Cerc. si Amenajări Silvice. Seria a II-a: 1–48.
- NIȚU C., RĂIESCU V., CREANGĂ JI. 1984. Cercetări privind comportarea proveniențelor de molid testate în diferite condiții staționale. Min. Silviculturi, Inst. Cerc. si Amenajări Silvice. Seria a II-a: 1–35.
- NOGOWICZ P. 1990. Wkraczanie świerka (*Picea abies*) do olsu (*Ribo nigri-Alnetum*) w Puszczy Białowieskiej. MSc. thesis, Białowieska Stacja Geobot. UW, Białowieża.
- NOSKO P., BRASSARD P., KRAMER J. R., KERSHAW K. A. 1988. The effect of aluminum on seed germination and early seedlings establishment, growth, and respiration of white spruce (*Picea glauca*). Can. J. Bot. 66: 2305–2310.
- NOVOTNÝ J., FILO J. 1997. The Forestry of the Slovak Republic. POLY-Kontakt. 85 pp.
- NOWOTNY I., DÄHNE J., KLINGELHÖFER D., ROTHE G. M. 1998. Effect of artificial soil acidification and liming on growth and nutrient status of mycorrhizal roots of Norway spruce (*Picea abies* [L.] KARST.). Plant and Soil 199: 29–40.
- NUNBERG M. 1930. Przyczynę do znajomości bleskotek (*Chalcididae*) jako pasożytów korników (*Ipidae*). Polskie Pismo Entomol. 9 (3–4): 200–208.

- NUNBERG M. 1967. Obumierki – *Rhizophagidae*. Klucze do oznaczania owadów Polski. 19, 64. PWN, Warszawa. 15 pp.
- NUNBERG M. 1976. Łyszczynkowate – *Nitidulidae*. Klucze do oznaczania owadów Polski. 19, 65. PWN, Warszawa. 92. pp.
- NYLUND J.-E. 1981. The formation of ectomycorrhiza in conifers: Structural and physiological studies with special reference to mycobiont, *Piloderma croceum* ERIKSS. & HJORTST. Acta Univ. Upsalensis, Abstr. Uppsala Dissert. Fac. Sci. 615: 1–34.
- NYLUND J.-E. 1988. The regulation of mycorrhiza formation. Carbohydrate and hormone theories reviewed. Scand. J. For. Res. 3: 465–479.
- NYLUND J.-E., DAHLBERG A., HOGBERG N., KÅREN O., GRIP K., JONSSON L. 1995. Methods for studying species composition of mycorrhizal fungal communities in ecological studies and environmental monitoring. In: STOCCHI V., BONFANTE P., NUTI M. (eds). Biotechnology of Ectomycorrhizae, Plenum Press, New York. pp.: 229–239.
- NYLUND J.-E., UNESTAM T. 1982. Structure and physiology of ectomycorrhizae I. The process of mycorrhiza formation in Norway spruce in vitro. New Phytol., 91: 63–79.
- NYS C. 1981. Réponse d'un peuplement adulte d'épicéa commun (*Picea abies* Karst.) a la fertilisation dans le Limousin. Rev. For. Franc. 33 (3): 217–227.
- OBMIŃSKI Z. 1947. Botanika leśna z krótkim zarysem botaniki ogólnej. Wyd. Spółdzielni Las, Warszawa. 112 pp.
- OBMIŃSKI Z. 1977. Ogólny zarys ekologii. In: BIAŁOBOK S. (ed.). Świerk pospolity, *Picea abies* (L.) KARST. Nasze drzewa leśne. PWN, Warszawa–Poznań 5: 332–371.
- OCHYRA R., ŻARNOWIEC J., BEDNAREK-OCHYRA H. 2003. Census Catalogue of Polish Mosses. Institute of Botany, Polish Academy of Sciences, Kraków. 372 pp.
- ODÉN P. C., ANDERSSON B., GREF R. 1982. Identification of gibberellin A9 in extracts of Norway spruce (*Picea abies* (L.) KARST.) by combined gas chromatography-mass spectrometry. J. Chromatogr. 247: 133–140.
- ODÉN P. C., SCHWENEN L., GRAEBE J. E. 1987. Identification of gibberellins in Norway spruce (*Picea abies* (L.) KARST.) by combined gas chromatography-mass spectrometry. Plant Physiol. 84: 516–519.
- ODÉN P. C., WANG Q., HOGBERG K. A., WERNER M. 1994. Quantification of gibberellins A9, A1 and A3 in relation to flower bud differentiation in *Picea abies*. Scand. J. For. Res. 9: 341–34.
- ODÉN P. C., WANG Q., HOGBERG K. A., WERNER M. 1995. Transport and metabolism of gibberellins in relation to flower bud differentiation in Norway spruce (*Picea abies*). Tree Physiol. 15: 141–145.
- OGNER G., BJØR K. 1988. Concentrations of elements in annual rings of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) from Arendal, in southern Norway. Medd. Norsk Inst. Skogforsk. 40 (10): 1–8.
- OHENOJA E. 1993. Effect of weather conditions on the larger fungi at different forest sites in northern Finland in 1976–1988. Ph. D. Thesis, Dept. Bot., Oulu Univ., Finland.
- OHENOJA E., KOISTONEN R. 1984. Fruit body production of larger fungi in Finland. 2. Edible fungi in northern Finland 1976–1978. Ann. Bot. Fenn. 21: 357–366.
- OHNO T., SUCOFF E. I., ERICH M. S., BLOOM P. R., BUSCHENA C. A., DIXON R. K. 1988. Effects of aluminum on the growth and nutrient uptake of red spruce seedlings. J. Environ. Qual. 17: 666–672.
- OHWI J. 1965. Flora of Japan. Washington, 1066 pp.
- OKOŁÓW C. 1963. Materiały do fauny żerowisk korników – *Scolytidae* Puszczy Boreckiej. Polskie Pismo Entomol., Ser. B 1–2 (29–30), (2): 15–20.
- OKOŁÓW C. 1982. Naturalne czynniki ograniczające liczebność populacji kornika drukarza (*Ips typographus* L.) w warunkach lasu pierwotnego i lasów zagospodarowanych Puszczy Białowieskiej (założenia i metodyka badań). Zesz. Probl. Post. Nauk Roln. 251: 115–120.
- OLEKSYN J., MODRZYŃSKI J., TJØELKER M. G., ŻYTKOWIAK R., REICH P. B., KAROLEWSKI P. 1998. Growth and physiology of *Picea abies* populations from a broad elevational transect: common garden evidence for altitudinal ecotypes and cold adaptation. Funct. Ecol. 12: 573–590.
- OLSEN H. C. 1978. Blomstringsinduction hos rødgran. Forstl. Forsøgsv. Denmark 36 (2): 231–266.

- OPSAHL W. 1951. On relation between summer temperature and seed ripening of Norway spruce. Medd. Norske Skogforsøk. 11: 619–662.
- ORLENKO E. G., RUDENKOVA O. F. 1972. Rannaya dyagnostika bystroty rosta potomstva plusovykh derev'iev eli obyknovennoy. In: Problemy Eksperiment. Genet. Nauka i tekhnika, Minsk, pp.: 132–136. [Ref. Zh. 1.56.98]
- ORLOV A. YA. 1957. Observations on absorbing roots of spruce (*Picea excelsa* Link) in natural conditions. Bot. Zh. 42: 1172–1181.
- ORLOV A. YA., KOSHEL'KOV S. P., PETROV-SPIRIDONOV A. A. 1987. Primenenie azotnykh udobreniy dlya uskoreniya rosta elovogo podrosta na vyрубkakh. Lesoved. (5): 20–28.
- ORŁOŚ H. 1952. Fitopatologia leśna. PWRiL, Warszawa.
- OSIECKA A. 1989. Wpływ terminu sadzonkowania na korzenie się sadzonek trzewch karłowych odmian świerka. Rośliny Ozdobne. Prace ISiK, Ser. B 14: 105–116.
- OSTAPENKO B. F., CHRISTUK YU. S. 1982. K voprosu o genezise nasazhdeniy na kamenistykh morfakh elovykh tipov leśa v Karpatakh. Lesovod. Agrolesomel. 62: 30–35.
- OSZAST J. 1973. The Pliocene profile of Domański Wierch near Czarny Dunajec in the light of palynological investigations (Western Carpathians, Poland). Acta Paleobot. 14 (1): 1–42.
- OSZLANYI J. 1997. Forest health and environmental pollution in Slovakia. Environ. Poll. 98: 389–392.
- OTS K., RAUK J. 2001. Defoliation of Scots pine and Norway spruce under alkaline dust impact and its relationship with radial increment. Oil Shale 18: 223–237.
- OVINGTON J. D. 1959. The calcium and magnesium contents of tree species grown in close stands. New Phytol. 58 (2): 164–175.
- OWENS J. N., JOHNSEN Ø., DÆHLEN O. G., SKRØPPA T. 2001. Potential effects of temperature on early reproductive development and progeny performance in *Picea abies* (L.) Karst. Scand. J. For. Res. 16: 221–237.
- PACZOSKI J. 1925. Świerk w ostępach Białowieży. Las Polski 5 (8): 358–371; 5 (9): 397–411.
- PACZOSKI J. 1930. Lasy Białowieży. Państwowa Rada Ochr. Przyr., Monogr. Nauk. 1: 1–575.
- PAGAN J. 1992. *Picea abies* (L.) KARST. Lesnicka Dendrologia. Technicka Univ., Zvolen. pp.: 5–25.
- PAGANELLI D. J., SEILER J. R., FERET P. P. 1987. Root regeneration as an indicator of aluminum toxicity in loblolly pine. Plant and Soil 102: 115–118.
- PAKKANEN A., NIKKANEN T., PULKKINEN P. 2000. Annual variation in pollen contamination and outcrossing in a *Picea abies* seed orchard. Scand. J. For. Res. 15: 399–404.
- PALTSEV A. M. 1978. Geograficheskie kul'tury eli v Solechnogorskom leskombinate. Les. Khoz. (5): 62–65.
- PALTSEV A. M. 1980. Sezonnyy rost geograficheskikh kul'tur eli obyknovennoy v moskovskoy oblasti. Lesoved. (6): 11–18.
- PALTSEV A. M. 1989. Khod rosta geograficheskikh ekotipov eli. Les. Khoz. (1): 46–48.
- PALOMÄKI V., HOLOPAINEN T. 1994. Effects of phosphorus deficiency and recovery fertilization on growth mineral concentration and ultrastructure of Scots pine needles. Can. J. For. Res. 24: 2459–2468.
- PANCER-KOTEJOWA E. 1965. Zbiorowiska leśne Wzniesienia Gubałowskiego. Fragm. Flor. Geobot. 11 (2): 241–305.
- PANCER-KOTEJOWA E. 1973. Zbiorowiska leśne Pienińskiego Parku Narodowego. Fragm. Flor. Geobot. 19 (2): 197–258.
- PANKOW W., NIEDERER M., WESER U., SCHMID B., BOLLER T., WIEMKEN A. 1989. Biochemical symptoms of stress in the mycorrhizal roots of Norway spruce (*Picea abies*). Trees 3: 65–72.
- PANOV A. 1950. O fruktifikaciyi nashikh chetinar. Šum. List 74 (9–10): 346–359. [FA. 13, 144]
- PARIBOK T. A., SAZYKINA N. A., TOPORSKIY V. N. 1989. Soderkhanie stronciya i rubidiya v gorodskikh rasteniyakh. Bot. Zh. 74 (4): 528–533.
- PARKER D. R., KINRAIDE T. B., ZELAZNY L. W. 1989. On the phytotoxicity of polynuclear hydroxyaluminium species. Soil Sci. Soc. Am. J. 53: 789–796.
- PARROT L. 1960. De la variabilité génétique de la densité du bois chez l'épicéa (*Picea excelsa* LINK.). Ann. Ec. Eaux Forêts, Nancy 17 (3): 267–334. [FA. 22, 2776]

- PARUSEL J. B. 1991. *Salicetum silesiacae* ass. nova w piętrze subalpejskim Babiej Góry w Karpatach Zachodnich. *Fragm. Flor. Geobot.* 35 (1–2): 283–293.
- PARUSEL J., HOLEKSA J. 1991. Relationship between the herb layer and the tree stand in the spruce forest of the upper montane belt in the Western Carpathians. *Phytocoenosis N.S. Suppl. Cartogr. Geobot.* 2: 223–229.
- PASTORINO J. M., GREGORIUS H. R. 2002. How many macrogametophytes per individual should be analyzed to genotype conifer seed trees at genetic markers? *For. Genet.* 9: 47–53.
- PARAMESWARAN N., FINK S., LIESE W. 1985. Feinstrukturelle Untersuchungen an Nadeln geschädigter Tannen und Fichten aus Waldschadensgebieten im Schwarzwald. *Eur. J. For. Path.* 15: 168–182.
- PASUTKOVÁ J. 1981. Pufráční kapacita jehličí smrku jako indikátor rezistence k působení SO_2 . *Práce VÚHLM* 58: 139–151.
- PAULE L. 1980. Predbežné výsledky provenienčného pokusu so smrekom (*Picea abies* KARST.). Sborník Referátů z konference Provenienční výzkum lesních dřevin. Praha pp.: 39–54.
- PAULE L. 1986. Strategy of choice of Norway spruce provenances for high altitudes. Provenances and Forest Tree Breeding for High Latitudes. *Proc. Frans Kempe Symposium. Umeå, Sweden, Report* 6: 33–55.
- PAULE L., LINDGREN D., YAZDANI R. 1993. Allozyme frequencies, outcrossing rate and pollen contamination in *Picea abies* seed orchards. *Scand. J. For. Res.* 8: 8–17.
- PAULE L., ŠKOLEK J. 1983. Príspevok k autovegetatívneho rozmnožovaniu hlavných lesných drevín. *Acta Fac. For., Zvolen* 25: 77–88.
- PAVES CH. K. 1982. Ocenka rosta posadochnogo materiala eli obyknovennoy razlichnogo geograficheskogo proiskhozhdeniya v Estonskoy SSR. *Geograficheskie opyty v lesnoy selekcii Pribaltiki. Zinatne, Riga*: 42–46.
- PAWLACZYK P. 1991. Wegetatywne odnowienie, rozrost i rozmnażanie się drzew w warunkach naturalnych. *Phytocoenosis N.S., Semin. Geobot.* 1: 275–297.
- PAWŁOWSKI B. 1925. Geobotaniczne stosunki Sądeckizny. *Prace Monogr. Kom. Fizjogr. PAU* 1: 1–342.
- PAWŁOWSKI B. 1956. *Flora Tatr*, 1. PWN, Warszawa. 672 pp.
- PAWŁOWSKI B., SOKOŁOWSKI M., WALLISCH K. 1928. Zespoły roślinne w Tatrach. Cz. 7. Zespoły roślinne i flora Morskiego Oka. *Bull. Acad. Pol. Sci. Lett., Cl. Sci. Math. Nat., Ser. B., Suppl.* 2: 205–272.
- PAWŁOWSKI B., STECKI K. 1927. Zespoły roślin w Tatrach. Cz. 4. Zespoły roślinne w Dolinie Miętusiej i na głównym masywie Czerwonych Wierchów. *Bull. Acad. Pol. Sci. Lett., Cl. Sci. Math. Nat., Ser. B., Suppl.* 2: 79–121.
- PAX. F. 1918. *Pflanzengeographie von Polen (Kongress-Polen)*. Berlin.
- PEACE E. A., LEA P. J., DARRALL N. M. 1995. The effect of open-air fumigation with SO_2 and O_3 on carbohydrate metabolism in Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). *Plant Cell Environ.* 18 (3): 277–283.
- PEACE T. R. 1962. *Pathology of trees and shrubs*. Clarendon Press, Oxford.
- PEARCE R. B., MCLEOD A. R. 1995. Effects of sulphur dioxide and ozone on stilbenes and disease resistance in spruce trees from the Liphook Forest Fumigation Project. *Plant Cell Environ.* 18: 303–307.
- PELKONEN P. 1981. Vegetative propagation in Finland of conifers through cuttings. *Proc. Symposium on clonal forestry, Uppsala, April 8–9, 1981*: 101–104.
- PENDER K. 1975. Zbiorowiska leśne Gór Sowich. *Acta Univ. Wratislav.* 169, *Prace Bot.* 20: 1–76.
- PERCY K. E., RIDING R. T. 1978. The epicuticular waxes of *Pinus strobus* subjected to air pollutants. *Can. J. For. Res.* 8: 474–477.
- PERRIN R., GARBAYE J. 1983. Influence of ectomycorrhizae on infectivity of *Pythium*-infested soils and substrates. *Plant and Soil* 71: 345–351.
- PERSSON A. 1994. Stem cracks in Norway spruce in southern Scandinavia: causes and consequences. *Ann. Sci. For.* 51 (3): 315–327.

- PERSSON A., PERSSON B. 1992. Survival, growth and quality of Norway spruce (*Picea abies* (L.) KARST. provenances at the three Swedish sites of the IUFRO 1964/68 provenance experiment. Dept. of Forest Yield Res. Report 29. 1–67.
- PETER M., AYER F., EGLI S. 2001a. Nitrogen addition in a Norway spruce stand altered macromycete sporocarp production and below-ground ectomycorrhizal species composition. *New Phytol.* 149: 311–325.
- PETER M., AYER F., EGLI S., HONNEGER R. 2001b. Above- and below-ground community structure of ectomycorrhizal fungi in three Norway spruce (*Picea abies*) stands in Switzerland. *Can. J. Bot.* 79: 1134–1151.
- PICHÉ Y., FORTIN J. A., LAFONTAINE, J. G. 1981. Cytoplasmatic phenols and polysaccharides in ectomycorrhizal and non-mycorrhizal short roots of pine. *New Phytol.* 88: 695–703.
- PIERRE M., QUEIROZ O. 1988. Air pollution by SO₂ amplifies the effects of water stress on enzymes and total soluble proteins of spruce needles. *Physiol. Plant.* 73: 412–417.
- PIGOTT C. D. 1982. Survival of mycorrhizas formed by *Cenococcum geophilum* Fr. in dry soil. *New Phytol.* 92: 513–517.
- PILET P. E., ROLAND J. C. 1972. Effects physiologiques et ultrastructuraux du fluor sur des tissus de Ronce cultivés in vitro. *Ber. Schweiz. Bot. Ges.* 82: 269–283.
- PISEK A., WINKLER E. 1959. Licht und Temperaturabhängigkeit der CO₂ Assimilation von Fichte (*Picea excelsa* LINK), Zirbe (*Pinus cembra* L.) und Sonnenblume (*Helianthus annuus* L.). *Planta* 53: 532 – 550.
- PLAUT M. 1910. Über die Veränderungen im anatomischen Bau der Wurzel während des Winters. *Jahrb. Wissensch. Bot.* 48 (2): 143–154.
- PLESNIK P. 1971. Horná hranica lesa vo Výsokých a Belanských Tatrách. SAV, Bratislava. 238 pp.
- PLIURA A., GABRILAVICIUS R. 1993. Adaptability of Lithuanian Norway spruce provenances. Norway spruce provenances and breeding. Proc. of IUFRO (S2.2–11). Symposium, Riga pp.: 119–127.
- PLOSHCHAKOVA-BALEVSKA L. 1970. Biologicheski osobennosti pri formirane i razvite na generativnite organi na *Picea excelsa* var. *erythcarpa* i var. *chlorocarpa*. *Gorskostopanska Nauka* 7 (3): 25–32.
- POETHIG R. S. 1990. Phase change and the regulation of shoot morphogenesis in plants. *Science* 250: 923–930.
- POLAKOWSKI B. 1962. Bory świerkowe na torfowiskach (zespół *Piceo-Sphagnetum girgensohni* ass. nov.) w północno-wschodniej Polsce. *Fragm. Flor. Geobot.* 8 (2): 139–156.
- POLANSKÝ B., VACL V. 1933 Několik předběžných zkoušek s umělým opylováním u lesních dřevin jehličnatých. *Vist (Bull.) Českoslov. Akad. Zeméd.* 9: 283–85.
- POLLE A., PFIRRMAN T., CHAKRABARTI S., RENNENBERG H. 1993. The effects of enhanced ozone and enhanced carbon dioxide concentrations on biomass, pigments and antioxidative enzymes in spruce needles (*Picea abies* L.). *Plant Cell Environ.* 16: 311–316.
- POLUNIN O., STANTON A. 1984. *Flowers of the Himalaya*. Oxford University Press. Oxford–New York. 580 pp.
- POPIVSHCHII I. I., SHAPKIN O. M. 1986. The response of young Scotch pine and Norway spruce plants to growth regulators and trace elements. *For. Abstr.* 1988, 049–03376.
- POPOV P. P. 1982. Izmenchivost' chisla semyadoley z eli evropeiskoy u eli sibirskoj. *Lesoved.* (5): 18–22.
- POULSEN H. D., SIMONSEN V., WELLENDOFF H. 1983. The inheritance of 6 izoenzymes in Norway spruce (*Picea abies* L. KARST.). *For. Tree Improv.* 16: 12–32.
- PRAVDIN L. F. 1972. Introgressivnaja gibrizacijazija eli evropejskoj (*Picea abies* (L.) KARST.) i eli sibirskoj (*Picea obovata* LEDEBOUR). *Les. Khoz. Les. Promyshl. SSSR.* Pp.: 325–328. [Ref. Zh. 12. 56.69]
- PRAVDIN L. F. 1975. El' evropejskaya i el' sibirskaya v SSSR. *Nauka, Moskva*, 176 pp.
- PRAVDIN L. P., ROSTOVTSSEV S. A. 1979. Norway spruce provenance experiments in the USSR. IUFRO Norway spruce-Meeting S. 2.03.11–S. 2.02.11. Bucharest, 85–99.
- PRAVDIN L. F., ROSTOVTSSEV S. A. 1980. Vliyanie proizchozhdeniya semyan eli obyknovennoy na rost kul'tur iz nikh. *Lesoved.* (6): 3–10.

- PRESCHE F. 1982. Testning av tillväxtrytm och tillväxtförmåga för bruksprovenienser av gran. SLV, Rapp. Inst. Skogsproduktion 10: 1–58.
- PROKAZIN E. P. 1962. Metod massovogo poluchenia mezhvidovyykh i mezhrodovyykh privivok w polevykh usloviakh. Bot. Zh. 47 (7): 987–990.
- PROKUBIN YU. N. 1987. Opredelitel vysshikh rastieni Ukrainy. Naukova Dumka, Kijev, 546 pp.
- PROSINSKI S. 1984. Chemia drewna. PWRiL, Warszawa.
- PRUŠA E. 1985. Die böhmischen und mährischen Urwälder. Academia, Praha. 578 pp.
- PRUS-GŁOWACKI W., GODZIK S. 1995. Genetic structure of *Picea abies* trees tolerant and sensitive to industrial pollution. Silvae Genet. 44: 62–65.
- PRZEBÓRSKI A. 1974. Wpływ okresu ekspozycji pniaków sosny zwyczajnej na ich zasiedlenie przez grzyb *Fomes annosus* (FR.) CKE i przez inne grzyby. Zesz. Probl. Post. Nauk Roln. 160: 87–111.
- PSOTA V., SEBANEK J., KLICOWA S., KRÁLIK J., VITKOVA H. 1992. Changes in the content of beta-indolylacetic acid in the needles of the species *Picea abies* (L.) KARST. in the course of the year. Biologia, Bratislava. 47: 295–299.
- PUCHALSKI T. 1968. Wzrost drzew i drzewostanów. [Growth of trees and stands]. PWRiL, Warszawa.
- PUCHALSKI T. 1970. Wybrane zagadnienia z hodowli lasu. Ekologia, pielęgnowanie i selekcja drzew. [Selected elements of forest tree breeding. Ecology, cultivation and selection of trees]. Skrypt. WSR. Poznań.
- PUCHALSKI T. 1972. Rębnie w gospodarstwie leśnym. [Cutting systems in Forestry]. PWRiL, Warszawa. 258 pp. (in Polish).
- PUCHALSKI T., PRUSINKIEWICZ Z. 1990. Ekologiczne podstawy siedliskoznawstwa leśnego. PWRiL, Warszawa. 619 pp.
- PUKACKI P. 1980. Temperature of Norway spruce and Scots pine buds. Arbor. Kórnickie 25: 277–287.
- PUKACKI P. 1981. The light transmission by Norway spruce bud scales as dependent on humidity, polythene covers and position in the crown. 6th Ann. Rep. 1980–1981, FG-Po-342 (JB-7), Institute of Dendrology, Kórnik. pp.: 30–32.
- PUKACKI P. M., MODRZYŃSKI J. 1998. The influence of ultraviolet-B radiation on the growth, pigment production and chlorophyll fluorescence of Norway spruce seedlings. Acta Phys. Plant. 20 (3): 245–250.
- PUKACKI P., CHAŁUPKA W. 1982. Pomiar przepuszczalności światła przez łuski pąkowe drzew przy zastosowaniu światłowodów. Mat. III Krajowego Symp. Światłowodowy i ich zastosowania, Jabłonna, 1982. 1: 204–209.
- PUKACKI P., GIERTYCH M. 1982. Seasonal changes in light transmission by bud scales of spruce and pine. Planta 154: 381–383.
- PUKKALA T. 1987a. Kuusen ja männyn siemensadon ennustemalli. Silva Fenn. 21 (2): 135–144.
- PUKKALA T. 1987b. Siementuotannon vaikutus kuusen ja männyn vuotuiseen kasvuun. Silva Fenn. 21 (2): 145–158.
- PULKKINEN P., PÖYKKÖ T. 1990. Inherited narrow crown form, harvest index and stem biomass production in Norway Spruce *Picea abies*. Tree Physiol. 6 (4): 381–391.
- PULS J., RADEMACHER P. 1986. Chemische Untersuchungen an Fichten aus Waldschadensgebieten. Holz. Roh Werkstoff 44: 307–312.
- PURO T. 1977. Operaatio metsänlannoitus II. Folia Forest. Inst. For. Fenn. 304: 1–15.
- QAMARUDIN M., DORMLING I., EKBERG I., ERIKSSON G., TILLBERG E. 1993. Abscissic acid content at defined levels of bud dormancy and frost tolerance in two contrasting populations of *Picea abies* grown in a phytotron. Physiol. Plant. 87: 203–210.
- QIAN X. M., KOTKE I., OBERWINKLER F. 1998. Influence of liming and acidification on the activity of the mycorrhizal communities in a *Picea abies* (L.) KARST. stand. Plant and Soil 199: 99–109.
- QINGHONG L., HYTTBORN H. 1991. Gap structure, disturbance and regeneration in a primeval *Picea abies* forest. J. Veg. Sci. 2: 391–402.
- RABIEN I. 1953. Zur Bestimmung fossiler Knospenschuppen. Paläontol. Z. 27: 57–66.
- RACHWAŁ L. 1983. Tolerance variability of trees and shrubs to high concentrations of SO₂ and heavy metals. Aquilo, Ser. Bot. 19: 324–353.

- RACHWAŁ L., OLEKSYN J. 1987. Growth and development of black pine (*Pinus nigra* ARN.) and Norway spruce (*Picea abies* (L.) KARST.) in the Niepolomice forest provenance experiments. *Acta Agr. Silv.* 26: 163–181.
- RACHWAŁ H. 1996. Zmiany chemizmu igieł świerka *Picea abies* (L.) KARST. w Puszczy Białowiejskiej. *Prace IBL, Warszawa* 825–828: 63–75.
- RACIBORSKI M. 1912. Rozmieszczenie i granice drzew oraz ważniejszych krzewów i roślin na ziemiach polskich. *Encyklopedia Polska*, 1: 349–355. Kraków.
- RACIBORSKI M., SZAFAER W. 1919. *Picea* LINK, Świerk. W: RACIBORSKI M., SZAFAER W. (red.). *Flora Polska* 1: 44–46 + mapa. AU, Kraków.
- RADDI P., RINALDO C. 1989. Variation in needle wax degradation in two silver fir provenances differentiated by tolerance to air pollution. In: SCHOLZ F., GREGORIUS H. R., RUDIN D. (eds.). *Genetic Effects of Air Pollutants in Forest Tree Populations*. Berlin, Heidelberg, pp.: 67–76.
- RADDI S., STEFANINI F. M., CAMUSSI A., GIANNINI R. 1994. Forest decline index and genetic variability in *Picea abies* (L.) KARST. *For. Genet.* 1: 33–40.
- RADEMACHER P., BAUCH J., PULS J. 1986. Biological and chemical investigations of the wood from pollution-affected spruce (*Picea abies* (L.) KARST.) *Holzforschung* 40: 331–338.
- RADOSTA P. 1987. Ekonomické a biologické hodnocení dosavadních technologií řízkování smrku ztepilého [*Picea abies* (L.) KARST.]. *Lesnictví* 33 (6): 541–550.
- RAIZADA M. B., SAHNI K. C. 1958 Living Indian Gymnosperms, 1. *Indian For. Rec.* 5 (2): 120–122.
- RAJSKA-JASIEWICZOWA M. 1983. Isopollen maps for Poland 0 – 11 000 years B.P. *New Phytol.* 14: 133–175.
- RANFT H., DÄSSLER H.-G. 1970. Rauchhartetest an Geholzen im SO₂-Kabinenversuch. *Flora* 159 (8): 573–588.
- RANGER J., CUIRIN G., BOUCHON J., COLIN M., GELHAYE D., MOHAMED AHAMED D. 1992. Biomasse et minéralomasse d'une plantation d'épicéa commun (*Picea abies* KARST.) de forte production dans les Vosges (France). *Ann. Sci. For.* 49: 651–668.
- RANTANEN L., PALOMÄKI V., HOLOPAINEN T. 1994. Interactions between exposure to O₃ and nutrient status of trees: effects on nutrient content and uptake, growth, mycorrhiza and needle ultrastructure. *New Phytol.* 128: 679–687.
- RAU H. M. 1983. Die Entwicklung des deutsch-polnischen Fichten-Provenienzversuches in Hessen. *Forstarchiv* 54 (1): 15–19.
- RAU H. M. 1993. The IUFRO 1964/68 Norway spruce provenance trial in Germany after 25 years of observation. Norway spruce provenances and breeding. *Proc. of IUFRO (S2.2–11)*. Symposium, Riga, Latvia: 128–132.
- RAUTER M. R. 1971. Spruce breeding at the southern research station, Maple, Ontario. *Proc. 12th meet. comm. For. Tr. Breed. in Canada* 2: 47–51.
- RAYNALL D. J., JOSLIN J. D., THORNTON F. C., SCHAEDEL M., HENDERSON G. S. 1990. Sensitivity of tree seedlings to aluminium; III. Red spruce and loblolly pine. *J. Environ. Qual.* 19: 180–187.
- READ D. J. 1991. Mycorrhizas in ecosystems. *Experientia* 47: 376–391.
- RED'KO G. I., DURSIN A. D. 1982. Geograficheskie kul'tury eli. Lektsii po kursu Lesnye kul'tury, dlja studentov spetsjal'nosti 1512, Leningrad. pp.: 1–59.
- REHDER A. 1977. *Manual of Cultivated Trees and Shrubs*. New York.
- REHDER A., WILSON E. H. 1916. *Plantae Wilsonianae* 2: 22–36. Cambridge.
- REHMAN A. 1895. *Ziemia dawnej Polski*. 1. Karpaty. Lwów.
- REMRÖD J. 1972. Försök med blomningsstimulering i en granfröplantage. *Föreningen Skogsträdsförädling Inst. Skogsför.*: 161–178.
- REMRÖD J., ERICSSON T., ANDERSSON G. 1972. Norrländska granproveniensförsök. *Föreningen Skogsträdsförädling, Årsbok* 1972: 140–197.
- REPÁČ I. 1996. Inoculation of *Picea abies* (L.) KARST. seedlings with vegetative inocula of ectomycorrhizal fungi *Suillus bovinus* (L.:FR.) O. KUNTZE and *Inocybe lacera* (FR.) KUMM. *New For.* 12: 41–54.
- REUTZE M., SCHMITT U., LIESE W. 1989. Strukturelle Veränderungen in Tannen und Fichtennadeln aus Begasungsexperimenten. *Mitt. Bundesforschungsanstalt Forst Holzwirtschaft, Reinbek bei Hamburg* 163: 197–214.

- REY A., JARVIS P. G. 1997. Growth response of young birch trees (*Betula pendula* ROTH.) after four and half years of CO₂ exposure. *Ann. Bot.* 80: 809–816.
- RICHARDS B. N. 1979. Wstęp do ekologii gleby. PWN, Warszawa. pp.: 234–267.
- RICHARDSON S. D. 1964. The external environment and tracheid size in conifers. In: ZIMMERMANN M. H. (ed.). The formation of wood in forest trees: 367–388.
- RICHTER C. M., WILD A. 1992. Phenolic compounds in Norway spruce trees in relation to novel forest decline. I. Studies on trees from a site in the northern Black Forest. *Biochem. Physiol. Plant.* 188: 305–320.
- RIDING R. T., PERCY K. E. 1985. Effects of SO₂ and other air pollutants on the morphology of epicuticular waxes on needles of *Pinus strobus* and *Pinus banksiana*. *New Phytol.* 99: 555–563.
- RIEGER A., GUTTENBERGER M., HAMPP R. 1992. Soluble carbohydrates in mycorrhized and non-mycorrhized fine roots of spruce seedlings. *Z. Naturforsch.* 47c: 201–204.
- RIKALA R. 1979. Lannoitteiden levitystavan vaikutus kouluttujen männyn ja kuusen taimien kehittymiseen taimitarhalla. *Folia Forest. Inst. For. Fenn.* 394: 1–15.
- RIMMELT M. 1994. Tylenchids Parasite of Insects. *Ostrom. Inst. Franc. Rech. Sci. Devel. Coop., Paris.* 145 pp.
- RINCON A., GERARD J., DEXHEIMER J., LE TACON F. 2001. Effect of an auxin transport inhibitor on aggregation and attachment processes during ectomycorrhiza formation between *Laccaria bicolor* S238N and *Picea abies*. *Can. J. Bot.* 79: 1152–1160.
- RISHBETH J. 1950. Observations on the biology of *Fomes annosus*, with particular reference to East Anglian pine plantations. I. The outbreaks of disease and ecological status of the fungus. *Ann. Bot.* 14: 365–383.
- RISHBETH J. 1951a. Observations on the biology of *Fomes annosus*, with particular reference to East Anglian pine plantations. II. Spore production, stump infection and saprophytic activity in stumps. *Ann. Bot.* 15: 1–21.
- RISHBETH J. 1951b. Observations on the biology of *Fomes annosus*, with particular reference to East Anglian pine plantations. III. Natural and experimental infection of pines, and some factors affecting severity of the disease. *Ann. Bot.* 15: 221–246.
- RITLAND K., EL-KASSABY Y. A. 1985. The nature of inbreeding in a seed orchard of Douglas-fir as shown by an efficient multilocus model. *Theor. Appl. Genet.* 71: 375–384.
- RITTER T., WEBER G., KOTTKE I., OBERWINKLER F. 1989. Zur Mykorrhizaentwicklung von Fichten und Tannen in geschädigten Beständen. *Biol. Zeit* 19: 9–15.
- RIVOLI J. 1884. O geograficznem rozsiadleniu świerka. *Sylwan* 1–7: 47–54; 101–105.
- RIVOLI J. 1921. Badania nad wpływem klimatu na wzrost niektórych drzew europejskich. *Prace Nauk. Uniw. Poznańskiego, Sekcja Rolniczo-Leśna*, 1.
- ROBAK H. 1962a. (Central European spruce in W Norway). *Tidsskr. Skogsbr.* 70 (3): 129–150. [FA. 24, 1896]
- ROBAK H. 1962b. Nye planteskoletforsøk over sambandet mellom sommer daglengden og avslutningen av første års vekst hos gran og Douglas. *Medd. Vestland. Forstl. Forsøksst.* 36: 11 (4): 199–246.
- ROBAK H. 1969. Aluminium plants and conifers in Norway. In: *Air Pollution Proceedings of the First European Congress on the Influence of Air Pollution on Plants and Animals*. Wageningen, April 22–27: 27–32. Pudoc, Wageningen.
- ROBAK H., MAGNESEN S. 1970. Contribution to the knowledge of the ecology of growth termination in spruce seedlings of Norwegian and Central European provenances. *Silvae Genet.* 19 (5–6): 188–190.
- ROBAKOWSKI P. 1997. Wpływ promieniowania ultrafioletowego (UV-B) na wybrane proveniencje niektórych gatunków drzew i roślin runa leśnego. Ph.D. thesis Forest Faculty, Poznań.
- ROBERTNTZ P., LINDER S. 1999. Effects of long-term CO₂ enrichment and nutrient availability in Norway spruce. II. Foliar chemistry. *Trees* 14 (1): 17–27.
- ROBERTS D. R. 1991. Absciscic acid and mannitol promote early development, maturation and storage protein accumulation in somatic embryos of interior spruce. *Physiol. Plant.* 83: 247–254.
- ROBERTS D. R., DUMBROFF E. B. 1986. Relationships among drought resistance, transpiration rates, and absciscic acid levels in three northern conifers. *Tree Physiol.* 1. 161–167.

- ROBERTS D. R., FLINN B. S., WEBB D. T., WEBSTER F. B., SUTTON B. C. S. 1990. Absciscic acid and indole-3-butyric acid regulation of maturation and accumulation of storage proteins in somatic embryos of interior spruce. *Physiol. Plant.* 78: 355–360.
- ROBERTS T. M., BROWN K. A., BLANK L. W. 1987. Methodological aspects of the fumigation of forest trees with gaseous pollutants using closed chambers. In: MATHY P. (ed.). *Air pollution and ecosystems. Proceedings of International Symposium held in Grenoble, France, 18–22 May 1987.* pp.: 338–360.
- ROBERTS T. M., SKEFFINGTON R. A., BLANK L. W. 1989. Causes of type 1 spruce decline in Europe. *Forestry*, London 62 (3): 179–222.
- ROGOZIŃSKA J. H. 1967. The occurrence of cytokinins in Scots pine. *Bull. Acad. Pol. Sci.* 15: 789–794.
- ROHMEDE E. 1971. Die Züchtung der Fichte auf frühzeitige und starke Borkenbildung. *Forstw. Cbl.* 90 (2): 74–87.
- ROHMEDE E., BEUSCHEL G. 1970. Die Fichtenherkunftsversuch in Bischofsreut/Bayer Wald nach 32 jähriger Wuchszeit. *Forstw. Cbl.* 89 (2): 78–87.
- ROHMEDE E., SCHÖNBORN A. V. 1965. Der Einfluss von Umwelt und Erbgut auf die Widerstandsfähigkeit der Waldbäume gegenüber Luftverunreinigung durch Industrieabgase. Ein Beitrag zur Züchtung einer relativ rauchresistenten Fichtensorte. *Forstw. Centbl.* 84 (1–2): 1–13.
- ROLLER K. J. 1971. Survival and height growth of Norway spruce in central Manitoba. *Bi-monthly research notes. Min. Forestry, Canada.* 27 (4): 28.
- ROLL-HANSEN F. 1974. Nytt om lokkrusten (*Pucciniastrum padi*). *MEDD. Nrske Skogelsk.* 34: 503–510.
- ROMANOWSKA M. 1934. Zmiany w zalesieniu Królestwa Polskiego w ostatniem stuleciu. *Czasopismo Geogr.* (1934) (3–4): 2–40.
- ROMMELL L. G. 1938. A trenching experiment in spruce forest and its bearing on problems of mycotrophy. *Svensk Bot. Tidskr.* 32: 89–99.
- ROMMELL L. G. 1939. The ecological problem of mycotrophy. *Ecology* 20: 163–167.
- RONE V. 1984. Firmie egļu provenienču vērtēšanas rezultāti Latvijā. *Jaunākis Mežsaimniecībā*, Rīga 26: 33–38.
- RONE V. M. 1970. Izmenčivost' plotnosti drevesiny i dliny tracheid v potomstve eli obyknovennoj. *Lesoved.* (5): 78–82.
- RONIS E. 1983. Maleinhidrazida ietekme uz poteto egļu augšanu un ziedēšanu. *Jaunākis Mežsaimniecībā*, Rīga 25: 43–47.
- ROSS S. D. 1988. Effects of temperature, drought, and gibberelin A₄₇ and timing of treatment on flowering in potted *Picea engelmanni* and *Picea glauca* grafts. *Can. J. For. Res.* 18: 163–171.
- ROSS S. D. 1990. Control of sex expression in potted *Picea engelmanni* grafts by gibberellin A₄₇ and the auxin, naphthaleneacetic acid. *Can. J. For. Res.* 20: 875–879.
- ROSS S. D. 1991. Effect of heat sum and of heat applied separately to shoots and roots on flowering in potted *Picea glauca* grafts. *Can. J. For. Res.* 21: 672–769.
- ROSTOVTSSEV S. A. 1967. Geograficheskie posevy eli obyknovennoj v pitomnikakh Moskovskoy oblasti. *Les. Khoz. Ref. Inform.* 22: 12–14. [Ref. Zh. 6. 56.68]
- ROSTOVTSSEV S. A., KURAKIN B. N. 1981. Geografičeskaja izmenčivost' eli obyknovennoj v evropejskoj časti SSSR. *Les. Khoz.* 12: 14–17.
- ROST-SIEBERT K. 1983. Aluminum – Toxizität und -Toleranz an Keimpflanzen von Fichte (*Picea abies* KARST.) und Buche (*Fagus sylvatica* L.). *Allg. Forst Holzwissch.* Ztg. 26/27: 686–680.
- ROSVALL O., ERICSSON T. 1981. Förflyttningseffekter i norrländska granproveniensförsök. Föreningen Skogsträdsförädling och Inst. Skogsförbättring, Årsbok 1981: 85–117.
- ROTH D. R., FAHEY T. J. The effects of acid precipitation and ozone on the ecto-mycorrhiza of red spruce samplings. *Water, Air, Soil Poll.* 103: 263–276.
- ROTHER A. 1994. Saure Beregnung und Kalkung, Auswirkungen auf Bodenchemie und Wasserqualität. *Allg. Forstztg.* 38: 686–689.
- ROTHER G. M. 1990. Identifizierung von Fichtenklonen durch Isozymanalysen an Nadeln. *Allg. Forst- Jagdztg.* 161 (5): 103–107.

- ROTTMANN M. 1983. Schneebruchschäden bei Fichten. Dissert. Forstwissenschaftl. Fak. Ludwig-Maximilians-Univ., München. 256 pp.
- ROULUND H. 1969. Artskrydningsforsøg i slægten *Picea*. Dansk Skovforen. Tidsskr. 54: 222–233.
- ROULUND H. 1974. Comparative study of characteristics of seedlings and clonal cuttings. N. Z. J. For. Sci. 4: 378–386.
- ROULUND H. 1975. The effect of the cyclophysis and the topophysis on the rooting and behavior of Norway spruce cuttings. Acta Hort. 54: 39–50.
- ROULUND H. 1979. Topophysis studies on cuttings of Norway spruce. Proc. IUFRO Norway Spruce Meeting, Sept. 24, 1979, Bucharest.
- ROVIRA A. D. 1969. Plant root exudates. Bot. Rev. 35: 35–57.
- RUBNER K. 1957. Ergebnisse eines heute 20 jährigen Fichtenherkunftsversuches. I Teil. Die Fläche in Bayern. Silvae Genet. 6: 65–74.
- RUBNER K. 1960. Die pflanzengeographischen Grundlagen des Waldbaues. Neumann Verlag, Radebeul u. Berlin. 620 pp.
- RUBTSOV N. J. 1952. O razmnozhenii eli otrodkami. Bot. Zh. 37 (5): 685–687.
- RUDEN T. 1963. Results from an 11-year old progeny test with *Picea abies* (L.) KARST. in south-eastern Norway (FAO/FORGEN 63) 1: 2a/9.
- RUDOLF P. O., SLABAUGH P. E. 1958. Growth and development of 12 seed sources of Norway spruce in Lower Michigan (15 year results). Tech. Note Lake St. For. Exp. Sta. 537.
- RUETZ W. F., BERGMANN F. 1989. Möglichkeiten zum Nachweis von autochthonen Hochlagenbeständen der Fichte (*Picea abies*) in den Berchtesgadener Alpen. Forstw. Cbl. 108 (3): 164–174.
- REUTZE M., SCHMITT U. 1988. Histologie der Alterung von Fichtennadeln. Angewandte Bot. 62: 9–20.
- REUTZE M., SCHMITT U., KÜPPERS K., LIESE W. 1988. Histologische Untersuchungen an Fichtennadeln (*Picea abies* L. KARST.) nach Begasung mit SO₂, O₃ und NO₂. Allg. Forst- Jagdztg. 159: 195–203.
- RÜHLING A., BÅÅTH E., NORDGREN A., SÖDERSTRÖM B. 1984. Fungi in metal contaminated soil near the Gsum. Bross Mill, Sweden. Ambio 13: 34–36.
- RÜHM W. 1956. Die Nematoden der Ipiden. Fischer Verlag, Jena. 147 pp.
- RUNIONS C. J., CATALANO G. L., OWENS J. N. 1995. Pollination mechanism of seed orchard interior spruce. Can. J. For. Res. 25 (9): 1434–1444.
- RUTH B., WEISEL B. 1993. Investigations on the photosynthetic system of spruce affected by forest decline and ozone fumigation in closed chambers. Environ. Poll. 79: 31–35.
- RUZICKA S., EDGERTON D., NORMAN M., HILL T. 2000. The utility of ergosterol as a bioindicator of fungi in temperate soils. Soil Biol. Biochem. 32: 989–1005.
- RYBNÍČKOVÁ E., RYBNÍČEK K. 1988. Isopollen maps of *Picea abies*, *Fagus sylvatica* and *Abies alba* in Czechoslovakia – their applications and limitations. W: LANG, SCHUSTLER (red.). Lake, mire and river environments during last 15 000 years. Balkema, Rotterdam.
- RYGIEWICZ, P. T., BLEDSOE C. S., ZASOSKI R. J. 1984. Effects of ectomycorrhizae and solution pH on ¹⁵[N] ammonium uptake by coniferous seedlings. Can. J. For. Res. 14: 885–892.
- RYKOWSKI K., SIEROTA Z. 1973. Badania nad przydatnością preparatu Agrico do zwalczania huby korzeni. Inst. Bad. Leśn., Warszawa.
- RYŠKOVÁ L. 1977. Stanovení poškození dřevin měřením vodivosti výluhu jejich asimilačních orgánů. Práce VÚLHM 51: 107–123.
- SABOR J. 1984. Pędzenie wiosenne świerka pospolitego (*Picea abies* (L.) KARST.) w rocznym cyklu przyrostowym proveniencji objętych doświadczeniem IPTNS-IUFRO 1964/68 w Krynicy. Acta Agr. Silv. 23: 53–69.
- SABOR J. 1989. The age x age of spring flushing correlation and the selection of resistant to spring frost Norway spruce provenances of IPTNS-IUFRO 1964/68 experiment in Krynica. Inst. Forest Improvement, Uppsala. Rep.11: 142–152.
- SABOR J., MIKOŁAJCZAK K., BARAN S. 1994. Ocena poziomu akumulacji składników odżywczych w igłach drzew selekcyjnych doświadczenia proveniencyjnego świerka IPTS-IUFRO 1964/68 w Krynicy. Biul. Reg. Zakł. Dor. Roln. AR, Kraków 308: 101–116.

- SÆTERS DAL L. S. 1956. Investigations on respiration and assimilation rates of various provenances of Norway spruce (*Picea excelsa*) in winter and spring. Årbok Univ. Bergen, Naturvitenskape-ling Rekke 6: 1–46.
- SÆTERS DAL L. S. 1963. The rate of drying of young excised plants of various provenances of Norway spruce and Douglas fir. Medd. Vestland. Forstl. Forsøksst. 38 12 (1): 1–88.
- SAKAI A., LÄRCHER W. 1987. Frost Survival of Plants. Responses and Adaptation to Freezing Stress. Springer Verlag, Berlin, Heidelberg, New York, London, Paris, Tokyo. 321 pp.
- SALMANOWICZ B., NYLUND J.-E. 1988. High performance liquid chromatography determination of ergosterol as a measure of ectomycorrhizal infection of Scots pine. Eur. J. For. Path. 18: 291–298.
- SALZER P., HAGER A. 1991. Sucrose utilization of the ectomycorrhizal fungi *Amanita muscaria* and *Hebeloma crustuliniforme* depends on the cell wall-bound invertase activity of their host *Picea abies*. Bot. Acta 104: 439–445.
- SALZER P., HAGER A. 1993. Characterization of wall-bound invertase isoforms of *Picea abies* cells and regulation by ectomycorrhizal fungi. Physiol. Plant. 88: 52–59.
- SAMPANGI R., PERRIN R., LE TACON F. 1986. Disease suppression and growth promotion of Norway spruce and Douglas-fir seedlings by the ectomycorrhizal fungus *Laccaria laccata* in forest nurseries. In: Mycorrhizae: physiology and genetics, 1st ESM, Dijon, 1–5 July 1985, INRA, Paris, 1985. pp.: 799–806.
- SAMUELSON K. R. 1979. Possibilities of seed orchards in Norway spruce. Proc. IUFRO Joint Mtg. of WPs on Norway spruce provenances and Norway spruce breeding, Bucharest: 129–139.
- SANCHEZ A., CADAHIA C., EYMAR E., MASAGUER A. 2000. Study of conifer nutrition using hydroponic cultures: Application to fertigation systems. J. Plant Nutr. 23 (7): 1007–1024.
- SANDBERG G. 1988. Effects of growth regulators on germination of *Picea abies* and *Pinus sylvestris* seeds. Scand. J. For. Res. 3: 83–95.
- SANDBERG G., ERNSTSEN A. 1987. Dynamics of indole–3-acetic acid during germination of *Picea abies* seeds. Tree Physiol. 3: 185–192.
- SANDERMAN H., SCHMITT R., HELLER W., ROSEMAN D., LANGEBARTELS C. 1989. Ozone-induced early biochemical reactions in conifers. In: LONGHURST J. W. S. (ed.). Acid Deposition. Sources, Effects and Controls. pp.: 243–254.
- SANDERMANN W. 1960. Naturharze, Terpeninöl, Tallöl. Springer, Berlin–Göttingen–Heidelberg.
- SANIGA M., SKLENDER P. 1989. Štruktúra, vyvoj, produkčné a regeneračné pomery prírodných lesov v ŠPR Pilsko. In: Stav, vyvoj, produkčné schopnosti a funkčné využívanie lesov v oblasti Babej Hory a Pilska. Zwolen. pp.: 26–49.
- SANTAMOUR F. S. 1960. New chromosome counts in *Pinus* and *Picea*. Silvae Genet. 9: 87–88.
- SANTANEN A., SIMOLA L. K. 1999. Metabolism of L[U–1⁴C]-arginine and L[U–1⁴C]-ornithine in maturing and verbalized embryos and megagametophytes of *Picea abies*. Physiol. Plant. 107: 433–440.
- SARAMAKI J., VALTANEN E. 1981. Toistuvan tyypilannoituksen vaihtus nuoren metsikon rakenteeseen ja kehitykseen. Folia Forest. Inst. For. Fenn. 479: 1–16.
- SARNACKIY V. V. 1988. Analiz vliyaniya mineral'nykh udobreniy i rubok ukhoda na zapas stvalovoy drevesiny elovych nasazhdeniy. Lesoved. Les. Khoz. (23): 18–21.
- SARTER T. 1986. Variabilité de la vigueur et de propriétés mécaniques du bois dans une plantation comparative de 16 provenances d'espèce commun (*Picea excelsa* LINK.). INRA Station Amélior. Arbres Forest. Doc. 332: 1–30.
- SARVAS R. 1955. Investigations into the flowering and seed quality of forest trees. Comm. Inst. For. Fenn. 45.7.
- SARVAS R. 1957. Studies on the seed setting of Norway Spruce. Medd. Norske Skogforsøk. 14: 529–556.
- SARVAS R. 1968. Investigations of the flowering and seed crop of *Picea abies*. Comm. Inst. For. Fenn. 67.5.
- SARVAS R. 1970. Establishment and registration of seed orchards. Folia Forest. Fenn. 89.
- SARVAS R. 1972. Investigations on the annual cycle of development of forest trees. Active period. Comm. Inst. Forest. Fenn. 76.3.

- SATO Y., MUTO K. 1953. Fundamental studies on the nutritional physiology of *Picea* spp. (I). Res. Bull. Exp. For. Hokkaido Univ. 16 (2): 206–227. [FA. 15, 80]
- SAVULESCU T., RAYSS T. 1928. Un parasite des pins peu connu en Europe *Neopeckia coulteri* (PECK.) SACC. J. Epiphyt. 14: 322–353.
- SAX K., SAX H. J. 1933. Chromosome number and morphology in the conifers. J. Arnold Arbor. 14: 356–375.
- SAXE H. 1989. Diagnostic parameters for selecting against novel spruce (*Picea abies*) decline: IV. Response of photosynthesis and transpiration to SO₂ + NO₂ exposures. Physiol. Plant. 76 (3): 362–367.
- SAXE H. 1993. Triggering and predisposing factors in the “Red” decline syndrome of Norway spruce (*Picea abies*). Trees 8: 39–48.
- SAXE H., CANNEL M. G. R., JOHNSEN Ø., RYAN M. G., VOURLITIS G. 2001. Tree and forest functioning in response to global warming. New Phytol. 149: 369–400.
- SAXE H., MURALI N. S. 1989a. Diagnostic parameters for selecting against novel spruce (*Picea abies*) decline: II. Response of photosynthesis and transpiration to acute NO_x exposures. Physiol. Plant. 76 (3): 349–355.
- SAXE H., MURALI N. S. 1989b. Diagnostic parameters for selecting against novel spruce (*Picea abies*) decline: III. Response of photosynthesis and transpiration to O₃ exposures. Physiol. Plant. 76 (3): 356–361.
- SCHAAF W., ZECH W. 1993. Düngung mit gebranntem Magnesit und Magnesiumhydroxid zur Standortmelioration in einem stark geschädigten Fichtenökosystem. Ztschr. Pflanzenernährung Bodenkunde 156 (4): 357–364.
- SCHACHLER G., MATSCHKE J. 1984. Stand und Perspektiven zur autovegetativen Vermehrung von Fichte. Beitr. Forstwirtschaft 18 (1): 19–24.
- SCHACHLER G., MATSCHKE J. 1991. Controlling flower induction in conifers. Holzzucht. 45: 25–27.
- SCHÄDELIN W. 1934. Die Durchforstung als Auslese- und Veredelungsbetriebshöchster Wertleistung. Haupt, Bern–Leipzig.
- SCHAEFFER C., WALLEND T., GUTENBERGER M., HAMPP R. 1995. Acid invertase in mycorrhizal and non-mycorrhizal roots of Norway spruce (*Picea abies* [L.] KARST.) seedlings. New Phytol. 129: 417–424.
- SCHAEZL R. J., BURNS S. F., JOHNSON D. L., SMALL T. W. 1989. Tree uprooting: review of impacts on forest ecology. Vegetatio 79: 165–176.
- SCHUEMANN W., HOFFMANN K. 1967. Die serienmäßige Prüfung der Frostresistenz einjähriger Fichtensämlinge. Arch. Forstw. 16 (6/9): 701–705.
- SCHIER G. A. 1985. Response of red spruce and balsam fir seedlings to aluminium toxicity in nutrient solution. Can. J. For. Res. 15: 29–33.
- SCHIER R. 1973. Beobachtungen an der natürlichen Fichtengrenze in Südschweden. Mitt. Dtsch. Dendr. Ges. 66: 49–59.
- SCHIFFENS-GRÜBER A., LÜTZ C. 1992. Ultrastructure of mesophyll cell chloroplast of spruce needles exposed to O₃, SO₂ and NO₂ alone and in combination. Environ. Exp. Bot. 32: 243–254.
- SCHLECHTE G. 1986. On the mycorrhizal fungus flora of damaged forest stands. Ztschr. Mykolog. 52 (1): 225–232.
- SCHLEE D., KÖCK M. 1987. Wirkung von abiotischen Stressoren auf den Proteinabbau und die Proteinsynthese in höheren Pflanzen. Biol. Rundsch. 25: 35–44.
- SCHLEGEL H., GODBOLD D. L., HUTTERMANN A. 1987. Whole plant aspects of heavy metal induced changes in CO₂ uptake and water relations of spruce (*Picea abies*) seedlings. Physiol. Plant. 69 (2): 265–270.
- SCHLENKER G. 1967. Stabile und labile Fichtenstandorte. Allg. Forst-Ztschr. 22: 308–309.
- SCHLENKER G., DENNO D. 1971. Die Auswirkung der Laubholz- bzw. Fichtenbestockung auf den Regenwurmbesatz in Parabraunerden und Pseudogleyen des Neckarlandes. Mitt. Vereins Forstl. Standortskunde Frostpflanzenzüchtung 21: 60–66.
- SCHLÜTER H. 1969. Das *Calamagrostis villosae*-Piceetum des Thüringer Waldes im Vergleich zu anderen Mittelgebirgen. Vegetatio 17 (1–6): 157–164.

- SCHMID I., KAZDA M., HASENAUER H. 2000. Forest ecosystem restoration: ecological and economical impacts of restoration processes in secondary coniferous forests. Proceedings of the International Conference, Vienna, Austria, 10–12-April 2000. pp.: 241–246.
- SCHMIDT-VOGT H. 1964. Der Johannistriebtest als Hilfsmittel zur Feststellung der Bodenständigkeit von Fichtenbeständen in Hochlagen. Forstsamengewinnung und Pflanzenanzucht für das Hochgebirge. BLV Verlag, München: 93–100.
- SCHMIDT-VOGT H. 1972. Wachstum und Schneebruchresistenz von Fichtenherkünften des Bayerischen Alpenvorlandes der Bayerischen Alpen und des Bayerischen Waldes. Forstw. Cbl. 91 (6): 339–357.
- SCHMIDT-VOGT H. 1974. Die systematische Stellung der Gemeinen Fichte (*Picea abies* (L.) KARST und die sibirischen Fichte (*Picea obovata* LEBED.) in der Gattung *Picea*. Allg. Forst- Jagdztg. 145: 45–60.
- SCHMIDT-VOGT H. 1975. Analyse der Fichtenbestände nach Provenienzen und deren ökologisches Verhalten. Allg. Forst-Ztschr. 30: 2.
- SCHMIDT-VOGT H. 1977 (ed.). Die Fichte. 1. Taxonomie, Verbreitung, Morphologie, Ökologie, Waldgesellschaften. Parey, Hamburg u. Berlin. 647 pp.
- SCHMIDT-VOGT H. 1978. Monographie der *Picea abies* (L.) KARST. unter Berücksichtigung genetischer und züchterischer Aspekte. Forstw. Cbl. 6: 281–302.
- SCHMIDT-VOGT H. 1982. Morphologische und physiologische Beurteilung von Forstpflanzen. Forst. Holzwirt. 10: 264–268.
- SCHMIDT-VOGT H. 1986. Die Fichte. II/1 – Wachstum. Züchtung. Boden. Umwelt. Holz. Verlag Paul Parey, Hamburg and Berlin. 563 pp.
- SCHMIDT-VOGT H. 1989. Die Fichte. II/2 – Krankheiten. Schäden. Fichtensterben. Verlag Paul Parey, Hamburg and Berlin. 607 pp.
- SCHMIDT-VOGT H. 1991. Die Fichte. II/3: Waldbau – Ökosysteme – Urwald – Wirtschaftswald Ernährung – Düngung – Ausblick. Parey, Hamburg u. Berlin. 781 pp.
- SCHMIDT-VOGT H., KOCIEŃSKI S. 1985. Entwicklung des IUFRO-Fichtenherkunftsversuches 1972 auf süddeutschen Versuchsflächen bis zum Alter 10. Forstarchiv 56 (4): 138–142. [FA. 49, 2897]
- SCHMIDT-VOGT H., WÜTHERICH G., DEICHNER P. 1987. Untersuchungen zur Sturmstabilität von Fichten und Tannen in Fichten-Tannen-Mischbeständen auf verschiedenen Standorten Süddeutschlands. Allg. Forst- Jagdztg. 158 (2/3): 42–50.
- SCHMITT U., REUTZE M. 1990. Structural changes in spruce and fir needles. Environ. Poll. 68: 345–354.
- SCHMITT U., REUTZE M., LIESE W. 1989. Microstructural analysis of pollution damaged conifer needles. Aquilo, Ser. Bot. 27: 15–18.
- SCHMITT U., REUTZE M., LIESE W. 1988. Feinstrukturelle Untersuchungen von Koniferennadeln aus Begasungsversuchen. Mitt. Bundesforschungsanstalt Forst Holzwirtschaft, Reinbek bei Hamburg 160: 191–199.
- SCHMITZ H., LOFFEL U., WEIDNER M. 1993. The rate of protein synthesis in needles of Norway spruce (*Picea abies*): light stimulation, regulation through photophosphorylation, stress enhancement. Physiol. Plant. 87 (2): 237–247.
- SCHMUCKER T. 1942. Die Baumarten der nördlich-gemäßigten Zone und ihre Verbreitung *Silvae Orbis* 4. CIC, Berlin-Wannsee.
- SCHÖNBACH H. 1957. Ergebnisse eines heute 20 jährigen Fichtenprovenienzversuches. *Silvae Genet.* 6: 74–91.
- SCHÖNHAR S. 1989. Pilze als Schaderreger. In: SCHMIDT-VOGT H. Die Fichte. II/2 – Krankheiten. Schäden. Fichtensterben. Parey, Hamburg and Berlin. pp.: 3–39.
- SCHÖNHERR J. 1976. Water permeability of isolated cuticular membranes: The effect of cuticular waxes on diffusion of water. *Planta* 132: 159–164.
- SCHÖNNAMSGRUBER H. 1958. Die Aufnahme der Phosphorsäure aus Thomasphosphat durch junge Holzpflanzen. *Phosphorsäure, Essen* 18 (1): 24–41.
- SCHRAMM J. R. 1966. Plant colonization studies on black waste from anthracite mining in Pennsylvania. *Trans. Am. Philos. Soc.* 56: 1–194.

- SCHROEDER P., WOLF A. E. 1996 Characterization of glutathione S-transferases in needles of Norway spruce trees from a forest decline stand. *Tree Physiol.* 16: 503–508.
- SCHUBERT R., MÜLLER-STARCK G., RIEGEL R. 2001 Development of EST-PCR markers and monitoring their intrapopulational genetic variation in *Picea abies* (L.) KARST. *Theor. Appl. Genet.* 103: 1223–1231.
- SCHULZ H. 1989. Biochemische Indikation mit Koniferennadeln – Ein Verfahren zur Früherkennung von Immissionswirkungen. *Biochem. Physiol. Pflanzen* 184: 419–432.
- SCHÜTT P., SCHUCK H. J. 1972. Zusammenhänge zwischen Rauchhärte und Cuticularwachsen bei Konifern. *Mitt. Forst. Budn. Wien* 97: 399–418.
- SCHWACKE R., HAGER A. 1992 Fungal elicitors induce a transient release of active oxygen species from cultured spruce cells that is dependent on Ca^{2+} and protein-kinase activity. *Planta* 187: 136–141.
- SCHWANZ P., HABERLE K. H., POLLE A. 1996. Interactive effects of elevated CO_2 , ozone and drought stress on the activities of antioxidative enzymes in needles of Norway spruce trees (*Picea abies* [L.] KARSTEN) growth with luxurious N-supply. *J. Plant Physiol.* 148: 351–355.
- SCHWARTZENBERG K. von, HAHN H. 1991. The cytokinin content in needles of Norway spruce (*Picea abies* (L.) KARST.) with different degree of damage. *J. Plant Physiol.* 139: 218–223.
- SCHWEINGRUBER F. H., ALBRECHT H., BECK M., HESSEL J., JOOS K., KELLER D., KONTIC R., LANGE K., NIEDERER M., NIPPEL C., SPANG S., SPINNLER A., STEINER B., WINKLER-SEIFERT A. 1986. Abrupte Zuwachsschwankungen in Jahrringabfolgen als oekologische Indikatoren. *Dendrochronologia* 4: 125–183.
- SCHWERTFEGER F. 1970. Die Waldkrankheiten. Ein Lehrbuch der Forstpathologie und des Forstschutzes. Parey, Hamburg und Berlin. 509 pp.
- SEABY D. A., SELBY C. 1990. Enhanced seedling root development in eight conifer species induced by naphthalene acetic acid. *Forestry, Oxford* 63: 197–207.
- SEBANEK J., KLIČOVÁ S., PSOTA V., KRALÍK J., VITKOVÁ H., KUDOVÁ D. 1991. Changes in the level of endogenous gibberellins and cytokinins in spruce *Picea abies* (L.) KARST. needles during the year. *Acta Univ. Agric. Fac. Hort.* 6: 27–36.
- SEHMER L., FONTAINE V., ANTONI F., DIZENGREMEL P. 1998. Effects of ozone and elevated atmospheric carbon dioxide on carbohydrate metabolism of spruce needles. Catabolic and detoxification pathways. *Physiol. Plant.* 102: 605–611.
- SEITH B., GEORGE E., MARSCHNER H., WALLENDEN T., SCHAEFFER C., EINIG W., WINGLER A., HAMPP R. 1996. Effects of varied soil nitrogen supply on Norway spruce (*Picea abies* [L.] KARST.). I. Shoot and root growth and nutrient uptake. *Plant and Soil* 184 (2): 291–298.
- SEKIYA J., WILSON L. G., FILNER P. 1982. Resistance to injury by sulfur dioxide. *Plant Physiol.* 70: 437–441.
- SEMEŇOVA V. G. 1971. Khimicheskiy sostav kory drevesiny eli, berezy i lipy. *Lesoved.* 1971 (6): 71–74.
- SENICZAK S. 1968. Zasiadlanie stref koron świerkowych przez korniki i towarzyszącą im entomofaunę w zależności od piętra drzewostanu w Nadleśnictwie Doświadczalnym Łaski. *Prace Komisji Nauk Rolniczych i Komisji Nauk Leśnych PTPN* 25: 325–354.
- SETZER B., MOHR H. 1998. Ammoniumstress bei Jungpflanzen von Tanne und Fichte. *Allg. Forst-Jagdztg.* 169 (2): 26–29.
- SEVEROVA A. I. 1951. Vegetativnoe razmnozhenie khvojnykh. *Akademia Nauk SSSR, Moskva.*
- SEVOLA Y. 1999. Forest Finland in Brief. Finnish Forest Research Institute. 47 pp.
- SHAW D. V., ALLARD R. W. 1982. Estimation of outcrossing rates in Douglas-fir using isozyme markers. *Theor. Appl. Genet.* 62: 113–120.
- SHAW D. V., KAHLER A. L., ALLARD R. 1981. A multilocus estimator of mating system parameters in plant populations. *Proc. Nat. Acad. Sci. USA* 78: 1298–1302.
- SHAW P. J. A., DIGTHON J., POSSKITT J., MCLEOD A. R. 1992. The effects of sulphur dioxide and ozone on the mycorrhizas of Scots pine and Norway spruce in a field fumigations system. *Mycol. Res.* 96: 785–791.

- SHCHERBAKOVA M. 1989. Growth characteristic feature of the spruce geographical cultures in Karelia. Proc. IUFRO Symp. on Forest genetics, breeding and physiology of woody plants, Voronezh. pp.: 225–226.
- SHEA K. L. 1987. Effects of population structure and cone production on outcrossing rates in Engelmann spruce and subalpine fir. *Evolution* 41: 124–136.
- SHEEDY G. 1982. Results of NPK fertilization of young plantations of Norway spruce, black spruce and jack pine established on two site types. Note, Service Rech. Terres Forests, Quebec 18: 1–9. [FA. 44, 5347]
- SHEN H. H., RUDIN D., LINDGREN D. 1981. Study of the pollination pattern in a Scots pine seed orchard by means of isozyme analysis. *Silvae Genet.* 30: 7–15.
- SHITOVA A. E. 1969. Suskka rezonansovoj drevesiny. *Drev. Promysl.* 18 (2): 27–28.
- SHUTYAEV A. M. 1989. Spruce geographical variability. Proc. IUFRO Symp. on Forest genetics, breeding and physiology of woody plants, Voronezh: 177–178.
- SHUTYAEV A. M. 1995a. Populyatsionno-geograficheskaya izmenchivost' opusheniya pobegov eli. *Lesoved.* (2): 70–76.
- SHUTYAEV A. M. 1995b. Geograficheske kul'tury vidov eli v central'nom chernozyem'e. *Lesoved.* (3): 8–18.
- SIEK M. 1970. Badania porównawcze własności drewna morfologicznych odmian świerka pospolitego. *Sylvan* 114 (7): 27–32.
- SIEROTA Z. 1995. Rola grzyba *Phlebiopsis gigantea* (Fr.: Fr.) Julich w ograniczaniu huby korzeni w drzewostanach sosny zwyczajnej (*Pinus sylvestris* L.) na gruntach porolnych. *Prace JBL. ser. A*, 810: 1–180.
- ŠIKA A. 1966. Výzkum kořenového systému smrku na provenienčních plochách v Beskydech. *Práce VÚLHM* 33: 101–126.
- SILA B., SEKULSKI K. 1961. Kwasy tłuszczowe w suchej żywicy świerkowej. *Folia Forest. Polonica, Ser. B* 3: 165–168.
- SILIM S. N., GUY R. D., LAVENDER D. P. 1993. Mefluidide-induced drought resistance in seedlings of three conifer species. *Can. J. Bot.* 71: 1087–1092.
- ŠIMAK M., GUSTAFSSON A., CHING KIM 1968. Occurrence of a mosaic-aneuploid in polyembryonic Norway Spruce seed. *Stud. Forest. Suec.* 67: 1–8.
- ŠIMAK M., KAMRA S. 1970. Germination studies on Norway spruce (*Picea abies*) seed of different provenances under alternating and constant temperatures. *Proc. Int. Seed. Test. Ass.* 35 (2): 383–391.
- ŠINDELÁŘ J. 1983. Potomstva uznanych jednotek smrku ztepilého, *Picea abies* (L.) KARST., na oviřovacích plochách. *Lesnictví* 29 (4): 285–302.
- ŠINDELÁŘ J. 1984. Nikteré otázky resistance potomstev uznanych jednotek smrku ztepilého *Picea abies* (K.) KARST. *Práce VÚLHM* 64: 9–42.
- ŠINDELÁŘ J. 1987. Genetické a šlechtitelské aspekty záchrany genofondu ohrožených populací lesních dřevin vegetativním množením. *Lesnictví* 33 (6): 485–490.
- SIREN G. 1955. The development of spruce forest on raw humus sites in northern Finland and its ecology. *Acta For. Fenn.* 62: 3–408.
- SIRÉN G., BERGMAN F. 1951. Mycorrhizal fungi and our forest trees. *Skogsbruket* 21: 39–43.
- SITOWSKI L. 1930. Spostrzeżenia nad pasożytami korników (*Ipidae*). *Polskie Pismo Entomol.* 9 (1–2): 1–13.
- SJÖRS H. 1965. Forest regions. *Acta Phytogeogr. Suec.* 50: 48–63.
- SKALICKÁ A., SKALICKÝ V. 1988. *Picea* A. DIETR. In: HEJNÝ S., SLAVIK B. (ed.) Květena ČR., 1: 317–326. Academia, Praha.
- SKEFFINGTON R., ROBERTS M. 1985. Effect of ozone and acid mist on Scots pine and Norway spruce – an experimental study. *VDI Berichte* 560: 747–760.
- SKOKLEFALD S. 1970. The effect of nitrogen-phosphorus fertilization on cone and seed production in shelterwood stands in Norway Spruce. Proc. IUFRO Mtg. on Sexual Reproduction of Forest Trees. Varparanta, Finland: II/30.
- ŠKOLEK J. 1987. Doterajšie výsledky s skúsenosti s autovegetatívnym množením lesných drevín na Slovensku. *Lesnictví* 33 (6): 559–564.

- SKOV E., WELLENDORF H. 1994. An isozyme study in Norway spruce on the effect on population genetic parameters of juvenile selection followed-up by clonal propagation by cuttings. *For. Tree Improv.* 25: 13–35.
- SKRE O., MORTENSEN L. M. 1990. Effects of ozone on frost resistance, growth and carbohydrate status in Norway spruce seedlings (*Picea abies*). *Aquilo*, Ser. Bot. 29: 51–68.
- SKRØPPA T. 1993. Variation and inheritance in diallel crosses within natural populations of Norway spruce. Norway spruce provenances and breeding. *Proc. of IUFRO (S2.2–11)*. Symposium, Riga, Latvia: 240 pp.
- SKRØPPA T. 1994. Growth rhythm and hardiness of *Picea abies* progenies of high altitude parents from seed produced at low elevations. *Silvae Genet.* 43 (2/3): 95–100.
- SKRØPPA T., DIETRICHSON J. 1986a. Genetic Variation and Ortet/Ramet Relationship in a clonal Test with *Picea abies*. *Scand. J. For. Res.* 1: 323–332.
- SKRØPPA T., DIETRICHSON J. 1986b. Winter damage in the IUFRO 1964/68 provenance experiment with Norway spruce (*Picea abies* (L.) KARST.). *Medd. Norsk. Inst. Skogforsk.* 39 (10): 161–183.
- SKRØPPA T., JOHNSEN Ø. 1990. The genetic response of plant populations to a changing environment: the case for non-Mendelian processes. In: *Biodiversity – Temperate Ecosystems and Global Change*. NATO ASI Ser. 1 (20): 183–199.
- SKRØPPA T., JOHNSEN Ø. 2000. Patterns of adaptive genetic variation in forest tree species, the reproductive environment as an evolutionary force in *Picea abies*. In: MÁTYÁS C. (ed.) *Forest Genetics and Sustainability*. Kluwer Academic Publishers. pp.: 49–58.
- SKRØPPA T., LINDGREN D. 1994. Male fertility variation and non random segregation in pollen mix crosses of *Picea abies*. *Forest Genet.* 1: 13–22.
- SKRØPPA T., MAGNUSSEN S. 1993. Provenance variation in shoot growth components of Norway spruce. *Silvae Genet.* 42 (2/3): 111–120.
- SKRØPPA T., NIKKANEN T., RUOTSALAINEN S., JOHNSEN Ø. 1994. Effects of sexual reproduction at different latitudes on performance of the progeny of *Picea abies*. *Silvae Genet.* 43 (5/6): 298–304.
- SKRØPPA T., TUTTUREN R. 1985. Flowering in Norway spruce seed orchards. *Silvae Genet.* 34: 90–95.
- SKVORTSOVA E. B., ULANOVA N. G., BASEVICH V. F. 1983. *Ekologicheskaya rol' vetrovalov. Lesnaya Promyshlennost'*, Moskva. 190 pp.
- SLABAUGH P. B., RUDOLF P. O. 1957. The influence of seed source on the development of Scotch pine and Norway spruce planted in Lower Michigan (fifteen year results). *Pap. Mich. Acad. Sci.* 42: 41–52.
- ŚLASKI J., SĘKOWSKI B. 1988. Szkółkarstwo szczegółowe drzew i krzewów ozdobnych oraz użytkowych. *PWRiL*, Poznań.
- SLOBODYAN M. P. 1962. Materiali do vivchennya prirodnogo poshirennya yalini evopejskoj na Ukrain's'komy Polissi. *Ukr. Bot. Zh.* 19 (4): 79–83.
- SLOCUM R. D., KAUR-SAHWNEY R., GALSTON A. W. 1984. The physiology and biochemistry of polyamines in plants. *Arch. Biochem. Biophys.* 235: 283–303.
- SLOVIK S. 1996. Early needle senescence and thinning of the crown structure of *Picea abies* as induced by chronic SO₂ pollution. II. Field data basis, model results and tolerance limits. *Global Change Biol.* 2: 459–477.
- SMIRNOV K. A. 1981. Vliyanie povrezhdeniy kory eli losem na prirost i smenu porod v yuzhnoj tayge. *Lesoved.* (4): 56–65.
- SMITH R., GREENWOOD M. 1995. Effects of gibberellin A₁₇, root pruning and cytokinins on seed and pollen cone production in black spruce (*Picea mariana*). *Tree Physiol.* 15: 457–463.
- SMITH S. E., READ D. J. 1997. *Mycorrhizal Symbiosis*. 2nd Edition, Academic Press, London.
- SÖDERSTRÖM B. E. 1977. Vital staining of fungi in pure cultures and in soil with fluorescein diacetate. *Soil. Biol. Biochem.* 9: 59–63.
- SOIKKELI S. 1981a. The types of ultrastructural injuries in conifer needles of northern industrial environments. *Silva Fenn.* 15: 399–404.
- SOIKKELI S. 1981b. Comparison of cytological injuries in conifer needles from several polluted industrial environments in Finland. *Ann. Bot. Fenn.* 18: 47–61.

- SOIKKELI S. 1981c. The effects of chronic urban pollution on the inner structure of Norway spruce needles. *Savonia* 4: 1–10.
- SOIKKELI S. 1981d. A review of the structural effects of air pollution on mesophyll tissue of plants at light and transmission electron microscope level. *Savonia* 4: 11–34.
- SOIKKELI S., KÄRENlampi L. 1984a. Cellular and ultrastructure effects. In: TRESHOW M. (ed.). *Air pollution and plant life*. John Wiley and Sons Ltd. pp.: 159–174.
- SOIKKELI S., KÄRENlampi L. 1984b. The effects of nitrogen fertilization on the ultrastructure of mesophyll cells of conifer needles in northern Finland. *Eur. J. For. Path.* 14 (3): 129–136. [FA. 46, 1839]
- SOIKKELI S., PAAKKUNAINEN T. 1981. The effect of air pollution on the ultrastructure of the developing and current year needles of Norway spruce. *Mitt. Forst. Budn. Wien* 137: 159–164.
- SOIKKELI S., TUOVINEN T. 1979. Damage in mesophyll ultrastructure of Norway spruce in two industrial environments in Central Finland. *Ann. Bot. Fenn.* 16: 50–64.
- SOKOLOV S. YA., SVIAZEVA O. A., KUBLI V. A. 1977. Arealy derevev i kustarnikov SSSR, 1: 11–18. Nauka, Leningrad.
- SOKOŁOWSKI A. W. 1968a. Sosnowo-świerkowy bór mieszany (zespół *Calamagrosti arundinaceae-Piceetum*) w północno-wschodniej Polsce. *Prace IBL, Warszawa* 350: 215–231.
- SOKOŁOWSKI A. W. 1968b. Zespoły leśne nadleśnictwa Zwierzyniec w Puszczy Białowieskiej. *Prace IBL, Warszawa* 354: 1–130.
- SOKOŁOWSKI A. W. 1968c. Zespoły leśne południowo-wschodniej części Niziny Mazowiecko-Podlaskiej. *Monogr. Bot.* 16: 1–176.
- SOKOŁOWSKI A. W. 1972. Świerk [*Picea abies* (L.) KARSTEN] na Wysoczyźnie Drohickej. *Sylvan* 116 (5): 1–6.
- SOKOŁOWSKI A. W. 1974a. Rozmieszczenie roślin naczyniowych na Wysoczyźnie Drohickej. W: CZECZUGA B. (red.). *Przyroda Białostoczczyzny i jej ochrona*. *Prace Białostockiego Tow. Nauk.* 19: 103–134.
- SOKOŁOWSKI A. W. 1974b. Zbiorowiska leśne Suwalskiego Parku Krajobrazowego. In: CZECZUGA B. (ed.). *Przyroda Białostoczczyzny i jej ochrona*. *Prace Białostockiego Tow. Nauk.* 19: 67–83.
- SOKOŁOWSKI A. W. 1980. Zbiorowiska leśne północno-wschodniej Polski. *Monogr. Bot.* 60: 1–205.
- SOKOŁOWSKI A. W. 1993. Fitosocjologiczna charakterystyka zbiorowisk leśnych Białowieskiego Parku Narodowego. *Parki Narod. Rez. Przyr.* 13 (3): 1–190.
- SOKOŁOWSKI A. W., KAWECKA A. 1970. Zespoły leśne nadleśnictwa Złota Wieś w Puszczy Knyszyńskiej. *Prace IBL, Warszawa* 369: 1–64.
- SOKOŁOWSKI M. 1928. O górnej granicy lasu w Tatrach. Zakłady Kórnickie, Zakład Badania Drzew i Lasu, 1. Fundacja Zakłady Kórnickie, Kraków. 188 pp.
- SOKOŁOWSKI S. 1921. *Hodowla lasu*. Lwów–Warszawa.
- SOMORA J. 1958. O rozšíreni niektorých leśných drevin v skupine Lomnického Štitu. *Wyd. Osveta, N. P. Martin*, 148 pp.
- SORENSEN F. C. 1982. The role of polyembryony and embryo viability in the genetic system of conifers. *Evolution* 36: 725–733.
- SPŁAWA-NEYMAN S., OWCZARZAK Z. 1993. Użytkowa gatunki drewna. *Vademecum, Przemysł Drzewny* 5/93.
- SPOREK K., WOŹNIAK Z. 1993. Deforestacja obszarów górskich a zasoby wodne. *Las Polski* (10): 18–19.
- SPURR S. H., BARNES B. V. 1980. *Forest Ecology*. John Wiley and Sons. New York–Singapore. 687 pp.
- SRIVASTAVA M. 1963. Secondary phloem in the *Pinaceae*. *Univ. Calif. Publ. Bot.* 36 (1): 1–142.
- ŚRODOŃ A. 1947. The upper limit of forest in the Czarnohora Mts. and the Czwyczyn Mts. (Eastern Carpathians). *Bull. Acad. Pol. Sci. Lett., Cl. Sci. Math.-Nat., Sèr. B*. Kraków.
- ŚRODOŃ A. 1967a. O świerku pospolitym w czwartorzędzie Polski. Materiały z konferencji poświęconej badaniom nad świerkiem pospolitym w Polsce, 5–8. Kórnik.
- ŚRODOŃ A. 1967b. Świerk pospolity w czwartorzędzie Polski. *Acta Paleobot.* 8 (2): 1–60.
- ŚRODOŃ A. 1977. Świerk w historii naszych lasów. W: BIAŁOBOK S. (red.). *Świerk pospolity – Picea abies* (L.) KARST. *Nasze drzewa leśne* 5: 7–19. PWN, Warszawa–Poznań.

- ŚRODOŃ A. 1990. Postglacial history of the common spruce (*Picea excelsa* (LAM.) LK.) in the Low Beskids separating the east from the west Carpathians. *Acta Paleobot.* 30 (1–2): 221–239.
- STAHL E. 1900. Der Sinn der Mycorrhizenbildung. *Jahrb. Wissensch. Bot.* 34: 539–668.
- STAIRS G. R., ADAPA S. 1969. Seed source and growth rate effects on wood quality in Norway spruce (*Picea abies* L.) *Proc. 16th NE For. Tree Improv. Conf. Quebec* 1968: 61.
- STALFELT M. G. 1961. On the distribution of the precipitation in a spruce stand. *British Ecological Society*. In: RUTTER A. J., WHITEHEAD F. H. (eds.). *The water relations of plants. Symp. mat.* 554/63: 115–126.
- STARCHENKO I. I. 1964. Ranne plodonoshenie eli obyknovennoy. *Bot. Zh.* 49 (1): 132–133.
- STASOLLA C., KONG L. S., YEUNG E. C., THORPE T. A. 2002. Maturation of somatic embryos in conifers: morphogenesis, physiology, biochemistry and molecular biology. *In Vitro Cell. Develop. Biol., Plant.* 38: 93–105.
- STASZKIEWICZ J. 1966. Wstępne badania nad zmiennością szyszek świerka pospolitego (*Picea abies* (L.) KARST. subsp. *excelsa*) z Polski. *Fragm. Flor. Geobot.* 12: 349–371.
- STASZKIEWICZ J. 1967. Zmienność szyszek świerka pospolitego (*Picea abies* (L.) KARST. subsp. *abies* z Polski. W: BIAŁOBOK S. (red.). *Materiały z konferencji poświęconej badaniom nad świerkiem w Polsce. Zakład Dendrologii PAN, Kórnik*. pp.: 9–18.
- STASZKIEWICZ J. 1976. Zmienność szyszek świerka pospolitego (*Picea abies* (L.) KARST.) w Karpatach. *Fragm. Flor. Geobot.* 22, 1–2: 35–42.
- STASZKIEWICZ J. 1977. Systematyka. In: BIAŁOBOK S. (red.). *Świerk pospolity *Picea abies*. Nasze Drzewa Leśne*, 5: 20–36. PWN Warszawa–Poznań.
- STEBBINS G. L. 1958. Zmienność i ewolucja roślin. PWN, Warszawa. 470 pp.
- STECKI K., KOŚCIELNY S. 1955. Zasięgi drzew. W: KULESZA W. *Klucz do oznaczania drzew i krzewów*. PWRiL, Warszawa. 282 pp.
- STEEN I. 1972. Growth regulators in *Picea abies*. *Physiol. Plant.* 26: 92–97.
- STEFANSSON E. 1948. Strangulering av fröträdsställningar. *Skogen* 35 (8). [FA. 3, 12406]
- STEFANSSON E. 1953. Preliminära resultat av proveniensförsök med gran utlagda av Kramfors AB. *Norrlands Skogsv. Förb. Tidskr.* (2): 335–366. [FA. 15, 206]
- STEIJLEN I., ZACKRISSON O. 1987. Long-term regeneration dynamics and successional trends in a northern Swedish coniferous stand. *Can. J. Bot.* 65: 839–848.
- STERN K. 1966. (Evaluating the characters 'start of flushing' in a Norway spruce breeding programme in Schleswig – Holstein). *Forstarchiv* 37 (3): 70–74. [FA. 27, 5384]
- STERN K., ROCHE F. 1974. *Genetics of forest ecosystems*. Springer, Berlin.
- STIENEN H., BAUCH J. 1988. Element content in tissues of spruce seedlings from hydroponic cultures simulating acidification and deacidification. *Plant and Soil* 106 (2): 231–238.
- STOCKMAN L., HÄGGLUND E. 1948. *Svensk Papperstidn.*
- STOJANOV N. 1963. *Picea* DIETR. In: JORDANOV D. (ed.). *Flora na Narodna Republika Bylgariya*, 1. Sofia pp.: 58–59.
- STRZELECKI H. 1894. O przyrodzonym rozsiedleniu drzew leśnych w Galicji. *Sylvan* (12): 295–306.
- STUHLIKOWA B., STUHLIK L. 1962. Geobotaniczna charakterystyka pasma Policy w Karpatach Zachodnich. *Fragm. Flor. Geobot.* 8 (3): 230–395.
- STURE S. 1986. Fertilizer experiments in young Norway spruce stands. *Rap. Norsk Inst. Skogforsk.* 4/86: 1–24. [FA. 50, 2958]
- SUCHARA J. 1980. Literární zhodnocení sadovnických použitelných druhů dřevin z hlediska jejich vhodnosti pro území se znečištěným ovzduším. VIII Symp. o zeleni Flora Bratislava '80, duben 1980, Bratislava: 3–33.
- SUKATCHEV V. N. 1928. *Lesnye porody*, 1. Khvojnye. Nauka, Moskwa.
- SUNDSTRÖM E. 1998. Afforestation of low-productive peatlands in Sweden – a tree species comparison. *Silva Fenn.* 32 (4): 351–361.
- SUREWICZ W. 1971. *Podstawy technologii mas włóknistych*. Warszawa.
- SURMIŃSKI J. 1994. *Żywiec naturalne*. Wydawnictwo AR, Poznań.
- SURMIŃSKI J. 1996. Kora – budowa anatomiczna, skład chemiczny, możliwości wykorzystania. *Wydawnictwo AR, Poznań*.

- SUSS R., EWALD D., MATSCHKE J. 1990. Erzeugung somatischer Embryonen aus Saatgut der gemeinen Fichte (*Picea abies* (L.) KARST. Beitr. Forstwirtschaft 24: 126–130.
- SUTINEN S. 1987a. Ultrastructure of mesophyll cells of spruce needles exposed to O₃ alone and together with SO₂. Eur. J. For. Path. 17: 362–368.
- SUTINEN S. 1987b. Cytology of Norway spruce needles. I. Changes during ageing. Eur. J. For. Path. 17: 65–73.
- SUTINEN S. 1987c. Cytology of Norway spruce needles. II. Changes in yellowing spruces from the Taunus mountains, West-Germany. Eur. J. For. Path. 17: 74–85.
- SUTINEN S. 1989. Ultrastructure of conifer needles exposed to O₃ and O₃ + SO₂ compared to the needle structure in the field in Finland, Sweden and West Germany. Aquilo., Ser. Bot. 27: 29–34.
- SUTINEN S., SKARBY L., WALLIN G., SELLDEN G. 1990. Long-term exposure of Norway spruce, *Picea abies* (L.) KARST., to ozone in open-top chamber. II. Effects on the ultrastructure of needles. New Phytol. 115 (2) 345–355.
- SUTINEN S., WALLIN G., SKARBY L., SELLDEN G. 1989. Effects of long term exposure of ozone on ultrastructure and net photosynthesis of Norway spruce. Seminar by the Nordic Forest Research Committee (SNS) 24–26 October 1988. "Air pollution as stress factor in the Nordic forests. Modelleiser fra Norsk Institutt for Skogforskning 42: 67–72.
- SVOBODA P. 1953. Lesní dřeviny a jejich porosty, vol. 1. Statní Zemedel. Naklad., Praha.
- SWAN H. S. D. 1972. Foliar nutrient concentrations in Norway spruce as indicators of tree nutrient status and fertilizer requirement. Wldls. Rept., Pulp Pap. Res. Inst. Can. 40: 1–20.
- SWIECKI T. J., ENDRESS A. G., TAYLOR O. C. 1982. The role of surface wax in susceptibility of plants to air pollutant injury. Can. J. Bot. 53. 1063–1071.
- SYLVEN N. 1909. Studien über den Formenreichtum der Fichte, besonders die Verzweigungstypen derselben und ihren forstlichen Wert. Mitt. Forstl. Anst. Schwedens.
- SYRACH LARSEN C. 1956. Genetics in Silviculture. Oliver and Boyd, Edinburgh and London.
- SZAFER W. 1916. Flora W: ROMER E. (red.). Atlas ziem polskich. Lwów.
- SZAFER W. 1921. Nieco o rozmieszczeniu geograficznym świerka w Polsce. Sylwan 39: 76–91.
- SZAFER W. 1931. The historical development of the geographical area of the spruce (*Picea excelsa* LINK) in Poland. Przegl. Geogr. 11: 1–8.
- SZAFER W. 1935. The significance of isopollen lines for the investigation of the geographical distribution of trees in the post-glacial period. Bull. Int. Acad. Pol. Sci. Lettr., Ser. B, 1: 235–239.
- SZAFER W. 1937. Flora. W: ROMER E. (ed.). Powszechny atlas geograficzny. Książnica-Atlas, Lwów–Warszawa.
- SZAFER W. 1959. Zasięgi drzew. W: SZAFER W., ZARZYCKI K. (red.). Szata roślinna Polski. PWN, Warszawa–Kraków.
- SZAFER W. 1972. Zasięgi drzew. W: SZAFER W., ZARZYCKI K. (red.). Szata roślinna Polski. Wyd. 2, PWN, Warszawa–Kraków.
- SZAFER W., PAWŁOWSKI B., KULCZYŃSKI S. 1923. Zespoły roślin w Tatrach. Cz. 1. Zespoły roślin w Dolinie Chochołowskiej. Bull. Acad. Pol. Sci. Lett., Cl. Sci. Math. Nat., Ser. B. Suppl. 3: 1–66.
- SZAFER W., SOKOŁOWSKI M. 1926. Zespoły roślin w Tatrach. Cz. 5. Zespoły roślinne w dolinach położonych na północ od Giewontu. Bull. Acad. Pol. Sci. Lett., Cl. Sci. Math. Nat., Ser. B., Suppl. 3: 123–140.
- SZCZEPAŃSKI H. 1960. Materiały do znajomości błęskotek (*Hymenoptera, Chalcidoidea*) w Puszczy Boreckiej. Polskie Pismo Entomol. 30 (23): 405–416.
- SZŐNYI L., UJVÁRI F. 1975. First results of the international (IUFRO) Norway spruce provenance experiment. Erdészeti Kutatások 71 (2): 139–147.
- SZUBERT M. 1830. Opisanie świerku. Sylwan 7 (3): 302–322. 5
- SZUJECKI A. 1960. Materiały do poznania *Staphylinidae* (*Coleoptera*) Polski. Fragm. Faun. 8 (22): 321–335.
- SZUJECKI A. 1976. Kusakowate – *Staphylinidae*, Wydłużaki – *Xantolininae*. In: Klucze do oznaczania owadów Polski. 19, 24d: 1–44.

- SZUJECKI A. 1978. Drapieżne kusakowate, omarlicowate, gnilirowate, przekraskowate, skórnikowate, obumierkowate. In: BOCZEK J., LIPA J. J. (eds.). Biologiczne metody walki ze szkodnikami roślin. PWN, Warszawa. 603 pp.
- SZUJECKI A. 1980. Kusakowate – *Staphylinidae*, kusaki – *Staphylininae*. In: Klucze do oznaczania owadów Polski. 19, 24e: 1–44.
- SZUJECKI A. 1996. Kusakowate (Coleoptera, Staphylinidae) Bieszczadów Zachodnich. PWN, Warszawa. 224 pp.
- SZWAGRZYK J. 1994. Co nauka jest winna ochronie przyrody? Przegl. Przyr. 5 (3/4): 3–16.
- SZWAŁKIEWICZ J. 1996. Szkodniki wtórne świerka – problem lasów Polski północno-wschodniej z uwzględnieniem powierzchni prawem chronionych. Mscr. mat. Konf., Jarnołtówek 1996. Dyrekcja Generalna Lasów Państwowych. pp. 75–78.
- SZYDLARSKI M. 1980. Wczesne obradanie świerka pospolitego (*Picea abies* (L.) KARST.) w Nadleśnictwie Lipusz (OZLP Toruń). Roczn. Dendrol. 33: 103–111.
- SZYMAŃSKI S. 1973. Struktura grubości drzew oraz słoistości drewna świerka istebniańskiego na przykładzie rodzimego drzewostanu nasiennego. [Thickness structure of trees and the grain of Norway spruce wood from the Istebna Forest District as an example of a native seed stand]. Prace Kom. Nauk Roln. i Kom. Nauk Leśn. PTPN. 36.
- SZYMAŃSKI S. 1975. Analiza porównawcza cech hodowlanych i przyrostowych świerka w Beskidzie Śląskim i w Beskidzie Żywieckim. [Comparative analysis of the growth and breeding characteristics of Norway spruce in the Śląski and Żywiecki Beskids Mts]. Prace Kom. Nauk Roln. i Kom. Nauk Leśn. PTPN. 50.
- SZYMAŃSKI S. 1989. Analiza naturalnego boru świerkowego w pasie walki z kosodrzewiną u górnej granicy lasu na Pilsku. Roczn. AR, Poznań 207: 129–113.
- TABOR C. A. 1990. Recurrent appearance of bisporangiate strobili with proliferation on *Picea abies*. Rhodora 92 (872): 257–263.
- TAKAHARA S., NOBUCHI T., HARADA H., SAIKI H. 1983. Wall structure of parenchyma cells surrounding axial resin canals in the wood of European spruce. J. Jap. Wood Res. Soc. 29 (5): 355–360.
- TAMM C. O. 1968. An attempt to assess the optimum nitrogen level in Norway Spruce under field conditions. Stud. Forest. Suec. 61.
- TAN W. X., BLAKE T. J. 1993. Drought tolerance, abscisic acid and electrolyte leakage in fast and slow-growing black spruce (*Picea mariana*) progenies. Physiol. Plant. 89: 817–823.
- TAUSCH M., MÜLLER M., STABENTHEIMER E., GRILL D. 1994. Stress physiological investigations and chromosomal analysis on Norway spruce [*Picea abies* (L.) KARST.] a field study. Phytom 34 (2): 291–308.
- TAYLOR A. F. S., ALEXANDER I. J. 1990. Demography and population dynamics of ectomycorrhizas of Sitka spruce fertilized with nitrogen. Agric. Ecosyst. Environ. 28: 493–496.
- TAYLOR A. F. S., ALEXANDER I. J. 1991. Ectomycorrhizal synthesis with *Tylospora fibrilosa*, a member of the *Corticaceae*. Mycol. Res. 95: 381–384.
- TAYLOR D. L., BRUNS T. D. 1999. Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: minimal overlap between the mature forest and resistant propagule communities. Mycol. Ecol. 8: 1837–1850.
- TAYLOR R. J. 1993. *Picea*. In: Flora of North America, 2: 369–373. Oxford University Press, Oxford, U.K.
- TEICH A. H. 1972. Some characteristics of selected and unselected populations of Norway spruce. For. Chron. 48 (4): 1–3.
- TEICH A. H., MORGESTERN E. K. 1969. Early growth of Norway spruce in a continental Canadian climate. Bi-Monthly Res. Not. Dep. Fish. For. Canada 25 (4): 37.
- TENBERGE K. B. 1992. Ultrastructure and development of the outer epidermal wall of spruce (*Picea abies*) needles. Can. J. Bot. 70: 1467–1487.
- TENTER M., WILD A. 1991. Investigation on the polyamine content of spruce needles relative to the occurrence of novel forest decline. J. Plant Physiol. 137: 647–654.
- TEPLOUKHOV TH. 1868. Ein Beitrag zur Kenntnis der sibirischen Fichte-*Picea obovata* LEDEB. Bull. Soc. Nat. Moscou 3: 244–252.

- TERASMAA T. 1971. Karyotype analysis of Norway spruce, *Picea abies* (L.) KARST. *Silvae Genet.* 20 (5–6): 179–182.
- TERASMAA T. 1972. A comparative karyomorphological study of Estonian and Lapland provenances of *Picea abies* (L.) KARST. *Ann. Bot. Fenn.* 9: 97–101.
- TERPIŃSKI Z. 1984. Szkółkarstwo ozdobne [Ornamental nurseries]. PWRiL, Warszawa.
- TERRASSON D. 1992. Le programme de vergers à graines de l'Etat une étape dans la stratégie de diffusion des variétés améliorées. Proc. AFOCEL-IUFRO Symposium on Mass Production Technology for Genetically Improved Fast Growing Forest Tree Species, Bordeaux: 97–105.
- TESCHE M. 1989. Umweltstreß. In: SCHMIDT-VOGT H. Die Fichte. II/2-Krankheiten, Schäden, Fichtensterben. Ver. Paul Parey, Hamburg and Berlin. pp.: 346–384.
- TESCHE M., FEILER S., MICHAEL G., RANFT H., BELLMANN C. 1989. Physiologische Reaktionen der Fichte (*Picea abies*) auf komplexen SO₂- und Trockenstress. Teil 1. Reaktionen auf gleichzeitiges Einwirken von SO₂ und Trockenheit. *Eur. J. For. Path.* 19: 281–292.
- THIERCELIN F. 1970. Tardiveté du débourrement et densité du bois das une population adulte de *Picea abies* KARST. *Ann. Sci. For.* 27 (3): 243–254.
- THOENE B., RENNENBERG H., WEBER P. 1996. Absorption of atmospheric NO₂ by spruce (*Picea abies*) trees. II. Parametrization of NO₂ fluxes by controlled dynamic chamber experiments. *New Phytol.* 134: 257–266.
- THOR E. 1976. Tree breeding at the University of Tennessee 1959–75. *Univ. Tenn. Bull.* 554: 1–48.
- THÖRNOVIST T. 1986. Influence of air pollution on wood properties. *Sveriges Lantbruksuniversitet, Institutionen för virkeslära Uppsats* 159, 22S.
- THORNTON F. C., SCHAEDEL M., RAYNAL D. J. 1987. Effects of aluminum on red spruce seedlings in solution culture. *Environ. Exp. Bot.* 27: 489–498.
- TIBBETT M., SANDERS F. E., CAIRNEY J. W. G. 1998. The effect of temperature and inorganic phosphorus supply on growth and acid phosphatase production in arctic and temperate strains of ecto-mycorrhizal *Hebeloma* species in axenic culture. *Mycol. Res.* 102: 129–135.
- TIGERSTEDT P. M. A. 1974. Genetic structure of *Picea abies* populations as determined by the isozyme approach. Proc. Joint IUFRO Meet. S.02.04, 1–2 Stockholm 283–291.
- Timber Bulletin for Europe 31 (3,2) [1978]; 31 (5,3) [1979]; 32 (3,4) [1979]; 33 (10) [1981]; 33 (7) [1983].
- TIMELL T. E. 1973. Ultrastructure of the dormant and active cambial zones and the dormant phloem associated with formation of normal and compression woods in *Picea abies* (L.) KARST. State Univ. New York. Tech. Publ. 96.
- TIMELL T. E. 1980. Organization and ultrastructure of the dormant cambial zone in compression wood in *Picea abies*. *Wood Sci. Techn.* 14 (3): 161–179.
- TINGEY D. T., ANDERSEN C. P. 1991. The physiological basis of differential plant sensitivity to changes in atmospheric quality. In: TAYLOR G. E., PITELKA L. F., MCLEGG M. T. (eds.). *Ecological Genetics and Air Pollution*. Springer, New York. pp.: 209–234.
- TINGEY D. T., PHILLIPS D. L., JOHNSON M. G., STORM M. J., BALL T. J. 1997. Effects of elevated CO₂ and N fertilization on fine root dynamics and fungal growth in seedlings *Pinus ponderosa*. *Environ. Exp. Bot.* 37: 73–83.
- TIREN L. 1935. Om granens kottsättning, dess periodicitet och samband med temperatur och nederbörd. *Medd. Statens Skogsförsöksanst.* 28: 413–524.
- TISHECHKIN A. N., KORABLEV V. N. 1980. Geograficheskie kul'tury eli v usloviyakh Permskoy oblasti. *Lesa Urala i khozjaistvo v nich, Sverdlovsk* 12: 163–171. [Ref. Zh. 11.56.53]
- TOBOLSKI K. 1976. Przemiany klimatyczno-ekologiczne w okresie czwartorzędu a problem zmian we florze. *Phytocoenosis.* 5 (3–4): 187–197.
- TOBOLSKI K. 1991. Biostratygrafia i paleoekologia interglacjału eemskiego i zlodowacenia Wisły regionu konińskiego. W: STANKOWSKI W. (ed.). *Przemiany środowiska geograficznego obszaru Konin–Turek.*: 45–87. UAM, Poznań.
- TOCAN M., PETREA G., ILIESCU G. 1963. Celuloza si Hirtie. 12 (7): 214–222; ibidem, (9): 281–287.
- TOMALAK M., MICHALSKI J., GROCHOLSKI J. 1984. The influence of *Nematoda* on the structure of guthalia of *Tomiscus piniperda* (*Coleoptera: Scolytidae*). *J. Invertebr. Path.* 43: 358–362.
- TOMANEK J. 1966. Botanika leśna. PWRiL, Warszawa.

- TOMESCU A., FLORESCU I., MICHALAHE A., STRÎMBEI M., AVRAMESCU C. 1967. Cercetări fenologice la principalele specii forestiere autohtone din Republica Socialistă România. Sinteză pentru perioada 1956–1965. Inst. Cercetări Silvice, Centrul Document. Tehnica Economia For-est., București.
- TOMKOVÁ E., KRAJŇÁKOVÁ J., STEINHÜBEL G. 1987. Výsledky kvantitatívno – morfologického rozboru vegetatívne namnoženého smreka pre imisnú oblasť Slovenských Beskyd. Lesníctví 33 (6): 551–558.
- TOMLINSON P. 1985. An aid to the identification of fossil buds, bud-scales and catkin-bracts of Brit-ish trees and shrubs. Circaea 3 (2): 45–130.
- TOMPSETT P. B., FLETCHER A. M. 1977. Increased flowering of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) by high temperature in a polythene house. Silvae Genet. 26 (2–3): 84–86.
- TOMPSETT P. B., FLETCHER A. M. 1979. Promotion of flowering on mature *Picea sitchensis* by gib-berellins and environmental treatments. The influence of timing and hormonal concentration. Physiol. Plant. 45: 112–116.
- TOUZET G., HEINRICH J. C., NOHN I. 1970. Foliar analysis and growth rate. C. R. Ass. For. -Cell. 1969: 17–57. [FA. 32, 100]
- TOWPASZ K. 1975. Rośliny naczyniowe południowo-wschodniej części Beskidu Wyspowego, cz. 2. Monogr. Bot.: 4–140.
- TRANQUILLINI W. 1979. Physiological Ecology of the Alpine Timberline. Tree Existence at High Al-titudes with Special Reference to the European Alps. Springer Verlag, Berlin Heidelberg New York. 137 pp.
- TRANQUILLINI W., LECHNER F., OBERHARZBACHER P., UNTERHOLZNER L., HOLZER K. 1980. Über das Höhenwachstum von Fichtenklonen in verschiedener Seehöhe. Mitt. Forst. Budn. Wien 129: 7–25.
- TRAPPE J. M. 1962. Fungus associates of ectotrophic mycorrhize. Bot. Rev. 28: 538–606.
- TRAUTMANN W. 1953. Zur Unterscheidung fossiler Spaltöffnungen der mitteleuropäischen Coniferen. Flora 140: 523–533.
- TRENDELENBURG R., MAYER-WEGELIN H. 1955. Das Holz als Rohstoff. München.
- TRESCHOW C. 1958. Forsøg med rødgranracers resistens overfor angreb af *Fomes annosus* (FR.) CKE. Forstl. Forsøgsv. Danmark 25 (1): 1–23. [FA. 20, 711]
- TRIMBLE J. L., SKELLY J. M., TOLIN S. A., ORCUTT D. M. 1982. Chemical and structural character-ization of the needle epicuticular wax of two clones of *Pinus strobus* differing in sensitivity to ozone. Phytopathology 72: 652–656.
- TROEGER F. R. 1958. Die Fichten-Provenienz-Versuche in Württemberg. Allg. Forst-Ztschr. 13 (9): 109–114.
- TROŠT T., AGERER R., URBANČIĆ M., KRAIGHER H. 1999. Biodiversity of ectomycorrhizae in a Nor-way spruce stand on Pokluka. Phytol. 39: 225–232.
- TRYANINA N. F., KONSTANTNAYA A. A. 1965. Les. Zh. (3): 121–123.
- TUNG G., TEMPLE P. J. 1996. Histological detection of lead in plant tissues. Environ. Toxicol. Chem. 15: 906–914.
- TUOMISTO H. 1988. Use of *Picea abies* needles as indicators of air pollution: epicuticular wax mor-phology. Ann. Bot. Fenn. 25: 351–364.
- TUOMISTO H., NEUVONEN S. 1993. How to quantify differences in epicuticular wax morphology of *Picea abies* (L.) KARST. needles. New Phytol. 123 (4) 787–799.
- TURNAU K., KOTTKE I., OBERWINKLER F. 1993. Element localization in *Paxillus involutus* – *Pinus sylvestris* mycorrhizas using electron energy loss spectroscopy and imaging. Bot. Acta: 245–249.
- TURUNEN M., HUTTUNEN S. 1990. A review of the response of epicuticular wax of conifer needles to air pollution. J. Environ. Qual. 19: 35–45.
- TWARÓG J. 1990. Rębnie w górach. [Cutting systems in the mountains]. PWRiL, Warszawa.
- TYLER G. 1972. Heavy metal pollute nature, may reduce productivity? Ambio 1: 52–59.
- TYMRKIEWICZ W. 1935. Wyspy świerka (*Picea excelsa* LINK.) na Polesiu i Wołyniu na tle podylu-wialnej historii świerka we wschodniej Polsce. Sylwan 53: 1–22.
- TYSZKIEWICZ S. 1934a. Nowa forma szyszek świerka (*Picea excelsa* LINK.). Las Polski (11–12): 319–325.

- TYSZKIEWICZ S. 1934b. Przyczynek do wyjaśnienia kwestii dwu zasięgów świerka w Polsce. Instytut Badawczy Lasów Państwowych, Ser. A, 6: 41–58.
- TYSZKIEWICZ S. 1949. Nasiennictwo leśne. Instytut Badawczy Leśnictwa, Warszawa.
- TYSZKIEWICZ S. 1968. Phenological observations. In: TYSZKIEWICZ S. (ed.). Population studies of Norway spruce in Poland. IBL, Warszawa. pp.: 66–77.
- TYSZKIEWICZ S., OBMIŃSKI Z. 1963. Hodowla i uprawa lasu. PWRiL, Warszawa.
- TZSCHACKSCH O., WEISS M. 1972. Die Variation der SO₂ Resistenz von Provenienzen der Baumart Fichte. (*Picea abies* (L.) KARST.). Beitr. Forstwirtschaft 6 (3): 21–23.
- UJVÁRI E., UJVÁRI F. 1979. Results of a 10-year old IUFRO international provenance trial Norway spruce (IPTNS – 1964/68) and their introduction in breeding and in practice. Proc. IUFRO Joint Meet. WPs Norway spruce provenances and breeding. Bucharest: 475–486.
- UJVÁRI E., UJVÁRI F. 1993. Geneecological investigation of Norway spruce provenances. Norway spruce provenances and breeding. Proc. of IUFRO (S2.2–11). Symposium, Riga, Latvia: 147–150.
- UJVÁRI F. 1986. A IUFRO lucfenyő-származási Kísérlet gyakorlatban hozsnosítható eredményei. Erdészeti Kutatások 78: 203–210. [FA. 51, 5526]
- ULRICH B. 1981. Die Rolle des Waldes für die Wassergüte. Allg. Forst-Ztschr. 36: 1107–1109.
- ULRICH B., MAYER R., KHANNA P. K. 1980. Chemical changes due to acid precipitation in a loess-derived soil in central Europe. Soil. Sci. 130: 193–199.
- ULRICH B., MEYER H. 1987. Chemischer Zustand der Waldböden Deutschlands zwischen 1920 und 1960. Ursachen und Tendenzen seiner Veränderung. Ber. Forschungsz. Waldökosysteme/Waldsterben. Univ. Göttingen 6: 1–133.
- URBAŃSKI K. 1987. Wpływ suszy w latach 1982–1984 na przyrost wysokości polskich proveniencji świerka pospolitego (*Picea abies* (L.) KARST.) w Leśnym Zakładzie Doświadczalnym Siemianice. Sylwan 131 (4): 31–35.
- USKOV S. P. 1962. K voprosu plodonosheniya elovykh drevostoev. Trudy Inst. Lesa Drev. AN SSSR 53: 3–24.
- VAGNER M., VONDRAKOVA Z., STRNADOVA Z., EDER J., MACHACKOVA I. 1998. Endogenous level of plant growth hormones during early stages of somatic embryogenesis of *Picea abies*. Adv. Hortic. Sci. 12: 11–18.
- VAN DE SYPE H., ROMAN-AMAT B. 1989. Analyse au stade juvenile d'un test multilocal de clones d'epicea commun (*Picea abies* (L.) KARST.). Variabilite genetique. Ann. Sci. For. 46 (1): 15–29.
- VAN DEUSEN J. L., NIENSTAEDT H. 1978. A trial of eleven sources of *Picea abies* in North Dakota and Minnesota. Ann. Proc. N. Dakota Acad. of Sci. 31 (2): 32–39.
- VAN GARDINGEN P. R., GRACE J., JEFFREE C. E. 1991. Abrasive damage by wind to the needle surface of *Picea sitchensis* (BONG.) CARR. and *Pinus sylvestris* L. Plant Cell Environ. 14: 185–193.
- VAN PRAAG H. J., WEISSEN F., SOUGNEZ-REMY S., CARLETTI G. 1985. Aluminum effects on spruce and beech seedlings. II. Statistical analysis of sand culture experiments. Plant and Soil 83: 339–356.
- VANČURA K. 1993. Norway spruce (*Picea abies* (L.) KARST.) provenances in air polluted area of Krušné hory Mts. Norway spruce provenances and breeding. Proc. of IUFRO (S2.2–11). Symposium, Riga, Latvia: 151–153.
- VANČURA K., MALA J. 2000. Information on research dealing with Genetics and Breeding of Frest Tees. Czechia. In: TEISSIER DU CROSS E. (ed.). Proceeding of the First Brain Storming Meeting, INRA, Orléans, France. Janvier 2000. 17–20.
- VANČURA K., VINŠ B. 1983. Preliminary evaluation of international provenance trial with Norway spruce *Picea abies* (L.) KARST. ČSR-GDR 1972/76–77. Comm. Inst. Forest. Czech. 13: 147–169.
- VANSELOW K. 1943. Über Ursachen der annähernd gleichen Massenleistungen unserer Reinbestände bei verschiedener Durchforstung. Forstw. Cbl.
- VÄRE H. 1990. Aluminium polyphosphate in the ectomycorrhizal fungus *Suillus variegatus* (Fr.) O. KUNTZE as revealed by energy dispersive spectrometry. New Phytol. 116: 663–668.
- VARNELL R. J., ROMBERGER J. A. 1967. Comparative development of vegetative and generative shoots of *Picea abies*. Amer. J. Bot. 54 (5, 2): 635. [FA. 29, 137]

- VASENEV I. I., PROSVIRINA A. P. 1988. Vliyanie vetroval'nykh narushenij na pochvennyy pokrov. In: UTKIN A. I., ORLOV A. YA. (eds.). Korennye temnochojnyje lesa juzhnoj tajgi. Nauka, Moskva. pp.: 184–197.
- VASILEV J. J., UKHANOV W. W. 1949. *Picea* DIETR. W: Dierevia i kustarniki SSSR, 1:122–153. Izd. AN SSSR, Moskva–Leningrad.
- VELKOV D., PLOSHCHAKOVA L., TILEV G. 1967. Formiranie i zreenie na shisharkite i semenata pri smrca. Gorskostop. Nauka 4: 65–83.
- VENN A. 1964. Foreløping melding om det internasjonale granproveniensforsøket av 1938 i Vest-Norge. Medd. Vestland. Forstl. Forsøksst. 39 12 (2): 87–125.
- VERESIN M. M., IVANOV S. M. 1970. Ekotipy eli obyknovennoi v gyeograficheskikh kul'turakh Voronyezhskogo lyeskhoza. Lyesn. genet. selektsya i syemyenovodstvo. Petrozavodsk, Karyeliya: 416–422. [Ref. Zh. 1.56.97]
- VIDAKVIĆ M. 1982. Cetinjace-morfologija i varijabilnost. Zagreb, 710 pp.
- VIIDIK P. 1973. The effect of squirrel damage on Norway spruce (*Picea abies* (L.) KARST.). Bi-monthly Res. Not. Min. Forestry, Canada. 29 (2): 14.
- VILHAR U., KRAIGHER H. 1999. Types of ectomycorrhizae on Pohorje. Phytion 39: 203–206.
- VINCENT G., FLEK J. 1953. Pokusné plochy provenienčne se smrkem. Práce Výzkum. Úst. Les. ČSR 3: 207–236.
- VINCENT G., VINCENT J. 1964. Ergebnisse des Internationalen Fichtenprovenienzversuches. Silvae Genet 13: 141–146.
- VINŠ B. 1963. Report on the state and preliminary evaluation of Czechoslovak provenance trial plots of Norway spruce in the international series from the year 1938 (FAO/FORGEN 63) 1: 3/6.
- VINŠ B. 1967. A. Contribution to the Norway spruce provenance research. Papers XIV IUFRO Congress, Munchen, III: 743–754.
- VINŠ B. 1976. Mezinárodní provenienční pokus se smrkem IUFRO – série 1938 2. sdělení: Taxační vyhodnocení pokusných ploch v Beskydech v roce 1974. Acta Mus. Silesiae, Dendrologia 25: 1–23.
- VINŠ B., VANČURA K. 1977. Provenance trial with spruce (*Picea abies* (L.) KARST.) IUFRO 1964/68 in Czechoslovakia. Comm. Inst. Forest. Czech. 10: 89–109.
- VINŠ B., VANČURA K. 1979. Mezinárodní provenienční pokus se smrkem (*Picea abies* (L.) KARST.) IUFRO 1964/68 – PPP Hluboká n. Vlt. Práce VÚLHM 54: 69–106.
- VISHNYAKOV YU. E. 1969. Geograficheskie kul'tury eli obyknovennoy v usloviyakh pikhtovoy zony Kazakhstanskogo Altaya. Lesn. Selektysya, Semenovodstvo Introduk. Kazachstane. Referaty dokl. nauchno-metod. konf. pri KazNIILCh, Alma-Ata: 48–49.
- VISKARI E. L., HOLOPAINEN T., KARENLAMPI L. 2000. Response of spruce seedlings (*Picea abies*) to exhaust gas under laboratory conditions – II – ultrastructural changes and stomatal behaviour. Environ. Poll. 107: 99–107.
- VODNIK D., GOGALA N. 1997. Inoculation of Norway spruce (*Picea abies* [L.] KARSTEN) with mycorrhizal fungi: the impact on growth and development in a tree nursery and after transplantation. Zbornik Gozdarstva i Lesarstva 54: 87–108.
- VODZINSKIY *et al.* 1969. Gidroliznaya y lesokhimicheskaya prom. 22 (4): 7–9.
- VOGELEI A., ROTHE G. M. 1988. Die Wirkung von Säure und Aluminiumionen auf den Nährelementgehalt und den histologischen Zustand nichtmykorrhizierter Fichten wurzeln (*Picea abies* [L.] KARST.). Forstw. Cbl. 107 (6): 348–357.
- VOGELLEHNER D. 1977. Phylogenie, Taxonomie und Verbreitung der Gattung *Picea*. W: SCHMIDT-VOGT H., Die Fichte, 1: 1–163. Paul Pary, Hamburg u. Berlin.
- VOGL M. 1960. Blattdüngung bei Fichten mit Radiophosphor. Arch. Forstw. 9 (12): 1125–1139.
- VOGT K. A., BLOOMFIELD J., AMMIRATI J. F., AMMIRATI S. R. 1992. Sporocarp production by basidiomycetes with emphasis on forest ecosystems. In: CAROLL C. G., WICKLOW D. T. (eds.). The fungal community its organization and role in the ecosystem. Marcel Dekker, New York. pp.: 563–581.
- VOLNÁ M., HAUCK O., RYCHNOVSKÁ A. 1990. Jednoduché způsoby zakořeňování smrku ztepilého (*Picea abies* (L.) KARST.). Lesnictví 36 (7): 553–569.

- VOLNÁ M., RADOSTA P. 1985. Morfologická charakteristika řízkovanců smrku ztepilého [*Picea abies* (L.) KARSTEN] a posouzení jejich kvality pro účely zalesňování. Acta Univ. Agric., Ser. C 54 (1–2): 49–77.
- VOLNÁ M., RADOSTA P. 1987. Vliv velikosti, hmotnosti a okamžité vlhkosti řízků na zakořenění a další vývin řízkovanců smrku ztepilého [*Picea abies* (L.) KARST.]. Lesnictví 33 (6): 511–524.
- VOL'SKIY L., SCHMIDT 1970. Khimicheskiy sostav oleoresin eli. Sibirsk. Otd. AN SSSR, Ser. Khim. Nauk 2: 132–134.
- WACHTER H. 1985. Zu Lebenslaner von Fichtennadeln in einigen Waldgebieten Nordrhein-Westfalens. Forst- Holzwirt. 40 (16): 420–425.
- WAGA J. 1848. Flora polska jawnokwiatowych rodzajów, 2. Strąbski, Warszawa. 679 pp.
- WAGNER Ch. 1923. Blendersaumschlag und sein System. 3 Aufl. Tübingen. Parey, Berlin.
- WALAS J. 1933. Roślinność Babiej Góry. Państw. Rada Ochr. Przyr., Monogr. Nauk. 2: 1–68.
- WALENDA T., KOTTKE I. 1998. Nitrogen deposition and ectomycorrhiza. New Phytol. 139: 169–187.
- WALLES B. 1967. The homozygous and heterozygous effect of an *Aurea* mutation on plastid development in spruce (*Picea abies* (L.) KARST. Stud. Forest. Suec. 60: 1–20.
- WALLIN G., SKÄRBY L., SELLDEN G. 1990. Long-term exposure of Norway spruce, *Picea abies* (L.) KARST. to ozone in open-top chambers. I. Effects on the capacity of net photosynthesis, dark respiration and leaf conductance of shoots of different ages. New Phytol. 115: 335–344.
- WANG CH.-W. 1961. The Forest of China with and survey of Grassland and Desert Vegetation. Cambridge, 313 pp.
- WANIN S. 1953. Nauka o drewnie. Warszawa.
- WAREING P. F. 1959. Problems of juvenility and flowering in trees. Bot. J. Linn. Soc. 56: 282–289.
- WARING R. H. 1991. Response of evergreen trees to multiple stresses. In: MOONEY H. A., WINNER W. E., PELL E. J. (eds.). Response of plants to multiple stresses. Academic Press Inc., San Diego–Toronto. pp.: 371–390.
- WEBER C. A. 1898. Über eine omorikaartige Fichte aus einer dem älteren Quartäre Sachsens angehörenden Moorbildung. Englers Bot. Jhrb. 24: 510–540.
- WEBER P., THOENE B., RENNENBERG H. 1998. Absorption of atmospheric NO₂ by spruce (*Picea abies*) trees. III. Interaction with nitrate reductase activity in the needles and phloem transport. Bot. Acta 111: 377–382.
- WECK J. 1955. Forstliche Zuwachs und Ertragskunde. 2. Aufl. Redebeul–Berlin.
- WEDLER M., WEIKERT R. M., LIPPERT M. 1995. Photosynthetic performance, chloroplast pigments and mineral content of Norway spruce (*Picea abies* (L.) KARST.) exposed to SO₂ and O₃ in open-air fumigation experiment. Plant Cell Environ. 18: 263–276.
- WEETE J. D. 1989. Structure and function of sterols in fungi. Adv. Lipid Res. 23: 115–167.
- WEIHE J. 1973. Die Reaktion von Buchen- und Fichtenbeständen auf den Regen. Allg. Forst-Ztschr. 28: 956–957.
- WEIHE J. 1984. Benetzung und Interzeption von Buchen- und Fichtenbeständen. IV. Die verteilung des Regen unter Fichtenkronen. Allg. Forst- Jagdztg. 155 (10/11): 241–252.
- WEINGES K. 1960. Die Lignane des Überwallungsharzes der Fichte. Tetrahedron Letters, London 10: 1–2.
- WEISER J. 1954. Příspevek k znalosti cizopasníku kurovce IPS TYPOGRAFUS L. Vestn. Českoslov. Zool. Spol. 18 (3): 217–224.
- WEISGERBER H. 1979. Norway spruce provenance experiments in Central Europe. Proc. IUFRO Joint Meet. WPs Norway spruce provenances and breeding. Bucharest: 57–73.
- WEISGERBER H., DIETZE W., KLEINSCHMIT J., RACZ J., DIETERICH H., DIMPFLMEIER R. 1977. Ergebnisse des internationalen Fichten-Provenienzversuches 1962. Allg. Forst- Jagdztg. 148 (12): 217–226.
- WEISGERBER H., DIMPFLMEIER R., KLEINSCHMIT J., WIDEMAIER T. 1985. Results of the international Norway spruce provenance trial (IUFRO 1964/68) in the Federal Republic of Germany after 18 years' observation. Materials from the IUFRO S2.02.11 Meeting on Norway Spruce Provenances, Vienna: 1–11.

- WEISGERBER H., DIMPFLMEIER R., RUETZ W., KLEINSCHMIDT J., WIDMAIER T. 1984. Ergebnisse des internationalen Fichten Provenienzversuches 1962. Entwicklung bis zum Alter 18. Allg. Forst Jagd. 155 (4/5): 110–121.
- WEISS M. 1981. Ergebnisse eines Baumschulversuches mit verschiedenen Provenienzen von *Picea abies*. Beitr. Forstwirtschaft 15 (3–4): 131–134.
- WEISS M., AGERER R. 1988. Studien an Ektomykorrhizen XII. Drei nichtidentifizierte Mykorrhizen an *PICEA ABIES* (L.) KARST. Aus einer Baumschule. Eur. J. For. Path. 18: 26–43.
- WEISS M., HOFFMANN J. 1968. Möglichkeiten zur heistungssteigerung durch Anbau geeigneter Fichtenprovenienzen. Social. Forstwirtschaft 18 (8): 241–245, 256.
- WEISS M., HOFFMANN J. 1969. Neue Ergebnisse einer Provenienzversuches mit Fichte (*Picea abies* (L.) KARST) im Erzgebirge und Thüringer Wald. Arch. Forstw. 18 (4): 443–466.
- WEISCH P. B. 1977. Biologia ogólna. PWN, Warszawa. 743 pp.
- WELTEN M., SUTTER R. 1982. Verbreitungsatlas der Fern- und blütenpflanzen der Schweiz. Birkhäuser, Basel–Boston–Stuttgart.
- WENG CH., JACKSON S. T. 2000. Species differentiation of North American spruce (*Picea*) based on morphological and anatomical characteristics of needles. Can. J. Bot. 78: 1367–1383.
- WENTZEL K. F. 1968. Empfindlichkeit und Resistenzunterschiede der Pflanzen gegenüber Luftverunreinigung. Forstarchiv 39 (9): 189–194.
- WENTZEL K. F. 1971. Habitus – Änderung der Waldbäume durch Luftverunreinigung. Forstarchiv 42: 165–172.
- WERLICH I., LYR H. 1957. Über die Mykorrhizausbildung von Kiefer (*Pinus sylvestris* L.) and Buche (*Fagus sylvatica* L.) auf verschiedenen Standorten. Arch. Forstw. 6: 1–23.
- WERNER A. 1982. Histological changes induced in Weigelia, Japanese larch, and Scots pine leaves by SO₂. Arbor. Kórnické 26: 189–201.
- WERNER A. 1989. Pathological changes induced in anatomical structure of leaves by industrial gases. Aquilo, Ser. Bot. 27: 35–43.
- WERNER M. 1976. Preliminära resultat från första revisionen av skogsförbättrings gran proveniensserie från år 1969. Mat. konf. Gran förädling. Bogesund, Institutionen för skogsgenetik. Skogshögskolan, Stockholm: 41–47.
- WERNER M. 1979. Present methods of propagation of Norway spruce and future aspects. IUFRO Norway Spruce Meeting S 2.03.11 – S 2.02.11 Bucharest: 117–128.
- WERNER M. 1980. Gran ett besvarligt olantagetrad? Skogsgenetik och skogstradsförädling. Sveriges Skog. Förb. Tidskr. 78 (1/2): 78–88. [FA. 43, 334]
- WERNER M., PETTERSSON H. 1981. Klonskogsbruk med gran. Särtryck ur Föreningen Skogsträdsförädling och Institutet för skogsförbättring, Arsbok 1981: 118–153.
- WESSLER A., WILD A. 1993. Investigations on the content of indole–3-acetic acid in spruce needles of healthy and damaged trees of various sites. J. Plant Physiol. 141: 615–620.
- WESTMAN C. J., NUMMI T., LEIKOLA M. 1985. Käytännön typpilannoituksen vaikutus varttuneiden kuusikoiden kasvuun ja tuotokseen. Silva Fenn. 19 (4): 393–406.
- WESTMAN L. 1974. Air pollution indications and growth of spruce and pine near a sulphite plant. Ambio 3 (5) 189–193.
- WETTSTEIN-WESTERSHEIM W. 1961. Möglichkeit einer Transgressionszucht bei Fichten. Z. Pflanzenzücht 46 (3): 347–350. [Ref. Zh. 12.5.146]
- WHEELER N. C., JECH K. S. 1992. The use of electrophoretic markers in seed orchard research. In: ADAMS W. T., STRAUSS S. H., COPES D. L., GRIFFIN A. R. (eds) Population Genetics of Forest Trees. Kluwer Academic Publishers. pp: 311–328.
- WHITE T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63: 90–105.
- WHITMORE T. C. 1982. On pattern and process in forest. In: NEWTON E. J. (ed.). The plant community as a working mechanism. Blackwell Sci. Publ., Oxford. pp.: 45–57.
- WIĄCKOWSKI S. 1956. Wyniki hodowli pasożytów owadów leśnych. Część I. Polskie Pismo Entomol. 26 (21): 311–320.

- WIEBE H. H. 1980. Morphological adaptations to water stress. In: TURNER N. C., KRAMER P. J. (eds.) Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York-Toronto. pp.: 439-443.
- WIEDEMANN E. 1936. Die natürliche Verjüngung der Fichte. Mitt. Forstw. 7: 40-54.
- WIERDAK S. 1927a. O kresowych stanowiskach naszych drzew. Sylwan 45: 103-114.
- WIERDAK S. 1927b. Rozsiedlenie świerka, jodły i buka w Małopolsce. Sylwan 45: 347-370.
- WIESER G., HASLER R., GOTZ B., KOCH W., HAVRANEK W. M., FÜHRER J. 2000. Role of climate, crown position, tree age and altitude in calculated ozone flux into needles of *Picea abies* and *Pinus cembra*: a synthesis. Environ. Poll. 109: 415-422.
- WIESER G., HAVRANEK W. M. 1993. Ozone uptake in the sun and shade crowns of spruce: quantifying the physiological effects of ozone exposure. Trees 7 (4): 227-232.
- WIESER G., HAVRANEK W. M. 1996. Evaluation of ozone impact on mature spruce and larch in the field. J. Plant Physiol. 148: 189-194.
- WIESER G., HAVRANEK W. M., LOIDOLDT-NAGELE M., KRONFUSS G., POLLE A. 1998. Response of photosynthesis, carbohydrates and antioxidants in needles of Norway spruce to slow and rapid changes in ozone. Bot. Acta 111: 35-41.
- WIKLUND K., NILSSON L. O., JACOBSSON S. 1995. Effect of irrigation, fertilization and artificial drought on basidioma production in a Norway spruce stand. Can. J. Bot. 73: 200-208.
- WILCZEK Z. 1995. Zespoły leśne Beskidu Śląskiego i zachodniej części Beskidu Żywieckiego. Uniw. Śląski, Katowice. 131 pp.
- WILCZEK Z., CABAŁA S. 1989. Zespoły leśne grupy Klimczoka w Beskidzie Śląskim. Cz. 1. Zespoły borowe. Acta Biol. Sil. 12 (29): 71-77.
- WILD A., SCHMITT V. 1995. Diagnosis of damage in Norway spruce (*Picea abies*) through biochemical criteria. Physiol. Plant. 93: 375-382.
- WILKINS D. A., HODSON M. J. 1989. The effects of aluminium and *Paxillus involutus* Fr. on the growth of Norway spruce [*Picea abies* (L.) KARST.]. New Phytol. 113: 225-232.
- WILKSCH W., SCHMITT V., WILD A., PAOLETTI E. 1998. Ethylene biosynthesis in cinifers: investigations on the emission of ethylene and the content of ACC and MACC in Norway spruce (*Picea abies*) and silver fir (*Abies alba*). Chemosphere 36: 883-888.
- WILLENBORG A., SCHMITZ D., LELLEY J. 1990. Effects of environmental stress factors on ectomycorrhizal fungi. Can. J. Bot. 68: 1741-1746.
- WILLENBRINK J., SCHATTEN T. 1993. CO₂-fixation and assimilate distribution in spruce under long-term fumigation with ozone. Forstw. Cbl. 112: 50-56.
- WILLIAMS K. A. 1982. Tolerances of four species of southern pine to aluminium in solution cultures. Ms Thesis, Univ. of Florida, Gainesville.
- WILSON E. J., SKEFFINGTON R. A. 1994. The effects of excess nitrogen deposition on young Norway spruce trees. Part II. The vegetation. Environ. Poll. 86 (2): 153-160.
- WINIARSKI M. 1886. Szyszki na 10-letnim świerku. Sylwan 4: 270.
- WITT H. H. 1987. Bedarforientierte Düngung bei Containerpflanzen. Dtsch. Baumschule 39 (5): 211-214.
- WŁOCZEWSKI T. 1968. Ogólna hodowla lasu. PWRiL, Warszawa. 499 pp.
- WODZICKI T. J., WITKOWSKA L. 1961. On the photoperiodic control of extension growth and wood formation in Norway Spruce [*Picea abies* (L.) KARST.]. Acta Soc. Bot. Pol. 30 (3/4): 755-764.
- WODZICKI T., WODZICKI A. 1981. Modulation of the oscillatory system involved in polar transport auxin by other phytohormones. Physiol. Plant. 53: 176-180.
- WOJTEWSKI T., KASPROWICZ M. 1985. Le relief de la pente et la végétation a travers les etages dans le massif de Babia Góra (Hautes Beskides) dans les Carpathes Occidentales. Coll. Phytosociol. 13: 257-265.
- WOJTEWSKI T., KASPROWICZ M., ŁUSZCZYŃSKI J. 1982. Der Karpatische Fichtenwald an der oberen Waldgrenze im Babia Góra- Massiv (Hohe Beskiden) und seine Struktur. In: DIERSCHKE H. (ed.). Struktur und Dynamik von Wäldern. Ber. Int. Symp. IVV: 345-353.
- WÖLLMER H., KOTTKE I. 1990. Fine root studies *in situ* in the laboratory. Environ. Poll. 68: 383-407.
- WOLSKI R. 1966. Zwalczanie kornika drukarza w lasach Warmii i Mazur. Sylwan 110 (11): 43-50.

- WORRALL J. 1975. Provenance and clonal variation in phenology and wood properties of Norway spruce. *Silvae Genet.* 24 (1): 2–5.
- WORRALL J., MERGEN F. 1967. Environmental and genetic control of dormancy in *Picea abies*. *Physiol. Plant.* 20: 733–745.
- WRIGHT J. 1955. Species crossability in spruce in relation to distribution and taxonomy. *For. Sci.* 1 (4): 319–349.
- WRIGHT J. 1962. Genetics of Forest Tree Improvement. FAO Forestry and Forest Products Studies 16, Rome.
- WÜHLISCH G. VON 1984. Propagation of Norway Spruce Cuttings Free of Topophysis and Cyclophysis Effects. *Silvae Genet.* 33 (6): 215–219.
- WÜHLISCH G. VON, MUHS H. J. 1987. Effect of spacing on growth, especially predetermined and free shoot growth on Norway spruce (*Picea abies* (L.) KARST.). *Silvae Genet.* 36 (2): 72–76.
- WULFF A., AHONEN J., KÄRENlampi L. 1996a. Cell ultrastructural evidence of accelerated ageing of Norway spruce needles in industrial areas. *New Phytol.* 133: 553–561.
- WULFF A., ANTONEN S., HELLER W., SANDERMANN H. JR., KÄRENlampi L. 1996b. Ozone-sensitivity of Scots pine and Norway spruce from northern and local origin to long-term open-field fumigation in central Finland. *Environ. Exp. Bot.* 36: 209–227.
- WULFF A., KÄRENlampi L. 1996. Effects of long-term open-air exposure to fluoride, nitrogen compounds and SO₂ on visible symptoms, pollutant accumulation and ultrastructure of Scots pine and Norway spruce seedlings. *Trees* 10: 157–171.
- WUTZ A. 1955. Anatomische Untersuchungen über System und periodische Veränderungen der Lentizellen. *Bot. Stud.* 4: 43–72.
- WYTENBACH A., TOBLER L. 1988. The seasonal variation of 20 elements in 1st and 2nd year needles of Norway spruce, *Picea abies* (L.) KARST. *Trees* 2 (1): 52–64.
- WYTWER T. 1970. Badania nad głębokością wnikania środków grzybobójczych do drewna świerkowego. *Zesz. Nauk. SGGW, Leśnictwo* 14: 105–122.
- XIE C. Y., KNOWLES P. 1992. Male fertility variation in an open-pollinated plantation of Norway spruce (*Picea abies*). *Can. J. For. Res.* 22: 1463–1468.
- XIE C. Y., KNOWLES P. 1994. Mating system and effective pollen immigration in a Norway spruce (*Picea abies* (L.) KARST) plantation. *Silvae Genet.* 43: 48–52.
- YANG C., WESSLER A., WILD A. 1993. Studies on the diurnal courses of the contents of abscisic acid, 1-aminocyclopropane carboxylic acid and its malonyl conjugate in needles of damaged and undamaged spruce trees. *J. Plant Physiol.* 144: 624–626.
- YAZDANI R., LINDGREN D., RUDIN D., SZMIDT A. E. 1985. Genetic structure of a *Pinus sylvestris* L. seed-tree stand and naturally regenerated understory. *For. Sci.* 31: 430–436.
- YEE-MEILER D. 1978. Der Einfluß von kontinuierlichen niedrigen SO₂-Begasungen auf den Phenolgehalt und der Phenoloxidase-Aktivität in Blättern einiger Waldbaumarten. *Eur. J. For. Path.* 8: 14–20.
- ZABOLOTNOVA Z. I. 1972. O gibrizacji eli kolyuchej s elyu obyknovennoy. *Nauch. Trudy Mosk. Lesotechn. Inst.* 43: 25–29. [Ref. Zh. 3.56.101]
- ZAGÓRSKA-MAREK B. 1995. Stałość i zmienność ulistnienia i waskularyzacji pędu. Materiały konferencji i sympozjów 50 Zjazdu PTB, Kraków: 464.
- ZAGWIŃ W. H. 1992. The beginning of the ice age in Europe and its major subdivisions. *Quater. Sci. Rev.* 11: 583–591.
- ZAJĄC A., ZAJĄC M. (eds.) 2001. Distribution Atlas of Vascular Plants in Poland. Laboratory of Computer Chorology, Institute of Botany, Jagiellonian University, Kraków. 716 pp.
- ZAJĄCZKOWSKI J. 1991. Odporność lasu na szkodliwe działanie wiatru i śniegu. Wydawnictwo Świat, Warszawa. 221 pp.
- ZAJĄCZKOWSKI J. 1994. Biogrupy drzew w drzewostanach – możliwości i celowość ich wykorzystania przy prowadzeniu trzebieży. *Prace IBL, Warszawa, Ser. A* 778: 5–38.
- ZAK B. 1964. Role of mycorrhiza in root disease. *Ann. Rev. Phytopathol.* 2: 377–392.
- ZARZYCKI K. 1963. Lasy Bieszczadów Zachodnich. *Acta Agr. Silv., Ser. Silv.* 3: 1–132.
- ZARZYCKI K. 1981. Rośliny naczyniowe Pienin. PWN Warszawa-Kraków, 256 pp.

- ZARZYCKI K. 1984. Ekologiczne liczby wskaźnikowe roślin naczyniowych Polski. PAN – Instytut Botaniki, Kraków. 45 pp.
- ŽDÁRSKÁ D. 1968. Severské provenience smrku *Picea excelsa* LINK. Sborník Ved. Les. Ust. Vysoké Školy Zemed. 11: 91–131.
- ŽDÁRSKÁ D. 1973. Předběžné hodnocení provenienčního pokusu se smrkem. Sborník Ved. Les. Ust. Vysoké Školy Zemed. 15–16/1972: 39–84.
- ŽDÁRSKÁ D. 1980. Předběžné hodnocení růstu provenienci smrku. Sborník referátů z konference *Provenienční Výzkum Lesních Dřevin*. Praha 1979: 55–73.
- ŽDÁRSKÁ D. 1988. Vyhodnocení růstu autovegetativně množených jedinců smrku ztepilého (*Picea abies* KARST.). Sborník. Úst. Aplikované Ekol. Ekotechn. Vysoké Školy Zemed. 7: 3–15.
- ZECH W. 1968. Kalkhaltige Böden als Nährsubstrat für Koniferen. Ökologische Studien in Süddeutschland. München.
- ZECH W. 1970. Besonderheiten im Ernährungszustand chlorotischer Fichten auf kalkreichen Böden. Forstw. Cbl. 89 (1): 1–9.
- ŻELAWSKI W., WODZICKI T. 1960. Różnicowanie słoja drewna siewek świerka pospolitego (*Picea excelsa* L.) w związku z rytmią dziennego oświetlenia. Folia Forest. Polonica, Ser. A 22: 113–121.
- ZELLNIG G., GAILHOFER M., PFEIFHOFER H. W., GRILL D. 1989. Ultrastructure and pigment composition of chloroplasts of differently damaged green and yellowed needles of *Picea abies*. Phyton 29 (2): 213–225.
- ZENKTELER M., WOŹNIAK H. 1965. Odczyn drewna niektórych krajowych gatunków drzew. Sylwan 109 (2): 49–53.
- ZIENTARSKI J. 1985. Wpływ wzniesienia oraz wielkości masywu górskiego na kształtowanie się górnej granicy lasu w Polsce. PhD. Thesis, AR Poznań.
- ZIENTARSKI J. 1989. Studia nad górną granicą lasu w Polsce. Roczn. AR, Poznań 204: 63–68.
- ZNAIMER H., WAZDA F. 1967. Kompostierung des Rindes. Holzforschung und Holzverwertung 19 (2): 29.
- ZÖTTL H. W. 1990. Ernährung und Düngung der Fichte. Forstw. Cbl. 109 (2–3): 130–137.
- ZUKRIGL K. 1991a. Succession and regeneration in the natural forests in Central Europe. Geobios 18: 202–208.
- ZUKRIGL K. 1991b. Ergebnisse der Naturwaldforschung für den Waldbau (Österreich). Schriftenr. Vegetationsk. 21: 233–246.
- ZVIEDRE A. A. 1970. Vliyanie ekologicheskikh factorov na determinaciyu generativnykh pochetk eli obyknovennoy v Latviyskoy SSR. Lesoved. (6): 26–29.
- ZWIAZEK J. J., SHAY J. M. 1987. Fluoride- and drought-induced structural alterations of mesophyll and guard cells in cotyledons of jack pine (*Pinus banksiana*). Can. J. Bot. 65: 2310–2317.
- ŻYBURA H. 1983. Wpływ drzewostanu osłaniającego na dynamikę odnowień podokapowych świerka w drzewostanach z udziałem sosny i świerka w północno-wschodniej części Polski. Sylwan 127 (9/10): 41–52.
- ŻYBURA H. 1990. Lasotwórcza rola świerka pospolitego (*Picea abies* L. KARST.) w Polsce ze szczególnym uwzględnieniem obszaru nizinnego. [The forest-forming role of Norway spruce (*Picea abies* L. Karst.) in Poland with emphasis on the lowland region]. SGGW-AR, Warszawa. 90 pp.
- ZYKOV P. V. 1967. O prognozirovanii plodonosheniya eli po generativnym pochkam. Les. Khoz. 20 (2): 23–24.

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