

# Part one

# Introduction

# 1 Ecology and biogeography of *Pinus*: an introduction

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## 1.1 Introduction

Pines are important, and very often dominant, components of the vegetation over large parts of the northern hemisphere (Fig. 1.1). Besides having major economic value as sources of timber, pulp, nuts, resin and other products, pines also influence ecosystems in many ways. They affect biogeochemical processes, hydrological and fire regimes, and provide food and create habitats for animals. The boreal forest, of which pines are an important component, plays a significant role in determining regional and global climate. For example, the presence of forest in these northern latitudes masks the high reflectance of snow, leading to warmer winter temperatures than would be the case if trees were absent (Bonan, Pollard & Thompson 1992). Pines featured in ancient myths and rituals, have influenced human history, and have been celebrated in visual art, prose, poetry and music (as in Ottorino Respighi's 'The Pines of Rome'). 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. *Pinus* is without a doubt the most ecologically and economically significant tree genus in the world.

This chapter provides an introduction to this volume by placing the genus in perspective. We discuss the origin and evolution of pines, the features that distinguish them from other woody taxa, and the position of pines in the landscape in each of the major habitats in which they occur. We consider some of the many interactions between pines and humans, and discuss some recent developments in the study of pines.

## 1.2 The origin and evolution of pines

The expansion of angiosperms and the concurrent decline of gymnosperms was one of the most important phytogeographic processes in the history of the earth. The earliest-known angiosperms arose in the Early Cretaceous (c. 120 million years ago), and there are now between 250 000 and 300 000 extant species. Gymnosperms arose much earlier (Middle Devonian, 365 million years ago), but there have never been more than a few thousand species. Evidence from fossilized cones shows that ancestors of Pinaceae had evolved by the mid-Jurassic, and that *Pinus* had evolved by the Lower Cretaceous. There is some evidence that *Cedrus* and possibly *Larix* appeared before the Tertiary, but the other genera of the family appeared only in the early Tertiary or later (Stewart 1983).

The current diversity of conifers (gymnosperms excluding cycads, *Ephedra*, *Ginkgo*, *Gnetum* and *Welwitschia*) comprises eight families, 68 genera, 629 species and about 176 intraspecific taxa. A large proportion of extant conifers occur in the northern hemisphere: seven families and about 70% of both genera and species (Farjon 1998). More than a third of extant gymnosperm species belong to the Pinaceae, by far the largest family of modern conifers, which is divided into 10 or 11 genera (Chap. 2, this volume). Species of all the large genera in the Pinaceae (notably *Pinus*, *Picea*, *Abies* and *Larix*) are widely distributed throughout the temperate parts of both Old and New Worlds. There are concentrations of species in all these genera in North America and eastern Asia. More than half the species in the Pinaceae (and almost 20% of all gymnosperm species) are included in the remarkable genus *Pinus* which, according to the treatment accepted for this volume (see Chap. 2), contains 111 species (Table 1.1).

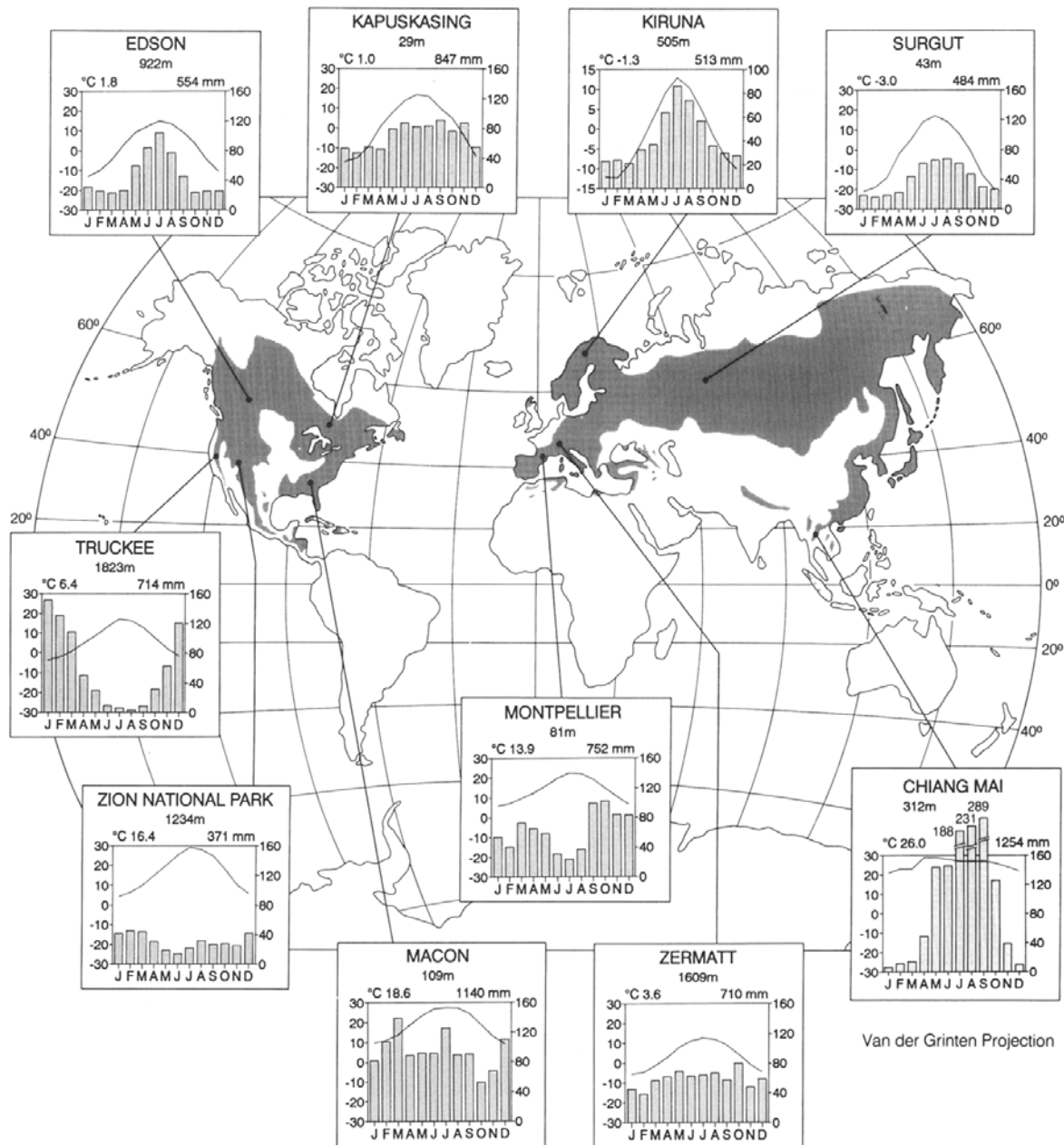


Fig. 1.1. The distribution of *Pinus* (based on Critchfield & Little 1966) with climographs for representative sites in each of the major habitat categories (see text). Mean monthly temperatures are

indicated by the line and mean precipitation for each month is shown by the bars. Station elevation, mean annual temperature, and mean annual precipitation appear at the top of each climograph.

By the end of the Mesozoic, pines had diversified into two major groups, or subgenera; representatives of both subgenera, *Strobus* (haploxylon or soft pines, with one fibrovascular bundle in the needle) and *Pinus* (diploxylon or hard pines, with two fibrovascular bundles in the needle), survive today. Several early subsections within these subgenera had also evolved by this time, including *Australes*, *Canarienses*, *Cembroides*, *Gerardiana*, *Pineae*, *Pinus*,

*Ponderosae* and *Strobi* (Millar & Kinloch 1991). At this stage, pines had migrated throughout the middle latitudes of the northern hemisphere super-continent, Laurasia. Major environmental changes in the Early Cretaceous, between 130 and 90 million years ago, led to the diversification and rapid spread of angiosperms throughout middle latitudes, initiating profound changes in terrestrial ecosystems (Crane, Friis & Pedersen 1995). As the

<i>Pinus</i> taxon <sup>a</sup>	Common name <sup>b</sup>	Needle no. <sup>c</sup>	Needle length (m) <sup>c</sup>	Needle longevity (yrs) <sup>c</sup>	Cone length (cm) <sup>c</sup>	Height (m) <sup>c</sup>	Biogeographic region <sup>d</sup>	Habitat <sup>e</sup>
<i>P. albicaulis</i>	whitebark pine	5	3-7	5-8	4-8	5-10(30)	W North America	subalpine
<i>P. aristata</i>	Colorado, or Rocky Mountain	5	3-4	10-20	5-6(11)	5-15(30)	Rocky Mts, North America	subalpine
<i>P. armandii</i>	bristlecone pine Chinese white, Armand's, or David's pine	5	8-15(18)	2-3	8-14	20-30	W & C China and Taiwan	temperate montane
<i>P. attenuata</i>	knobcone pine	3	9-15	4-5	8-15	10-20	Baja California, California, SW Oregon	mediterranean coastal
<i>P. ayacahuite</i>	Mexican white pine	5	8-15(22)	3	10-40	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, N 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	E Medit. Basin	mediterranean coastal
<i>P. bungeana</i>	lacebark pine	3	6-8	3-4	5-6	15(30)	C and N 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)	C Europe	subalpine
<i>P. cembroides</i>	Mexican pinyon	(2)3(4)	2-6(7)	3-4	1-3.5	5-10(15)	NW Mexico, Texas	arid/montane
<i>P. chiapensis</i>	Chiapas white pine	5	10-12	?	7-16	40	S-C to S Mexico, Guatemala	tropical
<i>P. clausa</i>	sand pine	2	6-9	2-3	3(4-8)	6(10)	SE USA	temperate
<i>P. contorta</i>	lodgepole pine	2	2-8	3-8	2-6	3-46(50)	W USA	temperate
<i>P. c. subsp. bolanderi</i>	Bolander pine	2	2.5-4	(1)2-3	4-5	6-15	California	montane/subalpine
<i>P. c. subsp. contorta</i>	shore, or beach pine	2	4-6(7)	3-4	4-7	3-10(16)	coastal N 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, S to Baja California	temperate
<i>P. cooperi</i>	Cooper pine	5(6-8)	8-10	?	6-10	30-35	W Mexico	montane/subalpine
<i>P. coulteri</i>	Coulter, or bigcone pine	3	16-30	3-4	20-36	15-25	California, Baja California	tropical montane
<i>P. cubensis</i>	Cuban pine	3	10-14	?	4.5	?	Cuba	mediterranean coastal
<i>P. culminicola</i>	Potosi pinyon	(3-4)5(6)	3-5	?	3-5	1-5	NE Mexico	tropical/savanna
<i>P. dabeshensis</i>	Dabie Shan white pine	5	5-14	?	11-14	20-30	E China	tropical montane/subalpine
<i>P. dalatensis</i>	Dalat, or Vietnamese white pine	5	4-10	?	5-10	40	Vietnam	temperate
<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>	Michoacan pine	5	20-35	?	20-30	20-30	Mexico, Guatemala	temperate montane
<i>P. discolor</i>	border pinyon	3	2-6	?	2-3	5-10	SW USA, C & NW Mexico	arid/montane
<i>P. donnell-smithii</i>	Donnell Smith pine	5-6(7-8)	15-22	?	10-13	25	Guatemala	tropical/subalpine
<i>P. douglasiana</i>	Douglas pine	5	20-35	?	7-10	20-35	W Mexico	tropical
<i>P. durangensis</i>	Durango pine	6(7-8)	12-20	?	7-10	30-40	N & C Mexico	tropical
<i>P. echinata</i>	shortleaf pine	2(3)	4-7	3-5	4-7	15-30(35)	SE USA	tropical
<i>P. edulis</i>	Colorado pinyon	2	2-4	4-6	3-6	5-15	SW USA	temperate
<i>P. elliotii</i>	slash pine	2-3	15(30)	2	8-18	25-30	SE USA	temperate
<i>P. engelmannii</i>	Apache pine	(2)3-4(5)	25-35	?	(10)-15	25(-30)	W Mexico, Arizona, New Mexico	temperate/montane
<i>P. fenzliana</i>	Fenzel pine	5	4-18	?	6-10	13-20(50)	S China to C Vietnam	temperate

Table 1.1. 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 parentheses indicate exceptional dimensions). Only those subspecific taxa that are discussed in detail in this volume are included.

<i>Pinus</i> taxon <sup>a</sup>	Common name <sup>b</sup>	Needle no. <sup>c</sup>	Needle length (m) <sup>c</sup>	Needle longevity (yrs) <sup>c</sup>	Cone length (cm) <sup>c</sup>	Height (m) <sup>c</sup>	Biogeographic region <sup>d</sup>	Habitat <sup>e</sup>
<i>P. flexilis</i>	limber, or Rocky Mountain white pine	5	3–8	5–6	7–15	7–15 (247)	W 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	SE USA	temperate
<i>P. greggii</i>	Gregg's pine	3	8–15	2–3	5–14	10–15(25)	E Mexico	tropical
<i>P. halepensis</i>	Aleppo pine	2(3)	6–12(15)	2	5–12	10–20(25)	Medit. Basin	mediterranean coastal
<i>P. hartwegii</i>	Hartweg pine	3(4–5)	8–16	?	8–14	20–30	Mexico, Guatemala	tropical/subalpine
<i>P. heldreichii</i>	Heldreich whitebark, or Bosnian pine	2	6–10	2–3(67)	7–8	20(30)	Balkan Peninsula and Italy	temperate
<i>P. herreriae</i>	Herrera pine	3	10(10–25)	?	2–3(4)	20–25(35)	W Mexico	tropical
<i>P. hwangshanensis</i>	Hwangshan (Huangshan) pine	2	5–9	?	4–6	25	C and E China	temperate
<i>P. jaliscana</i>	Jalisco pine	4–5	12–16	?	4–8	20–30	W 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	NE Mexico	arid/montane
<i>P. juarezensis</i>	Sierra Juarez pinyon	5	1.5–4	?	3.5–5	15	Baja California, S California	arid/montane
<i>P. j. x. P. monophylla</i> [= <i>P. quadrifolia</i> ]	Parry pinyon	4	3–5	?	4–6	5–10	Baja California	arid/montane
<i>P. kesya</i>	Khasi, or Khasya pine	3	12–20(22)	2	5–7(10)	20–35(45)	SE Asia	tropical
<i>P. koraiensis</i>	Korean stone pine	5	(6)8–13	2	9–20	20–35	Korea, Japan, NE China, Siberia	temperate montane
<i>P. krempfi</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	S Mexico	tropical
<i>P. leiophylla</i>	smooth-leaved, or Chihuahuan pine	5	5–9(15)	2	4–6(5)8	20–25(30)	Mexico, Arizona, New Mexico	temperate montane
<i>P. longaeava</i>	western, Great Basin, or Intermountain bristlecone pine	5	1.5–3	10–33(45)	6–9.5	16	W USA	subalpine
<i>P. luchuensis</i>	Luchu pine	2	15–20	?	<5	<20	Japan, Ryukyu Islands	temperate
<i>P. lumholtzii</i>	Lumholtz pine	3	(15)20–30	?	4–5(7)	10–20	C Mexico	tropical
<i>P. massoniana</i>	Masson, or Chinese red pine	2	15–20	?	5–6	30–40	C and E China, Taiwan	temperate montane
<i>P. maximartinezii</i>	Martinez, or Maxi pinyon	5	7–11	5	15–23	6–10	C Mexico	arid/montane
<i>P. maximinoi</i>	Maximino pine	5	15–28	?	5–8	20–35	S Mexico, Central America	tropical
<i>P. merkusii</i>	Merkus, or Tenasserim pine	2	17–25	1.5–2	5–9	20–35	SE 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	SW USA to N Baja California	arid
<i>P. monticola</i>	western white pine	5	(4)7–13	3–4	14–25(30)	50–55(70)	W 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	NE Mexico	arid
<i>P. nigra</i>	European black, or Austrian pine	2	8–16	4(8)	3–10	20–40	Europe, Medit. Basin	temperate
<i>P. nubicola</i>	Perry's pine	5–6(7–8)	25–43	?	10–15	25–30	S Mexico, Central America	tropical
<i>P. occidentalis</i>	Hispaniolan pine	(3)4–5	11–18	?	5–7(8)	18	Hispaniola, W Cuba	tropical montane
<i>P. occarpa</i>	eggcone pine	(3–4)5	20–25	?	6–10	15–30	Mexico & Central America	tropical
<i>P. palustris</i>	longleaf pine	3(57)	20–45	2	15–25	25–30	SE USA	temperate
<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	E Mexico	tropical
<i>P. peuce</i>	Macedonian, or Balkan (white) pine	5	6–12	?	8–15	20–30	Balkan Peninsula	temperate montane

Table 1.1. (cont.)

<i>P. pinaster</i>	maritime, or cluster pine	2	(10)15–20(25)	3	10–22	20–35(40)	W Medit. Basin	mediterranean coastal
<i>P. pinocarpa</i>	weeping, or Pince pinyon	3	6–8(14)	7	5–10	4–10	NE 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	Medit. 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)	W USA	temperate montane
<i>P. praetermissa</i>	Styles' pine	5	8–16	7	3–5	15	W Mexico	tropical
<i>P. pringlei</i>	Pringle's pine	3(4–5)	15–25	7	5–8	15–30	S Mexico	tropical
<i>P. pseudostrobus</i>	Mexican false white, or false Weymouth pine	5(6–8)	20–25	7	8–15	30–40	S Mexico, Guatemala	tropical montane
<i>P. pumila</i>	dwarf stone pine	5	4–6	5	3–5(6)	1–4	E Asia	boreal forest, subalpine
<i>P. pungens</i>	Table Mountain pine	2	5–7(9)	3	6–10	15–20	NE USA	temperate
<i>P. radiata</i>	Monterey, or radiata pine	(2)3	9–15	3–4	7–15	10–30(40)	California, Baja California	mediterranean coastal
<i>P. remota</i>	Texas, or paper-shell pinyon	2	3–5	?	2.5–3.5	3–8	Texas, NE Mexico	arid
<i>P. resinosa</i>	red pine	2	12–18	4–5	3.5–6	20–30(40)	NE USA, Canada	temperate
<i>P. rigida</i>	pitch pine	(2)3	5–10(12)	2–3	3–4(5–10)	10–25(30)	NE USA	temperate
<i>P. roxburghii</i>	Chir pine	3	20–30	1–3	10–15(20)	40–50+	Himalayas	temperate montane
<i>P. rzędowskii</i>	Rzędowski pinyon	(3)4(5)	6–10	?	10–15	15–30	SW 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	5	15–20	2–3	5–8	20	SE USA	temperate
<i>P. sibirica</i>	Siberian stone pine	5	(5)10–13	7	6–12	20–35	Central Asia	boreal forest
<i>P. squamata</i>	Qiaojia pine	5	9–17	?	9	?	SW China	subtropical montane
<i>P. strobus</i>	eastern white pine	5	6–10(12)	2–3	8–20	25–30(40)	NE 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)	N & W-C China	temperate montane
<i>P. taeda</i>	loblolly pine	3	12–22	3–4	6–12(15)	20–30	SE 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	7	4–7	50	Central America	tropical
<i>P. teocote</i>	twisted-leaved, Mexican small-cone, 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)	E 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	SW 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

## Notes:

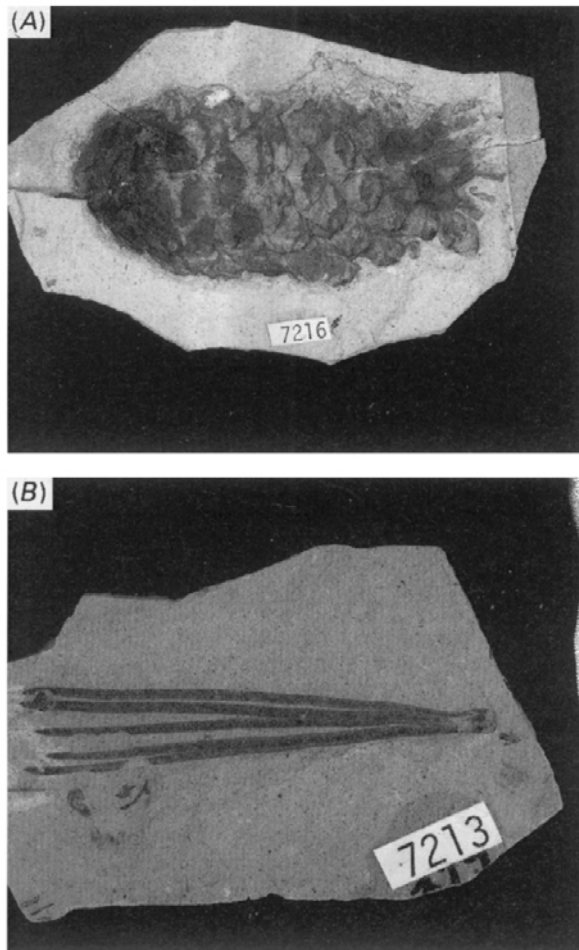
<sup>a</sup> Nomenclature follows Price, Liston & Strauss (Chap. 2, this volume).

<sup>b</sup> Criteria used in compiling the list of common names included: (1) the extent and history of common usage in English (some misnomers were discarded); (2) where several names exist we chose the one(s) that describe clearly recognizable features of the pine as first choice, next the geographical range or habitat of the species, next the anglicized version of the latin name. Preference was also given to common names that allude to the position of taxa within super-specific taxa (e.g. \_\_\_\_ white pine for the taxa in section *Strobus*, subsection *Strobbi*). In all cases, the first name given is the recommended common name. In a few cases, changes from current common usage are suggested (e.g. *P. brutia* for which we prefer the name East Mediterranean pine; *P. pinea*, commonly known as the Italian stone pine, but here called the Mediterranean stone pine; *P. sabiniana* where foothill pine is used in preference to Digger pine). The new English names for *P. nubicola* and *P. praetermissa* proposed here honour their respective describers, Jesse P. Perry and Brian T. Styles, both prominent scholars of Mexican pines. For a more comprehensive list of names, readers should refer to the Glossary of common names (p. 490).

<sup>c</sup> Main sources of data: Original species descriptions and Looek (1950); Den Ouden & Boom (1965); Dallimore & Jackson (1966); Mirov (1967); Farjon (1984); Perry (1991); Vidaković (1991); Young & Young (1992); Kindel (1995).

<sup>d</sup> Main sources of data: Critchfield & Little (1966); Perry (1991).

<sup>e</sup> Main source of data: Mirov (1967); Perry (1991); Kindel (1995).



**Fig. 1.2. Evidence reviewed in Chap. 3 (this volume) suggests that pines made their first Tertiary appearance at many middle-latitude locations during the Oligocene, recolonizing areas where they had occurred in the Mesozoic. The figure shows a fossilized cone (A) and needles (B) from the Late Oligocene Creede flora from Colorado, USA (c. 27.2 million years ago; see Table 3.4, p. 79 for palaeo-coordinates). These specimens (UCMP 7213 and 7216) have been assigned to *Pinus crossii*, an ancestor of the extant bristlecone and foxtail pines in subsection *Balfourianae*. Taxa of this subsection, whose basal position in the phylogeny of the haploxyton pines has been confirmed by recent biochemical studies (Chap. 2, this volume), were probably confined to middle-latitude refugia in the Rocky Mountains during the early Tertiary (photographs kindly supplied by D.M. Erwin, Museum of Paleontology, University of California, Berkeley).**

angiosperms diversified and spread they began to replace the formerly dominant gymnosperms. The latter were deposited to small, cool or dry refugia in polar latitudes and scattered upland refugia at middle latitudes (e.g. the present Rocky Mountains and Japan). These habitats have remained the principal domain of gymnosperms. The widespread displacement of gymnosperms by the rampant angiosperms led to the splitting of several subsections of *Pinus* into northern and southern groups. Kremenetski *et al.* (Chap. 4, this volume) discuss the impor-

tance of the division of subsection *Pinus* into northern refugial populations in western Siberia, mid-latitude populations in eastern Asia, and southern refugial populations in other parts of Asia and Europe for evolution within the genus. Intensive mountain-building events in some areas, with further climate change, created the environmental heterogeneity that drove the radiation of pine taxa in several areas which became secondary centres of diversification in *Pinus* (notably Mexico and north-eastern Asia). Angiosperms which were adapted to tropical conditions declined dramatically throughout middle latitudes following climatic deterioration at the end of the Eocene. This permitted pines to expand their ranges (Fig. 1.2). Radiations of subsections *Contortae*, *Oocarpae* and *Ponderosae*, and of many species within subsections seem to date to this period. Millar & Kinloch (1991) provide an excellent review of the events described above, and Millar (Chap. 3, this volume) describes in more detail the role of Eocene phenomena in shaping the ecology and biogeography of *Pinus*.

Like the Eocene, the Pleistocene was also characterized by profound environmental changes. However, whereas events in the Eocene completely reshuffled elements of the genus (Millar 1993), Pleistocene changes caused pine species and populations to shift first south, then north (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. For example, populations of the progenitor of *P. banksiana* and *P. contorta* were separated into disjunct eastern and western populations (Critchfield 1985; see also section 1.6.8 and Chapters 6 and 9, this volume, for further discussion). Whereas North America and northern Europe experienced massive glaciations during the Pleistocene, northern Asia did not. This region was, nonetheless, affected by significant changes in climate associated with the alternation between glacial and non-glacial periods. These fluctuations probably caused the separation of closely related species such as *P. pumila* and *P. sibirica* during glacial periods, and may have played a role in speciation or at least the preservation of distinctive genotypes (Chap. 4, this volume). Although phenomena such as these have been important for the evolution of pines, Pleistocene events seem to have been less pivotal than those of the Eocene (see Chap. 3, this volume). 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, semi-disjunct populations. Such distributions may have served to promote interspecific diversity while not necessarily promoting speciation (see Chap. 6, this volume). Geological history prevented pines from migrating south of the Sahara, south of Nicaragua in the Americas, or from entering the Australian continent; their

recent success in the southern hemisphere shows that large parts of these regions are most suitable for pines.

The previous paragraphs have given a very brief (and highly simplified) account of some prominent events that have influenced the evolution and migration of pines since the Cretaceous. To understand the current distribution of pines, however, the changes in abundance and geographic ranges that have occurred since the end of the last glacial period, i.e. during the last 10 000 years, are especially important. The study of fossil pollen from sediments has facilitated the compilation of detailed pollen maps (e.g. Huntley & Birks 1983). Analysis of these has shown that pines generally expanded their ranges more rapidly into deglaciated regions of North America and Europe than other tree taxa in most areas (Chapters 4–6, this volume). Different taxa moved at different rates and different habitats showed different degrees of resistance to invasion by pines and other taxa. Recorded rates of spread of *Pinus* species range from 81–400 m yr<sup>-1</sup> in North America to 1500 m yr<sup>-1</sup> in Europe (MacDonald 1993). Species such as *P. banksiana* and *P. contorta* in the western interior of North America probably reached their current distributions relatively recently, whereas others such as *P. sylvestris* migrated rapidly in the early postglacial. Estimates of population growth also vary greatly, with a doubling time of 73 years for *P. sylvestris* to over 1000 years for *P. contorta* subsp. *latifolia* and other undifferentiated pine species (references in MacDonald 1993). Significant variation in population growth, even within a species, has also been observed. For instance, MacDonald & Cwynar (1991) found a high degree of regional variability in population growth rates of *P. contorta* subsp. *latifolia*, suggesting that invading populations spread and/or grew at different rates in different regions. The rates and patterns of these postglacial migrations have left clear imprints on patterns of genetic variation between and within pine taxa (Cwynar & MacDonald 1987; Chap. 13, this volume). Ledig (1993) discusses the examples of *P. jeffreyi* and *P. monticola* which show little genetic differentiation among sites or elevations in the northern parts of their ranges, but substantial differentiation in California. This is presumably because too few generations have passed since they colonized the northern areas to permit genetic adaptation of populations to local environments. Another classic example is the evolution of pygmy-forest edaphic subspecies of *P. contorta* on marine terraces in coastal northern California (Aitken & Libby 1994; see section 1.6.7).

The Quaternary history of the climate and vegetation of southwestern North America was poorly understood until the discovery by Wells & Jorgensen (1964) that middens built by packrats (*Neotoma* spp.) provide abundant plant fossils. Recent analyses of middens preserved for up to 40 000 years at many sites in the Rocky Mountains, the Great Basin, and deserts throughout the western USA and

Mexico, have greatly improved our understanding of the history of pines in these areas. Probably the most dramatic floristic change revealed by the study of these ‘natural time capsules’ was the replacement of pinyon–juniper woodland by desert scrub in the Great Basin between two and three thousand years after a period of rapid warming 13 000–14 000 years ago (Long *et al.* 1990; see Chap. 9, this volume, for further discussion).

The chapters in Part III – *Historical biogeography* describe the events that have shaped pine distribution in four important regions: northern Asia (Chap. 4), Europe (Chap. 5), northern North America (Chap. 6), and Mexico and Central America (Chap. 7). Two chapters in Part IV – *Recent biogeography* describe in more detail the role of events over the past few centuries on the distribution of pines in the Mediterranean Basin (Chap. 8) and the American Southwest (Chap. 9).

### 1.3 Pines compared with other conifers and broadleaved trees

Pines share certain features with the other genera in the Pinaceae (*Abies*, *Cathaya*, *Cedrus*, *Keteleeria*, *Larix*, *Nothotsuga*, *Picea*, *Pseudolarix*, *Pseudotsuga* and *Tsuga*). Price *et al.* (Chap. 2, this volume) show that pines are most similar to *Cathaya* and *Picea* in overall morphology, and to *Cathaya*, *Larix* and *Picea* if one considers wood anatomy and seed and cone-scale morphology. The immunological comparisons of seed proteins reviewed in Chap. 2 (this volume) suggest that pines and spruces occupy relatively basal positions in the phylogeny of Pinaceae, a finding that is consistent with the fossil record. In terms of ecology, pines are closest to firs (*Abies* spp.) and spruces (*Picea* spp.) with which they frequently co-occur; these three genera are very prominent in the northern hemisphere and often dominate the vegetation in which they occur. It is, however, in the role of aggressive post-disturbance colonizers that pines are most clearly differentiated from firs, spruces, other conifers, and angiosperm trees. An idealized ‘pine prototype’ would conform with the following profile: a light-demanding, fast-growing, sclerophyllous 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. That this is an oversimplification becomes obvious when one considers the wide range of habitats in which pines occur (see later) and the range of life-history syndromes evident in the genus (Chap. 12, this volume).

Among the factors that have contributed to the rapid migration and population increases of pines in the Holocene are: their abundant output of seeds from an



early age; their ability to recruit dense daughter stands on exposed sites soon after disturbance; effective mechanisms for long-distance seed dispersal; a mating system that permits inbreeding and selfing in isolated trees; and various life-history traits that confer resilience at the population level under a wide range of disturbance regimes; and the ability to colonize nutrient-poor sites. These attributes enabled pines to undergo rapid range changes through a combination of neighbourhood diffusion and long-distance dispersal. In such a 'stratified dispersal process', their initial range expansion occurs mainly through the recruitment (in response to disturbance) of large numbers of offspring near parent plants. However, as the range of the founding population expands, new colonies created by long-distance migrants increase in number to cause an accelerating range expansion in the later phase. Pine expansion provides a model case of the stratified diffusion process described by Hengeveld (1989; see also Shigesada, Kawasaki & Takeda 1995). This behaviour also explains the response of pines to recent changes in disturbance regimes (see below).

*Abies*, *Picea* and *Pinus* are all listed as prominent taxa in six of Takhtajan's (1986) 35 floristic regions of the world (Circumboreal; Eastern Asiatic; North American Atlantic; Rocky Mountain; Irano-Turanian; and Madrean). In these regions, pines generally thrive on the poorest soils, whereas firs and spruces require slightly more fertile (and heavier in *Picea*) soils. Pines are also prominent in Takhtajan's Mediterranean Region, which lacks *Picea* and has very limited representation of *Abies* which requires better soils. Regions with the greatest diversity of dominant pine species are the Madrean (29 species listed), North American Atlantic (14 species), Eastern Asiatic (9 species), Rocky Mountain (8 species) and Mediterranean (6 species). Regions where *Abies* and *Picea* are prominent but where *Pinus* is absent as a recognized dominant include Takhtajan's Manchurian Province (Eastern Asiatic Region) and Western Asiatic Subregion (Irano-Turanian Region). Taxa of the other northern hemisphere conifer genera are represented in far fewer floristic regions, and are less abundant and generally less important in ecosystems than pines. Pines also differ from southern hemisphere conifers which, with a few exceptions (e.g. *Agathis australis* in New Zealand and *Araucaria araucana* and *Fitzroya cupressoides* in Chile; Enright *et al.* 1995), are usually relatively minor components of the vegetation or have highly localized occurrences.

#### 1.4 Morphological traits of pines

##### 1.4.1 Growth form and size

Pines, like many other conifers, have the characteristic of monopodial growth and large size. The largest species of

pines in the world are centred in distribution in California and the Pacific Northwest of the USA. Growth conditions in these regions favour immense size in many genera, including *Abies*, *Picea*, *Pseudotsuga*, *Sequoia*, *Sequoiadendron*, *Thuja* and *Tsuga* (Waring & Franklin 1979). The largest species of pine in both height and girth is *P. 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 (Table 1.1). Many Mexican pines grow in mountain areas with annual rainfalls of 1200–2000 mm or more (e.g. *P. ayacahuite*, *P. hartwegii*, *P. maximinoi*, *P. tecunumanii*), but they usually reach heights of only 20–50 m. Similarly, *P. caribaea* var. *hondurensis* which grows in Belize, Honduras and Nicaragua, in probably the wettest habitats of any pine where annual rainfall may commonly reach 2000–3000 mm, reaches only 20–30 m in height.

Pines can, however, be quite short in stature in more extreme habitats. The pinyon pines as a group (11 species in section *Parrya*, subsection *Cembroides*), growing in habitats with 300–600 mm of rain annually, usually attain heights of 5–10 m when mature (Table 1.1). Timberline pines also may be low-growing, particularly when they occur as *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 favourable conditions. At least two species, however, *P. mugo* in the European Alps, and *P. pumila* in East Asia and Japan, occur most characteristically with a low shrubby growth form.

The characteristic monopodial growth form of pines is absent in the unusual *P. sabintiana* in the foothills of California, which lacks apical dominance after the juvenile period and has a branched main trunk like that of hardwood species. *Pinus bungeana* from China and *P. maximartinezii* from Mexico have similar habits. Monopodial growth may also be lost in *krummholz* growth forms of pines which attain a distinctly shrubby canopy.

##### 1.4.2 Whole-tree longevity

Many pines are very long-lived, and the two bristlecone pines, *P. aristata* and *P. longaeva* (Fig. 1.3), are the oldest living organisms in the world, with the latter reaching documented ages of nearly 5000 years (Currey 1968). The oldest living *P. aristata* was aged to 2435 years (Brunstein & Yamaguchi 1992). Nooden (1988) lists two other pine species, *P. cembra* (1200 years) and *P. sylvestris* (500 years) among the longest-lived plants in the world, but several other pines could also make this list. According to Schweingruber (1993), *P. balfouriana* may live as long as the bristlecone pines, *P. flexilis* can live for more than 2000 years, *P. jeffreyi* and *P. ponderosa* for >1000 years, and *P. con-*



Fig. 1.3. Western bristlecone pines, *Pinus longaeva*, growing on poor soils on the White Mountains of California, USA, which are characterized by a cold and dry climate. Trees at this site have been aged to nearly 5000 years – the oldest living organisms on Earth. Tree rings from three trees that give a continuous time series from 8000 years ago to the present were analysed for the composition of stable hydrogen isotopes. This record, which shows the presence of a postglacial climate optimum 6800 years ago and a continuous cooling since then, serves as a reference for other climate indicators (Feng & Epstein 1994) (photo: W.D. Stock).

*torta* subsp. *murrayana* and *P. monticola* for up to 500 years. *Pinus heldreichii* has been aged to >800 years in Calabria, southern Italy (Serre Bachet 1985).

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 (Fritts 1976). Douglas, an astronomer, became Director of the Lowell Astronomical Observatory in Flagstaff, Arizona, in 1894. With research interests in sunspot activity and possible related impacts on climate, Douglas was drawn to the possibility that tree rings might contain climatic records that would not otherwise be available from existing weather stations. Working with *P. ponderosa* in the Flagstaff area, Douglas developed the concept of cross-dating to compare and extend these tree-ring measures over broad regional areas to identify year-to-year variation in climate. It was this pine research that led him to establish the Laboratory of Tree Ring Research at the University of Arizona in 1906.

Collaborative work beginning in 1914 by Douglas with Clark Wissler, a prominent anthropologist at the American Museum of Natural History, 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 >2000 years, and had profound impacts in the field of anthropology.

Although the field of dendrochronology has expanded greatly in scope and depth since these early studies and involves work with many tree genera throughout the world (Schweingruber 1993), research with pines still



Fig. 1.4. Cross-section of *Pinus ponderosa* from Kings Canyon National Park, California, showing a record of fire scars from 1722 to 1994. This section was collected by Chris Baisan, Kiyomi Morino, James Risser and Robert Shay of the University of Arizona's Laboratory of Tree-Ring Research.

forms the heart of this field (see e.g. Cook & Kairiukstis 1990). Pines contain the longest single chronologies available (*P. longaeva* in the western USA; Fig. 1.3) and some of the most sensitive chronologies for evaluating regional patterns of climate (e.g. Brunstein 1996 and references therein). Tree-ring chronologies are also proving to be valuable records of alteration of typical forest growth regimes resulting from atmospheric pollution or other causes. Fire histories over long periods can be inferred from scars on pines (Arno & Sneek 1977; Fig. 1.4), providing useful records of past conditions at a site.

#### 1.4.3 Cone and seed morphology

The form and morphology of pine cones is highly variable, with obvious relationships to the reproductive biology of individual species (Chap. 12, this volume). In terms of size, the greatest length of cone in any pine occurs in *P. lambertiana*, where the elongate cones reach up to 50 cm in length. In terms of weight of fresh cone, the record probably belongs with the large globular cones of *P. coulteri* from California which are 20–35 cm in diameter and may weigh as much as 2.3 kg. Large cones are also present in the Mexican taxa *P. ayacahuite*, *P. devoniana* and *P. maximartinezii*