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Biology and Ecology of Norway Spruce

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1. PALEORECORD OF NORWAY SPRUCE

ANDRZEJ ŚRODOŃ, 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. engleri* in Paleogenian 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.

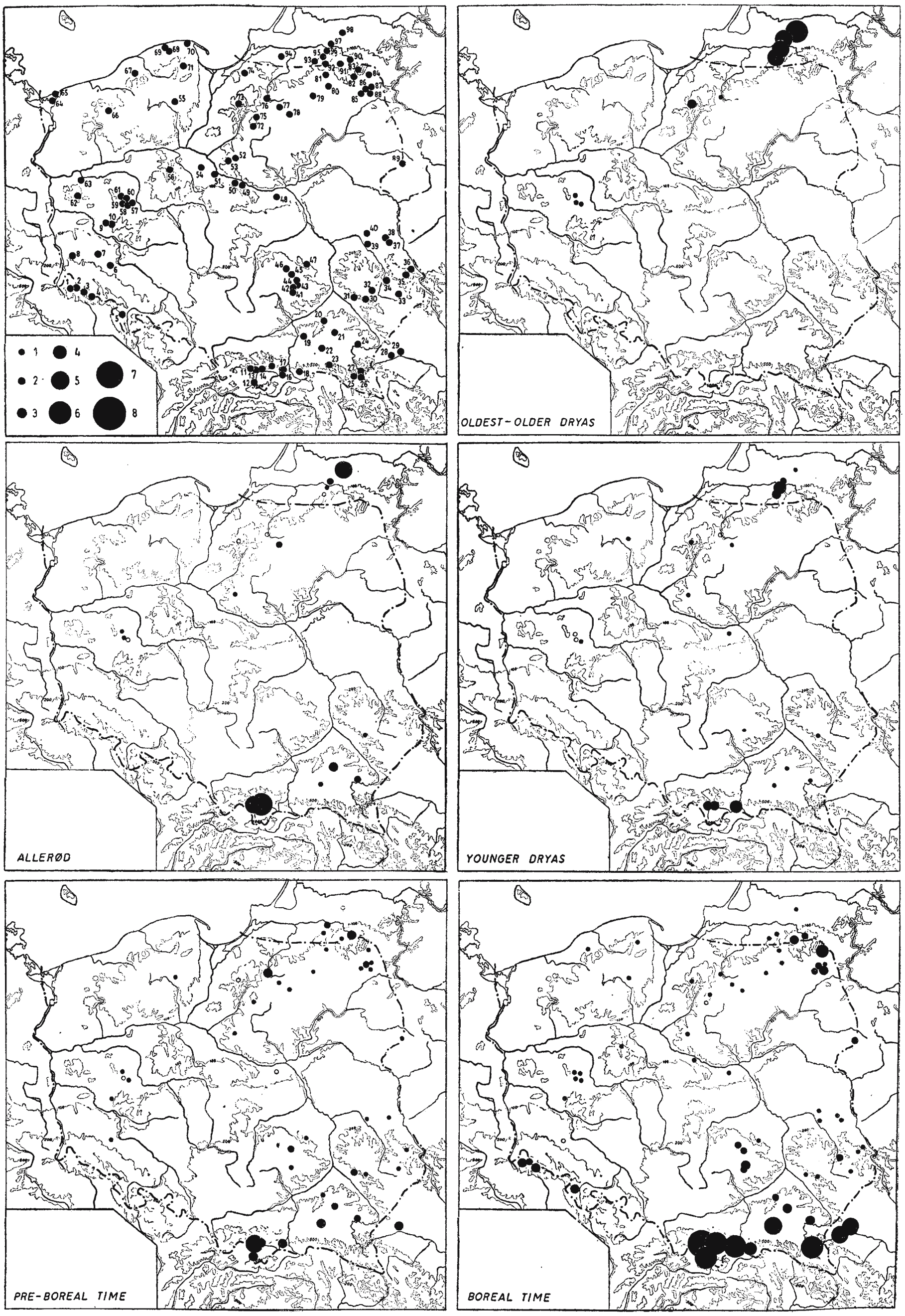
The northern portion of the contemporary range of spruce was likely formed through a northern migration route, which quite early divided into two pathways. One path traversed northern Scandinavia where range expansion occurred somewhat more slowly. This is evidenced by the relatively late proliferation 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-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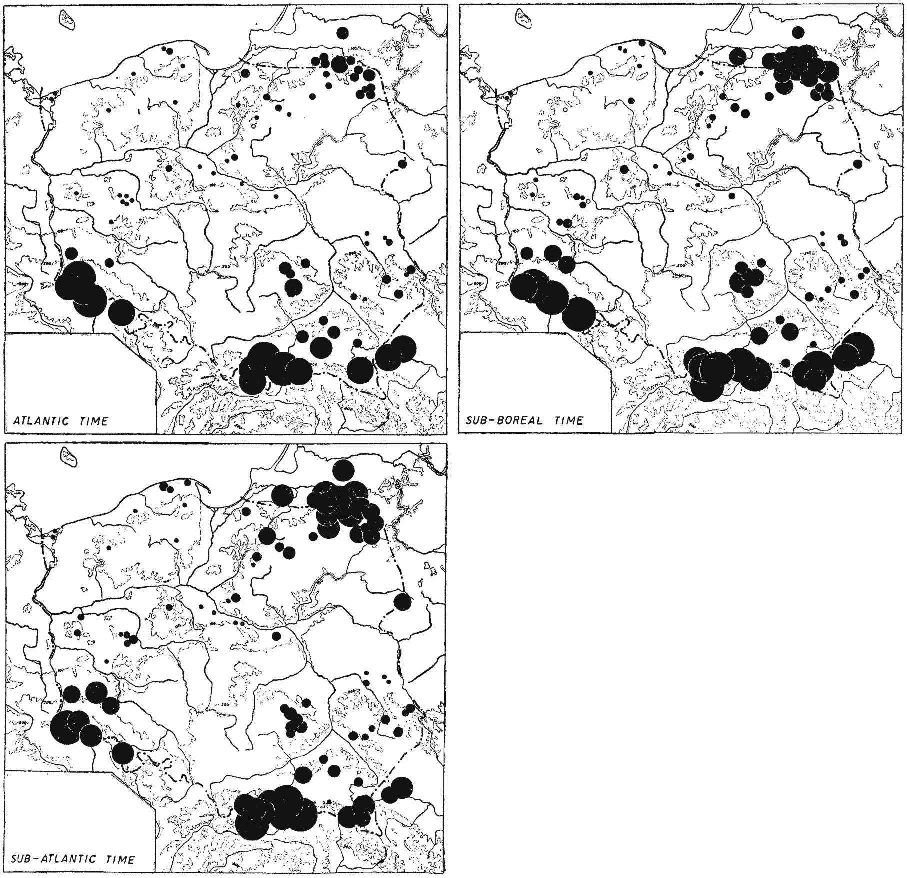

Figure 1.1. Distribution of spruce in the Late Glacial and Holocene periods. Locations numbers are shown on the first panel (ŚRODOŃ, 1967b)

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 m^2 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 grayer. 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 grayer-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 monecious; 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 stamina, 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

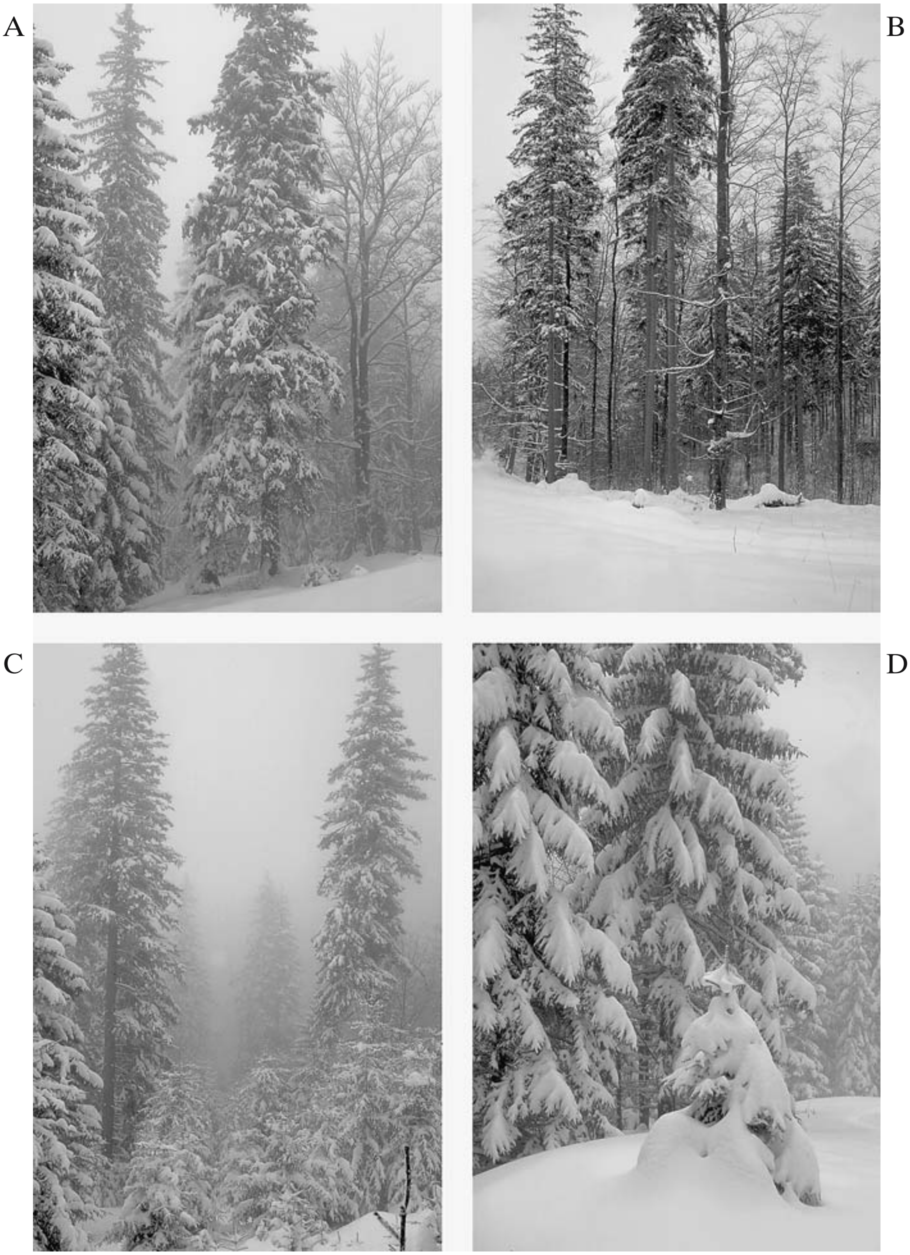

Figure 2.2. Norway spruce trees in the lower montane belt (photo A. BORATYŃSKI)

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 back 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 m^2 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 diameter) 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 m^2/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 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-

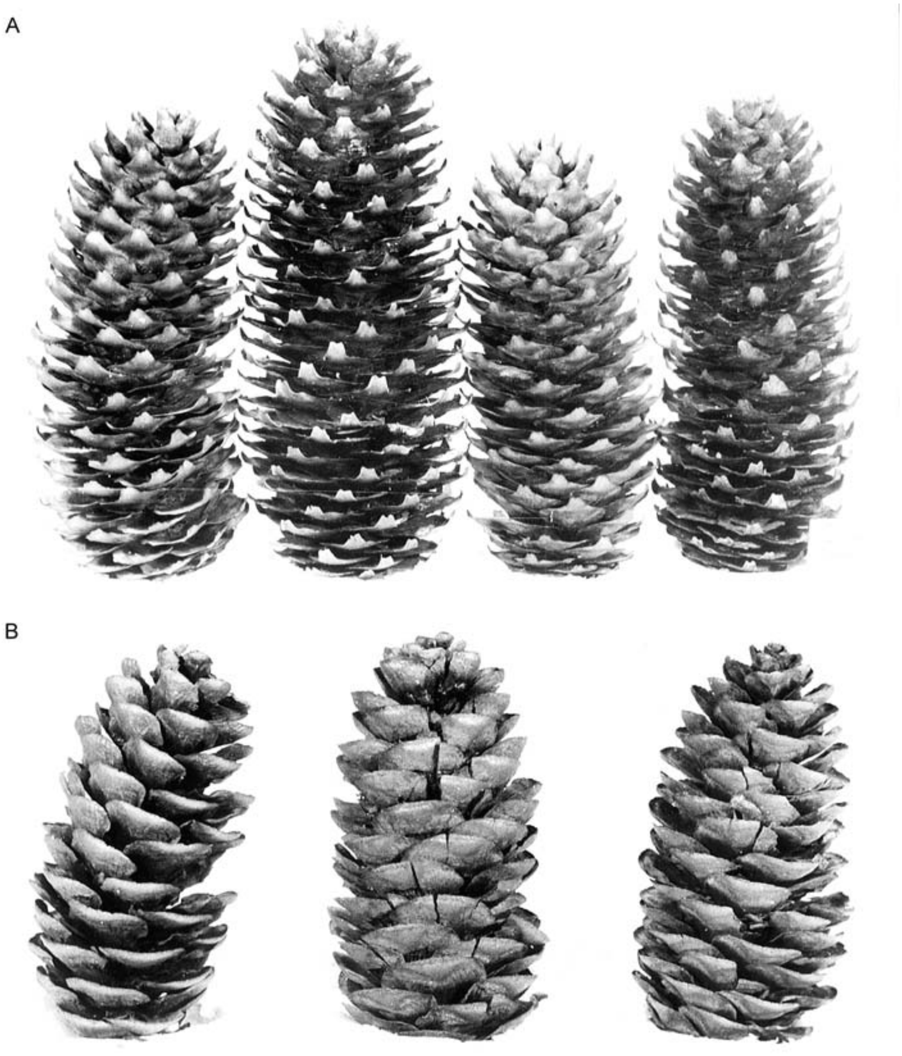

Figure 3.1. Cones of Picea abies (photo E. SZUBERT)

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 ½ 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 ¾ 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*

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

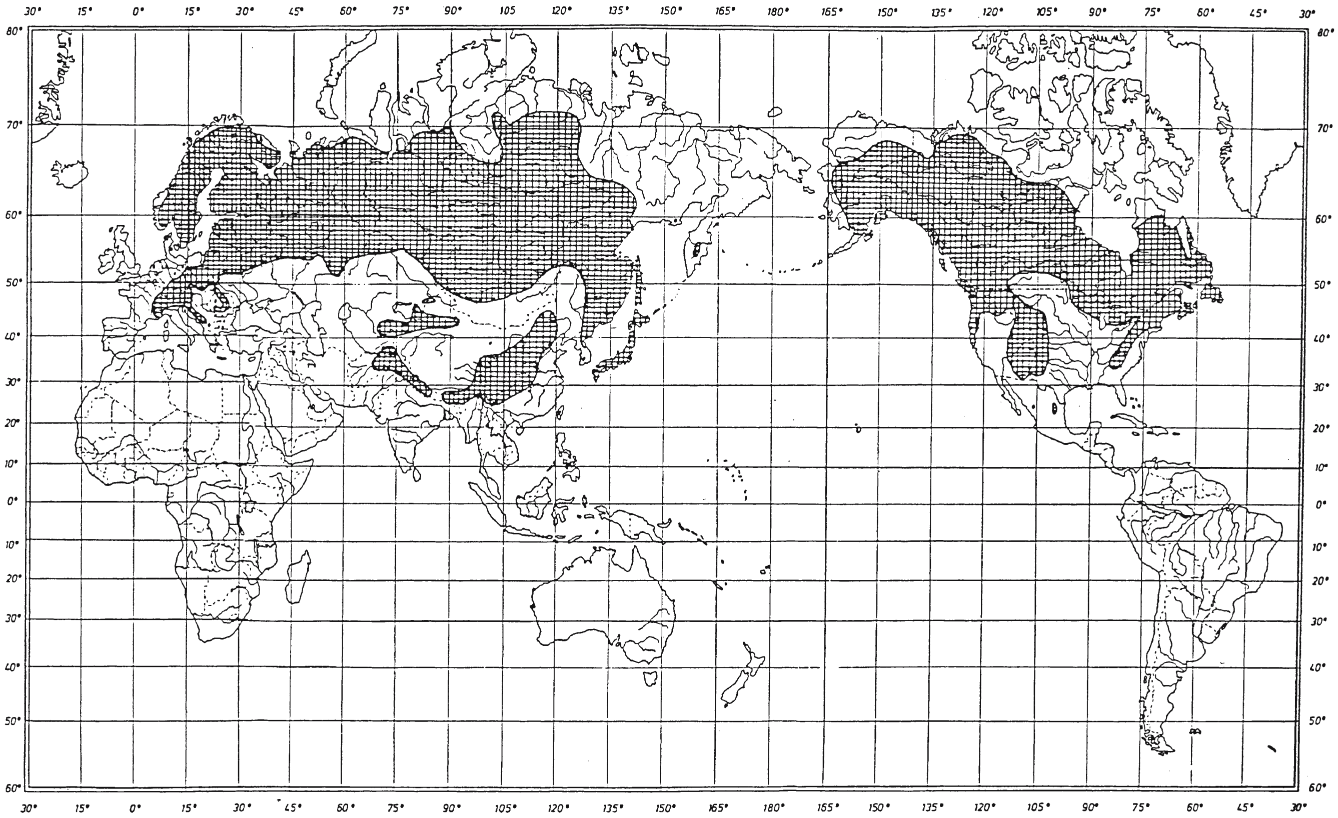

Figure 4.1. Native geographic range of the genus Picea (compiled from LITTLE *1971;* JALAS *and* SUOMINEN *1973;* HORIKAWA *1976;* SOKOLOV *et al. 1977;* SCHMIDT-VOGT *1977;* BROWICZ *1982)*