

## 4 The late Quaternary dynamics of pines in northern Asia

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### Introduction

Northeastern Asia is home to about 20 *Pinus* species. A diverse fossil flora of pines attests to the presence of the genus in northern Asia since at least the Cretaceous (Millar 1993), making this a potential region of origin of *Pinus* (Mirov 1967; Millar 1993). However, the reclassification of purported Jurassic and Cretaceous Asian pine fossils into extinct pinaceous genera makes the case for an Asian centre of origin less compelling than previously thought (Millar 1993; Chap. 3, this volume). During Eocene climatic shifts northern Asia appears to have served as a refugium for pines displaced from more southerly zones. These displacements occurred because of warm conditions and increased competition from angiosperms (Millar 1993). The division of subsections such as *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 was extremely important for evolution within the genus. *Pinus sylvestris* seems to have its origins in a northern Asian Eocene refuge, while *P. densiflora* and *P. thunbergii* may have arisen from a mid-latitude location near eastern China and Japan (Millar 1993).

Although northern Asia did not experience the massive Pleistocene glaciations of North America and northern Europe, the region was affected by significant changes in climate associated with the alternation between glacial and non-glacial periods (Velichko *et al.* 1984). These climatic variations caused major alterations in vegetation, including the distribution of pines. Although Millar (1993; Chap. 3, this volume) does not believe that these Pleistocene shifts were as significant for the evolution of pines in Asia as were the earlier Eocene events, the separation of closely related species such as *P.*

*pumila* and *P. sibirica* during glacial periods may have played a role in speciation or at least the preservation of distinctive genotypes. In any case, the modern distribution of pines reflects changes in abundance and geographic ranges that have occurred since the end of the last glacial period. In this chapter we will examine the late Quaternary history of pines in Siberia-Mongolia, China and Japan. Where possible, we will outline the possible locations of refugial populations of *Pinus* during the last glacial maximum. We will attempt to infer the environmental factors that influenced the postglacial distributions of *Pinus* species in northern Asia. Finally, we will discuss some evolutionary implications of the Quaternary history of pines in northern Asia.

Reconstruction of the postglacial history of pine in northern Asia is based mainly upon fossil pollen sampled from peat, lake sediment and loess. Pine macrofossils are also an important source of data. Such palaeoecological data are available from a number of sites in Siberia, China and Japan. Similar data are extremely sparse from southern Asia. *Pinus* pollen cannot be subdivided beyond the section *Strobos* and section *Pinus*. However, macrofossil remains of pines are sometimes encountered and allow for greater floristic precision. As in most parts of the world, pine pollen tends to be over-represented relative to the actual percentages of pine trees in the vegetation. This is because of (1) the high production of pollen by pines, (2) the potential of the grains for long-distance aerial transport, and (3) their high potential for preservation. For example, in Inner Mongolia, eastern Tibet, and southeastern Qinghai, which are near the distributional limits of pines, *Pinus* contributes 10% or more of the total pollen sum (Li 1991; K.-b. Liu, unpublished data). *Pinus* pollen

occurs sporadically in surface samples from the interior plateaus and desert basins of Tibet and Xinjiang, hundreds of kilometres beyond the limits of pine (Li 1991). Most strikingly, Wu & Xiao (1995) found 10–40% (mean = 26.5%, of total pollen sum) *Pinus* pollen in the Zabuye Salt Lake area of southwestern Tibet, where the nearest pine trees are at least 400 km away. Studies of modern pollen deposition in Zhongtiao Shan & Kunming also demonstrated that *Pinus* pollen occurs at 20–30% in surface sample sites where pine trees are locally absent (Wu & Sun 1987; Yao 1989). The over-representation of pine, particularly in cases where its pollen occurs beyond the range of the genus, argues for caution in attempting to delineate exact range boundaries from the fossil record. The pine pollen record can be considered to provide, at best, an indication of general regions where pine was present in the past.

All ages presented here are radiocarbon years Before Present (BP) with present being taken as AD 1950. Radiocarbon years do not exactly equal calendar years and this difference increases with age (Stuiver & Reimer 1993). For example, a radiocarbon age of 10 000 BP is roughly equivalent to a calendar date of 12 000 years ago.

## 4.2 Siberia and Mongolia

### 4.2.1 Introduction

Siberia and Mongolia experienced pronounced changes in vegetation due to climate variations related to glacial cycles. The three common pines that we will discuss are *P. pumila* (dwarf stone pine), *P. sibirica* (Siberian stone pine) and *P. sylvestris* (Scots pine). *Pinus pumila* and *P. sibirica* are members of the section *Strobus* and their pollen cannot be separated. *Pinus sylvestris* belongs to the section *Pinus* and has pollen that is distinctive from the other two species. Sufficient fossil pollen sites exist to produce tentative maps of the postglacial spread of these three species. These maps are based on the assumption that the first continuous appearance of *Pinus* pollen at a site represents the presence of the genus in the regional vegetation (Ritchie & MacDonald 1986). Macrofossil records are present at some sites, but are less common than pollen records.

### 4.2.2 *Pinus sylvestris*

*Pinus sylvestris* is extremely widespread in Eurasia (Fig. 4.1) and occupies a number of environmental settings (Fig. 4.2). The northeastern limit of the species in Siberia probably reflects its inability to withstand cool summers and extremely cold winters (Vakovski 1958). The southern limits appear to be determined by the aridity of the steppe zone.

From available Russian studies, a preliminary map of



Fig. 4.1. Modern distribution of *Pinus sylvestris* in Asia and the postglacial spread of the species as evidenced from fossil pollen and plant macrofossil records (based on data from: Neustadt 1967, 1976; Vipper 1968; Kind, Gorshkov & Chernysheva 1969; Levkovskya *et al.* 1970; Neustadt & Selikson 1971; Zubakov 1972; Kutafieva 1973, 1975; Volkov *et al.* 1973; Glebov *et al.* 1974; Kind 1974; Vipper & Golubova 1976; Vipper *et al.* 1976; Khotinsky 1977; Koltsova, Starikov & Zhidovlenko 1979; Arkhipov & Votakh 1980; Koshkarova 1981, 1986, 1989; Zubarev 1981; Firsov *et al.* 1982; Levina *et al.* 1983, 1987; Krivonogov 1988; Glebov 1988; Klimanov & Levina 1989; Chernova *et al.* 1991; Kulagina & Trofimov 1992; Kremenetski, Tarasov & Cherkinski 1994).

the postglacial spread of *P. sylvestris* can be developed (Fig. 4.1). Most records are from fossil pollen as macrofossils of the species are very rare in Siberia. During the last glacial there were probably only a few isolated locations in Siberia where *P. sylvestris* persisted. A good candidate would be the upper Irtysh River valley where the species has likely been present for the past 14 000 years and perhaps the Ob valley near the city of Novosibirsk where it has been present for at least 10 000 years (Fig. 4.1).

*Pinus sylvestris* appears to have moved northwards during the early postglacial and grew beyond its present limits along the Yennisy River by 8000 BP. This northward extension of *P. sylvestris* along the Yennisy is convincingly proven by the presence of seeds in a radiocarbon-dated peat deposit (Koshkarova 1986). The species retreated to its present northern limits later in the Holocene, probably as a result of climatic cooling. Expansion southeastward was slower and the species did not reach its northeastern range limits in Siberia until about 6000 BP. It is not clear when it reached its extreme southeastern limits along the Amur River. *Pinus sylvestris* was not present at its extreme southern limits in Siberia and Mongolia until 5000 BP. The relatively slow spread southwards may reflect warm and dry conditions during the early to mid-Holocene, or the



Fig. 4.2. *Pinus sylvestris* occurs in a wide range of habitats in Eurasia, ranging from rocky sites to moist bog margins. The picture shows Scots pine on a rock outcrop on the NW shore of Lake Baikal, Siberia (Russia). Rocky sites such as this provide habitats which are seldom affected by high-intensity, stand-replacing fires. Extremely old pines can be found on such sites (photo: J.G. Goldammer).

relative sparseness of suitable sites for the species in those regions.

#### 4.2.3 *Pinus sibirica*

*Pinus sibirica* has a more restricted range than *P. sylvestris*, with which it is closely sympatric (Fig. 4.3). In general, its northern and eastern range is controlled by summer and winter cold, while to the south, aridity is the main determinant of distribution.

The pollen of *P. sibirica* cannot be distinguished from that of *P. pumila*. However, the ranges of the two species overlap only in Trans-Baikal region and southern Yakutia (Figs. 4.2, 4.3), where *P. pumila* often grows as understorey in *P. sibirica* forests. Thus, over most of the modern range, pollen of the section *Strobus* can be attributed to *P. sibirica*.

It is likely that the main glacial refuges for *P. sibirica* lay to the southwest in the upper part of the Irtysh River valley where evidence of presence of the species extends back to 12 000 BP (Fig. 4.3). Other refugia include the Yennisy,



Fig. 4.3. Modern distribution of *Pinus sibirica* in Asia and the postglacial spread of the species as evidenced from fossil pollen and plant macrofossil records (based on data from: Neustadt 1967, 1976; Vipper 1968; Kind *et al.* 1969; Levkovskya *et al.* 1970; Neustadt & Selikson 1971; Volkov *et al.* 1973; Glebov *et al.* 1974; Kind 1974; Vipper & Golubova 1976; Vipper *et al.* 1976; Khotinsky 1977; Koltsova *et al.* 1979; Arkhipov & Votakh 1980; Arkhipov, Levina & Panychev 1980; Koshkarova 1981, 1986, 1989; Zubarev 1981; Levina *et al.* 1983; Krivonogov *et al.* 1985; Krivonogov 1988; Glebov 1988; Klimanov & Levina 1989; Chernova *et al.* 1991; Kulagina & Trofimov 1992).

Kriaz, Tuva and northern Mongolian intermountain valleys (Vipper *et al.* 1976; Levina *et al.* 1987; Krivonogov 1988). The postglacial spread of the species appears to have been in an easterly direction and occurred slightly more slowly than *P. sylvestris* (Fig. 4.1). *Pinus sibirica* may not have been present at its modern southern range limits in Siberia and Mongolia until 6000–5000 BP (Fig. 4.3). It did not advance to its present eastern limits until 6000–4000 BP. The wide range of arrival dates in most regions suggests that the spread and subsequent population growth of *P. sibirica* occurred by the founding of small populations with variable growth rates. The main period of spread and population growth for *P. sibirica* occurred between roughly 8000 and 4000 BP. This may reflect the predominance of warm conditions in Siberia at that time.

#### 4.2.4 *Pinus pumila*

*Pinus pumila* occupies the major part of Russian Far East, Medny Island (Komandorski archipelago), Kurily Islands, Sakhalin and adjacent portions of the Japanese Islands, Korea and China (Fig. 4.4). It grows as far west as the Lena and Oleniek River basins and occurs at alpine treeline sites down to sea level. *Pinus pumila* dominates the vegetation over much of the Russian Far East, but may also occur as an understorey tree in *Larix* forests. It is able to extend its



Fig. 4.4. Modern distribution of *Pinus pumila* in Asia, and: fossil pollen sites with evidence of *P. pumila* presence throughout the Holocene; macrofossil sites presenting evidence of *P. pumila* northern range extension during the Holocene; location of disjunct stands of *P. pumila* along the Oleniok River (based on data from: Tikhomirov 1946, 1949; Korzhuyev & Federova 1962, 1970; Serebrianny 1965; Belorusova *et al.* 1977; Khotinsky 1977; Nikolskaya 1980; Yegorova 1982; Stefanovich *et al.* 1986; Andreev *et al.* 1989; Andreev & Klimanov 1991; Lozhkin & Federova 1989).

range into regions with extremely cold winters due to its prostrate habit during the winter.

Given its ability to withstand cold conditions, during the last glacial maximum *P. pumila* may have been present in many parts of its modern range on isolated sites that possessed suitable soil and microclimatic conditions. If this is the case, the general range of *P. pumila* did not change much from the end of the last glacial through the postglacial and *P. pumila* populations in the mountains of Japan, Korea and China may well be relicts from the period of the last glaciation. Although full glacial records are rare, work from some postglacial sites in Siberia support this contention. In the region of Lake Baikal *P. pumila* was probably present during the whole Holocene. In the Lena River basin of Yakutia (Andreev & Klimanov 1991; Andreev *et al.* 1989) pollen of *P. pumila* occurs without any major fluctuation during the entire Holocene. On Sakhalin Island (Khotinsky 1977) abundant pollen of *P. pumila* is found in deposits from the end of the late glacial. Results of pollen investigations in Kamchatka suggest that thickets of *P. pumila* from the mountains to near sea level have been present since the beginning of the Holocene (Khotinsky 1977). However, near Magadan on the eastern coast of northern Asia the species appears to have been absent until 9000 BP (Lozhkin *et al.* 1993). It is possible that dry-cold conditions during the winter restricted the occur-

rence of the species in the Far East during the last glacial maximum (Lozhkin *et al.* 1993). These small populations, persisting on favourable sites, then expanded during the early postglacial, allowing the rapid appearance of the species in a number of regions.

Detailed analysis shows that there have been changes in *P. pumila* distribution and population density near the edges of its present range. In the southeast there has been an increase in the importance of the species in the late Holocene. At Kradeno Lake near Yakutsk (Khotinsky 1977) there is a rise of *P. pumila* pollen after 5000–4500 BP, which seems representative of an expansion of *P. pumila* thickets in the mountains due to climatic cooling. A similar expansion is reported from near Magadan (Lozhkin *et al.* 1993). A major expansion of *P. pumila* thickets also occurred in Kamchatka after c. 5000 BP (Yegorova 1982).

In contrast, northern regions have witnessed a contraction in *P. pumila* range in the late Holocene. Pollen data (Stefanovich *et al.* 1986) show that in the area of Penzhina Bay the species was most widespread between 8000 and 5200 BP. A pollen diagram from Elchikanski Lake demonstrates that the expansion of thickets of *P. pumila* in the Kolyma Mountains began at 8000 BP (Lozhkin & Federova 1989). At 5000 BP an expansion of *P. pumila* thickets occurred in the upper part of Indigirka River basin (Belorusova, Lvelius & Ukraintseva 1977). *Pinus pumila* bark was identified in a layer of peat in the first terrace of the Lena River (not in the floodplain) near Chekurovka (Korzhuyev & Federova 1962, 1970). The layer of peat is dated  $5610 \pm 200$  BP (Serebrianny 1965). Seeds of *P. pumila* were also identified in non-dated Holocene peat in the eastern part of the Taymyr Peninsula (Nikolskaya 1980). These finds, coupled with the presence today of isolated *P. pumila* in the Oleniok River basin (Fig. 4.4), suggest that between 8000 and 5000 BP the range of *P. pumila* in north-east and north-central Siberia extended further northwest than now. Restriction of *P. pumila* range in this part of Siberia and the isolation of stands in the Oleniok River basin was probably caused by climatic cooling at 5000–4500 BP. At the same time climatic deterioration favoured an expansion of *P. pumila* in the subalpine belt in the southeastern Siberian mountains.

## 4.3 China

### 4.3.1 Modern distribution

There are 22 species of *Pinus* in China, including 12 species of the section *Strobus* and 10 species of the section *Pinus* (Zheng 1983). Pines are widely distributed throughout the forested regions of China (Fig. 4.5), from the tropical monsoonal rain forest in Yunnan, Guangdong, Hainan and

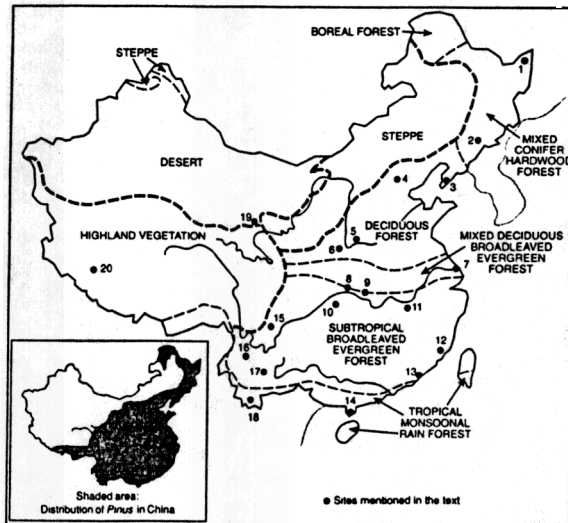


Fig. 4.5. Map of key *Pinus* pollen sites discussed in the text, in relation to the vegetation regions of China: 1. Qindeli, Sanjiang Plain (Xia 1988), 2. Gushantun Bog, Changbai Mountain (Liu 1989), 3. Pulandian, Liaodong Peninsula (Guiyang Institute of Geochemistry 1977), 4. Fenzhuang, Beijing (Kong & Du 1980), 5. Zhongtiao Mountain (Yao 1989), 6. Beizhuangcun, southern loess plateau (Wang & Sun 1994), 7. Qidong, Yangtze River delta (Liu *et al.* 1992), 8. Shennongjia, middle Yangtze River valley (Liu 1990), 9. Jiang-Han Plain, middle Yangtze River valley (Liu 1991), 10. Nanping Bog, Hubei (Gao 1988), 11. Lushan (Li 1985), 12. Daiyun Mountain, Fujian (Liu & Qiu 1994), 13. Han Jiang delta (Zheng 1991), 14. Leizhou Peninsula (Lai & Zheng 1993), 15. Lake Shayema, Sichuan (Jarvis 1993), 16. Xi Hu, Yunnan (Liu *et al.* 1986), 17. Dianchi, Yunnan (Sun *et al.* 1986), 18. Xishuangbanna, Yunnan (Liu *et al.* 1986), 19. Qinghai Lake (Du *et al.* 1989), 20. Zabuye Salt Lake, Tibet (Wu & Xiao 1995). The insert map shows the general distribution of the genus *Pinus* in China. The thick broken lines are the primary vegetation boundaries between the forest, steppe, desert, and highland biomes. The thin broken lines separate different forest regions within the forest biome.

Taiwan in the south to the taiga in Xiao Xingan Ling in the extreme northeast. It extends westwards beyond the forest-steppe ecotone and exists in the grassland regions of southeastern Inner Mongolia, the Loess Plateau, the southeastern part of the Qinghai-Tibetan Plateau, and along the Himalayas. It is absent in the vast desert and plateau regions west of Qinghai Lake, except for the Altai Mountain in the extreme northwestern corner of China (*P. sibirica*). Altitudinally, *Pinus* grows from coastal plains to 3600 m (*P. densata*) in the mountains of western Sichuan and southeastern Tibet (Zheng 1983). The large number of sympatric species means that the following discussion of the history of pine in China must be organized by regions, rather than by species.

*Pinus* pollen generally accounts for 20–60% of the arboreal pollen (AP) sum in forested regions. In the temperate mixed conifer/hardwood forest of the Northeast, *Pinus* accounts for 15–50% of arboreal pollen and usually co-dominates with *Betula* in the surface samples from the Changbai Mountain (Zhou *et al.* 1984; Sun & Wu 1988a). In the temperate deciduous forest of the Zhongtiao

Mountains *Pinus* co-dominates with *Betula*, *Carpinus* or *Quercus*, and accounts for 30–90% of the arboreal pollen (Yao 1989). In the Shennongjia Mountains of the northern subtropical broadleaved evergreen forest, even where pine trees are locally absent, it still accounts for 10–30% of the modern pollen rain (Liu 1990). In surface samples from Lushan in the northern part of the subtropical broadleaved evergreen forest, *Pinus* occurs at 15–90% and co-dominates with *Castanopsis* and *Quercus* (Li 1985). In surface samples from Yunnan and Sichuan in the south-western part of the subtropical broadleaved evergreen forest, *Pinus* is present at 20–85% and co-dominates with *Alnus*, *Cyclobalanopsis*, or *Castanopsis/Lithocarpus* (Wu & Sun 1987; Sun & Wu 1988b; Jarvis & Clay-Poole 1992).

#### 4.3.2 Early Quaternary occurrence of pine

*Pinus* pollen is abundant (40–80% of AP sum) in the classical Early Pleistocene Nihewan Formation in North China (Liu 1988), suggesting that pines were an important component of the glacial-stage vegetation at that time. These pollen assemblages also contain much *Abies* and *Picea*, with a mixture of Tertiary relicts such as *Podocarpus*, *Dacrydium*, *Keteleeria* and *Tsuga*. The data imply that pine existed in an Early Pleistocene forest in North China that was probably without modern equivalent. *Pinus* pollen is present consistently in several long boreholes from the North China Plain and the Lower Yangtze River valley (Liu & Ye 1977; Liu 1988), suggesting that pine persisted in these regions throughout the Quaternary. Nevertheless, fluctuations in *Pinus* pollen percentages in these long records may imply significant changes in pine population size in response to environmental changes in the Quaternary.

#### 4.3.3 Northeast China

Several well-dated pollen records from Northeast China show major changes in the abundance of *Pinus* during the late Pleistocene and Holocene. Pollen assemblages co-dominated by *Pinus* and *Picea/Abies* dating to 23 000–40 000 BP indicate that pine was an important component of the coniferous forest that prevailed in Northeast China before the last glacial maximum (c. 18 000 BP) (Liu 1988). The widespread occurrence of *Coelodonta* and *Mammuthus* fossils and relict periglacial features suggests that late Pleistocene climate was much colder than the present. Pollen data directly dated to the last glacial maximum are rare from this region. Wang & Sun (1994) inferred that much of today's temperate mixed forest and deciduous forest regions of Northeast China and North China were covered by *Artemisia* steppe with some open woodland under a cold and arid climate during the glacial maximum. It is reasonable to expect, however, that *Pinus* was not completely eliminated from the Northeast but

instead survived in small populations in favourable habitats throughout the cold and dry stage. Its populations were probably decimated on the alluvial lowlands and plains, where pine trees are uncommon even today. The mountain ranges (Changbai Mountain and Xiao Xingan Range) may have provided refuge for pine and other conifers (spruce and fir) to survive the increased aridity of the glacial maximum.

*Pinus* populations in Northeast China were still quite small and restricted during the late glacial and early Holocene. At the Gushantun bog (elevation 500 m) in the Changbai Mountain, *Pinus* pollen is present at 5–10% of a total pollen sum in the basal pollen zone dating to 9500–13 000 BP (Liu 1989). At Qindeli on the Sanjiang alluvial plain near the extreme northeastern 'horn' of Northeast China, *Pinus* pollen is essentially absent in the basal sediments dated to 10 000–12 000 BP (Xia 1988). *Pinus* pollen is also essentially absent in the basal sediments of 8000–10 000 BP age in the Pulandian peatland in the Liaodong Peninsula (Guiyang Institute of Geochemistry 1977). The late glacial to early Holocene pollen spectra from Northeast China are typically dominated by *Betula*, accompanied by relatively high percentages of *Picea/Abies* or *Artemisia*. Pine must have been only a minor component of this *Betula*-dominated forest or woodland.

Pine populations remained small in Northeast China from 10 000 to about 4000 BP. During the mid-Holocene, the climate in Northeast China became warmer and more humid, allowing deciduous hardwoods such as *Corylus*, *Juglans*, *Quercus* and *Ulmus* to increase in abundance (Liu 1988). Since about 5000–4000 BP, *Pinus* populations have increased dramatically throughout Northeast China. In many pollen records *Pinus* increased sharply from <5 to >30%, accompanied by a slight increase in *Picea/Abies* and a remarkable decline in the pollen of deciduous hardwood trees. The expansion of pine in the Northeast during the late Holocene is probably due to climatic cooling, which favoured the temperate pine species like *Pinus koraiensis* over the thermophilous hardwoods. Human disturbance was not the cause for this vegetational change, because the northern part of Northeast China remained sparsely populated until the 20th century.

#### 4.3.4 North China and Northwest China

A pollen record from Beizhuangcun (altitude 570 m) south of the Loess Plateau shows episodic expansions and contractions of *Pinus* populations between 27 000 and 23 000 BP, followed by a decline in forest and expansion of steppe (Wang & Sun 1994). By 18 000 BP forest had virtually disappeared and much of North China was covered by *Artemisia* steppe or open woodland (Wang & Sun 1994). As in the case of Northeast China, pine populations in North China were probably reduced and restricted to favourable

habitats during the last glacial maximum. In a pollen diagram from Fenzhuang near Beijing, *Pinus* pollen increases to nearly 20% briefly after 13 000 BP in a pollen zone dominated by *Abies*, *Larix* and *Picea*, followed by a slight decline and some fluctuations over the next three millennia (Kong & Du 1980). In most sites *Pinus* is an important component of the pollen assemblages throughout the Holocene. During the mid-Holocene deciduous hardwood trees increased at the expense of pine, but pine increased again after 5000–4000 BP in response to climatic cooling (Zhou *et al.* 1984; Li & Liang 1985; Liu 1988). In some pollen records *Pinus* pollen percentages show some remarkable fluctuations during the Holocene (Kong, Du & Zhang 1982; Xu *et al.* 1991). However, these pollen changes do not exhibit a regionally consistent pattern and may only reflect variations in local vegetation or sedimentary changes.

A pollen diagram from Qinghai Lake (near the present western limit of *Pinus* in Northwest China) provides a sensitive record of changes in *Pinus* distribution over the last 11 000 years (Du, Kong & Shan 1989). *Pinus* pollen is essentially absent from the sediments of Qinghai Lake before 8000 BP. During the mid-Holocene (8000–3500 BP), *Pinus* pollen increased to 20–50% of all pollen and spores. This was followed by fluctuating but declining values between 3500 and 1500 BP. *Pinus* pollen has declined to about 5% since 1500 BP. The data therefore suggest that *Pinus* probably extended its range westwards to invade the southern edge of the steppe during the mid-Holocene, in response to a warmer and more humid climate due to a stronger summer monsoon.

#### 4.3.5 Tropical and subtropical China

Pollen data from a long borehole in the Yangtze River delta (Liu & Ye 1977) suggest that southeastern China was forested throughout the Quaternary, and *Pinus* has generally been an important component of the regional vegetation. Superimposed on this general trend are several episodes of *Pinus* population expansion and contraction that have been documented from various sites across the vast territories of the Chinese tropics and subtropics.

Two detailed pollen records from the Hanjiang delta and the Leizhou Peninsula in the tropical monsoonal region of coastal Guangdong document an expansion of *Pinus* populations between 28 000 and 23 000 BP. The increase in *Pinus* pollen is accompanied by peaks in the pollen of subtropical broadleaved deciduous elements (*Carpinus*, *Fagus*, *Quercus*) and tropical alpine conifers (*Dacrydium*, *Podocarpus*, *Taxus*, *Tsuga*), suggesting climatic cooling of about 4 °C in the Chinese tropics (Zheng 1991; Lei & Zheng 1993). By contrast, in Xishuangbanna, Southwest Yunnan, *Pinus* pollen declined abruptly during an interval inferred to be around 30 000 BP when

Podocarpaceae (*Dacrycarpus*, *Dacrydium*) pollen was most abundant, perhaps reflecting a climate with wetter, though not cooler, winters (Liu *et al.* 1986). These pollen changes probably reflect local population changes in the watershed around the lake basin instead of large-scale ecological movements or range shifts.

During the last glacial maximum the winter and summer temperatures of the South China Sea were about 6 °C and 2 °C cooler than the present, respectively (Wang & Sun 1994). Significant cooling on land is also evident from the limited pollen data available. *Abies* and *Picea* pollen increased considerably between 21 000 and 14 000 BP in two pollen records from the Hubei Province in the north-central subtropics (Gao 1988; Liu 1991). *Pinus* pollen percentages were also relatively high (10–30%) at that time. At Xi Hu (altitude 1980 m), northwestern Yunnan, *Abies* and *Picea* descended at least 500 m downslope during the period 17 000–15 000 BP when the mean annual temperature was estimated to be 2.5–4.0 °C cooler than the present (Lin, Qiao & Walker 1986). The vegetation of the lower slopes around the lake basin shortly after the last glacial maximum was inferred to be dominated by *Pinus* and evergreen *Quercus* mixed with some *Abies*, *Picea*, *Sabina* and *Tsuga*. *Pinus* pollen accounts for 30–90% of all pollen from trees and shrubs during this period, and remains dominant throughout the entire pollen record spanning the last 17 000 years (Lin *et al.* 1986).

The pollen records from Yunnan suggest that *Pinus* has remained an important or dominant component of the vegetation throughout late-glacial and Holocene times (Lin *et al.* 1986; Sun *et al.* 1986). Some fluctuations do occur in the *Pinus* pollen curve during the last 14 000 years, but precise reconstruction of its history is complicated by problems in dating and the over-representation of *Pinus* pollen. In core DZ18 from Dianchi *Pinus* pollen seems to decrease from 60 to 20% during an unspecified interval around 10 000 BP (Sun *et al.* 1986). *Pinus* pollen becomes more frequent during 10 000–7500 BP in Xi Hu (Lin *et al.* 1986). In another core (DZ13) from Dianchi *Pinus* pollen decreases remarkably between 8000 and 4000 BP, perhaps in response to a more equable climate with warmer winters and reduced rainfall seasonality (i.e. less intense spring drought). *Pinus* expanded again after 4000 BP when the modern climatic pattern with strong rainfall seasonality began to develop (Sun *et al.* 1986).

Elsewhere in the Chinese subtropics *Pinus* also seems to dominate the vegetation during the late Pleistocene and Holocene with only minor population changes. No major changes in *Pinus* abundance were detected in the middle or lower reaches of the Yangtze River valley (Liu 1991; Liu *et al.* 1992). In Lake Shayema (altitude 2400 m), southwestern Sichuan, *Pinus* pollen percentages were relatively low (18% of total pollen sum) between 11 000 and 10 000 BP. It

increased rapidly to 50–60% after 10 000 BP and occurred persistently at about 40% throughout the Holocene (Jarvis 1993).

A pollen study from the Daiyun Mountain of central Fujian provides insight into the origin of the pine woodland in the Chinese subtropics (Liu & Qiu 1994; Qiu 1994). The pine woodland, characteristically dominated by *P. masoniana* with a dense ground cover of *Dicranopteris* ferns and grasses, is a very common secondary vegetation type on the denuded hill slopes of subtropical Southeast China today. A pollen record from a subalpine site (altitude 1360 m) presently surrounded by open pine woodland shows that the basin slopes were originally covered by a dense subtropical mixed conifer–hardwood forest in which pine was absent or rare. The pollen of *Castanopsis*, *Cryptomeria* and *Quercus* declined abruptly about 1100 years ago, apparently as a result of deforestation caused by humans. This was followed by a dramatic increase in *Pinus*, Poaceae, and *Dicranopteris*, indicating the development of the pine woodland (Liu & Qiu 1994; Qiu 1994). The study implies that the ubiquitous pine woodland landscape of Southeast China is a landmark of intensified human disturbance in the Chinese tropics and subtropics during the last one or two millennia.

#### 4.4 Japan

##### 4.4.1 Introduction

Much of the knowledge of the postglacial vegetation history of Japan available in the English-language literature comes from the efforts of Tsukada (1967, 1983, 1985, 1988). This brief account will draw heavily from his published work. Common pine species in Japan include *P. pumila* on alpine sites, *P. koraiensis* and *P. parviflora* in subalpine forests, and *P. densiflora* and *P. thunbergii* in more temperate and coastal forests. *Pinus* pollen is well represented in the modern pollen rain of Japan, ranging from c. 6% to 74% of the total sum (Tsukada 1988). The first three species listed above are from the section *Strobus* and not generally differentiated on the basis of pollen. *Pinus densifolia* and *P. thunbergii* are from the section *Pinus* and have so-called diploxylon pollen. They can be differentiated from the other three species, but not from each other. The degree of sympatry between the species makes it difficult to unravel their individual histories except where macrofossils are available.

##### 4.4.2 Glacial distribution

Pine was an important component of the glacial vegetation (Fig. 4.6) of Japan from the northern island of Hokkaido (likely *P. pumila*), through the northeastern

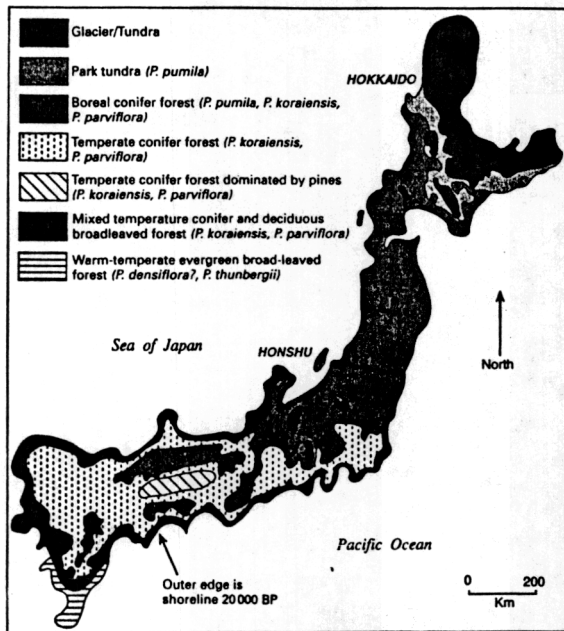


Fig. 4.6. Glacial vegetation of Japan (c. 20 000 BP) and probable distribution of pine species (vegetation map after Tsukada 1985, 1988).

portion of the main island, Honshu (probably *P. koraiensis* and *P. parviflora*) and down to lowlands of the south (Tsukada 1985, 1988). The inferred dominance of *P. pumila* in the north reflects the potential of that species to survive the cold conditions that existed during the last glacial maximum. It was probably important in the park tundra of northernmost unglaciated Hokkaido (Fig. 4.6). In Honshu a large number of *P. koraiensis* macrofossil have been recovered from glacial-age sediments (Tsukada 1985). These provide proof of the widespread presence of that species at that time. The general absence of diploxylon pine pollen (Tsukada 1988) argues against the presence, or at least importance, of *P. densiflora* or *P. thunbergii* in the glacial vegetation of the archipelago.

#### 4.4.3 Late-glacial and postglacial history

A decrease in *P. pumila* occurs in central Honshu around 16 000 to 15 000 BP and signals the transition from full-glacial to late-glacial conditions (Tsukada 1988). Further declines in pine pollen occurred between 13 000 and 10 000 BP. As climate warmed, deciduous trees became increasingly important, with *Fagus* reaching northern Honshu and *Quercus* reaching Hokkaido by 10 000 BP. The importance of pine in the temperate regions of the islands continued to decline in response to warm temperatures through the period 7000–4000 BP.

At approximately 2500 to 2000 BP climatic cooling during the late Holocene is manifested in an increase in

the importance of *P. pumila* on Hokkaido (Tsukada 1988). A dramatic increase in diploxylon pine pollen is registered in almost all regions of Honshu, Shikoku and Kyushu during the late Holocene. This is probably due to the increased importance of *P. densiflora* as a successional species on sites cleared for agriculture (Tsukada 1988). This rise is time transgressive in response to the spread of agriculture geographically. At some sites in the south the rise of pine occurs as early as 6000–4000 BP, while at northern sites it does not occur until 800–700 BP (Tsukada 1988). Thus, the present abundance of *P. densiflora* in Japan is largely an artefact of human activity.

#### 4.5 Discussion

*Pinus* is a highly diverse genus in terms of both number of species and intraspecific genetic variability (Chap. 13, this volume). Although Eocene events may be responsible for the main features of pine species diversity in eastern Asia (Millar 1993), the Quaternary history of the region has probably played a significant role in some aspects of both maintaining interspecific differences and also mitigating against speciation events. Three general patterns of pine distributional response to glacial conditions are evident. In the north, *P. sibirica* and *P. sylvestris* were essentially eliminated from their present eastern ranges in Siberia. In northern China, the middle portion of our study area, pine abundances decreased and populations were likely to have been restricted to scattered refugia. In southern China, the abundance of pine was at a maximum during the last glacial in a number of regions. This is also the case for some pines in parts of Japan. These distributional changes could have important impacts on genetic diversity.

In Siberia *P. sibirica* was absent from its modern range during the last glacial. In contrast, *P. pumila* probably persisted in areas of its present range. *Pinus pumila* and *P. sibirica* only became sympatric in the mid-Holocene. There have been as many as 17 glacial periods in the Quaternary, and they have generally lasted longer than interglacials (Bowen 1979). For much of the last 2 million years *P. sibirica* has been isolated from the closely related *P. pumila*. Similarly, *P. sylvestris* has been isolated from other members of the subsection *Sylvestres* such as *P. densiflora* and *P. thunbergii* in eastern Asia during both the last glacial and the Holocene. Such long allopatry would help to foster and maintain genetic differences between these related species.

The persistence of *P. pumila* in small isolated populations in Siberia during glacials and the separation of Japanese and mainland pine populations would serve to enhance genetic variability within the species by pro-



moting and preserving changes brought on by genetic drift and the different selective pressures that might be experienced by different refugial populations. A similar enhancement of genetic diversity through genetic drift and differing selection pressures may have affected pine species such as *P. armandi*, *P. bungeana*, *P. koraiensis* and *P. tabuliformis* that would have experienced population reductions and range fragmentation during glacial periods in northern China and adjacent areas. Conversely, in some southern portions of the study areas, it might be during interglacials, such as the Holocene, when certain pine species experience population declines and range fragmentation.

The high intraspecific genetic variability of pines would impart plasticity that is helpful in the shifting of ranges in response to Quaternary climatic oscillations. During the transitions from glacials to non-glacials and vice versa, pine species would have to accommodate to differing soils, climate, photoperiods and competitive pressures. The shifts in range and changes in abundance could also mitigate against speciation events. Genetically iso-

lated populations would be brought back into contact with other populations as ranges and pine abundance increased during favourable periods. In contrast to the Eocene, when climate oscillations occurred over a span of 20 million years, the Quaternary shifts have all occurred over 2 million years. The short duration of isolation and frequent changes in environmental selection pressures during Quaternary glacial and non-glacial episodes might enhance intraspecific variability but preclude the marked evolution of new species that accompanied the Eocene climate variations (Millar 1993).

### Acknowledgements

This work was supported by a NSERC Special Collaborative Grant and UCLA support to GMM, and a NOAA Grant (NA56GP0215) and NSF Grants (ATM-9410491, SES-9001343) to KBL. This chapter is PACT (Paleoecological Analysis of Circumpolar Treeline) Contribution 8.

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Ecology and  
Biogeography  
of *Pinus*

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