

competition as required. Release is necessary in high-density stands because stem diameter growth of walnut is extremely sensitive to the degree of crowding in a stand. Trees have been mechanically pruned to increase stem quality. Research and experience has shown that with proper thinning and pruning it is possible to produce 40 cm saw logs in 30–35 years and veneer logs (50 cm) in 40–50 years. Given a silvicultural objective of veneer logs, the recommended stocking and spacing for an average stand diameter of 50 cm dbh should be 62 trees per hectare at a spacing of 13 m between trees.

Pecans should be grown on sites that have well-drained, deep soils (1.2–2 m) with moderate soil moisture holding capacity. Pecan trees are native to river valley soils and have a relatively high water requirement. They do best on sandy loam soils but also can be grown on heavier soils such as clay loams if the soils are well drained. In areas where the soil is lighter and relatively dry, irrigation is required. When pecan trees are fully mature, approximately 20 years after planting, tree spacing should be approximately 20–25 m between rows and also between trees within rows, or 15–22 trees per hectare.

## Utilization

English walnut (*Juglans regia*) is native to the region in Eurasia extending from the Near East through to the Himalayas and on to Western China. This single species is known by various names: Persian, French, Turkish, Italian, Circassian, and Carpathian walnut. Walnuts must have been harvested from earliest times but the earliest records of growing of orchards of walnut trees go back to classical Greek and Roman times. Besides the nuts, trees are also a source of high-quality wood used for furniture and gunstocks. Growing of walnuts in Europe began in the 1500s; but by the 1600s walnut was replaced by mahogany as the wood most favored for furniture. They are now grown worldwide and the largest production is from California. Black walnut and other walnuts are used in much the same way as European walnut.

Hickories produce heavy, strong, shock-resistant wood with a high fuel value. These characteristics make hickory suitable for handles used in axes, hammers, and other striking instruments. Pecan is not only valuable as a fine furniture wood but the nut is prized for food. Species in the *Engelhardtia* and *Pterocarya* also produce fine cabinet woods.

See also: **Temperate and Mediterranean Forests:** Temperate Broadleaved Deciduous Forest. **Temperate**

**Ecosystems:** Fagaceae. **Tropical Forests:** Tropical Montane Forests.

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## Pines

**P W Rundel**, University of California, Los Angeles, CA, USA

**D M Richardson**, University of Cape Town, Cape Town, South Africa

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## Introduction

Pines clearly form the most ecologically and economically significant tree group in the world. The genus *Pinus* contains 110 species (Table 1), comprising more than half the species in the Pinaceae and almost 20% of all gymnosperm species. Ecologically, pines also influence the structure and function of many forest ecosystems. They affect biogeochemical processes, hydrological and fire regimes, and provide food and create habitats for animals. Pines are important, and very often dominant, components of the vegetation over large parts of the northern hemisphere (Figure 1). Economically, pines play a major role as sources of timber, pulp, resin, nuts, and other products. Pines have also been cultivated in many parts of the world, both within and well outside their natural range, and they form the foundation of exotic forestry enterprises in many southern hemisphere countries. Moreover, pines have featured in ancient myths and rituals throughout

human history, and have been celebrated in visual art, prose, poetry, and music.

Pines are found in a remarkably wide range of environments, from above the arctic circle where winters are very cold and growing seasons are short, to the tropics where frost never occurs and growth continues through the year. Pines are the dominant trees over large parts of the boreal forest, or taiga, which covers about 12 million km<sup>2</sup> of the northern hemisphere. In temperate latitudes of the northern hemisphere they occur abundantly in high mountains, in Mediterranean-climate regions, and mixed with junipers over extensive semi-arid woodlands. Some pine species form virtually monospecific forests over very large areas whereas others form mixed forests with other conifers (notably spruce and fir species) and broadleaved trees (notably oak, poplar, birch, and alder species), or form subtropical savannas or open woodlands. In temperate regions, and even more so in the tropics, pines are usually associated with acidic, nutrient-poor soils. Pines possess a range of specialized mechanisms that enable them to thrive (and usually attain dominance) in these harsh environments. That pines are not restricted to such sites is clearly shown by their ability to spread into more productive sites, both within and outside their natural ranges, following disturbance that reduces the competitive superiority of vigorous angiosperms. The disturbance regime is thus an important determinant of pine distribution and abundance in the landscape. Fire is the driving force in succession in nearly all pine habitats.

## The Origin and Evolution of Pines

The expansion of angiosperms and the concurrent decline of gymnosperms in the late Mesozoic had a significant impact on the phytogeographic history of the earth. The earliest-known angiosperms arose in the Early Cretaceous (130–90 million years ago), and there are now between 250 000 and 300 000 extant species. The first gymnosperms arose in the Middle Devonian (365 million years ago), much earlier than the angiosperms, but the group never achieved a high diversity of species. Evidence from fossilized cones shows that ancestors of the Pinaceae had evolved by the mid-Jurassic, and that pines themselves had evolved by the Early Cretaceous. Most of the other modern genera of the pine family appeared only in the Early Tertiary or later.

By the end of the Mesozoic (65 million years ago), pines had diversified into two major groups, or subgenera (Table 2); the subgenus *Pinus* (diploxylon or hard pines, with two fibrovascular bundles in each

needle) and subgenus *Strobus* (haploxylon or soft pines, with one fibrovascular bundle in each needle). At this stage, pines had migrated throughout the middle latitudes of the supercontinent Laurasia. However, as major environmental changes occurred in the Early Cretaceous (between 130 and 90 million years ago), the diversification and rapid spread of angiosperms throughout middle latitudes pushed most conifers to small, cool or dry refugia in polar latitudes and scattered upland refugia at middle latitudes.

Intensive mountain-building events in the Tertiary created the environmental heterogeneity that drove the radiation of pine taxa in secondary centers of diversification, notably Mexico and northeastern Asia. Angiosperms that were best adapted at that time to tropical and subtropical conditions declined dramatically throughout middle latitudes following climatic deterioration at the end of the Eocene, allowing pines to expand their ranges.

Like the Eocene, the Pleistocene was also characterized by profound environmental changes that influenced the evolution of pines. However, whereas events in the Eocene completely reshuffled elements of the genus, Pleistocene changes caused pine species and populations to shift first toward the equator, then poleward (and to lower, then higher elevations), following the cycle of glacial and interglacial periods. Such migrations had important influences on the genetic diversity of pines. In some areas, such as the Pacific Northwest of North America, pine distributions were not so much split into distinct ranges by glaciations, as fragmented into small, semidisjunct populations. Such migrations served to promote intraspecific diversity while not necessarily promoting speciation. Although geographic conditions prevented pines from migrating south of the Sahara Desert, Nicaragua in Central America, or Java and Sumatra in Asia, the success of planted pines in the southern hemisphere shows that large parts of this hemisphere are highly suitable for pine growth.

Many significant changes in the abundance and geographic ranges of pines have occurred since the end of the last glacial period as pines rapidly expanded their ranges into deglaciated regions of North America and Europe. Wood rat middens preserved over the past 40 000 years at many sites in the Great Basin and other parts of the southwestern United States show a replacement of pinyon-juniper woodland by desert scrub in the Great Basin with warming at the end of Pleistocene.

## Why Are Pines so Successful?

It is in the role of aggressive postdisturbance colonizers that pines are most clearly differentiated

**Table 1** List of *Pinus* taxa, with common names, selected morphological features, and biogeographic region and habitat; figures relate to conditions regularly observed in the field (figures in brackets indicate exceptional dimensions)

<i>Pinus</i> taxon	Common name	Needle number	Needle length (cm)	Needle longevity (years)	Cone length (cm)	Height (m)	Biogeographic region	Habitat
<i>P. albicaulis</i>	Whitebark pine	5	3–7	5–8	4–8	5–10(30)	Western North America	Subalpine
<i>P. aristata</i>	Colorado or Rocky Mountain bristlecone pine	5	3–4	10–20	5–6(11)	5–15(30)	Rocky Mts, North America	Subalpine
<i>P. armandii</i>	Chinese white, Armand('s), or David's pine	5	8–15(18)	2–3	8–14	20–30	West and central China, Taiwan	Temperate montane
<i>P. attenuata</i>	Knobcone pine	3	9–15	4–5	8–15	10–20	Baja California, California, southwest Oregon	Mediterranean coastal
<i>P. ayacahuite</i>	Mexican white pine	5	8–15(22)	3	25–45	35–50	Mexico, Central America, Arizona, New Mexico	Tropical montane
<i>P. balfouriana</i>	Foxtail pine	5	(1.5)3–4	10–30	6–9(12)	10–22	California	Subalpine
<i>P. banksiana</i>	Jack pine	2	2–5	2–4	3–3.5	10–18(20)	Canada, northern USA	Boreal forest
<i>P. bhutanica</i>	Bhutan white pine	5	12–28	2–3	12–20	25	Himalayas	Temperate montane
<i>P. brutia</i>	Eastern Mediterranean or Calabrian pine	2	8–15	?	6–9	10–25	Eastern Mediterranean Basin	Mediterranean coastal
<i>P. bungeana</i>	Lacebark pine	3	6–8	3–4	5–6	15(30)	Central and north China	Temperate montane
<i>P. canariensis</i>	Canary Island pine	3	20–30	2–3	10–20(25)	30	Canary Islands	Mediterranean
<i>P. caribaea</i>	Caribbean pine	(2)3(4–5)	15–25	2	5–12	20–30	Caribbean area, Central America	Tropical/savanna
<i>P. cembra</i>	Swiss stone or Arolla pine	5	7–9	3–12	4–10	8–20(25)	Central Europe	Subalpine
<i>P. cembroides</i>	Mexican pinyon	(2)3(4)	2–6(7)	3–4	1–3.5	5–10(15)	Northwest Mexico, southwest USA	Arid/montane
<i>P. chiapensis</i>	Chiapas white pine	5	10–12	?	7–16	40	South-central to south Mexico, Guatemala	Tropical
<i>P. clausa</i>	Sand pine	2	6–9	2–3	3(4–8)	6(10)	Southeastern USA	Subtropical
<i>P. contorta</i>	Lodgepole pine	2	2–8	3–8	2–6	3–46(50)	Western USA	Temperate montane/subalpine
<i>P. c. subsp. bolanderi</i>	Bolander pine	2	2–5	?	?	6–15	California	Temperate
<i>P. c. subsp. contorta</i>	Shore or beach pine	2	2–7	?	2–5	3–10(16)	Coastal north California to British Columbia	Temperate
<i>P. c. subsp. latifolia</i>	(Rocky Mountain) lodgepole pine	2	(4)5–8	5–18	?	40–46	Rocky Mts, North America	Temperate montane
<i>P. c. subsp. murrayana</i>	Sierra (Nevada) lodgepole pine	2	(5–8)	?	2–5	15–40(50)	Sierra Nevada to Baja California	Temperate montane/subalpine
<i>P. cooperi</i>	Cooper pine	5(6–8)	8–10	?	6–10	30–35	Western Mexico	Tropical montane
<i>P. coulteri</i>	Coulter or bigcone pine	3	16–30	3–4	20–35	15–25	California, Baja California	Mediterranean coastal
<i>P. cubensis</i>	Cuban pine	3	10–14	?	4.5	?	Cuba	Tropical/savanna

<i>P. culminicola</i>	Potosí pinyon	(3–4)5(6)	5–6	?	3–5	1–5	Northeast Mexico	Tropical
<i>P. dabeshenensis</i>	Dabie Shan white pine	5	5–14	?	11–14	20–30	Eastern China	Temperate
<i>P. dalatensis</i>	Dalat or Vietnamese white pine	5	4–10	?	5–10	?	Vietnam	Tropical
<i>P. densata</i>	Sikang or Gaoshan pine	2(3)	8–14	3	4–6	30	China	Temperate montane
<i>P. densiflora</i>	Japanese red pine	2	(6)9–12	2–3	3–5	20–30 (36)	Japan, Korea, China	Temperate
<i>P. devoniana</i>	Michoacán pine	5	20–35	?	20–30	20–30	Mexico, Guatemala	Tropical
<i>P. discolor</i>	Border pinyon	3	2–6	?	2–3	5–10	Southwest USA, central and northwest Mexico	Arid/montane
<i>P. donnell-smithii</i>	Donnell Smith pine	5–6(7–8)	5–22	?	10–13	25	Guatemala	Tropical/subalpine
<i>P. douglasiana</i>	Douglas pine	5	20–35	?	7–10	20–35	West Mexico	Tropical
<i>P. durangensis</i>	Durango pine	6(7–8)	12–20	?	7–10	30–40	Northern and central Mexico	Tropical
<i>P. echinata</i>	Shortleaf pine	2	7–11	3–5	4–7	15–30(35)	Southeastern USA	Subtropical
<i>P. edulis</i>	Colorado pinyon	2	2–4	4–6	3–6	5–15	Western USA	Arid
<i>P. elliotii</i>	Slash pine	2–3	15(–30)	2	8–18	25–30	Southeastern USA	Subtropical
<i>P. engelmannii</i>	Apache pine	(2)3(4–5)	25–35	?	(10)–15	25(–30)	West Mexico, Arizona, New Mexico	Temperate/montane
<i>P. fenzeliana</i>	Fenzel pine	5	4–18	?	6–10	13–50	South China to central Vietnam	Temperate
<i>P. flexilis</i>	Limber or Rocky Mountain white pine	5	3–8	5–6	7–15	7–15 (24?)	Western North America	Subalpine
<i>P. gerardiana</i>	Chilgoza or Gerard's pine	3	6–10	?	12–20	10–20(25)	Punjab, Afghanistan, Pakistan	Temperate montane
<i>P. glabra</i>	Spruce pine	2	(4)6–8	2–3	4–9	22–35	Southeastern USA	Temperate
<i>P. greggii</i>	Gregg's pine	3	8–15	2–3	8–14	10–15(25)	East Mexico	Tropical
<i>P. halepensis</i>	Aleppo pine	2(3)	6–12(15)	2	5–12	10–20(25)	Mediterranean Basin	Mediterranean coastal
<i>P. hartwegii</i>	Hartweg pine	3	8–16	?	8–14	20–30	Mexico, Guatemala	Tropical/subalpine
<i>P. heldreichii</i>	Heldreich whitebark or Bosnian pine	2	6–10	2–3(6?)	7–8	20(30)	Balkan peninsula, Greece	Temperate montane/subalpine
<i>P. herrerae</i>	Herrera pine	3	10(10–25)	?	2–3(4)	20–25(35)	West Mexico	Tropical
<i>P. hwangshanensis</i>	Hwangshan (Huangshan) pine	2	5–9	?	4–6	25	Central and eastern China	Temperate
<i>P. jaliscana</i>	Jalisco pine	4–5	12–16	?	4–8	20–30	West Mexico	Tropical
<i>P. jeffreyi</i>	Jeffrey pine	3	12–15(23)	4–6	15–30	25–50(60)	California, Baja California	Temperate montane
<i>P. johannis</i>	Zacatecas pinyon (pine)	3	3–5	?	3–4	2–4	Northeast Mexico	Arid/montane
<i>P. kesiya</i>	Khasi or Khasya pine	3	12–20(22)	2	5–7(10)	20–35(45)	Southeast Asia	Tropical
<i>P. koraiensis</i>	Korean stone pine	5	(6)8–13	2	9–20	20–35	Korea, Japan, northeast China, Siberia	Temperate montane
<i>P. krempfii</i>	Krempf pine	2	3–7	?	7–9	12–30	Vietnam	Tropical
<i>P. lambertiana</i>	Sugar pine	5	(5)8–10	2–4	25–50(60)	75	Baja California, California, Oregon	Temperate montane
<i>P. lawsonii</i>	Lawson's pine	3–5	15–20	?	6–8	25–30	South Mexico	Tropical

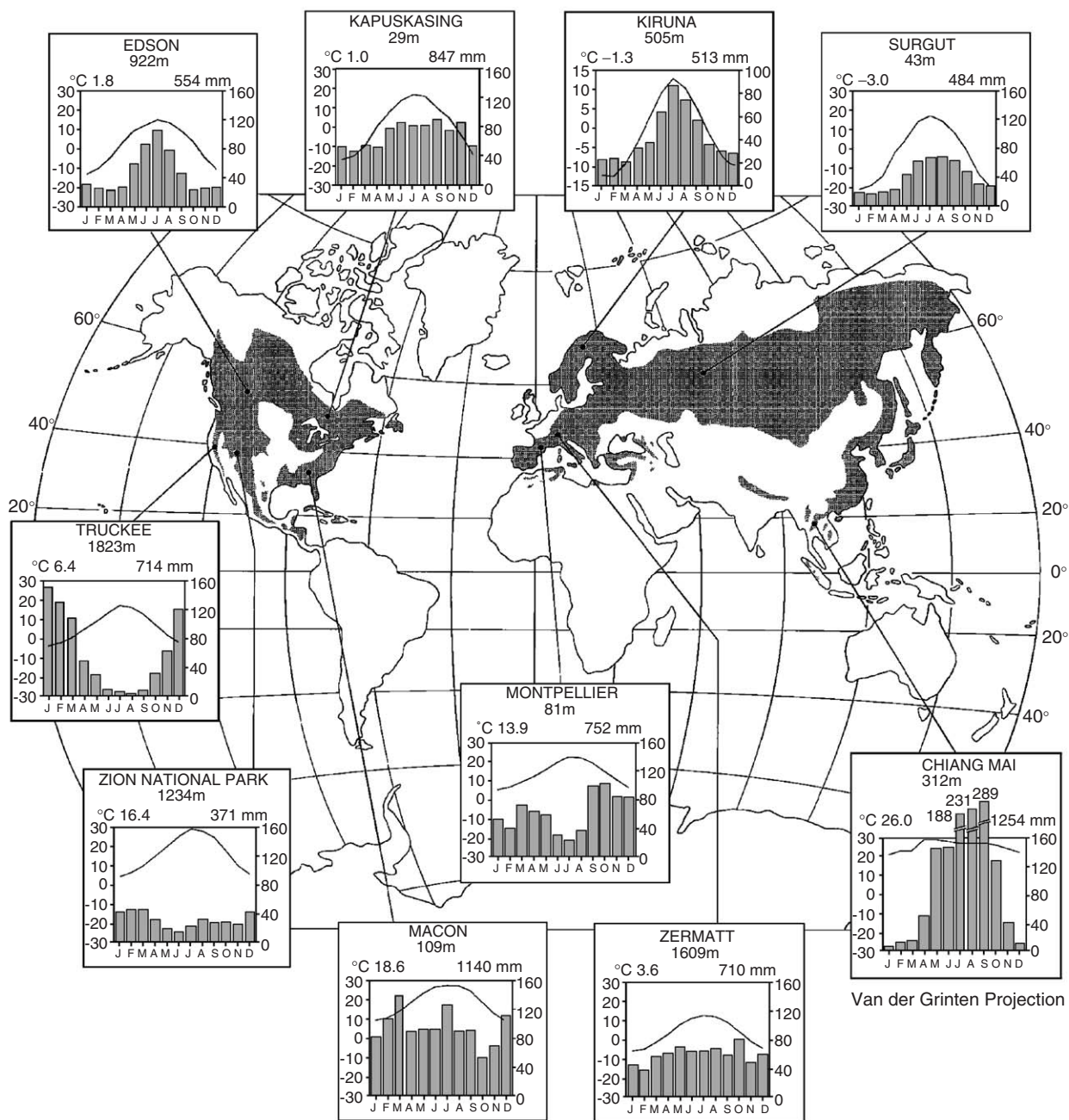
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Table 1 Continued

<i>Pinus taxon</i>	<i>Common name</i>	<i>Needle number</i>	<i>Needle length (cm)</i>	<i>Needle longevity (years)</i>	<i>Cone length (cm)</i>	<i>Height (m)</i>	<i>Biogeographic region</i>	<i>Habitat</i>
<i>P. leiophylla</i>	Smooth-leaved or Chihauhuan pine	5	5–9(15)	2	4–6.5(8)	20–25(30)	Mexico, Arizona, North Mexico	Temperate montane
<i>P. longaeva</i>	Western, Great Basin, or Intermountain bristlecone pine	5	1.5–3	10–33(45)	6–9.5	16	Western USA	Subalpine
<i>P. luchuensis</i>	Luchu pine	2	15–20	?	<5	<20	Japan, Ryukyu (Luchu) Islands	Temperate
<i>P. lumholtzii</i>	Lumholtz pine	3	(15)20–30	?	4–5(7)	10–20	Central Mexico	Tropical
<i>P. massoniana</i>	Masson, or Chinese red pine	2	15–20	?	5–6	8–25(30)	Central and eastern China, Taiwan	Temperate montane
<i>P. maximartinezii</i>	Martínez or Maxi pinyon	5	7–11	?	15–23	6–10	South Mexico	Arid/montane
<i>P. maximinoi</i>	Maximino pine	5	15–28	?	5–8	20–35	Mexico, Central America	Tropical
<i>P. merkusii</i>	Merkus or Tenasserim pine	2	17–25	1.5–2	5–9	20–30	Southeast Asia	Tropical/savanna
<i>P. montezumae</i>	Montezuma or roughbranched pine	(3–4)5(6–8)	15–25	3	(6)12–15	20–30(35)	Mexico, Guatemala	Tropical
<i>P. monophylla</i>	Singleleaf pinyon	1(2)	3–6	4–12	5–8	5–10	Southwestern USA to northern Baja California	Arid
<i>P. monticola</i>	Western white pine	5	(4)7–13	3–4	14–25(30)	50–55(70)	Western North America	Temperate montane
<i>P. morrisonicola</i>	Taiwan white pine	5	4–10	?	7–11	25(30)	Taiwan	Temperate
<i>P. mugo</i>	Dwarf mountain pine	2	3–8	5+	3–5(6)	2–6	Europe	Subalpine
<i>P. muricata</i>	Bishop pine	2	7–15	2–3	4–9	10–15(25)	California, Baja California	Mediterranean coastal
<i>P. nelsonii</i>	Nelson pinyon (pine)	3	5–10	?	7–12	5–10	Northeast Mexico	Arid
<i>P. nigra</i>	European black or Austrian pine	2	8–16	4(8)	3–10	20–40	Europe, Mediterranean Basin	Temperate
<i>P. nubicola</i>	Perry's pine	5–6(7–8)	25–43	?	10–15	25–30	South Mexico, Central America	Tropical
<i>P. occidentalis</i>	Hispaniolan pine	(3)4–5	11–18	?	5–7(8)	18	Caribbean Islands	Tropical montane/savanna
<i>P. oocarpa</i>	Eggcone pine	(3–4)5	20–25	?	6–10	15–30	Mexico and Central America	Tropical
<i>P. palustris</i>	Longleaf pine	3(5?)	20–45	2	15–25	25–30	Southeastern USA	Subtropical
<i>P. parviflora</i>	Japanese white pine	5	5–8	3–4	5–10	20–30	Japan	Subalpine
<i>P. patula</i>	Mexican weeping pine	3(4–5)	15–25(30)	3–4	7–10	30–35	East Mexico	Tropical
<i>P. peuce</i>	Macedonian or Balkan (white) pine	5	6–12	?	8–15	20–30	Balkan Peninsula	Temperate montane
<i>P. pinaster</i>	Maritime or cluster pine	2	(10)15–20(25)	3	10–22	20–35(40)	Western Mediterranean Basin	Mediterranean coastal
<i>P. pinceana</i>	Weeping or Pince pinyon	3	6–8(14)	?	5–10	4–10	Northeast Mexico	Arid/montane

<i>P. pinea</i>	Mediterranean stone, Italian stone, or umbrella pine	2	(8)12–15(20)	2–3	10–15	15–30	Mediterranean Basin	Mediterranean coastal
<i>P. ponderosa</i>	Ponderosa or western yellow pine	(2)3(4–5)	17–25	4–6	5–15	10–50(72)	Western USA	Temperate montane
<i>P. praetermissa</i>	Styles's pine	5	8–16	?	3–5	15	West Mexico	Tropical
<i>P. pringlei</i>	Pringle's pine	3(4–5)	15–25	?	5–8	15–30	South Mexico	Tropical
<i>P. pseudostrobus</i>	False Weymouth pine	5(6–8)	20–25	?	8–15	30–40	Mexico, Guatemala	Tropical
<i>P. pumila</i>	Dwarf stone pine	5	4–6	5	3–5(6)	1–4	East Asia	Boreal forest, subalpine
<i>P. pungens</i>	Table Mountain pine	2	5–7(9)	3	6–10	15–20	Northeastern USA	Temperate
<i>P. quadrifolia</i>	Parry pinyon	4–5	1.5–5	?	3.5–6	5–15	South California Baja California	Arid/montane
<i>P. remota</i>	Texas or paper-shell pinyon	2	3–5	?	2.5–3.5	3–8	Texas, northeast Mexico	Arid
<i>P. resinosa</i>	Red pine	2	12–18	4–5	3.5–6	20–30(40)	Northeastern USA, Canada	Temperate
<i>P. rigida</i>	Pitch pine	(2)3	5–10(12)	2–3	3–4(5–10)	10–25(30)	Northeastern USA	Temperate
<i>P. roxburghii</i>	Chir pine	3	20–30	1–3	10–15(20)	40–50 +	Himalayas	Temperate montane
<i>P. rzedowskii</i>	Rzedowski pinyon	(3)4(5)	6–10	?	10–15	15–30	Southwest Mexico	Tropical
<i>P. sabiniana</i>	Foothill or digger pine	3	15–25(30)	3–4	15–25	15–25	California	Mediterranean coastal
<i>P. serotina</i>	Pond pine	3	15–20	2–3	5–8	20	Southeastern USA	Temperate
<i>P. sibirica</i>	Siberian stone pine	5	(5)10–13	?	6–12	20–35	Central Asia	Boreal forest
<i>P. squamata</i>	Qiaojia pine	5	9–17	?	9	?	Southwest China	Subtropical montane
<i>P. strobus</i>	Eastern white pine	5	6–10(12)	2–3	8–20	25–30(40)	Northeastern USA and Canada	Temperate
<i>P. sylvestris</i>	Scots pine	2	3–7	2–8	3–6	30(35)	Europe, central Asia	Boreal forest, temperate, subalpine
<i>P. tabuliformis</i>	Chinese red pine	2–3	10–12(13–17)	?	4–9	25(30)	North and west central China	Temperate montane
<i>P. taeda</i>	Loblolly pine	3	12–22	3–4	6–12(15)	20–30	Southeastern USA	Temperate
<i>P. taiwanensis</i>	Taiwan red or Formosa pine	2	8–12	?	4–8	20–25(35)	Taiwan	Tropical montane
<i>P. tecunumanii</i>	Tecun Umán pine	4–5	14–21	?	4–7	50	Central America	Tropical
<i>P. teocote</i>	Twisted-leaved or Aztec pine	(2)3(4–5)	8–15	3	4–7	8–25(30)	Mexico, Guatemala	Tropical
<i>P. thunbergii</i>	Japanese black pine	2	7–12	3–4	4–6	30–40	Japan, Korea	Temperate
<i>P. torreyana</i>	Torrey pine	5	15–30	3–4	10–15	5–10(15)	California	Mediterranean coastal
<i>P. tropicalis</i>	Tropical pine	2(3)	15–30	?	?	?	Cuba	Tropical/savanna
<i>P. uncinata</i>	Swiss mountain pine	2	(3)5–6	5 +	4–6	10–20	Europe	Temperate montane
<i>P. virginiana</i>	Virginia or scrub pine	2	4–8	3–4	3–7	8–15(30)	Eastern USA	Temperate
<i>P. wallichiana</i>	Himalayan blue pine	5	11–18(20)	3–4	20–30	50 +	Himalayas	Temperate montane
<i>P. wangii</i>	Wang pine	5	2.5–6	?	4.5–9	20	Southwest China	Temperate
<i>P. washoensis</i>	Washoe pine	3	10–15	4–6	7–10	35(70)	Sierra Nevada	Temperate montane
<i>P. yunnanensis</i>	Yunnan (white) pine	2–3	15–20(30)	?	3–7(10)	15–30	China	Temperate montane

Adapted from Richardson D (ed.) (1998) *Ecology and Biogeography of Pinus*. Cambridge, UK: Cambridge University Press.



**Figure 1** The worldwide distribution of the genus *Pinus* with examples of the varied climate regimes in which pines occur. Reproduced with permission of Cambridge University Press from Richardson D (ed.) (1998) *Ecology and Biogeography of Pinus*. Cambridge, UK: Cambridge University Press.

from firs, spruces, other conifers, and from angiosperm trees. An idealized 'pine prototype' would conform with the following profile: a light-demanding, fast-growing tree that regenerates as even-aged cohorts following landscape-scale disturbance, and retains its position in the landscape by exploiting aspects of its regeneration biology. This is an oversimplification, however, when one considers the wide range of habitats in which pines occur,

and the range of life history syndromes evident in the genus.

Among the factors that have contributed to the ecological success of pines are their abundant output of seeds from an early age, their effective mechanisms for long-distance seed dispersal, their ability to colonize nutrient-poor and disturbed sites, and their mating system that permits inbreeding and selfing in isolated trees and confers resilience at

**Table 2** Systematic relationships within the genus *Pinus*. Subgeneric categories are based on data in Richardson (1998) and personal communications from Aaron Liston (Oregon State University)

Genus *Pinus*

Subgenus *Pinus*

Section *Pinus*

Subsection *Pinus* (Eurasia, North Africa, northeastern North America, Cuba):

*P. densata*, *P. densiflora*, *P. hwangshanensis*, *P. kesiya*, *P. luchuensis*,  
*P. massoniana*, *P. merkusii*, *P. mugo*, *P. nigra*, *P. resinosa*, *P. sylvestris*,  
*P. tabuliformis*, *P. taiwanensis*, *P. thunbergii*, *P. tropicalis*, *P. uncinata*, *P. yunnanensis*

Subsection *Pinaster* (Canary Islands, southern Europe, North Africa, West Asia, Himalayas):

*P. brutia*, *P. canariensis*, *P. halepensis*, *P. heldreichii*, *P. pinaster*,  
*P. pinea*, *P. roxburghii*

Section *Trifolius*

Subsection *Contortae* (North America):

*P. banksiana*, *P. clausa*, *P. contorta*, *P. virginiana*

Subsection *Australes* (Eastern USA, Caribbean, Central America):

*P. caribaea*, *P. cubensis*, *P. echinata*, *P. elliotii*, *P. glabra*, *P. occidentalis*, *P. palustris*,  
*P. pungens*, *P. rigida*, *P. serotina*, *P. taeda*

Subsection *Ponderosae* (Western North America to Central America):

*P. cooperi*, *P. coulteri*, *P. devoniana*, *P. donnell-smithii*, *P. douglasiana*,  
*P. durangensis*, *P. engelmannii*, *P. hartwegii*, *P. jeffreyi*, *P. maximinoi*,  
*P. montezumae*, *P. nubicola*, *P. ponderosa*, *P. pseudostrobus*, *P. sabiniana*,  
*P. torreyana*, *P. washoensis*

Subsection *Attenuatae* (Western USA, adjacent to Mexico):

*P. attenuata*, *P. muricata*, *P. radiata*

Subsection *Oocarpae* (Mexico, Central America):

*P. greggii*, *P. herrerae*, *P. jaliscana*, *P. lawsonii*, *P. oocarpa*, *P. patula*,  
*P. praetermissa*, *P. pringlei*, *P. tecunumanii*, *P. teocote*

Subsection *Leiophyllae* (Mexico and southwestern USA):

*P. leiophylla*, *P. lumholtzii*

Subgenus *Strobus*

Section *Parrya*

Subsection *Balfourianae* (Western USA):

*P. aristata*, *P. balfouriana*, *P. longaeva*

Subsection *Cembroides* (Southwestern USA, Mexico):

*P. cembroides*, *P. culminicola*, *P. discolor*, *P. edulis*, *P. johannis*,  
*P. maximartinezii*, *P. monophylla*, *P. pinceana*, *P. quadrifolia*, *P. remota*, *P. rzedowskii*

Subsection *Nelsoniae* (Mexico):

*P. nelsonii*

Section *Strobus*

Subsection *Gerardianae* (East Asia, Himalayas):

*P. bungeana*, *P. gerardiana*, *P. squamata*

Subsection *Kremfianae*

*P. krempfii*

Subsection *Quinquefolius* (North and central America, southeast Europe, Asia):

*P. albicaulis*, *P. armandii*, *P. ayachuite*, *P. bhutanica*, *P. cembra*,  
*P. chiapensis*, *P. dabeshanensis*, *P. dalatensis*, *P. fenzeliana*, *P. flexilis*,  
*P. koraiensis*, *P. lambertiana*, *P. monticola*, *P. morrisonicola*, *P. parviflora*,  
*P. peuce*, *P. pumila*, *P. sibirica*, *P. strobus*, *P. wallichiana*, *P. wangii*

the population level under a wide range of disturbance regimes.

## Morphological Traits of Pines

Pines, like many other conifers, typically have a main trunk which can grow to a large size. The largest species of pines in the world are found in California and the Pacific Northwest of the USA. Growth conditions in these regions favor immense size in many conifer genera, including *Abies*, *Picea*, *Pseudotsuga*, *Thuja*, *Tsuga*, *Sequoia*, and *Sequoiadendron*. The

largest species of pine in both height and girth is *Pinus lambertiana* which reaches over 75 m in height and more than 5 m in diameter in the Sierra Nevada of California. Three other pines from the western USA, *P. jeffreyi*, *P. monticola*, and *P. ponderosa*, all reach heights of 60 m or more.

Pines can, however, be quite short in stature in more extreme habitats. The pinyon pines usually attain heights of no more than 5–10 m when mature. Timberline pines also may be low growing, particularly when they occur as multistemmed krummholz shrubs at the upper limits of tree distribution. Most



of these timberline species have the genetic potential for taller growth, and may reach 10–20 m in height under more favorable conditions.

Many pines are very long-lived, and the two bristlecone pines, *Pinus aristata* and *P. longaeva*, are the oldest living organisms in the world, with the latter reaching documented ages of nearly 5000 years. *Pinus albicaulis*, *P. balfouriana*, and *P. flexilis* may live for more than 2000 years, while others such as *P. jeffreyi*, *P. monticola*, and *P. ponderosa* can reach ages beyond 1000 years. All of these are montane or timberline species from western North America.

Because of their great ages, pines have played a fundamental role in the development of the modern science of dendrochronology, beginning with the pioneering work of Andrew Douglas in the American Southwest. Douglas developed the concept of cross-dating to compare and extend tree ring measures over broad regional areas to identify year-to-year variation in climate. It was this research that led to the establishment of the Laboratory of Tree Ring Research at the University of Arizona in 1906. Collaborative work with anthropologists soon led to what were then revolutionary approaches to dating the construction of Indian dwellings in Chaco Canyon and Mesa Verde in the Southwest. These studies allowed the earliest measurement and linkages of floating chronologies to develop long-term records over more than 2000 years, and had profound impacts in the field of anthropology.

The field of dendrochronology has expanded greatly in scope and depth in recent decades. Chronologies of living *P. longaeva* tied to floating records in logs show promise of developing a 10 000-year record across the Holocene. Tree ring chronologies are also proving to be valuable records of alteration of typical forest growth regimes resulting from fires and from atmospheric pollution or other causes.

Although all pines share the defining morphological trait of possessing pine needles, there is a wide variation in the size and manner of needle display. Needles are arranged in bundles (generally termed fascicles or needle clusters), with the number of needles per fascicle being a reasonably constant and species-specific characteristic in many taxa. Most pine species have two, three, or five needles per fascicle, but other numbers are also present. Only one species has one needle per fascicle: *P. monophylla*, the singleleaf pinyon of the southwestern USA. At the other extreme, four species of typically five-needled Mexican pines (*P. cooperi*, *P. donnell-smithii*, *P. durangensis*, and *P. pseudostrabus*) frequently have six needles per fascicle, and sometimes up to eight.

Needle number does not have any established ecological correlation. Adaptive radiation within specific subsections of the genus *Pinus* has taken place, both with and without modifications of needle number per fascicle. For example, almost all of the 24 Old World pines of the subsections *Pinus* and *Pinaster* have two needles per fascicle (Table 2) – this despite the wide range of habitats occupied by taxa in this group (e.g., *P. resinosa* and *P. sylvestris* in boreal-type forest; *P. nigra* and *P. pinaster* in lower-elevation sites in the Mediterranean Basin; *P. heldreichii*, *P. mugo*, and *P. uncinata* at high-elevation sites in the Mediterranean Basin; *P. kesiya* and *P. merkusii* in tropical savannas; and a set of eastern Asian species that occupy a wide range of habitats). The white pines occupying varied montane and subalpine habitats all typically have five needles per fascicle. At the other extreme are the pinyon species of North America which include taxa with one to five needles per fascicle, despite the arid environments in which all these species occur.

The length and form of pine needles varies greatly among pine species. The longest needles of any pine species are those of the appropriately named longleaf pine, *P. palustris*, in the southeastern USA (up to 45 cm), and *P. nubicola* in Mexico which also reach lengths of over 40 cm. At the other extreme are many pines with very short needles in the 2–8 cm range of maximum lengths. These short-needled species are almost entirely confined to the arid-adapted pinyon pines, high-elevation, or timberline pines, and pines on low nutrient sites, suggesting a relationship with environmental stress.

There are other interesting needle traits in pines that have not been studied to assess ecological significance. Several Mexican pine species have drooping, or ‘weeping’, needles that hang downward, and there are intermediate morphologies in other species with relatively flexible needles. Such long, fine needles may aid the condensation and drip of fog moisture in tropical mountain areas or in coastal fog zones, as with *P. lumholtzii*, *P. nubicola* and *P. patula* in Mexico, *P. radiata* on Cedros Island and the coast of California, and *P. canariensis* in the Canary Islands. Such hypotheses remain conjectural, however. Another unusual needle morphology in pine is that of flattened needles which are characteristic of the rare *P. krempfii* from the central highlands of Vietnam.

One strong environmental correlate of needle traits in pines does exist. Needle longevity is strongly correlated with habitat water availability and nutrient relations and/or stress. Tropical pines such as *P. caribaea* and the southern USA species *P. palustris* keep needles for no more than 2–3 years,

and the Indian species *P. roxburghii* usually sheds its needles every year. Temperate forest pines commonly retain their needles for intermediate periods of 4–6 years. Pinyon pine leaves have relatively greater longevities of up to 10 years. Subalpine pines such as *P. longaeva* retain their leaves for up to 30 years or more, and even 45 years in extreme circumstances at the timberline in the White Mountains of California. This is the greatest needle longevity recorded for any conifer.

The form and morphology of pine cones is highly variable, with obvious relationships to the reproductive biology of individual species. The greatest length of cone in any pine occurs in *P. lambertiana*, where cones reach up to 50 cm in length. In terms of fresh cone weight, *P. coulteri* from California holds the record, with large globular cones 20–35 cm in diameter weighing as much as 2.3 kg. Large cones are also present in the Mexican taxa *P. ayacahuite*, *P. devoniana*, and *P. maximartinezii*. About one-third of pine species typically bear cones that are less than 5 cm long. As a broad generalization, it appears that taxa associated with stressful environments have smaller cones. *Pinus* is far more diverse in the morphology of its seeds than all other Pinaceae combined, a fact that certainly contributes to the wide range of habitats in which pines flourish. While most pines have wind-dispersed seed, the pinyon pines and many subalpine pines have large seeds dispersed by birds. It is intuitive to expect the largest seeds in species with the largest cones, but correlations between cone size and seed size is poor.

### Ecophysiological Traits of Pines

Coniferous forest trees characteristically utilize a very different strategy of canopy carbon gain than do hardwood trees. Compared to deciduous hardwoods, conifers generally show a relatively low level of carbon gain per unit of leaf area, but a far higher leaf area index (LAI). Needles are retained for several to many years, and a clustered arrangement of foliage and regular canopy architecture has evolved to allow maximum irradiance of older foliage. Thus, the net primary productivity of conifer forests with high LAI is typically as great or greater than that of deciduous hardwood forests in the same climatic regime despite the lower photosynthetic rates. However, most conifers are inherently slow in becoming established in successional sequences where environmental stress is not extreme because it takes them multiple years to attain a full canopy. Under these conditions, deciduous hardwood saplings which can attain a full canopy in a single year are much more competitive.

Pines differ from the typical conifer strategy in several respects. Typical ranges of LAI in field populations of pines are only  $2\text{--}4\text{ m}^2\text{ m}^{-2}$ , compared with values of  $9\text{--}11\text{ m}^2\text{ m}^{-2}$  in the more shade-tolerant genera *Abies*, *Picea*, and *Pseudotsuga*. The low LAI in pines largely results from the fact that many species carry relatively few years of needles compared to other conifers. Except in pines characteristic of environments of extreme cold or drought stress, 2–5 years of needles in the canopy at any time is typical. Thus, despite their relatively low LAI, pines are inherently more effective colonizers than many other conifers because they can attain a full canopy of foliage more rapidly early in succession. Many pines, however, can be selected for a higher LAI under plantation conditions where resources are not limiting. Highly productive plantations of commercial pine species such as *P. radiata* owe much of their productivity to LAIs two or three times those found under natural conditions.

It is interesting to speculate on the potential similarities of the rapid growth and colonizing abilities of many pines and the traits of early successional hardwood trees. The relatively low LAI of pines and their generally poor shade-tolerance are shared by such hardwoods as temperate *Eucalyptus* and many tropical pioneer trees. Shade-tolerant conifers such as *Abies*, *Picea*, *Pseudotsuga*, and *Sequoia* not only have high LAIs, but share a typical architectural form characterized by growth cycles that produce regular whorls of branches at levels determined by the height of the trunk meristem. In contrast to this pattern, most pines and many tropical colonizers (e.g., *Cecropia*, *Macaranga*, and *Musanga* spp.) are shade-intolerant and possess a canopy architecture with the cyclical addition of tiers of branches which are structurally identical to the trunk.

Considering the wide range of ecological habitats in which pines occur, it is noteworthy that there is relatively little variation in their photosynthetic characteristics. Maximum rates of photosynthetic capacity under field conditions within ecologically plastic species such as *P. contorta* and *P. sylvestris* appear to vary as much as within pines as a group. When grown under common garden conditions under nonlimiting conditions, pines from very different environments exhibit quite similar photosynthetic responses to irradiance, suggesting a considerable degree of phenotypic plasticity. This is equally true both for ecotypes of the same species and different species. Thus, variation in net primary production rates of pines in different environments is less a function of differences in photosynthetic capacity than of climatic factors of cold or drought

that limit the period of positive net carbon gain throughout the year.

Seasonal patterns of low temperatures in autumn and winter are clearly important components of the potential net primary production of pine species. Thus pines in cold-temperate environments or timberline habitats have high levels of positive canopy photosynthesis limited to relatively few months of the year. Subtropical and tropical species grow throughout the year, with light, LAI, and nutrient availability as the primary factors controlling net primary production. Although pine species may tolerate habitats over a wide range of annual precipitation, the response of individual species to limited water availability is surprisingly consistent, as with almost all conifers. Net photosynthesis in pines typically falls to zero at relatively modest tissue water stress, thereby limiting the growth potential of pines in semi-arid environments.

Other aspects of the ecophysiology of pines show highly adapted traits between species that adapt them to specific climatic or environmental conditions. As logic would suggest, pines of cold habitats commonly have much lower temperature optima for photosynthesis than do species of warm climates. A stomatal response to environmental water vapour deficit is another trait showing adaptive selection. Species of semi-arid environments are highly sensitive to small changes in vapor pressure, thereby regulating summer water loss, while subtropical species are quite insensitive to such changes. Clear differences in tolerance of low nutrient conditions are also apparent in pine species whose ranges overlap.

### Human Impacts on Pines and Pine Forests

Human-induced changes to pine forests have had significant impacts on the structure, dynamics, and biodiversity of these ecosystems for centuries. The consequences of human activities likely extend back thousands of years in the Mediterranean Basin where marked changes in human population numbers and far-reaching changes in land use practices have exerted major influences. Human impacts have come from logging and deforestation, land use practices that increase or decrease natural frequencies of fire, grazing, and plantation establishment outside of normal species ranges.

There is a massive literature on the history, policies, politics, and practices of logging in different parts of the range of pines. Logging takes place in natural pine forests around the world for construction-grade lumber, with varying levels of sustainability. Additionally, the need for fuelwood in many

parts of the natural range of pines in the developing world still accounts for a large part of the total area of pine forest cleared every year. While pines are important lumber sources, logging of hardwood forests has often led to a stimulation of pine establishment and dominance. For example, past clearing of broadleaved forests in the southeastern USA and areas of Asia has created suitable conditions for pines. Human-induced changes to natural fire regimes have had a particularly dramatic effect on pine ecosystems. This impact has been seen most strongly where human activities have led to increased fire frequency. In Central America, Mexico, and Southeast Asia this has often arisen through the agency of slash-and-burn agriculture. However, the opposite condition of reduced fire frequencies has also been widespread and has affected pine establishment. Heavy grazing of rangelands has reduced fire frequency in many parts of the American West by reducing fuel loads, and this has had a major impact on vegetation dynamics. Fire exclusion has allowed pines to spread into some areas where the natural fire regime excluded them, and has changed the forest composition in areas where the natural fire regime allowed pines to grow, but where changed fire characteristics have altered processes affecting vegetation dynamics. Some impacts of fire suppression in pine forests through the disruption of the relationships between pines, fire, pathogens and insects are complex.

Changes in grazing pressure have triggered changes in pine distribution in many regions, but the phenomenon has been best studied in North America. Grazing facilitates pine establishment in abandoned fields by reducing the cover of vigorous grasses and thus competition with pine seedlings. Areas subjected to heavy grazing often remain susceptible to colonization by pines long after grazing pressure has been greatly reduced or eliminated. Such effects have been documented for pine forests adjoining mesic subalpine meadows and mixed grass and brush in more arid regions.

Humans have harvested pines and their products for thousands of years. There are 29 pine species whose seeds are harvested for human consumption. In some societies, pine seeds harvested from natural forests are still important economic resources, as in Pakistan, India, China, and Mexico.

Pines have been widely planted in the Mediterranean Basin since prehistoric times, and more recently throughout the world. Some pines have proved highly successful for use in plantations outside their natural ranges where there is a shortage of coniferous species to produce fibers and solid wood products. This is particularly true of temperate

areas in the southern hemisphere where there are massive plantations of *Pinus radiata* and other pine species. Reasons for the widespread use of pines in exotic forestry plantations include their simple design with straight trunks and geometrical branching habitat that makes them ideal for timber production. Moreover, pines grow faster than many other potential species, are easy to manage in plantations, have easily collected seeds, and are ideally suited for planting in marginal forest lands where most plantations are desired. Many pine species – *P. caribaea*, *P. elliottii*, *P. kesiya*, *P. oocarpa*, *P. patula*, *P. radiata* and *P. taeda* – are widely grown in plantations in the tropics and subtropics.

## Threats to Pine Species

One-third of all pine species are either threatened in their entirety, or have subspecies or varieties that are threatened. This includes species with naturally restricted ranges and small population sizes as well as others that owe their threatened status to human activities. Even among pine taxa that occupy large ranges, large portions of their genetic diversity have been lost; this may have reduced their ability to respond to changing environmental conditions.

**See also:** **Biodiversity:** Biodiversity in Forests. **Ecology:** Plant-Animal Interactions in Forest Ecosystems. **Environment:** Environmental Impacts. **Genetics and Genetic Resources:** Population, Conservation and Ecological Genetics. **Hydrology:** Hydrological Cycle. **Landscape and Planning:** Perceptions of Forest Landscapes. **Mensuration:** Tree-Ring Analysis. **Plantation Silviculture:** Forest Plantations. **Temperate and Mediterranean Forests:** Mediterranean Forest Ecosystems; Northern Coniferous Forests; Southern Coniferous Forests; Sub-alpine and Boreal Forests; Temperate Broadleaved Deciduous Forest. **Tree Breeding, Practices:** *Pinus Radiata* Genetics. **Tree Physiology:** Canopy Processes. **Tropical Ecosystems:** Tropical Pine Ecosystems and Genetic Resources.

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## Poplars

**B Stanton**, Greenwood Resources, Clatskanie, OR, USA

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## Introduction

The genus *Populus* (family Salicaceae) comprises 29 diverse species found almost exclusively in forests of the northern hemisphere. Considered as a whole, *Populus* covers an impressive ecological amplitude from the tropics to the boreal forests. In China alone, an extraordinary number of species are found in the cold northeast, the arid northwest, and the subtropical Qinghai–Tibetan plateau. No less impressive is the close association between *Populus* forests and the development of humankind that has included their cultivation for shelterbelts, fuel, animal feed and forage, pulp, veneer, lumber, and more lately, engineered wood products. Moreover, this group of trees has lately assumed a vital ecological role in forestalling desertification in Asia and in restoring and maintaining many of the world's degraded rivers and floodplains (**Figure 1**). In the latter regard, conserving the genetic resources embodied in the natural stands of many *Populus* species is critically important. These genetic resources are also an indispensable foundation for many breeding programs that support ongoing *Populus* domestication efforts. As the global forest plantation industry becomes inexorably associated with high-yield plantations of the tropical and subtropical regions, such applied genetics programs will help to sustain *Populus* plantations as the only temperate-zone tree that can be managed for near-comparable yields.

This article is an overview of the genus *Populus* and its members, where they occur, examples of how