established using genetically modified *P. tremula*, *P. tremuloides, P. deltoides*, and *P. alba* × *P. tremula* selected varieties. The use of genetically modified plants has raised concerns over the risk posed to the fitness or future adaptability of wild relatives with whom transgenic plantations might reproduce. Consequently, a major ongoing effort has been sterility transformation that would prevent completely the sexual reproduction of transgenic plantations.

See also: **Genetics and Genetic Resources**: Propagation Technology for Forest Trees. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance; Genetics and Improvement of Wood Properties. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Breeding Theory and Genetic Testing; Conifer Breeding Principles and Processes; Economic Returns from Tree Breeding; Forest Genetics and Tree Breeding; Current and Future Signposts.

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Spruces, Firs and Larches

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Introduction

Together with the genera *Pinus* (subfamily Pinoideae), *Cathaya*, *Pseudotsuga* (subfamily Laricoideae), and *Cedrus, Keteleeria, Nothotsuga, Pseudolarix, Tsuga* (subfamily Abietoideae), the genera *Picea* (subfamily Piceoideae), *Abies* (subfamily Abietoideae), and *Larix* (subfamily Laricoideae) belong to the family Pinaceae. The subfamilies are distinguished by cone and seed characters like the existence of an umbo or the existence of resin vesicles on the seed.

Species of the genera *Picea* (spruce), *Abies* (fir), and *Larix* (larch) are exclusively distributed in the northern hemisphere from 22° N in the south to 73° N forming the polar borderline of trees. Several species of these genera cover wide areas in boreal Eurasia and North America. They contribute to a major extent to the northern coniferous forests which stretch from coast to coast across these latitudes and form the greatest expanses of continuous forests. Many species of these genera are also found in mountainous regions of the more temperate zones often forming the alpine tree border line.

Picea, Abies, and *Larix* species occur in a wide range of habitats with very different soil and climate conditions. They are associated with various tree species depending on certain site conditions but they can also be found in pure stands under extreme site conditions. Mainly reproducing sexually by wind pollination, vegetative reproduction is the dominant mode of propagation if sexual reproduction is limited due to climatic limitations.

The lifetime of *Picea, Abies*, and *Larix* species ranges variously from 150 to 900 years. Under favorable conditions they grow to tall trees often forming dense forests with considerable growing stocks. Among populations of most species genetic differences can be observed in various traits. Due to their wood characteristics, the timber of spruces, firs, and larches can be used for a wide variety of purposes and is therefore of high economical importance.

Spruces

The genus *Picea* (subfamily Piceoideae) is related most closely to the genus *Pinus* (subfamily Pinoideae), but differs significantly by, e.g., cone and seed characteristics, the absence of short shoots, or the period of cone maturing. *Picea* is a very uniform genus, showing no significant differences within the genus allowing the delineation of subgenera. The genus *Picea* includes 34 species of cone-bearing, tall evergreen trees with straight stems and regularly constructed crowns with columnar or pyramidal habit. The horizontally arranged and usually rather short branches are whorled. On young trees, the bark is rather thin, on old trees scaly. The buds are conical or ovate, resinous or without resin. The spirally arranged needles are either four-sided or flat on a short petiole which remains on the shoot after needle fall. Stomatal bands can be found on all four sides or in the case of flat needles on the lower surface.

Natural Distribution

Out of the 34 species of *Picea*, eight species occur naturally in North and Central America, and 26 species are distributed in Eurasia (**Table 1**). The greatest species diversity is found in China and the Himalayas often in single species stands.

Picea species are mainly distributed in the boreal and subboreal zones of the northern hemisphere as well as to a minor extent in the mountainous regions of the more southerly zones where *Picea* can be found up to the subalpine range forming the treeline (**Figure 1**). The species of the genus *Picea* can be divided in a northern and a southern group, the differences between the groups are important from the ecological and genetical point of view. *Picea* species of the northern group occur mainly in large, often overlapping natural distribution areas either from east to west only interrupted by the Atlantic Ocean and the Bering Sea like *Picea abies, P. glauca,* and *P. obovata* or from north to south like *P. engelmannii* (**Figure 1**). In contrast, the species of the southern group grow in small, often isolated natural occurrences, for example *P. omorika*.

The northern limit of distribution of *Picea* is reached at about 69° N in Norway (*P. abies*) and the Northwest Territory of Canada (*P. glauca, P. mariana*). In the south, *Picea* stands can be found up to 23° to 27° N at the eastern (*P. morrisonicola*) and up to 23° to 25° N at the western hemisphere (*P. chihuahuana*) (**Figure 1**). In warmer regions, the water supply is the limiting factor of distribution.

In the northern part of the distribution area, the vertical occurrence of *Picea* reaches from sea level in North America and Eurasia to 2250 m above sea level in the Central Alps (*P. abies*) and about 3700 m in the southern Rocky Mountains (*P. engelmannii*). In the southern part, *Picea* species with upright growth can be found in altitudes up to 4700 m in the Himalayas forming the most upper limit of closed forests in the world (*P. asperata*).

Table 1 The intragenetic classification and distribution of species of the genus *Picea*

Distribution	*Botanical name*	*Common name*
North America	*P. breweriana*	Brewer spruce
	P. chihuahuana	—
	P. engelmannii	Engelmann spruce
	P. glauca	White spruce
	P. mariana	Black spruce
	P. pungens	Blue spruce, Colorado spruce
	P. rubens	Red spruce
	P. sitchensis	Sitka spruce
Europe and Northern Asia	*P. abies*	Norway spruce
	P. obovata	Siberian spruce
	P. omorika	Serbian spruce
	P. orientalis	Oriental spruce
Central Asia and Himalayas	*P. schrenkiana*	Schrenk spruce
	P. smithiana	Himalayan spruce
	P. spinulosa	—
East Asia including islands	*P. alcoquiana*	Alcock spruce
	P. glehnii	Sakhalin spruce
	P. jezoensis	Hondo spruce, Yezo spruce
	P. koraiensis	—
	P. koyamae	Koyama spruce
	P. maximowiczii	—
	P. morrisonicola	—
	P. torano	Japanese spruce
Central China and South Asia	*P. asperata*	Chinese spruce
	P. aurantiaca	—
	P. brachytyla	—
	P. crassifolia	—
	P. farreri	—
	P. likiangensis	Purple spruce
	P. meyeri	—
	P. neoveitchii	—
	P. purpurea	—
	P. retroflexa	—
	P. wilsonii	—

Climate and Soils

Picea species can withstand extremely cold temperatures down to -60°C. The amplitude of temperature varies from -60°C to 35°C. The mean annual precipitation ranges from 230 to 4000 mm with the maximum falling outside the vegetation period. The vegetation period ranges from 26 to 175 days, the shorter growing season in the north counterbalanced by longer periods of daylight and the ability of spruces to assimilate down to temperatures of -6 to -7°C.

Picea species are not very demanding of soil conditions with the exception of the water supply.

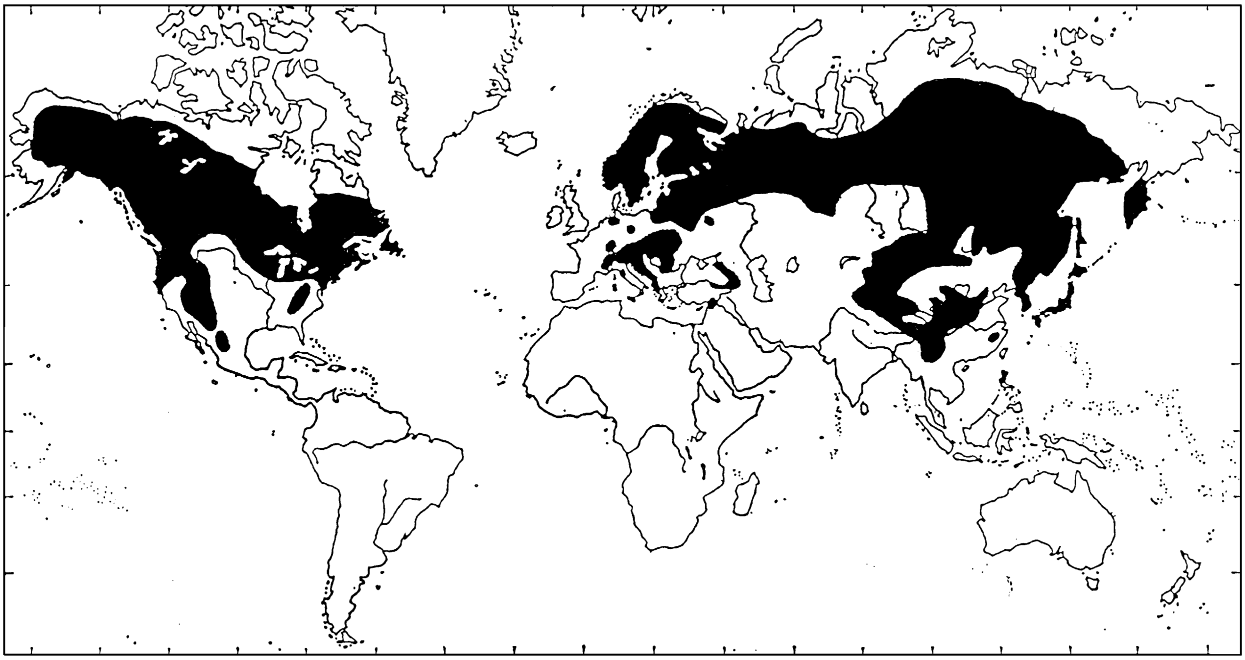

Figure 1 Natural distribution area of spruces (*Picea* spp.) Adapted with permission from Kruessmann G (1983) *Handbuch der Nadelgehoelze*. Berlin: Parey-Verlag.

In the northern part of the distribution area, *Picea* species occur on all soils showing the best growth on well-aerated, deep, acidic to slight alkaline soils with an intermediate nutrient supply and water supply over average. In the southern part, they are restricted to wet, cold or shallow soils of bogs.

Associated Forest Cover

Growing at extreme site conditions, *Picea* species can be found in pure, often uneven-aged stands. Under more favorable conditions, however, *Picea* species are associated with species of the genera *Abies, Chamaecyparis, Larix, Pinus, Pseudotsuga, Thuja,* and *Tsuga* as well as *Acer, Alnus, Betula, Populus, Prunus, Quercus,* and *Salix* in North America. In Eurasia, the species admixed to *Picea* belong to the genera *Abies, Juniperus, Larix, Pinus, Taxus, Thuja,* and *Tsuga* as well as *Betula, Fagus, Quercus, Populus,* and other deciduous broadleaved species.

Reproduction and Growth

Flowering starts between the age of 10–50 years. Male and female flowers are inserted in axils of needles of the previous year's shoots on different branches of the same tree, the female flowers inserted upright in the upper part of the crown. The flowering period varies from April to July. Peak flowering can be observed from every second year to every 13th year, in average from the third to the sixth year. Pollination is by wind over long distances due to the light weight and the low falling speed of the pollen grains which contain air vesicles. The yellowish green, crimson, or purple-colored cones ripen in the same year turning color during ripening. A ripe cone consists of brownish, woody scales, each bearing two brown to black seeds at the base. The ovate seeds are winged and mainly dispersed by wind during autumn and winter. The empty cones do not disintegrate and remain on the trees for about 1 year. Germination capacity varies from 75% to 95%. The weight of spruce seeds shows a big variation and ranges from 60 000 (*Picea torano*) to 890 000 (*P. mariana*) cleaned seeds kg^{-1}.

Seeds of most *Picea* species show no dormancy and germinate promptly without stratification. However, seeds of some species may require light for germination but prechilling will usually overcome the light requirement. Under natural conditions, seeds germinate on almost any seedbeds including rotten wood, but survival may be low. The germination is most successful on a mineral or mixed mineral and organic soil seedbed, especially under light shade, as long as drainage is adequate and the soil provides sufficient nutrients. The germination is epigeal, the four to 15 cotyledons rising above the ground.

If sexual reproduction is limited or nonexistent due to climatic limitations at the arctic or alpine tree line, vegetative reproduction of *Picea* species by layering is apparently the dominant mode of propagation.

Roots are also known to produce shoots. Artificially, vegetative propagation is easily possible by rooting of softwood cuttings from juvenile material or grafting.

Similar to that of *Abies* and *Pseudotsuga*, the root growth of *Picea* species starts before the shoot growth. The development of the root system is generally influenced by the existing soil conditions of which the oxygen supply may play an important role. Growing at sites with unfavorable soil conditions (e.g., near surface water table, clay-containing or compacted soil), *Picea* species develop an extremely shallow lateral root system near to the surface. On deep, porous, and well-drained soils, the lateral root system penetrates the soil by layer roots to a depth of 2.5 m and more.

The average age of *Picea* species varies from 250 to 800 years (*P. sitchensis*). Under favorable conditions, the average height of mature trees ranges from 25 to 40 m, some species reaching heights between 50 and 60 m (*P. sitchensis*). The mean diameter at breast height (dbh) of mature spruces ranges from 50 to 150 cm. Under favorable conditions, *Picea* forests produce timber volumes between 190 and 690 $m^3 ha^{-1}$, and at exceptionally good sites between 870 and 1200 $m^3 ha^{-1}$ (*P. abies, P. sitchensis*).

Species of the genus *Picea* have intermediate tolerance of shade, the tolerance decreasing with increasing age. Height growth is slow in the first few years but increases rapidly thereafter. When mixed with other species, *Picea* species can also survive and grow in the understory using occasional stand disturbances to rise up in the overstory.

Silviculture

Depending on the site conditions, even-aged as well as uneven-aged silvicultural systems are appropriate for the regeneration of *Picea* forests. The even-aged methods include clear-cutting and shelterwood cutting. Seed tree cuttings are not suitable for the regeneration of spruce due to its susceptibility to windthrow. Appropriate uneven-aged cutting methods are individual tree and group selection cuttings and their modifications. Thinning in young *Picea* stands enhances the growth of diameter and the crown development improving the stability of spruces.

In deep shade, lower branches soon die, decay, and break off, the resinous stubs remaining for many years. *Picea* species only exceptionally develop sprouts from adventitious buds along the stem related to light intensity, e.g., after thinning.

Pests and Diseases

Picea species are subject to damage from abiotic agents, pathogens, insects, and animals. Among abiotic agents windthrow is the most serious especially after initial or partial cuttings in old-growth stands. Species of the genus *Picea* are also sensitive to air pollution. However, most common diseases of spruces are caused by wood-rotting fungi resulting in loss of volume and predisposition of trees to windthrow and wind break. In pure stands, the mass propagation of bark beetles can cause serious damage. Due to their thin bark, *Picea* species can also be damaged by game animals that peel the bark.

Genetics

Compared to *Picea* species growing in the northern part of the distribution area, the species from the southern part show a greater systematic uniformity. Most of the *Picea* species of the northern part can be separated into geographical races or systematic varieties indicating genetic differences. The differences can be seen in phenological, morphological, quantitative, and qualitative characters as well as in resistance against pest and diseases influencing the suitability of the provenance in question for cultivation out of its natural distribution area. In North America and Asia, spontaneous hybridization between *Picea* species can be observed in common growing zones of the species in question. In Germany, the UK, and Scandinavia, *P. abies* and *P. sitchensis* in particular are the subjects of intense breeding programmes for commercial plantation forestry.

Uses

The strong, lightweight, light-colored, fine-grained, even-textured, and long-fibered wood makes most spruce species useful timber trees. The timber can be used as lumber, construction wood, rotary-cut veneer, furniture timber, posts, poles, and mine timber as well as plywood, pulpwood, and fuelwood. The high strength-to-weight ratio and the resonant qualities make the wood suitable for the construction of aircraft parts and musical instruments. Due to its wood qualities and yield, *Picea* is one of the most important commercial genus in the boreal forest. Several species like *P. abies, P. glauca, P. sitchensis,* or *P. omorika* are planted commercially outside their natural distribution area. Most *Picea* species are also important watershed protectors because of their occurrence at high elevations and on steep slopes.

Firs

Compared to the genus *Picea*, the genus *Abies* (subfamily Abietoideae) is a very heterogenous genus allowing the delineation of 10 sections with several subsections. The genus *Abies* includes 49 species of cone-bearing, tall evergreen trees with straight stems and regularly built-up crowns with pyramidal habit (**Table 2**). The horizontally arranged branches are distinctly whorled. On young trees, the bark is thin and smooth, often with resin blisters, in old trees often thick and fissured. The buds are usually resinous, globose, or ovate to fusiform. The linear–lanceolate, flat, singly borne needles are dark green above with two bluish or silvery-white stomatal bands on the lower surface. The needles which are widened like a shield at the base are inserted on long shoots usually in two ranks leaving a rounded scar after fall or removal.

Natural Distribution

Out of the 49 species of *Abies*, 15 species occur naturally in North and Central America, and 33 species are distributed in Eurasia (**Figure 2**). In contrast to *Picea* and *Larix*, one *Abies* species is found exclusively in northern Africa (**Table 2**). Similar to *Picea*, the greatest species diversity in *Abies* can be observed in China and the Himalayas.

Abies species occur from sea level to the timberline but the majority are found at middle to high elevations in mountainous areas. However, in North America as well as in North Asia, *Abies* species are found as components of boreal forests. Few species of the genus *Abies* grow as components of low-elevation, temperate forests. In North America, *Abies* species can be found from 64°30′ N in Yukon Territory, Canada (*Abies lasiocarpa*) to 14°49′ N in Central America (*A. guatemalensis*) and from 53° W in Newfoundland (*A. balsamea*) to 140° W parallel to the borderline between Alaska and Canada (*A. lasiocarpa*). The vertical distribution ranges from sea level to about 3600 m. In Eurasia and Africa, the distribution area extends from 67° 40′ N in the north (*A. sibirica*) to about 22° N in the south (*A. kawakamii*) and from 6° W in the west (*A. alba*) to 160° E in the east (*A. sachalinensis*). Vertically, firs grow at elevations from about 300 m to 4700 m in the Himalayas (*A. squamata*).

Climate and Soils

Since *Abies* species occur in very different regions of the northern hemisphere, the requirements of the climate also vary accordingly. The mean annual temperature ranges from −4°C to 11°C within the distribution area with an amplitude of temperature from −45°C to 41°C. The mean annual precipitation varies from 510 to 2540 mm with extremes between 390 and 6650 mm. In mountainous regions, between 50% and over 80% of the annual precipitation is snow and sleet. Snow packs between 3 and 12.7 m are

Table 2 The intragenetic classification and distribution of species of the genus *Abies*

Distribution	*Botanical name*	*Common name*
North America	*A. amabilis*	Pacific silver fir
	A. balsamea	Balsam fir
	A. bracteata	—
	A. concolor	White fir
	A. durangensis	—
	A. fraseri	Fraser fir
	A. grandis	Grand fir
	A. hickelii	—
	A. hidalgensis	—
	A. lasiocarpa	Subalpine fir
	A. magnifica	California red fir
	A. procera	Noble fir
	A. religiosa	—
	A. vejarii	—
Central America	*A. guatemalensis*	—
Europe and West Asia	*A. alba*	European silver fir
	A. borisii-regis	King Boris fir
	A. cephalonica	Greek fir
	A. cilicica	Cilician fir
	A. nebrodensis	Silician fir
	A. nordmanniana	Nordmann fir
Europe and North Africa	*A. pinsapo*	Spanish fir
North Africa	*A. numidica*	Algerian fir
Northern and Central Asia	*A. sibirica*	Siberian fir
Central Asia and Himalayas	*A. densa*	—
	A. pindrow	Pindrow fir
	A. spectabilis	Himalayan fir
Central China and South Asia	*A. chengii*	—
	A. chensiensis	—
	A. delavayi	—
	A. fabri	—
	A. fanjingshanensis	—
	A. fansipanensis	—
	A. fargesii	—
	A. forrestii	—
	A. recurvata	—
	A. squamata	—
	A. yuanbaoshanensis	—
	A. ziyuanensis	—
East Asia including islands	*A. beshanzuensis*	—
	A. firma	Japanese fir, Momi fir
	A. holophylla	Manchurian fir
	A. homolepis	Nikko fir
	A. kawakamii	—
	A. koreana	Korean fir
	A. mariesii	Maries fir, Shasta red fir
	A. nephrolepis	—
	A. sachalinensis	Sakhalin fir
	A. veitchii	Veitch fir, Veitch's silver fir

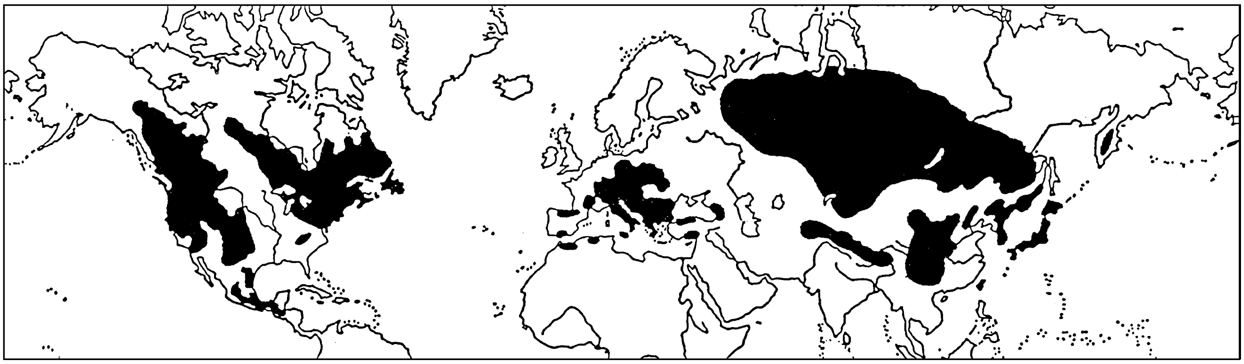

Figure 2 Natural distribution area of firs (*Abies* spp.) Adapted with permission from Kruessmann G (1983) *Handbuch der Nadelgehoelze*. Berlin: Parey-Verlag.

reported. The vegetation period ranges from 40 to 250 days, the shorter growing season in higher elevations being compensated by the ability of some fir species to assimilate down to a temperature of $-5°C$.

Due to its large distribution area with very different geological bedrocks, *Abies* species grow on a wide variety of soils developed from almost every kind of parent material. *Abies* species are tolerant of a wide range of soil conditions, nutrient content and availability as well as pH values. Species of the genus *Abies* are more dependent on moisture availability and temperature. However, the best growth of *Abies* species can be expected on deep, nutrient rich, fine to medium textured and well-drained soils.

Associated Forest Cover

Abies species seldom grow in pure, uneven-aged stands. Mainly, they can be found in mixed forests also under extreme site conditions. In North America, *Abies* species are associated more or less with the same species as *Picea* species. In Eurasia and Africa, the species mixed with *Abies* belong to the genera *Cedrus, Chamaecyparis, Juniperus, Larix, Picea, Pinus, Taxus, Thuja,* and *Tsuga* as well as *Acer, Betula, Fagus, Fraxinus, Quercus, Populus,* and other deciduous broadleaved species.

Reproduction and Growth

Flowering starts between the ages of 20 to 50 years. Male and female flowers occur separately on the same tree. The female flowers are typically inserted highly in the crown on the upper side of the previous year's shoot, the male flowers generally lower in the crown than female flowers densely along the undersides of 1-year-old twigs. The flowering period varies from April to July. Peak flowering can be observed from every second to every eighth year, on average from the second to the fourth year. Pollination by wind takes place mostly among neighboring trees due to the heavy weight and the fast sinking speed of the pollen despite the existence of air vesicles. The red or greenish conspicuous cones ripen the first year; a ripe cone consists of brownish, woody scales, each bearing two winged and typically ovate to irregularly triangular seeds at the base. The seeds with conspicuous resin blisters are mainly dispersed by wind from August to November. In contrast to other conifers, the erect cones disintegrate leaving only the spikelike cone axis on the tree. Germination capacity varies from 25% to 70% but it is very often low, around 30%. The weight of the comparatively heavy fir seeds ranges from 10 000 (*Abies cilicica*) to 200 000 (*A. koreana*) cleaned seeds kg^{-1}.

Since *Abies* seeds are disseminated in autumn under conditions which may allow an early germination, the germination is hampered by resins stored in the seed coat. Under forest conditions the dormancy is broken by evaporation of the resins during the winter after seed fall. The germination is most successful on a warm seedbed with moist mineral soil. The germination is epigeal, the three to 14 well-differentiated cotyledons rising above the ground.

Under natural conditions, most *Abies* species do not reproduce vegetatively either by sprouting or layering. Layering can be observed in few species growing in extreme conditions of the more northern and mountainous regions, e.g., *A. balsamea* or *A. lasiocarpa*. Artificially, vegetative propagation is possible by grafting or rooting of cuttings from juvenile material.

The root systems of *Abies* vary from shallow and widespread where the effective soil depth is limited by rocks or seasonable water tables, through relatively deep lateral root systems under more favorable conditions, to a deep and intensive taproot system which also develops under less favorable soil conditions.

The average age of *Abies* species varies from 150 to 500 years, exceptionally to 700 years (*A. procera*). Under favorable conditions, the average height of mature trees ranges from 20 to 50 m, several species reaching heights between 60 and 90 m (e.g., *A. alba, A. amabilis, A. grandis, A. procera, A. spectabilis*). The mean dbh of mature *Abies* trees ranges from 30 to 300 cm (*A. spectabilis*). Due to their capacity to maintain a high level of stand density and due to the generally low taper of *Abies* trees, a considerable growing stock can be observed between 450 and $600\,m^3\,ha^{-1}$ on average sites. Under favorable conditions, *Abies* forests produce timber volumes between 1000 and $1600\,m^3\,ha^{-1}$ (e.g., *A. alba, A. amabilis, A. concolor, A. grandis, A. procera*), and in exceptional cases up to $2300\,m^3\,ha^{-1}$ (*A. magnifica*).

Although *Abies* species grow well in full sunlight, most species can survive and grow for long periods in relatively dense shade and therefore they are classified as shade tolerant. However, some species are not too tolerant of shade especially if regeneration under a closed forest canopy is considered. Due to their shade tolerance over average compared to other tree species, *Abies* species can be found in mixed coniferous and conifer–broadleaved forests as well as in pure stands.

Silviculture

For most *Abies* species, uneven-aged silvicultural systems are the most appropriate way for regeneration. Appropriate uneven-aged cutting methods are individual tree and group selection cuttings and their modifications providing the necessary growth advantage several species need in front of competing species due to their slow growth in the juvenile stage.

Pests and Diseases

Abies species are subject to damage from abiotic agents, pathogens, insects, and animals. *Abies* species are very sensitive to air pollution. Due to their thin bark, *Abies* species are susceptible to severe damages and fire. Among pathogens, mistletoe causes major damage. In old-growth trees, wood rotting fungi cause major losses. Species of the genus *Abies* are also very sensitive to browsing and bark peeling by game.

Genetics

Several *Abies* species show a high self-fertility, up to 70% and more of sound seeds being produced by outcross pollination. Since the range in elevation and latitude is large in various *Abies* species and due to different evolutionary processes, differences among populations of several species can be observed in morphology, phenology, growth rate, monoterpenes, or isozyme patterns. In North America and Eurasia, spontaneous hybridization between *Abies* species is reported in common growing zones of the species in question. In the USA, selective breeding programs are practiced, particularly for the improvement of shape, size, and color of Christmas trees.

Uses

With the exception of the absence of primary resin canals, the characteristics and uses of fir wood are similar to them of spruce wood. Young trees of most *Abies* species are preferred Christmas trees. *Abies* species growing at high elevations and on steep slopes are also important for the protection of watersheds. Only few species of the genus *Abies* are planted commercially outside their natural distribution area, for example *A. grandis* or *A. nordmanniana*.

Larches

The genus *Larix* (subfamily Laricoideae) is the type genus of the subfamily mentioned before. The genus is divided into two groups separated by the position of the bracts (exserted or nonexserted). The genus *Larix* includes 11 species of cone-bearing, tall deciduous trees with straight stems and narrow, sometimes broad, mostly regularly built-up crowns. The horizontally arranged branches are not whorled. The bark is fissured, reddish-brown to gray-brown in color. The buds are small and ovate with a little number of short and imbricate scales. The soft and thin needles are inserted in bunches on short shoots and spirally on long shoots.

Natural Distribution

Out of the 11 species of the larches, three species occur naturally in North America, and eight species are distributed in Eurasia (**Table 3**). The conifer forests around the Arctic Circle are mainly formed by

Table 3 Intrageneric classification and distribution of species of the genus *Larix*

Distribution	*Botanical name*	*Common name*
North America	*L. laricina*	Tamarack
	L. lyallii	Alpine larch
	L. occidentalis	Western larch
Central Europe	*L. decidua*	European larch
North Eurasia	*L. czekanowskii*	—
	L. gmelinii	Dahurian larch
	L. sibirica	Siberian larch
China and Himalayas	*L. griffithii*	Sikkim larch
	L. mastersiana	—
	L. potaninii	Chinese larch
Japan	*L. kaempferi*	Japanese larch

Larix laricina, L. sibirica, and *L. gmelinii* with largely extended distribution areas. Other larches occur in the mountainous regions of more temperate latitudes, distributed in smaller and more scattered areas with extreme vertically extension.

In North America, species like *L. laricina* extend from 53° W in Newfoundland to 140° W parallel to the border of Alaska and Canada and from 40° N in the south to 67° N forming the northern treeline. The vertical distribution reaches from sea level to 1220 m above sea level in eastern North America (*L. laricina*) and from 180 to 3020 m (*L. lyallii*) in the west of North America.

In Eurasia, the distribution area of *Larix* species reaches from 68° N to 73° N (*L. gmelinii*), its northern limit forming the polar treeline. The southern limit can be found at about 22° N in the Himalayas and China (*L. griffithii, L. potaninii*). The west–east distribution reaches from 5° E in the western Alps (*L. decidua*) to about 170° E in East Siberia (*L. gmelinii*) (**Figure** 3). The vertical extent varies among the different parts of the natural distribution area. In Europe and North Asia, the genus ranges from the riverine lowlands of the north (*L. sibirica, L. gmelinii*) to elevations of 2400 m forming the alpine treeline in the western Alps (*L. decidua*) or in the Manchurian Mountains (*L. gmelinii*). *Larix* species grow in altitudes between 1000 and 2700 m on the island of Hondo in Japan (*L. kaempferi*), and they can be found between 2500 and 4000 m in the Himalayas and China (*L. griffithii, L. potaninii*).

Climate and Soils

Larix species can withstand extremely cold temperatures down to −70°C as well as a large range of temperatures from −70°C to 35°C. The mean annual precipitation varies from 180 to 2500 mm. In mountainous regions, about 75–80% of the annual precipitation is snow and sleet. The vegetation period ranges from 50 to 230 days, the shorter growing season in the north being counterbalanced by longer periods of daylight.

Species of the genus *Larix* can tolerate a wide range of soil conditions. Species forming the forests at the Arctic Circle grow most commonly on wet to moist organic, boggy, and acidic sites with a shallow layer of peat or soil over permafrost. The best growth of *Larix* species can be observed on moist and deep soils rich in nutrients with high water storage capacity.

Associated Forest Cover

Growing in extreme site conditions, species of the genus *Larix* can be found mainly in pure, often even-aged stands. Under more favorable conditions, however, *Larix* species are associated with species of the genera *Abies, Picea, Pinus, Pseudotsuga, Thuja,* and *Tsuga* as well as *Acer, Betula, Fraxinus, Populus,* and *Ulmus* in North America. In Eurasia, the species associated with larch belong to the genera *Abies, Picea,* and *Pinus* as well as *Betula, Fagus,* and *Populus.*

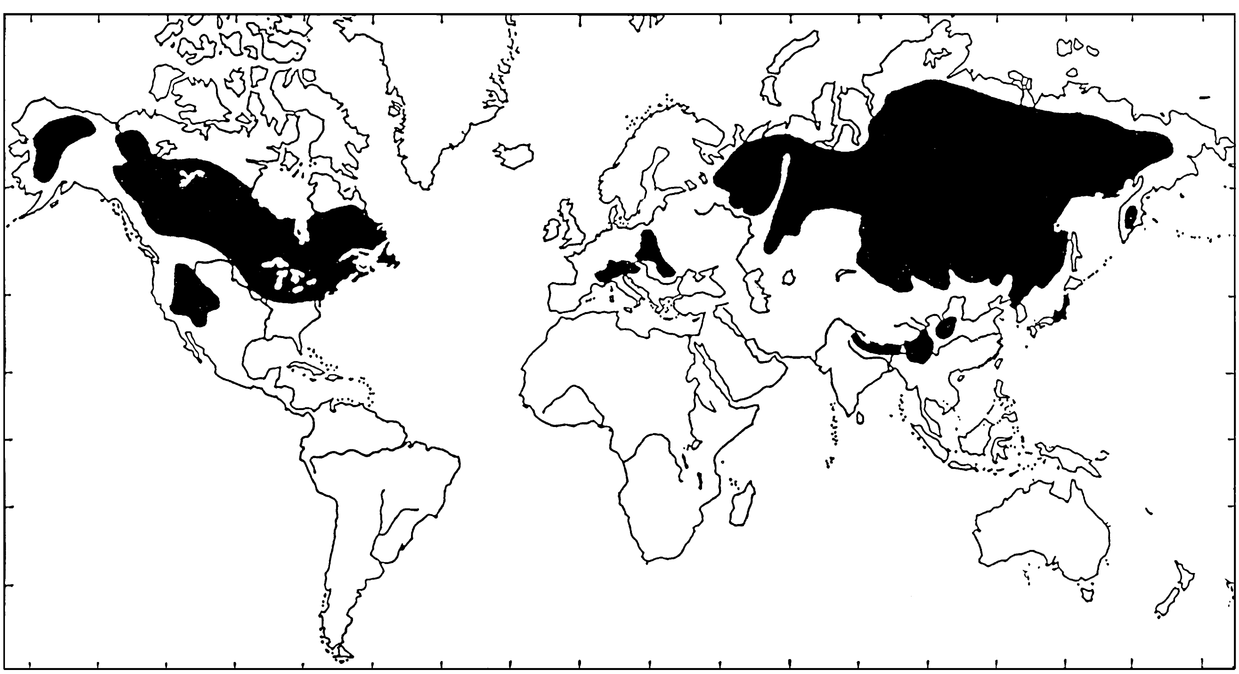

Figure 3 Natural distribution area of larches (*Larix* spp.) Adapted with permission from Kruessmann G (1983) *Handbuch der Nadelgehoelze*. Berlin: Parey-Verlag.

Reproduction and Growth

Flowering starts between the ages of 10 and 40 years. Male and female flowers occurring separately on the same tree open a few days before needle elongation or appear with the needles. The flowering period varies from March to June. Peak flowering can be observed from every year to every 10th year, on average from the third to the sixth year. Pollination by wind takes place mostly among neighboring trees due to the heavy weight and the fast falling speed of the pollen grains which lack air vesicles. The red or greenish cones ripen the first year; a ripe cone consists of brownish, woody scales, each bearing two seeds at the base. The winged and nearly triangular seeds are mainly dispersed by wind from September to spring. The empty cones do not disintegrate and remain on the trees for an indefinite period. Germination capacity varies from 15% to 50%. The small and lightweight *Larix* seeds range from 100 000 (*L. sibirica*) to 700 000 (*L. laricina*) cleaned seeds kg^{-1}.

With few exceptions internal seed dormancy ranges from none to mild. Under forest conditions any existing dormancy is broken during the winter after seed fall. The germination is most successful on a warm seedbed with moist mineral soil. Germination is epigeal, the five to seven cotyledons rising above the ground.

If sexual reproduction is limited or nonexistent due to climatic conditions along the northern limit of *Larix* species, e.g., in Canada and Alaska, layering is apparently the dominant mode of propagation. Roots are also known to produce shoots. Artificially, vegetative propagation is easily possible by rooting of softwood cuttings of juvenile material or grafting.

Species of the genus *Larix* have a very adaptable root system, coping with permafrost soil, rocky substrate, or deep and well-drained soils. Under favorable conditions, most *Larix* species develop a deep taproot with extensive and large lateral roots.

The average age of *Larix* species varies from 150 to 900 years (*L. occidentalis*). Under favorable conditions, the average height of mature trees ranges from 15 to 55 m, occasionally exceeding 60 m (*L. occidentalis*). The mean dbh of mature *Larix* trees ranges from 35 to 230 cm. In the most northern parts of the distribution area, a growing stock can be observed from 30 to 50 $m^3\,ha^{-1}$. Under favorable conditions, larch forests produce timber volumes between 300 and 550 $m^3\,ha^{-1}$ (*L. occidentalis*).

Larix species are highly intolerant of shade. Compared to other conifers, most *Larix* species show rapid juvenile growth, giving larches the height advantage they need to survive. When mixed with other species, *Larix* must be in the overstory and they are practically never found in the understory.

Silviculture

The requirements of *Larix* forests are best met by even-aged silvicultural systems of shelterwoods, seed tree cuttings, and clear-cuts. Thinning in young *Larix* stands enhances the growth of diameter and height during the juvenile years when response potential is greatest.

Compared to other conifers, *Larix* trees are good self-pruners, and boles of 25–30-year-old trees may be clear of branches for one-half or two-thirds their length. Older *Larix* sometimes produce sprouts from adventitious buds after thinning, the amount of sprouting increasing with the severity of thinning.

In natural forest stands located in the boreal zone, fire is essential for the maintenance of *Larix* forests. Fires thin stands, reduce fuels, regenerate the undergrowth, and prepare seed beds.

Pests and Diseases

Larix species are more resistant than other conifers to air pollution, mechanical damage or soil compaction. Some species with thin bark have low resistance to surface fire. In mountainous areas, snow avalanches and snow slides can cause serious damages. Outside the natural distribution area, *Larix* trees are very often subject to damage from pathogens and insects.

Genetics

Within *Larix* species growing over a wide range of sites as well as within species with a distribution area divided into different parts, significant differences of traits can be observed among provenances. The traits include morphological, quantitative, and qualitative characters as well as resistance against pests and diseases, influencing the suitability of the provenance in question for cultivation out of the natural distribution area. In North America and Asia, spontaneous hybridization between *Larix* species is reported in common growing zones of the species in question. In Europe, hybrids between *L. decidua* and *L. kaempferi* are planted commercially providing exceptional growth and resistance to canker.

Uses

Larix timber consists of a narrow, bright yellow sapwood and a reddish-brown heartwood which is hard, heavy, durable, and tough as well as fungi and acid resistant. The timber can be used as lumber, construction wood, fine veneer, furniture timber, posts, poles, and mine timber as well as pulpwood and fuel wood. Several species including

L. decidua, *L. kaempferi*, *L. laricina*, and *L. sibirica* are planted commercially outside their natural distribution areas.

See also: **Silviculture**: Natural Stand Regeneration. **Temperate and Mediterranean Forests**: Northern Coniferous Forests.

Further Reading

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Thinning *see* **Plantation Silviculture**: Forest plantations; Rotations; Stand Density and Stocking in Plantations; Tending; Thinning. **Silviculture**: Silvicultural Systems.

TREE BREEDING, PRACTICES

Contents

Biological Improvement of Wood Properties

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Introduction

The objective of this article is to discuss how wood can be changed either naturally or by manipulation and how these changes might affect the final product. All wood characteristics are the result of physiological effects (controls) on growth. When the physiological controls are determined by genetic or other within-plant influences, they are referred as internal. These are difficult to manipulate and require activities such as breeding to obtain the desired kind of wood. When the physiological controls are primarily influenced by forces outside the tree, such as weather, nutrient availability or other, one refers to them as external controls.

A good example of a wood property strongly controlled internally is wood density or wood specific gravity. This makes possible the development