PICEA

Picea, especially Picea growing in the Southeastern United States

Part three
including the pages 284-291 (of 247-305)
of the review with the title:

THE GENERA OF PINACEAE IN THE SOUTHEASTERN UNITED STATES

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2. **Picea** A. Dietrich, Fl. Gegend Berlin, 794. 1824.

Pyramidal evergreen trees (or shrubs under harsh conditions) with slender, more or less whorled branches. Branchlets pubescent with simple trichomes or glabrous, roughened by persistent leaf bases. Bark thin and scaly or sometimes furrowed. Wood with axial and radial resin canals and ray tracheids regularly present; axial parenchyma absent. Leaves spirally arranged, linear, 4-sided and then stomatiferous on all sides [or dorsiventrally flattened and stomatiferous on the lower—but morphologically adaxial—surface], acute to acuminate, often sharply pointed [or sometimes obtuse or emarginate]; fibrovascular bundle apparently single [or often double]; resin canals 2 [rarely 1], laterally placed; leaf bases persistent, ultimately woody. Pollen cones (microsporangiate strobili) subsessile [or stalked], borne singly in axils of leaves of previous year; microsporophylls many per strobilus, each with apex prolonged into a broad, nearly circular crest; microsporangia longitudinally dehiscent; pollen bisaccate. Ovulate cones borne at tips of previous year's growth, maturing in 1 year, before pollination erect on short stalks; mature cones ovoid to cylindrical, 2–7[–15] cm long, sessile or short stalked, pendulous; bracts much smaller than scales at maturity; ovuliferous scales persistent, obovate to oblong, with apex rounded [to rhombic], entire to denticulate [erose]. Seeds with thin terminal wing; body rounded on the sides and usually acute at base; seed coat without resin vesicles. Cotyledons ca. 6 [4–15], denticulate or entire. Chromosome number $2n = 24$. TYPE SPECIES: *Picea rubra* A. Dietr., *nom. illeg.*, = *P. Abies* (L.) Karst.; see Britton, N. Am. Trees, 54. 1908. (Classical Latin name for a conifer, from *pix,* pitch.)—SPRUCE.

A well-defined genus of approximately 35 species, *Picea* occurs widely in the boreal and temperate areas of the Northern Hemisphere, from the arctic of North America and Eurasia south to the higher mountains of Mexico and southern China. The greatest number of species (ca. 24) occurs in eastern and central Asia, where the taxonomic situation is particularly complex (see Cheng & Fu; Rehder, 1940; Schmidt-Vogt, 1977; Wright). Seven species are native to the United States and Canada; three of these occur in the eastern part, with only one, *P. rubens* Sarg., ranging south into our region.

Sections within *Picea* are not easily distinguished on the basis of overall morphology, chemistry, or crossability. Willkomm divided the genus into two sections, *Eupicea* Willk. (= sect. PICEA) and OMORIKA Willk., based on the cross-sectional form and stomatal arrangement of the needles. Mayr divided the genus into three sections, *Morinda* (= sect. PICEA), CASICTA, and OMORIKA, on the basis of cone-scale shape and texture, in addition to the needle characters noted above. A number of later authors (Bobrov, 1970; Dallimore & Jackson; Gaussen, 1966; Krüssmann; Rehder, 1940) have used this three-section classification, but there has been considerable disagreement over the placement of several species (see comparisons in Schmidt-Vogt, 1977). Wright, in a worldwide treatment utilizing both crossability data and comparisons of overall morphological similarity, found no clear-cut groups among the species. Thus neither his treatment nor the more recent monograph by Schmidt-Vogt (1977) divided the genus into sections. Preliminary comparisons of monoterpene profiles (Schantz & Juvonen; Von Rudloff, 1975), leaf phenolics (Wellendorf & Kaufmann), and electrophoretic alleles (Wellendorf & Simonsen), as well as further crossability data (Fowler; Mikkola, 1969, 1972), also did not yield groups concordant with the earlier morphological sections. Smaller groups of morphologically similar species recognized as series by Bobrov (1970) seem to be of greater utility.

Our only species, *Picea rubens* (*P. australis* Small; *P. rubra* (Du Roi) Link, non *P. rubra* A. Dietr.), red spruce, yellow spruce, he-balsam, $2n = 24$, a prominent forest tree of the cooler parts of northeastern United States and adjacent Canada, occurs from eastern Ontario east to Nova Scotia, south to Pennsylvania, northern New Jersey, and Delaware, and locally south in the Appalachians to the higher mountains of eastern Tennessee and western North Carolina (Little, 1971, *maps 41N, E*). The species occurs most commonly on well-drained, rocky slopes, as compared to the closely related black spruce (*P. mariana* (Miller) BSP.), which is generally found on wet, boggy soils where it overlaps the range of the red spruce in the northeastern United States and southeastern Canada (Gordon, 1976; Manley & Ledig).

Red spruce differs from black spruce in having lustrous dark or bright green (rather than glaucous) leaves and ovoid-cylindrical, reddish brown, ovulate cones that are usually deciduous at maturity (vs. ovoid, dull gray ones that persist for several years). Both red and black spruce have sharply pointed four-sided leaves and pubescent branchlets, and both are unusual in the genus in having terminal buds with awl-shaped points on their outer scales. Monoterpene profiles are also very similar for the two species (Von Rudloff, 1967a, b; Wilkinson & Hanover). Reports of *P. mariana* in the southern Appalachians (e.g., by Small) are erroneous and based on material of *P. rubens.*

Hybridization between red and black spruces is well documented (Gordon, 1976; Manley; Morgenstern & Farrar) in areas where the two come in contact in southern Canada, but the prevalence of intermediate plants is apparently limited by the habitat differences between the species, relatively low crossability between them (Gordon, 1976), and natural selection against hybrids and hybrid derivatives. Manley & Ledig reported a lack of heterosis and found that photosynthetic rates of hybrids and backcrosses were significantly lower than those of the parental species under all environmental regimes examined. Khalil, however, did find heterosis in hybrids from the lowlands of New Brunswick. The significant geographic variation in morphological and physiological characters within *Picea rubens* found in Khalil's long-term provenance studies appears to reflect selection along latitudinal and altitudinal gradients, as well as effects of hybridization and backcrossing.

During late Pleistocene times additional species of *Picea* occurred in the southeastern United States (Watts). Large cones (up to 10 cm long) that appear to represent an undescribed species similar to *P. glauca* (Moench) Voss, white spruce, have been found as fossils at sites in Louisiana, Tennessee, and Georgia (Critchfield; Delcourt & Delcourt).

Picea comprises a natural group, as is indicated by the overall similarity and genus. It differs from the other pinoid genera primarily in lacking their unusual derived features, as detailed in the family treatment. It also differs from each of these genera in having leaves that are squarish in cross section and with prominent, persistent bases. As noted in the family treatment, *Picea, Cathaya,* and *Pinus* are apparently the only genera in the Pinaceae that produce the unusual serratene triterpenoids (He *et al.*; Hegnauer, 1986). *Pinus* and *Picea* are quite similar in the details of their pollination mechanisms. *Picea* differs from *Pinus* and *Cathaya* in lacking cleavage polyembryony (Doyle & Brennan) and in having a more asymmetric karyotype.

Chromosome numbers have been reported for 22 of the 36 species of *Picea* recognized by Schmidt-Vogt (see particularly Kuo *et al.*; Santamour, 1960; Sax & Sax; Seitz), with all species having $2n = 24$. Aneuploid and polyploid seedlings have been found at very low frequency in nursery plantings of *P. Abies* (Kiellander), but these presumably would not survive in nature. Supernumerary (B) chromosomes have been reported from some populations of *P. sitchensis* (Bong.) Carr., *P. glauca,* and *P. obovata* Ledeb. (*P. Abies* var. *obovata* (Ledeb.) Fellm.) but are lacking in others (Herzog; Moir & Fox; Pravdin *et al.*). Increase in nuclear-DNA content with latitude has been reported for *P. glauca* and *P. sitchensis* by Miksche (1968, 1971), but this has not been confirmed in wider sampling by Teoh & Rees.

Intergradation or more limited hybridization among species is an important factor in the taxonomic complexity seen in *Picea.* Wright proposed that a number of Asian taxa of uncertain status were the variable products of interspecific hybridization. Among the North American species, *P. glauca* and *P. Engelmannii* Parry show an extensive zone of intergradation in western Canada and Montana (Daubenmire; La Roi & Dugle; Ogilvie & Von Rudloff; Roche), leading some authors (e.g., T. M. C. Taylor, 1959) to treat these taxa as ecogeographic subspecies. Relatively frequent hybridization in regions of sympatry is also seen between the more obviously distinct species *P. sitchensis* and *P. glauca* (Daubenmire; Nienstadt & Teich; Roche), as well as *P. rubens* and *P. mariana,* discussed above. In contrast, the widely sympatric *P. glauca* and *P. mariana* only rarely hybridize (Little & Pauley) and are very difficult to cross artificially (Fowler). The closely related *P. Engelmannii* and *P. pungens* Engelm. may hybridize to a limited degree in areas of sympatry in the southern Rocky Mountains, but no evidence for this was seen in the electrophoretic study of Mitton & Andalora.

Extensive programs of artificial interspecific crossing have been undertaken in *Picea* (Bongarten & Hanover; Fowler; Gordon, 1976; Mikkola, 1969, 1972; Wright), resulting in a substantial number of verified hybrid combinations, including several involving species from different continents. The infrageneric groupings proposed by Mikkola (1969) and Fowler on the basis of crossability agree poorly with those based on leaf anatomy. For example, *P. mariana* and *P. rubens* are more readily crossable with the morphologically dissimilar *P. omorika* (Pančić) Purkyne than they are with one another (Gordon, 1976), perhaps because of selection against hybridization in the two partially sympatric species (Fowler). Prezygotic barriers to hybridization (e.g., failure of the pollen tube to penetrate the nucellus) and early postzygotic barriers have been detailed

Detailed expositions of the comparative leaf anatomy of *Picea* are given by Marco and Colleau. Species assigned to sect. OMORIKA have needles dorsiventrally flattened to varying degrees and are unusual in generally having stomata only on the adaxial leaf surface, which faces downward due to twisting of the leaf base. *Picea sitchensis,* however, often has stomata on all four sides of the leaf (Marco). Colleau attempted to limit sect. OMORIKA to those species with a foliar stomatal density greater than 80 per mm^2, but it is unclear that this yields a more natural group. Resin canals in species of sect. OMORIKA are near the abaxial leaf surface, while those in the other species are usually adjacent to the lateral angles of the leaf. The leaf mesophyll is differentiated into palisade and mesophyll cells in some species with flattened needles and in some with quadrangular ones (Marco). Another interesting feature of the leaves is the variation in color from bluish to greenish in some species—for example, *P. pungens* (Colorado blue spruce)—due to differences in the amount and structure of the surface wax (Hanover & Reicosky).

Leaf-terpenoid patterns in *Picea* have been critically reviewed by Von Rudloff (1975), following the earlier treatment of Schantz & Juvonen. Von Rudloff found relatively minor differences between some of the species assignable to sects. OMORIKA (*P. omorika* and *P. Breweriana* S. Watson) and PICEA (*P. rubens* and *P. mariana*), but greater ones among other species assignable to the latter section or to sect. CASICTA. Schantz & Juvonen also found differences in leaf- and stem-terpenoid composition to be greater within than among the sections of *Picea.* The degree of geographic or intrapopulational variation in leaf-terpene composition is quite limited in some species (e.g., *P. mariana* and *P. rubens*; Von Rudloff, 1975) but quite variable in others (such as *P. Engelmannii*).

Leaf-stilbene spot patterns and their intensities were surveyed for 23 species of *Picea* by Wellendorf & Kaufmann, who found no clear-cut subgroups within the genus. It has been alleged that sect. OMORIKA is distinct in its leaf-stilbene profile, but this has not been substantiated (Hegnauer, 1962, 1986). Overall leaf-phenolic profiles have proved useful in differentiating *Picea* species in the western United States and Mexico (La Roi & Dugle; R. J. Taylor & Patterson).

A number of species of *Picea* are heavily utilized for pulpwood, lumber for construction, and specialized wood products, with *P. Abies* in Europe, and *P. sitchensis* and *P. glauca* in North America, being of particular economic importance. Acid rain has recently had serious effects on spruce forests in central Europe (e.g., the Black Forest in Germany) and is also adversely affecting *P. rubens* populations from northern Vermont southward in the Appalachian Mountains. Wood of *P. Abies* and *P. glauca* has been valued for violins and for the sounding boards of keyboard instruments, while the high strength-to-weight ratio of the wood of *P. sitchensis* made it particularly valuable for aircraft construction (Dallimore & Jackson). Spruces are frequently grown as ornamentals in the cooler parts of the North Temperate Zone, with Norway spruce (*P. Abies*) and Colorado blue spruce (the glaucous form of *P. pungens*) the most widely cultivated in the United States. Spruce beer, prepared from *P. rubens* and *P. mariana* in the United States and *P. Abies* in Europe by boiling the leafy shoots with flavorings and sugar, was used as an antiscorbutic on sea voyages, while spruce chewing gum was obtained from the resin of the former

1980). The purified resin of *P. Abies,* known as Burgundy pitch, has been used in medicinal plasters (Dallimore & Jackson), and the pitch of *P. rubens* was similarly utilized in the United States (Krochmal & Krochmal).

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END OF PICEA