

Picea A. Dietr.

spruce

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Growth habit, occurrence, and use. The spruce genus-*Picea*-includes 40 to 50 species of evergreen conifers native to the temperate and boreal regions of the Northern Hemisphere, occurring in Europe, Asia Minor, the Caucasus, Siberia, China, Japan, the Himalayas, and North America (table 1). The genus evolved from primordial ancestors in the northeastern mainland of Asia, with present-day Korean spruce likely the most primitive species. Most North American species probably arose through eastward migration and mutation of Ezo spruce (Wright 1955). More recent work suggests a strong relation between the Old World Serbian spruce and the New World black spruce (Fowler 1980). At least 12 species occur in China (Li and others 1990). Seven species are native in North America, excluding the rare and localized occurrence of Chihuahua spruce (*P. chihuahuana* Martinez) in northwest Mexico (Rushforth 1986; Patterson 1988). The genus name is derived from the Latin *pix* or *picis*, Apitch@, referring to the resinous qualities of the trees (Everett 1981) or of a pitch pine, probably Scots pine (*Pinus sylvestris* L.) (Little 1979).

The genus includes medium to tall conifers that range in height at maturity from 9 to over 70 m. Crowns of most species appear conical in outline. The generally small branches occur in whorls with common internodal branches. The needle-like leaves are borne on peg-like projections (pulvini) on the twigs, have angled or flattened cross section, and persist for several years. Needles fall readily from twigs on drying. The slender boles gradually taper along their entire length, sometimes from a buttressed base. The thin and scaly bark sometimes has furrows at the base of old trees. The generally shallow root systems have many long, stringy, and tough rootlets. Open grown trees retain live branches to the ground, and in black spruce and sometimes Norway, Ezo, and white spruces, layering occurs when branch tips come in contact with moist soil, take root, and develop into full-size trees (Nienstaedt and Zasada 1990; Nikolov and Helmisaari 1992; Stone and McKittrick 1976; Viereck and Johnston 1990).

Members of the spruce genus grow on various soils and at all elevations up to treeline in the more northern latitudes. In more southern latitudes, spruce species usually inhabit cold, wet, or shallow soils of bogs or higher elevations on mountain slopes. Shade-tolerant spruce species often replace stands of birch (*Betula*), quaking aspen (*Populus tremuloides* Michx.), or other pioneer species on disturbed areas (Dallimore and Jackson 1967). Nursery and greenhouse cultivation currently provide seedlings and transplants of 7 North American and 8 introduced species for forestry or horticultural purposes in the United States (table 1).

The strong, light-weight, light-colored, fine-grained, even-textured, long-fibered wood of Engelmann, white, black, red, and Sitka spruces result in high-value timber. However, the restricted range, occurrence in inaccessible locations, and propensity for developing knots limits

the commercial timber value of Brewer spruce (Thornburgh 1990). Specialty products have included violin faces and piano soundboards from Engelmann, white, red, and Sitka spruces; aircraft parts from Engelmann and Sitka spruces; and house logs from Engelmann and white spruces. The occurrence of most species at high elevations and on steep slopes or wet soils makes them important watershed protectors. The genus also provides important winter shelter for wildlife in the higher latitudes. Although some animals such as snowshoe hare (*Lepus americanus*), porcupine (*Erethizon dorsatum*), and black bear (*Ursus americanus*) may sometimes browse on spruce foliage or inner bark, neither wild nor domestic animals prefer spruce as a food source (Alexander and Shepperd 1990; Blum 1990; Dallimore and Jackson 1967; Harris 1990; Nienstaedt and Zasada 1990; Viereck and Johnston 1990).

Tolerance of extreme exposure to wind and cold temperatures makes spruce especially well-suited to some shelterbelt planting. White, Norway, blue, and Sitka spruces have been widely used for this purpose. The relatively shallow root systems of Engelmann, white, blue, red, and Sitka spruces make these species susceptible to windthrow, however, especially when growing on sites with moist soils or high water tables. The conical form and dense, persistent branches of spruce species make them highly desirable for environmental plantings. All 7 North American species and the introduced Norway, Ezo, dragon, and Serbian spruces are planted as ornamentals. Many cultivars featuring variations or extremes in crown height, shape and symmetry, or thickness; rate of height growth; branch angle and degree of twig droop; and needle color exist (Everett 1981, Huxley 1992). In general, spruce species do not tolerate droughty sites but do thrive on slightly acidic and moist but well-drained soils. Of all the species, Serbian spruce may best tolerate industrial air pollution (Dallimore and Jackson 1967).

Geographic races and superior strains. The wide ranges and diverse environments to which the spruce species have adapted provide an array of individual, ecological, and geographic variations. Natural hybridization and introgression commonly occur where ranges of compatible species overlap. Hybridization between white spruce and Sitka spruce (first reported by Little 1953 as *P. H lutzii*), occurs in British Columbia and throughout the Kenai Peninsula in Alaska (Copes and Beckwith 1977). This hybrid has demonstrated a genetically based resistance to attack by the Sitka spruce weevil *Pissodes strobi* Peck which causes severe height growth and stem form reduction in Sitka spruce (Mitchell and others 1990). Hybridization between white spruce and Engelmann spruce occurs in northern Montana and British Columbia (Daubenmire 1974). Artificial crosses of Engelmann spruce with Sitka spruce and blue spruce suggests the close relatedness of these North American species (Fowler and Roche 1977). Electrophoresis has yet to clearly identify hybrids of Engelmann spruce and blue spruce along a 1,200-m elevational transect in the Front Range of Colorado where the species grow together. Morphological similarity between the 2 species, such as number of bud scales, number of stomatal rows, and location of resin sacs, however, suggests either convergent evolution or the influence of environmental variation on the morphological characters (Mitton and Andalora 1981). Natural introgression between the maritime Sitka spruce and the more interior complex of white and Engelmann spruces occurs in a portion of British Columbia, and the hybrid fraction was estimated by restriction fragment length polymorphisms of the nuclear ribosomal RNA genes (Sutton and others 1994). Differences in monoterpene composition from black spruce oleoresin (including α -pinene, 3-carene, and terpinolene) vary among geographic origins in an east-west pattern, except for seeds from sources in New England that have close affinity in monoterpene composition to red spruce (Chang and Hanover 1991). Natural introgression of black spruce into red spruce may result in greater height and diameter growth in New Brunswick, yet the hybrid

performed unpredictably in managed stands (Fowler and others 1988).

Early crosses within the genus have provided a thorough background in potential crossability of the genus, including specimens from artificial crosses between nonsympatric species (Wright 1955). Analysis of morphological characteristics and monoterpene composition from artificial crosses between white, red, and blue spruces later verified the hybridity of the seedlings, evaluated the utility of spruce hybrids, and clarified the evolutionary relation among members of the genus (Bongarten and Hanover 1982). Height growth of Englemann spruce H Sitka spruce hybrids proved unsuitable for reforestation purposes in the north central interior of British Columbia (Kiss 1989). Hybrids of black spruce and Serbian spruce out-performed the black spruce parents in height and diameter growth and can be produced sexually *en masse* in seed orchards (Fowler 1980).

Seed source identification and provenance testing of native as well as exotic spruce species are important in selecting suitable races for various purposes. Seeds intended for use in artificial reforestation usually are collected from Asuperior@ trees growing in the same area that is to be replanted. Measurements of phenology and growthCboth adaptive characters closely related to survival and optimal utilization of the growing seasonCindicated a clinal variation pattern with photoperiod and temperature as primary factors in 100 seed sources of black spruce from natural stands in Alaska to Newfoundland. A 1E shift in latitude changed the seedlings= total height 2 to 11% (Morgenstern 1978). On a smaller scale, clinal variation in black spruce in the Maritime Provinces resulted in 3 overlapping breeding zones (Park and Fowler 1988). Within the range of black spruce, extensive gene flow between stands discourages formation of distinctive provenances. Phenotypic characteristics of cones, needles, twigs, percentage survival, and growth generally differ more within-populations than between-populations (Fowler and Mullin 1977; Parker and others 1983; Thomson and others 1990). In Alberta, black spruce populations growing on strongly contrasting environments, such as uplands adjacent to peatlands, exhibited similarity in isozyme variability (Wang and MacDonald 1992). In contrast, populations near the margins of the range, such as coastal regions in Newfoundland, better reflected provenance effects (Khalil 1984; Yeh and others 1986).

Genetic variation of Engelmann spruce may correlate with latitude and elevation; the species grows at 762 to 1,067 m in British Columbia and as high as 3,658 m in the southern Rocky Mountains (Alexander 1987). After 10 years, seedlings from more northern and lower elevation sources grew better than those from other sources within this wide geographical and elevational distribution when planted together at 2,930 m in central Colorado (Shepperd and others 1981). Lack of genetic variation of red spruce at the provenance level suggests a single broad seed and breeding zone for the Maritime Provinces (Fowler and others 1988). Genetic variation in natural populations of blue spruce has received considerable attention and seems to conform to a discontinuous (rather than clinal) pattern with extensive stand-to-stand and individual-tree variation (Diebel and Fechner 1988; Fechner 1985; Hanover 1975). Provenance research in genetic variation of white spruce indicates that distinct populations have evolved within broad ecological regions, thereby resulting in differences in rate of juvenile growth, response to calcium nutrition, wood density, late-season initiation of needle primordia, nuclear volume, DNA content, branch to bud morphology, optimal temperature for seed germination, terpene biochemistry, and isoenzymes (Alden 1985). A range-wide provenance study planted in Minnesota showed large differences for tree height at ages 9 and 19 among populations with relatively poor performance by northern and western populations. Yet, no apparent geographic pattern existed in allozyme variation due to high outcrossing rates and strong inbreeding

depression (Furnier and others 1991).

Norway spruce, perhaps the most intensively studied non-native species, shows strong latitudinal and elevational gradients. Seeds from northern latitudes and higher elevations weigh less than seeds from southern latitudes and lower elevations (Heit 1968; Tyszkiewicz 1968). Seed source also influences mineral nutrient content of seeds (Youngberg 1951) and early growth of seedlings in nursery beds (Heit 1968). Seed source of Serbian spruce can affect the crown shape and susceptibility to frost (Dirr and Heuser 1987).

Flowering and fruiting. The reproductive cycle in spruce takes 2 years; timing of various processes has been studied in detail for Engelmann spruce (Harrison and Owens 1983), white spruce (Owens and Molder 1977; 1984) (figure 1), and Sitka spruce (Owens and Molder 1976). Production of cones and filled seed varies with (1) the number of central or fertile ovuliferous scales formed in the cone-primordium; (2) the success of pollination and fertilization; (3) the degree of self-pollination; and (4) the loss to seed-eating animals and disease organisms (Caron and Powell 1989). Male and female strobili arise in spring in axils of elongating shoots, usually on different branches of the same tree. Bisexual cones occasionally occur; in interior Alaska, white spruce bisexual cones with the female portion at the apex are more common than those with the male portion at the apex (Zasada and others 1978). The pendant, yellow, bright purple, or crimson male strobili have ovoid to cylindrical shape and uniform distribution over the crown. Each scale (microsporophyll) bears 2 pollen sacs (microsporangia) and are spirally arranged on a central axis. Male strobili dry out and fall off soon after pollen-shedding.

The timing of female strobili differentiation is similar for most species of spruce that have been studied; female strobili become anatomically determined at the end of the period of bud-scale initiation and the end of lateral shoot elongation (Owens 1986). Female strobili arise near the apex of shoots on upper branches in crowns of Engelmann, Sitka, and white spruces; the seed-cone zone in black spruce occurs on the most vigorous 1-, 2-, and 3-year-old branches at the top of the tree (Caron and Powell 1992). Initially the female strobili are erect, yellowish green, crimson, or purple; cylindrical; and 5 to 20 mm in diameter. The ovuliferous scales are spirally arranged on a central axis and each bears 2 ovules (megasporeangia) at the base. Each species has a characteristic number of spirals per cone, and the number of seeds per cone depends in part on the pitch and diameter of the spirals as well as the length of the cones (Fogal and Alemdag 1989). The size of the preceding cone crop and climatic conditions at the time of cone bud differentiation influence the number of reproductive buds formed in white spruce (Zasada and others 1978). Checking female strobili in the fall preceding the seed year provides an early means of predicting potential cone crop size (Eis 1973).

Female strobili receive pollen when fully open, a period that lasts only a few days. Fechner (1974) determined that female strobili of blue spruce become receptive 1 to 5 days after the first pollen release, depending on elevation, and that cones tip over and become pendent within 3 to 4 weeks of initial receptivity. Fertilization may follow pollination within a few days or may be delayed until after cones become pendent (Fechner 1974); cones mature in late summer or autumn, depending on summer growing conditions (table 2). Embryo development (figure 2) of white spruce seeds in Alaska generally proceeds rapidly during July after completion of shoot, stem, and cone growth, although on any specific date, embryo length, percentage of embryo length, cotyledon length, and relative cotyledon length will differ among trees within a stand (Zasada 1988). Embryos of white spruce-Engelmann spruce hybrids in British Columbia typically fill the embryo cavity well before the seeds mature (Eremko and

others 1989). Cotyledon number between species differs from 4 to 15 (Dallimore and Jackson 1967) and may be under strong maternal control (Diebel and Fechner 1988).

The size of a cone crop for individual trees and stands tends to follow the phenomenon of alternate bearing, with heavy crops followed by light or no crops, because cones develop in terminal positions on the shoots, leaving fewer available locations for flower production the year after a good crop (Edwards 1986; Fechner 1985). Annual production of cones and seeds differs considerably, however, with the intervals between good cone crops ranging from 2 years in Brewer spruce to as long as 13 years in white and Norway spruces (table 2). Between 1969 and 1994, Engelmann spruce in central Colorado produced good cone crops in 8 of the 26 years (Shepperd 1995). Between 1957 and 1978, irregular production of white spruce cones and seeds in interior Alaska varied with environmental factors such as temperature during cone initiation; nutrient deficiencies; and losses to insects, diseases, and squirrels (Zasada 1980; Zasada and Viereck 1970).

At maturity, the pendent cones open to shed seeds during autumn and winter (table 2). Persistent cone scales on mature cones may have rounded, pointed, irregular, notched, or reflexed ends. Most species shed cones at the end of the season, but some cones may remain on the tree throughout the next growing season. Cones should be harvested before inclement weather reduces workers' productivity or losses to squirrels increase (Curran and others 1987). Cones may be collected before they are fully ripe and, if artificially ripened, release seeds with maximal germination capacity (Edwards 1980). Cones may be collected from standing trees, slash, or animal caches, although cones that have been in contact with the forest floor may acquire seed-killing fungi. Seeds generally reach maturity before cones show their characteristic ripe color (table 2). Time of ripening varies among cones on an individual tree and among trees in a single stand (Fechner 1974; Jensen and others 1967; Zasada 1988). Various measures of estimating seed maturity have emphasized (1) physical attributes such as color and firmness of cones; (2) moisture content and specific gravity of cones; (3) color of testa and brittleness of seeds (Crossley 1953; Edwards 1980); (4) a cone moisture content of 30% or less for Norway spruce; (5) specific gravity between 0.78 and 0.95 (Winston and Haddon 1981; Zasada 1973) and a soft spongy feel of cones when squeezed in the fingers for white spruce; or (6) dark brown or black testa and seeds that snap when cut with a sharp instrument. All of these indicate that cones are sufficiently ripe for harvest.

Morphological characteristics of seed maturity for white spruce embryos show 75 to 95% complete embryo development by the end of the growing season, depending on site characteristics of the stand. Continued embryo development in seeds of cones collected in high latitude forests at this stage of seed maturity requires careful handling of the cones (Zasada 1988). Changes in sugar content provide a biochemical measure of maturity in ripening seeds of Norway and Sitka spruces (Jensen and others 1967). Computation of average daily temperature and growing degree-day summations also indicates seed maturity. Zasada (1973) recommends 625 growing degree-days (above a threshold of 5 EC and summed from pollination date) as a minimal time for white spruce embryos in interior Alaska to fully develop; this heat sum is reached in early August. Other optimal growing degree-day sums include 912 for white spruce in Ontario (Winston and Haddon 1981) and 955 for white spruce and 1,050 for black spruce in Newfoundland (Curran and others 1987). Maximal cone maturity in blue spruce, measured as seed germinability, occurs 6 weeks before natural seed release for low-elevation trees and 4 weeks before natural seed release for high-elevation trees (Fechner 1974).

Recent work has expanded the understanding of seed production in relation to crown

structure and cone size. Cones of black spruce on trees of intermediate crown class initially produce almost twice as many seeds as those of either the dominant or the co-dominant trees, but disperse their seeds at a much faster rate during the first 5 to 6 seed-bearing years (Payandeh and Haavisto 1982). The number of black spruce seeds per cone and number of filled seeds per cone relate to cone size: cones in New Brunswick averaged from 26 to 30 mm long with 10 to 37 filled seeds per cone (Caron and Powell 1989) and the most common size of black spruce cones in Ontario averaged 20 to 28 mm long with potential yields of 74 to 94 seeds per cone and 38 to 44 filled seeds per cone (Haavisto and others 1988). Cones of white spruce from Ontario averaged 39 to 47 mm in length and contained an average of 46 to 62 filled seeds per cone; regression models developed from these results estimate the number of sound seeds per cone as a function of seeds per cone section, cone length, and cone diameter (Fogal and Alemdag 1989).

Attempts to enhance seed yields in seed orchard programs have been hampered by the relatively long period of tree growth before flowering begins. Documented minimal seed-bearing age (table 2) for most species ranges from 10 to 60 years, although crops of sufficient quantity to warrant collection may not occur until much later. Efforts to stimulate flowering in younger trees have involved girdling of the bole, nitrogen fertilization, and root pruning. Top pruning of grafted white spruce in seed orchards, done to maintain the cone-bearing branches at a height within reach of a short ladder, may also increase cone production and decrease the cost of cone collection (Nienstaedt 1981).

Several lines of research have attempted to define the physiological processes and procedures for large-scale stimulation of flowering to either shorten the length of breeding programs or to increase production of cones and seeds. Application of gibberellins A₄, A₇, and A₉ stimulated female cone production in grafted Norway spruce clones, although the response differed by year and clone (Dunberg 1980). Gibberellin A_{4/7} applied in the top 2 branch whorls of mature Sitka spruce grafts increased female flowering and seed production (Tompsett and others 1980); girdling in combination with stem injections of gibberellin A_{4/7} in grafted clones of Sitka spruce may stimulate pollen-cone production (Philipson 1985a); and top-pruning and stem injection of gibberellin A_{4/7} may increase cone production in the lower crown and increase the ease of cone collection (Philipson 1985b). Heat and drought also promote flowering, although by a different induction mechanism. Potted grafts of Engelmann spruce produced high numbers of both male and female cone buds after exposure to high temperature within heated polyethylene-covered houses when the exposure occurred during the late stage of slow shoot elongation, whereas drought during the period of rapid shoot elongation after vegetative bud burst enhanced female cone production (Ross 1985). Optimal daytime temperature is 22 to 25 EC (Ross 1988a). In contrast, polyhouse temperatures that frequently exceed 30 EC during the pollination sequence of Engelmann spruce resulted in accelerated pollen shed, increased underdevelopment of pollen cones, and reduced yields of seed (Ross 1988b). These results suggest a need for a year's rest between treatments to allow time for cone maturation and vegetative replenishment of shoots. Repeated injection of gibberellin A_{4/7} into container-grown grafts of Sitka spruce in a polyhouse during May and June effectively stimulated flowering (Philipson 1992). Application of gibberellin A_{4/7} also stimulated flowering of white spruce (Ho 1988b; Marquard and Hanover 1984), even though white spruce has been classed as recalcitrant because of its sporadic flowering and usually nominal response to gibberellin A_{4/7} alone (Pharis and others 1986). Stem injection of gibberellin A_{4/7} in combination with nondestructive girdling greatly increases flowering in mature white spruce trees (Pharis and others 1986) and grafted clones (Ross 1992). Whole-tree spraying of branches at relatively high concentrations (800 mg/l gibberellin A_{4/7})

during May through July promoted cone production the next year (Ho 1988b). In the Great Lakes region, elongating shoots sprayed in May produced more male and female strobili than shoots sprayed in June (Cecich 1985). Flowering of white spruce responded to heat similar to that of Engelmann spruce by enhanced pollen-cone production after subjecting potted grafts to 30 EC for 10 hours, whereas seed-cone production was enhanced after 5 hours at 20 EC (Ross 1991). Seed-cone production of black spruce also has been stimulated by application of gibberellin; the greatest increase occurred with 200 mg/l of gibberellin A_{4/7} sprayed repeatedly on young grafts during the period of rapid shoot elongation (Ho 1991). Seed-cone production also may be enhanced in field-grown seed orchards by applying a foliar spray of 400 mg/l gibberellin A_{4/7} during the period before lateral shoot elongation and bud-type differentiation (Ho 1988a), and in seed orchards of seedling origin by applying a foliar spray of 200 to 800 mg/l gibberellin A_{4/7} (Hall 1988). Attempts with several species to promote male flowering preferentially by the synthetic auxin naphthalene acetic acid (NAA) have been inconclusive (Hall 1988; Ross 1992).

Spruce seeds are small (2.5 to 5.0 mm long), oblong to acute at the base, with a single well-developed wing that is 2 to 4 times the length of the seed (figure 3). Wind is the primary agent for dispersal (Dobbs 1976; McCaughey and Schmidt 1987; Youngblood and Max 1992; Zasada and Lovig 1983). Dispersal of white spruce seeds begins in late August and extends throughout winter; however, seeds released before mid-October have higher viability because they tend to come from well-developed central cone scales, whereas seeds released either earlier or later tend to come from less-developed basal and apical scales (Dobbs 1976; Youngblood and Max 1992; Zasada and others 1978). Cones of red spruce release seeds in a similar manner. The semi-serotinous cones of black spruce remain partially closed, and disperse seeds for several years as the cone scales flex with repeated wetting and drying (Haavisto and others 1988; Viereck and Johnston 1990). Seed viability decreases only slightly during the first 3 years, then decreases rapidly to about 5% in cones up to 12 years old, and may remain almost constant for older cones (Payandeh and Haavisto 1982). Nonlinear equations have been developed to model dispersal of filled seeds into openings for Engelmann spruce (Alexander 1986; McCaughey and Schmidt 1987), white spruce (Dobbs 1976; Youngblood and Max 1992) and black spruce (Payandeh and Haavisto 1982). Once dispersed, spruce seeds remain viable for only a short period; Fraser (1976) reported that on a natural forest floor seedbed, black spruce seeds may lose viability completely after 16 months.

Cone and seed losses. Various agents destroy cones and seeds, including killing frosts, insects, diseases, birds, and mammals. Late frost during the spring may damage cones of white spruce; affected conelets become flaccid, die and turn black and do not produce seeds (Zasada 1971). Frost also commonly damages cones of Engelmann spruce (Cameron and Jenkins 1988).

Many insects feed on seeds and cone parts (table 3). Just 2 species of spruce cone seed maggot (*Hylemya anthracina* Czerny) and spruce seed moth (*Laspeyresia* (= *Cydia*) *youngana* Kearfott) cause the most widespread damage (Cameron and Jenkins 1988; Hedlin 1973; Hedlin and others 1980; Schmid and others 1981). Insect populations fluctuate with cone crop abundance and differ among spruce communities having dissimilar stand structure (Fogal and Larocque 1992). Greater seed and cone losses usually occur in years of below-average cone production (Schmid and others 1981; Werner 1964). Above-average summer temperatures may ameliorate seed losses in Ontario from *Laspeyresia* by contributing to greater insect mortality and preventing prolonged insect diapause (Fogal 1990). Damage to cones and seeds by insects has been reduced by soil application of carbofuran (Cerezke and Holmes 1986) or stem implants

of acephate (West and Sundaram 1992).

Basidiospore production of the inland spruce cone rust *Chrysomyxa pirolata* Winter coincides with the period when most spruce cones are receptive to pollen. This fungus sometimes causes severe damage to the cones of white, blue, Engelmann, and black spruces. Diseased cones contain fewer seeds, with reduced viability, and germinants may be abnormal (Summers and others 1986, Sutherland 1990). Coastal spruce cone rust *Chrysomyxa monesis* Ziller causes similar damage in Sitka spruce (Bega and Scharpf 1993). Pre-emergence seed losses caused by a soil-borne fungus *Geniculodendron pyriforme* G.A. Salt in Sitka spruce nurseries occur after cones come in contact with the ground during collection and cleaning of seeds (Sutherland and Woods 1978). Similarly, another fungus *Caloscypha fulgens* (Pers.) Boudier infects cones lying on the forest floor or in squirrel caches, spreads during stratification and presowing storage, and kills seeds of white, black, and Sitka spruces (Sutherland 1990). The seed-borne blight caused by *Sirococcus strobilinus* Preuss may damage seedlings of Engelmann, Sitka, and white spruces, and their hybrids (Sutherland and others 1981).

Many species of birds consume spruce seeds. Several finches (families *Fringillidae* and *Estrildidae*) feed almost exclusively on conifer seeds, including the common (red) crossbill (*Loxia curvirostra*), the two-barred (white-winged) crossbill (*L. leucoptera*), and the pine siskin (*Carduelis pinus*). Spruce seeds often provide an important winter food source for the American goldfinch *C. tristis*. In addition, the pine siskin and the pine grosbeak *Pinicola enucleator* may feed on reproductive buds (Benkman 1987; Clement and others 1993).

Pine squirrels (*Tamiasciurus hudsonicus fremonti*) harvest and cache Engelmann spruce cones (Alexander 1987). Red squirrels (*T. hudsonicus*) and northern red-backed voles (*Clethrionomys rutilus*) consume great quantities of seeds of white spruce during winter (Brink and Dean 1966; West and others 1980; West and deGroot 1990). Red squirrels also consume seeds of black spruce and clip twigs and terminals and eat reproductive and vegetative buds of red spruce (West 1989). In Newfoundland, the proportion of black spruce cones per tree harvested by red squirrels in years with small cone crops ranged from 64 to 96%, whereas in a year with a good cone crop, less than 1% of cones were taken (West 1989).

Extraction and storage of seeds. Spruce seeds require careful extraction and storage because cones often are collected before fully mature and seeds may continue to ripen within the cones (Caron and others 1990; Edwards 1980; Edwards 1986; Zasada 1973). Post-harvest ripening of prematurely collected cones, however, allows flexibility in collecting operations and extends the collection period by allowing the use of immature cones (Edwards 1986). Cones of white spruce may air-dry in half-filled burlap sacks or on open screens for a few weeks at 5 to 15 EC and 60 to 75% relative humidity (Alden 1985), or for up to 3 months at 5 EC and 75 to 90% relative humidity (Winston and Haddon 1981). Cones also may dry under field conditions of outside storage if ventilation is good (Caron and others 1990; Zasada 1973). Cones of Engelmann Sitka, and white spruces have been safely stored for up to 5 months without loss of seed quality (Edwards 1986).

Improper extraction, even from mature cones, will reduce viability of spruce seeds. Mature cones usually require additional drying with heat to fully flex the cone scales and ensure maximal seed recovery. Cones of Engelmann, Sitka, and white spruces require exposure to an air flow of gradually decreasing moisture content and increasing temperature in a convection kiln for 6 to 24 hours at 38 to 49 EC (Edwards 1986). Other workers suggest slightly lower maximal temperatures for white spruce (Alden 1985; Curran and others 1987). Kiln-drying requires careful monitoring of temperature because high temperature can cause physiological injury

(Carmichael 1958). After drying, tumbling or shaking loosens seeds from opened cones. If cones fail to open fully, complete extraction of seeds may require remoistening and redrying followed by additional tumbling or crushing (Alden 1985; Edwards 1986).

Black spruce cones present a greater challenge for seed extraction because of the tightly bonded scales. The following special extraction procedure has been developed for these semi-serotinous cones (Haavisto and others 1988):

1. Cones are soaked in lukewarm water for 2 hours.
2. Cones are oven-dried at 40 EC for 20 to 22 hours.
3. Cones are tumbled in a revolving screened drum for 30 minutes.
4. Steps 1 to 3 can be repeated for up to 16 times for complete extraction of seeds.

The weakly bonded seed wings separate readily from the seeds with little abrasive action (Edwards 1986). For small seedlots, the seeds can be gently rubbed by hand inside a moistened cotton bag (Alden 1985; Caron and others 1990). For larger lots, wings and chaff are separated from seeds using any commercial seed-processing device: an oscillating screen scalper, a fanning mill, an air-screen cleaner, or a small rotating cement mixer, for example (Alden 1985; Edwards 1986; Stiell 1976). In some cases, seeds may need remoistening with a fine mist to aid in cleaning, after which they can be dried again. Air and gravity separators not only remove empty seeds, wings, and debris, but also sort seeds into different density fractions. Cleaned seeds are prepared for storage by conditioning with low heat to achieve 4 to 8% moisture content. The number of cleaned seeds per weight ranges from about 50,000 to almost 900,000/kg (110,200 to 1,984,200/lb) for the various species (table 4).

Because cone- and seed-crops differ between years, seeds collected during good to excellent years are stored for use during poor crop years. Seeds from most species of spruce seem fairly similar in longevity characteristics and storage requirements; seeds have been safely stored for 10 to 20 years at moisture content of 4 to 8% and temperatures between -10 and +3 EC (Wang 1974). Seeds of Norway spruce, stored at 0 to 2 EC and 6 to 8% moisture content in glass carboys sealed with cork and wax, retained high percentage germination for 17 years (Hill 1976). Seeds of white spruce stored at -18 to +3 EC and 7% moisture content for 7 years retained their initial percentage germination (Stiell 1976). To assure maximal seed longevity, the specified moisture content must be maintained during the entire storage period. Polyethylene bags (4- to 10-mil) make satisfactory storage containers. Seeds treated with rodent repellent have longevity characteristics similar to untreated seeds (Radvanyi 1980). For longer storage, metabolic processes are halted; Ahuja (1986) found that Norway spruce seeds stored in liquid nitrogen (-196 EC) retained full germinability, suggesting this as a long-term storage method.

Pregermination treatments. Seeds of most species of spruce germinate promptly without pretreatment, but seeds of black, blue, Brewer, Engelmann, Ezo, Norway, Sakhalin, Sitka, and white spruces may germinate more rapidly after a stratification treatment. Seeds of Norway spruce may be stratified by conditioning for 3 weeks at cold temperature and may be soaked in water for 24 hours (Apriming@) before planting (Dirr and Heuser 1987). Seeds of red and white spruces stratified in newspaper and moist sand at 0 to 3 EC for 14 months showed only a slight loss of percentage germination; under these conditions black spruce lost about one-third of its percentage germination and germination of all 3 species declined to about 10% of the original capacity after 27 months (MacGillivray 1955). Prechilling, or cold stratification, may widen the range of temperatures over which seeds can subsequently germinate, increase the

maximal percentage germination at some temperatures, and increase the rate of germination at almost any temperature (Gosling and Rigg 1990). Prechilling of white spruce seeds at 2 to 4 EC for 6 weeks results in high percentage germination (Caron and others 1990). Other researchers have prechilled white spruce seeds by soaking them in cold running water for 24 hours, blotting them dry, and then refrigerating them at 4 EC for 3 weeks (Chanway and others 1991). Storage of cones at 5 EC for 4 weeks, however, may eliminate any subsequent need for stratification of white spruce seeds (Winston and Haddon 1981). White spruce seeds from high-latitude sites in Alaska (> 55E latitude) do not undergo dormancy, and stratification is detrimental for mature seeds (Alden 1995). Before nursery sowing, Engelmann spruce seeds need to be primed for 24 hours, then prechilled for 6 to 8 weeks at 2 EC in loosely closed polyethylene bags (Tanaka and others 1986). Unstratified seeds of black spruce incubated for 24 days at 3 or 20 EC germinated completely within 18 days with 14:10 (light:dark) hours of fluorescent light, whereas moist seeds prechilled for 24 hours at 3 EC in a polyethylene bag in the dark reached 95% germination within 12 days when incubated at 5 to 30 EC, regardless of lighting regime (Farmer and others 1984). Priming black spruce seeds for 5 to 6 days in water (until the radicles nearly emerge) and surface-drying before sowing accelerated germination by about 1 week (Malek 1992). Seeds of black spruce from high latitudes in Alaska, collected and immediately extracted in the spring, will germinate in 2 to 6 days after becoming fully imbibed with water; no dormancy exists and stratification is not required (Alden 1995). Dormancy of Sitka spruce seeds is broken and 95% germination is possible after priming for 72 hours (until seeds reach 30% moisture content), then chilling for 6 weeks in loosely closed polyethylene bags at 4 EC (Gosling and Rigg 1990).

Treating seedlots with various fumigants, insecticides, fungicides, and rodent repellents in storage or before sowing may reduce germination of seeds. Germination of white spruce seeds treated with a finely ground rodent repellent mixed with graphite declined slightly from that of untreated seeds after more than 5 years of storage (Radvanyi 1980). Aluminum powder, which is used as a lubricant on Sitka and white spruce seeds in bareroot nurseries in Canada, may decrease the percentage germination of treated seeds and reduce first-year survival of seedlings (Sutherland and others 1978). Embedding black spruce seeds in pellets may discourage their consumption by small mammals, depending on the material surrounding the seeds (Martell 1981). As always, pesticide users should closely follow the manufacturer's recommended dosages.

Seedlots of all spruce species should meet the quality standards of 95% purity and 80% viability recommended by the International Seed Testing Association and the Association of Official Seed Analysts for most species. Many spruce seedlots contain a fairly high percentage of empty seeds when extracted from the cones. Failure to remove these empty seeds during the cleaning process can seriously affect germination test results. Methods of germination testing are summarized in table 4 (Safford 1974p; Stein and others 1986). In all species, germination tests call for alternating temperatures of 20 EC for 16 hours and 30 EC for 8 hours (Stein and others 1986).

Germination and nursery practices. Germination of spruce seeds is epigeal (figure 4). Growers raise seedlings of spruce species in North America either as bareroot stock (2+0 or 3+0) in nursery beds or as container seedlings (1+0 or 2+0) in greenhouses. Nursery-grown transplants (2+2) of slow-growing species such as black spruce may have greater survivability (Mullin 1980). Seeds of blue, Engelmann, and Korean spruces may germinate at low temperatures in the fall and die over winter, making fall-sowing of these species in nursery beds highly risky (Heit 1968).

Under natural conditions, most species of spruce germinate on various media, including rotten wood, shallow duff, and mixtures of mineral and organic soil. Mineral soil makes an ideal seedbed because of greater water availability. Commercial growers raise white spruce seedlings with high stem caliper and stem height and heavy stem and root weight as container seedlings in either (1) a commercially prepared mixture composed of equal parts of sphagnum peat moss and vermiculite or (2) a mixture of equal parts of sphagnum peat moss, peat moss, and vermiculite (Lackey and Alm 1982). Germination of some seedlots of Sitka spruce has been improved by moistening the substrate with a 0.2% solution of potassium nitrate (Safford 1974).

Seeds of most species germinate promptly and completely under a wide range of temperatures either with or without light. Once germinated, seedlings in greenhouses require extended daylength to accelerate growth and prevent dormancy. Continuous fluorescent lighting providing about 150 Fmol/m²/sec photosynthetically active radiation at 25 EC allows continuous vigorous growth of blue spruce seedlings (Young and Hanover 1978). White spruce seedlings respond favorably to photoperiodic lighting intensities of about 414 to 4,150 Fmol/m²/sec, although Engelmann spruce has a much narrower response range of about 210 to 520 Fmol/m²/sec (Arnott and Macey 1985). Seedlings of white spruce also have been grown with photosynthetically active radiation at the seedling canopy level of about 300 Fmol/m²/sec in a 16-hour photoperiod at 23 EC and a night temperature of 17 EC (Chanway and others 1991). Failure of the lighting system for only a few days reduced the effectiveness of extended or intermittent photoperiod, leading to increased root rather than shoot growth in white spruce seedlings (Arnott and Simmons 1985). Under laboratory or greenhouse conditions, newly germinated seedlings of red spruce require a light period of at least 16 hours to prevent the onset of dormancy (Safford 1974).

In greenhouse management, imposing a reduced photoperiod will induce bud scale formation leading to dormancy and hardening-off in spruce seedlings. Without this stimulus, first- or second-year seedlings may not enter dormancy, regardless of temperature. Imposing nitrogen stress and moisture stress will also induce dormancy (Young and Hanover 1978). Once dormant, seedlings of most species require a 4 to 6-week cold treatment at 0 EC or lower to initiate new growth (Safford 1974).

Macro- and micro-nutrients introduced in the irrigation system commonly support spruce seedlings in accelerated growth conditions within a greenhouse (Landis and others 1989). In addition to fertilizer, addition of growth-promoting rhizobacteria such as *Bacillus* strains may stimulate the emergence rate of white spruce seedlings, possibly through induction of root elongation and the formation of lateral and adventitious roots (Chanway and others 1991). In Great Lakes region nurseries, stunting of first-year white spruce seedlings described as early cessation of growth, purple discoloration of foliage, and low foliage phosphorus concentration without a soil phosphorus deficiency may result from poor mycorrhizal development after soil fumigation (Croghan and others 1987).

Ectomycorrhizae may play an important role in seedling establishment, and a growing number of researchers are investigating the formation of mycorrhizae on seedlings. Black spruce seedlings inoculated soon after emergence with fungal plugs of the ectomycorrhizae-forming *Laccaria bicolor* (Maire) Orton or *L. laccata* (Fries) Berkely & Broome showed more second-order lateral roots and greater seedling dry weight and height (Thomson and others 1990).

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Figure 1 *Picea glauca*, white spruce: reproductive cycle (from Owens and Molder 1984, used with permission of the author and publisher).

Figure 2 *Picea glauca*, white spruce: diagrammatic longitudinal section of a mature seed at dispersal, showing seed coat, gametophyte, and fully developed embryo (from Alden 1985, used with permission of the author and publisher).

Figure 3 *Picea*, spruce: seeds with wings, H 2.

Figure 4 *Picea pungens*, blue spruce: seedling development at 2, 5, and 7 days after germination.

Table I—*Picea*, spruce: nomenclature and occurrence of native and cultivated species in North America

Scientific name & synonym(s)	Common name	Occurrence
<i>P. abies</i> (L.) Karst. <i>P. excelsa</i> Link	Norway spruce	Native of Fennoscandia, W Europe to Ural Mtns of central Russia; widely planted in NE & central US
<i>P. asperata</i> Mast. <i>P. crassifolia</i> Kamarov	dragon spruce, Chinese spruce	Native of NW China; occasionally cultivated in US
<i>P. breweriana</i> S. Wats.	Brewer spruce, weeping spruce	NW California & SW Oregon
<i>P. engelmannii</i> Parry ex Engelm. <i>P. columbiana</i> Lemmon <i>P. glauca</i> ssp. <i>engelmann</i> (Parry ex Engelm.) T.M.C. Taylor <i>P. engelmannii</i> var. <i>glabrata</i> Goodman	Engelmann spruce, mountain spruce	Rocky Mtns from British Columbia S to Arizona & New Mexico; Cascade Range in Washington & Oregon
<i>P. glauca</i> (Moench) Voss <i>P. alba</i> (Aiton) Link <i>P. alba</i> var. <i>albertiana</i> (S. Brown) Beiss. <i>P. albertiana</i> S. Brown <i>P. canadensis</i> B.S.P. <i>P. canadensis</i> var. <i>albertiana</i> (S. Brown) Rehder <i>P. glauca</i> var. <i>albertiana</i> (S. Brown) Sarg. <i>P. glauca</i> var. <i>posildii</i> Raup <i>P. nigra</i> var. <i>glauca</i> Carr.	white spruce, Canadian spruce, skunk spruce, cat spruce, Black Hills spruce, western white spruce, Alberta spruce, Porsild spruce	Norton Sound to Gulf of Alaska, E across Canada from British Columbia & SW Alberta to Labrador, Newfoundland; also in Black Hills of South Dakota
<i>P. glehnii</i> (Fr. Schmidt) Mast.	Sakhalin spruce	Native to Sakhalin & Hokkaido; planted in NE US to Newfoundland
<i>P. jezoensis</i> (Siebold & Zucc.) Carr.		Ezo spruce , yeddo spruce, Native of SE Russia, Shantar Islands, Kamchatka Peninsula, Sakhalin Island, S to NE China, N Korea, & N Japan
<i>P. ajanensis</i> (Lindley & Gordon) Fischer ex Carr. <i>P. kamchatkensis</i> LaCassagne <i>P. komarovic</i> Vasiljev <i>P. microsperma</i> (Lindley) Carr.	yezo spruce	
<i>P. koraiensis</i> Nakai	Korea spruce, Koyama spruce	N Korea, NE China, & Sikhote-Alin Mtns of SE Russia
<i>P. mariana</i> (Mill.) B.S.P.	black spruce, bog spruce, swamp spruce, eastern spruce	Alaska to Labrador, Newfoundland; NE & N central US
<i>P. obovata</i> Ledeb. <i>P. abies</i> var. <i>obovata</i> Lindquist	Siberian spruce	From White Sea & Kola Peninsula E across Russia to Sea of Okhotsk
<i>P. omorika</i> (Pancic) Purk.	Serbian spruce	SE Europe
<i>P. pungens</i> Engelm. <i>P. commutata</i> Horton <i>P. parryana</i> Sarg.	blue spruce, Colorado spruce, Colorado blue spruce	Rocky Mtns in Wyoming, Utah, & Colorado, scattered in Arizona & New Mexico

<p><i>P. rubens</i> Sarg. <i>P. australis</i> Small <i>P. nigra</i> (Ait.) Link var. <i>rubra</i> (Du Roi) Engelm. <i>P. rubra</i> (DuRoi) Link (not A. Dietrich)</p>	<p>red spruce, West Virginia spruce, eastern spruce, yellow spruce, he-balsam</p>	<p>Nova Scotia, S Quebec, New York, & S in Appalachian Mtns to North Carolina</p>
<p><i>P. sitchensis</i> (Bong.) Carr. <i>P. sitchensis</i> Bong. <i>P. falcata</i> (Rafin.) Suringar <i>P. menziesii</i> (D. Don) Carr. <i>Abies falcata</i> Rafin. <i>A. menziesii</i> (D. Don) Lindley <i>Pinus menziesii</i> Douglas</p>	<p>Sitka spruce, coast spruce, tideland spruce, yellow spruce, Alaska spruce</p>	<p>Gulf of Alaska & Kodiak Island to N California</p>
<p><i>P. smithiana</i> (Wall. Boss. <i>P. morinda</i> Link</p>	<p>Himalayan spruce, west Himalayan spruce</p>	<p>N India & Pakistan</p>

Sources: USDA ARS (2002), USDA NRCS (2001).

Table 2—*Picea*, spruce: height, seed-bearing age, and phenology of flowering and fruiting

Species	Mature height (m)	Minimal seed-bearing age (yr)	Flowering dates	Cone ripening dates	Cone size (cm)	Dispersal dates	Interval between large crops (yr)	Preripe cone color	Ripe cone color
<i>P. abies</i>	30–60	40–60	Apr–June	Sept–Nov	10–18	Sept–Apr	4–13	—	Brown
<i>P. asperata</i>	45	—	—	—	8–13	—	—	—	—
<i>P. breweriana</i>	25–30	20–30	—	Sept–Oct	—	Sept–Oct	2	Green	Dark brown, black
<i>P. engelmannii</i>	25–30	15–40	May–June	Aug–Sept	3–6	Sept–Oct	2–6	Green	Brown
<i>P. glauca</i>	15–30	30	May	Aug	3–5	Aug–May	2–13	Green	Pale brown
<i>P. glehnii</i>	30	—	—	—	6	—	—	—	Shiny brown
<i>P. jezoensis</i>	30–45	20–25	—	—	5–8	—	2–4	Crimson	Brown
<i>P. koraiensis</i>	18—	—	—	—	—	—	Green	Brown	—
<i>P. mariana</i>	9–27	10	May–June	Sept	2–4	Oct*	4	Green	Purple–brown
<i>P. obovata</i>	—	—	—	Sept	—	—	12–13	—	—
<i>P. omorika</i>	30	—	May	—	5	—	—	Bluish black	Cinnamon brown
<i>P. pungens</i>	21–50	20	Apr–June	—	7–10	—	1–3	Green	Pale brown
<i>P. rubens</i>	21–30	30–50	Apr–May	Sept–Oct	—	Oct–Mar	3–8	Green	Brown
<i>P. sitchensis</i>	18–73	20	May	Aug–Sept	—	Aug–Sept	3–4	Yellow-green	Brown
<i>P. smithiana</i>	61	20	Apr–May	Oct–Nov	10–18	Oct–Nov	—	Bright green	Brown

Sources: Alden (1955), Alexander (1987), Alexander and Shepperd (1984), Edwards (1980), Fechner (1985), Nikolov and Helmisaari (1992), Safford (1974), Zasada and Viereck (1970).

* Cones of *P. mariana* are semi-serotinous and release seeds throughout the year for several years.

Table 3—*Picea*, spruce: common cone- and seed-damaging insects

Insect species	Common name	Damage	Affected species*
<i>Choristoneura occidentalis</i> Freeman	Western spruce budworm	Larvae feed externally on cones	<i>P. engelmannii</i>
<i>Dasineura canadensis</i> Felt	Spruce cone gall midge	Larvae form gall on cone scale	<i>P. glauca</i>
<i>Dasineura rachiphaga</i> Tripp	Spruce cone axis midge	Larvae mine through scales into axis	<i>P. engelmannii</i> , <i>P. glauca</i> , <i>P. sitchensis</i> , <i>P. mariana</i>
<i>Dioryctria abietivorella</i> Grote	Fir cone moth	Larvae mine & riddle cone	<i>P. mariana</i> , <i>P. glauca</i> , <i>P. engelmannii</i> , <i>P. pungens</i> , <i>P. rubens</i>
<i>Henricus fuscodorsanus</i> Kearfott	Cone cochylid	Larvae feed on scales & seeds	<i>P. sitchensis</i> , <i>P. glauca</i>
<i>Hylemya anthracina</i> Czerny	Spruce cone seed maggot	Larvae tunnel around cone axis	<i>P. mariana</i> , <i>P. glauca</i> , <i>P. engelmannii</i> , <i>P. sitchensis</i>
<i>Laspeyresia youngana</i> Kerfott	Spruce seed moth	Larvae feed on seeds	<i>P. engelmannii</i> , <i>P. glauca</i> , <i>P. mariana</i> , <i>P. pungens</i> , <i>P. rubens</i> , <i>P. sitchensis</i>
<i>Mayetiola carpophaga</i> Tripp	Spruce seed midge	Larvae feed on seeds	<i>P. glauca</i>
<i>Megastigmus atedius</i> Walker	Spruce seed chalcid	Larvae feed on seeds	All native <i>Picea</i>
<i>Strobilomyia neanthracina</i> Michelson	Spruce cone maggot	—	<i>P. mariana</i>

Sources: Cameron and Jenkins (1988), Schmid and others (1981).

* Major hosts in **boldface type**.

Table 4—*Picea*, spruce: weight of cleaned seeds, methods of testing for laboratory germination, and additional directions

Species	Seeds/weight		Substrate	Test length (days)	Additional directions
	/kg	/lb			
<i>P. abies</i>	105,600–462,300	47,000–209,700	TB	16	—
<i>P. asperata</i>	154,300–165,400	70,000–75,000	—	—	—
<i>P. breweriana</i>	112,500–163,200	51,000–74,000	—	—	Prechill
<i>P. engelmannii</i>	152,200–710,000	69,000–322,000	TB,P	16	Prechill; light; sensitive to excess moisture; if dormant, use KNO ₃
<i>P. glauca</i>	298,000–884,200	135,000–401,000	TB	21	Prechill 14–21 days at 3–5 EC; light
<i>P. glehnii</i>	—	—	TB,P	14	Prechill 21 days at 3–5 EC
<i>P. jezoensis</i>	395,100–508,500	179,200–230,600	TB,P	14	Prechill 21 days at 3–5 EC
<i>P. koraiensis</i>	209,500–242,500	95,000–110,000	TB	21	Light
<i>P. mariana</i>	739,000–1,464,100	335,000–664,000	TB	—	Prechill or soak; light
<i>P. omorika</i>	277,000–377,500	125,600–171,200	TB	16	Light; sensitive to excess moisture
<i>P. pungens</i>	176,400–359,000	80,000–163,000	TB,P	16	Prechill
<i>P. rubens</i>	220,500–637,000	100,000–289,000	TB	28	Light
<i>P. sitchensis</i>	342,000–882,000	155,000–400,000	TB,P	21	Soak; prechill; light; sensitive to excess moisture; if dormant, use KNO ₃
<i>P. smithiana</i>	53,000–88,200	24,000–40,000	—	—	—

Sources: Dirr and Heuser (1987), Jeglum and Kennington (1993), Nikolov and Helmisaari (1992), Safford (1974), Stein and others (1986), Willan (1985).

Note: TB = top of blotters; P = petri dishes covered with blotters, filter paper, or sand.