

CONIFEROUS FORESTS OF THE TEMPERATE ZONE OF ASIA

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INTRODUCTION

The vegetation cover of Eastern Asia varies greatly in response to two basic climatic gradients characteristic for the territory. The area stretches from latitude 39°N to 73°N. In accordance with this wide latitudinal range, the climate ranges from temperate in the south to arctic in the north. The differentiation in climate causes a change in vegetation expressed from north to south as a sequence of phytogeographical zones of (1) polar deserts, (2) tundra, (3) dwarf-pine woodlands, (4) boreal forests, and (5) temperate hardwood-conifer and summer-green (deciduous) broadleaved forests. From the coast of the Pacific Ocean there is a continentality gradient towards the interior. The climate on the Komandorskiye and Kurilskiye islands is suboceanic with cold summers and mild winters. In the inner continental regions it changes to ultra-continental with very cold winters and warm summers. The territory of Far-East Asia is usually subdivided into five continentality sectors: (1) suboceanic, (2) maritime, (3) sub-maritime, (4) continental, and (5) ultra-continental (Krestov, 2003). The vegetation in each sector reflects a change in climate from a damp oceanic climate with relatively little seasonal variation to a dry climate with strong seasonal contrast in the inner regions. This change of climate in the temperate zone of Asia is associated with corresponding changes in the vegetation, which varies from mesic broadleaved-coniferous forests on the Pacific islands to excessively dry steppe and deserts in the interior areas on the eastern edge of the continent.

In this chapter we focus on forest vegetation of the temperate zone, characterized by the presence of mixed broadleaved-coniferous and broadleaved deciduous forests in the lower montane belt on zonal sites¹ with the following values of bioclimatic variables: Kira's warmth index² exceeding 45 (Miyawaki and Nakamura, 1988; Grishin, 1995); mean annual temperature exceeding 0°C; summer precipitation exceeding winter precipitation; precipitation always exceeding evaporation. This zone includes vegetation in eastern Japan, the southern Kurilskiye Ostrova, the southernmost area of Sakhalin (Mys Kril'on), North Korea, northeastern China and the southern part of the Russian Far East (Fig. 5.1). In different systems for vegetation classification this zone has been called the Far Eastern Broadleaved-coniferous Area (Y.Y. Vasiliev, 1947), the Pan-Mixed forest zone (Tatewaki, 1958), the broadleaved-Korean pine forest zone (Kolesnikov, 1961), the hemiboreal subzone of the boreal zone and the northern subzone of the temperate zone (Hämet-Ahti et al., 1974), the Cool-temperate mixed needle-leaved forest zone (Song, 1998), and the Cool Temperate region (Miyawaki and Nakamura, 1988).

AREA AND VEGETATION ZONALITY

Main divisions of the Asian temperate zone

The continental part of the Asian temperate zone comprises the southern part of the Russian Far East as well as northeastern China, in the basin of the Amur River on the spurs of the mountain ranges Sikhote Alin Gory, Badzhalskiy Khrebet, the Lesser Hingan

¹ "Zonal site" is a key term in biogeoclimatic ecosystem classification (Kojima, 1981; Pojar et al. 1987). In zonal sites, the vegetation reflects the climate, rather than local effects of soil, slope, insolation, snow packs, cold-air drainage and other non-climatic factors. Where such local influences are important, the site is described as "azonal".

² Kira's warmth index (WI) is defined as $WI = \sum \max \{0, (T_i - 5)\}$, where T_i is the mean temperature in °C of the i th month (Kira, 1945, 1977).

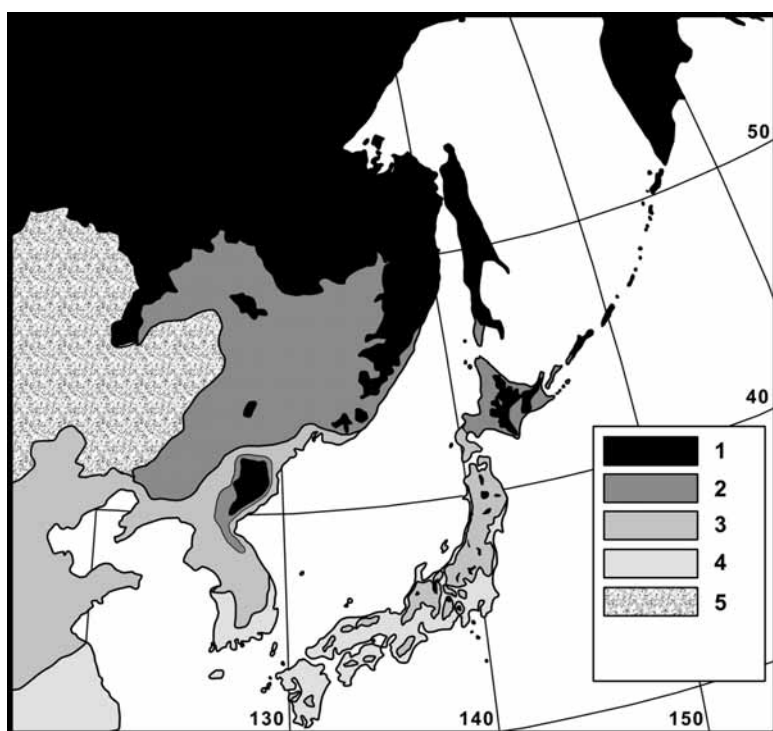


Fig. 5.1. Sketch of the main vegetation zones in temperate Asia: 1: boreal and oroboreal zone, 2: cold temperate zone and mountain belt, 3: cool temperate zone and mountain belt, 4: warm temperate zone and mountain belt, 5: temperate steppe and deserts in the continental sector of the cold and cool temperate zones.

Range, Changbai Shan and Laoye Ling. The valley of the Amur River permits oceanic air masses to penetrate deep into the interior, considerably shifting the eastern boundary of the continental climate inland. On the other hand, the influence of continental cold air masses tends to increase strongly in winter-time. This creates a contrast between summer and winter seasons in the area with very low winter temperatures (the average mean temperature in January is -20°C) and relatively high summer temperatures (mean August temperatures reach $+22^{\circ}\text{C}$), in addition the maritime region at 40°N also faces high humidity (Table 5.1). The high annual temperature ($+2-8^{\circ}\text{C}$) in combination with seasonal climatic contrast causes a great variety in vegetation types occurring on zonal sites in the zone.

The gradient of climate continentality causes a change in vegetation, which ranges from drought-tolerant oak forests in the interior to species-rich mixed broadleaved-conifer forests on the coastal areas. Along the gradient of continentality three areas are recognized as belonging to the cold temperate zone.

The **Daurian Mongolian oak area** lies mostly in northeastern China and extends in the west to northeastern Mongolia. In the Russian Far East, where it stretches over the upper part of the Amur River basin called Dauriya and the basin of Ozero Khanka (= Hanka). The basic forest type is the Mongolian oak (*Quercus mongolica*)³ in pure stands or mixed with *Betula davurica*. The conifer forests in the area are dominated by *Pinus densiflora*, which forms stands on the ridges and southern slopes, occasionally affected by fires near Ozero Khanka, and *Pinus sylvestris*, forming stands on sandy soils in the upper Amur regions.

The **Manchurian Broadleaved-Conifer area** lies on the spurs of the Sikhote Alin mountain range and on the southern spurs of the Lesser Hingan, the Bureinskiy and the Badzhal'skiy mountain ranges. The main vegetation type is broadleaved-Korean pine forests dominated by *Pinus koraiensis* and (south of 44° latitude) *Abies holophylla*, and a number of broadleaved species: *Betula costata*, *Fraxinus mandshurica*, *Kalopanax septemlobus*, *Phellodendron amurense*,

³ Nomenclature of vascular plants follows Kharkevich (1985-96) and Ito and Hinoma (1985-94).

Table 5.1
Climatic data in the temperate and orotemperate zone¹

Area and station	Latitude	Longitude	Mean temperature (°C)			Annual precipitation (mm)
			Annual	Coldest month	Warmest month	
Asian mainland						
Birobidzhan	49°N	133°E	-0.1	-24.6	20.3	761
Blagoveshchensk	50°N	127°E	0.0	-24.3	21.4	525
Khabarovsk	49°N	135°E	1.4	-22.3	21.1	569
Sovetskaya Gavan'	49°N	140°E	-0.4	-19.4	16.5	742
Dal'nerechensk	46°N	134°E	1.5	-21.9	20.7	627
Roshchino	46°N	135°E	0.3	-24.4	20.4	789
Terney	46°N	137°E	2.3	-14.0	17.4	813
Kirovskiy	45°N	134°E	1.9	-21.8	21.0	646
Ol'ga	44°N	135°E	3.6	-12.4	18.9	831
Ussuriysk	44°N	132°E	3.2	-19.1	21.2	599
Vladivostok	43°N	132°E	4.8	-13.5	21.0	831
Ryazanovka	43°N	131°E	5.2	-11.4	20.5	961
Changbai Res. St.			3.3	-19.5	19.2	733
Yeongju			11.6	-5.5	25.0	994
Islands						
Yuzhno-Sakhalinsk	47°N	143°E	2.1	-13.8	17.3	753
Ulegorsk	49°N	142°E	1.6	-14.8	17.0	600
Mys Kril'on	46°N	142°E	3.8	-7.6	15.9	960
Kurilsk	45°N	148°E	4.3	-7.2	16.0	1040
Okedo	44°N	144°E	5.7	-9.3	20.2	910
Shirataki	44°N	143°E	5.2	-9.5	19.5	981

¹ Simplified from Anonymous (1966–71).

Quercus mongolica, *Tilia amurensis*, *T. mandshurica* and *Ulmus japonica* (Kolesnikov, 1956a; Krestov, 1997). Normally in a forest community the number of tree dominants is 3–5 species. At an elevation of 600–800 m above sea level, the temperate forest communities may be enriched with the boreal dominants *Abies nephrolepis* and *Picea jezoensis*.

Other vegetation types in the area are broadleaved valley forests with *Fraxinus mandshurica* and *Ulmus japonica* in the old and stable parts of the river valleys, *Populus koreana* and *P. maximowiczii* in the younger parts of river valleys and *Chosenia arbutifolia* on the fresh alluvial deposits. The poorly drained parts of the Ussuri valley are occupied by grass meadows.

The amount of old-growth forests in the area has drastically decreased during the 20th century as a result of forest exploitation and fires. Secondary forests include mixed broadleaved forests with no conifers, *Betula platyphylla* and *Populus tremula* forests, and

Quercus mongolica forests with no conifers, depending on ecological features of the site and the factors causing damage.

The temperate forest vegetation in the suboceanic climate on southern Sakhalin and the southernmost Kuril'skiye islands (Kunashir, Shikotan, Habomai-shoto) differs from the temperate forest vegetation on the continent because of the dominants and the species composition reflecting the influence of the Sino-Japanese flora. The main vegetation type is mixed *Abies sachalinensis*–*Quercus crispula* forests with *Sasa*, which is a fruticose grass related to bamboo. The major part of the area lies on the island of Hokkaido north of the Kuromatsunai lowlands, where it borders on *Fagus crenata* forests (Miyawaki and Nakamura, 1988). The zonal vegetation in the area is mixed *Abies sachalinensis*–*Quercus crispula* forest with an admixture of broadleaved species such as *Fraxinus mandshurica*, *Kalopanax septemlobus* and *Tilia maximowicziana*.

The moist lowlands are occupied by wet meadows, swamp and bog with *Calamagrostis langsdorffii*, *Carex thunbergii* and *Myrica tomentosa* fringed by *Alnus japonica*–*Fraxinus mandshurica* forests. *Fraxinus mandshurica* and *Ulmus japonica* form forests with *Cercidiphyllum japonicum* in the second tree stratum and *Dryopteris crassirhizoma*, *Lysichiton camtschatcense*, *Symplocarpus renifolius* and *Trillium camtschatcense* in the understorey.

The Japanese Archipelago is affected by the oceanic climate, influenced by the cold Aleutian Current from the Pacific side, and the warm Japan Current from the Sea of Japan. The northern part of Tohoku and the southern part of Hokkaido within the latitudinal range from 39° to 42°N are in the cool temperate zone, and Hokkaido except the Oshima peninsula, the southern Kurilskiye islands and the southern part of Sakhalin from 42°N to 49°N are in the Pan-Mixed forest zone (Tatewaki, 1958) of the continent. The mean annual temperature is +6°C and the mean annual precipitation 815.3 mm (Abashiri climatic station in northern Hokkaido, observations of 1961–1990, unpubl. data). The boundary line between the boreal and temperate zones corresponds to Schmidt's Line, which crosses central Sakhalin as the floristic boundary line between the Euro-Siberian and Sino-Japanese floral regions (Tatewaki, 1958). The mixed forests of Hokkaido are composed of *Abies sachalinensis*, *Picea jezoensis* and *Quercus crispula*. On the other hand, the coniferous forests of Honshu (the zonal vegetation of the oroboreal belt) are composed of *Abies mariesii*, *A. veitchii*, *Larix kaempferi*, *Picea jezoensis* var. *hondoensis* and *Tsuga diversifolia*. Azonal vegetation, such as a convex site in the temperate zone, includes *Pinus densiflora*, *P. koraiensis*, *P. parviflora* var. *pentaphylla*, *Thuja standishii* and *Thujopsis dolabrata*.

Vertical distribution

Far-Eastern Asia is a montane area. Mountain systems vary greatly in origin, age, height, present geological processes, and basic orientation. The change of climate along the elevation gradient causes a change in vegetation. The areas described are characterized by a definite sequence of vertical belts and by the altitude at

which each zone occurs. The latter varies depending on a number of geomorphologic factors, among which the general exposure has the clearest effect on the altitude of a belt, making it higher on southern and lower on northern slopes (Fig. 5.2).

The general sequence of vertical zones in the subarctic sector of the temperate zone repeats the sequence seen from south to north, appearing from bottom to top as summer-green broadleaved forests, broadleaved–conifer forests, dark-conifer⁴ evergreen forests, *Betula ermanii* forests, *Pinus pumila* thickets and alpine tundra (Rozenberg and Vasiliev, 1967; Miyawaki and Nakamura, 1988; Okitsu, 2003). A vertical belt in most cases may be considered as an analogue of a horizontal zone in its physiognomy as well as its species composition. However, depending on the region, the species composition of a vertical zone may be enriched by species from the zones above or below it (Krestov, 1999).

Similarity of cold temperate and boreal forests

The position of the northern boundary of the temperate zone has been a subject of continuous discussion among phytogeographers since the beginning of the 20th century. This discussion is still ongoing because of the very complicated relationships between climate and topography in Far Eastern Asia. The boundary between the temperate and boreal zone along most of its length can be considered as altitudinal, but spatial proximity of two different vegetation types has a great mutual influence. This affects the controversial decisions of phytogeographers to treat the nemoral zone⁵ as an ecotone between the temperate and boreal zones (Walter and Breckle, 1987) or relate nemoral vegetation to the temperate zone (Tatewaki, 1958; Kolesnikov, 1961).

Similarity of oroboreal and boreal forests

The temperate zone in Far Eastern Asia with a humid montane climate is occupied by forests dominated by *Abies*, *Picea*, *Pinus* and *Tsuga*, which are more diverse and richer in species than the boreal forests. The distribution of many species including some forest dominants is restricted to the northern temperate zone.

⁴ In northern Eurasia, a distinction is made between "dark-conifer forests" dominated by spruce (*Picea abies*, *P. obovata*, *P. jezoensis*) and five-needle pines (*Pinus koraiensis*, *P. sibirica*) and "light-conifer forests" dominated by larch (*Larix cajanderi*, *L. dahurica*, *L. sibirica*) and two-needle pine (*Pinus sylvestris*). The proportions of these forest types in the boreal forests of Eurasia are about equal.

⁵ The term 'nemoral' (Lat. *nemus*=grove) is used in European and Russian geobotany for mesothermic broadleaved deciduous forests dominated by species of *Acer*, *Fagus*, *Fraxinus*, *Quercus*, *Tilia*, and other genera. One of the main features of nemoral forests is the relatively high shade tolerance of the trees and capability for regrowth under the canopy or in small gaps.

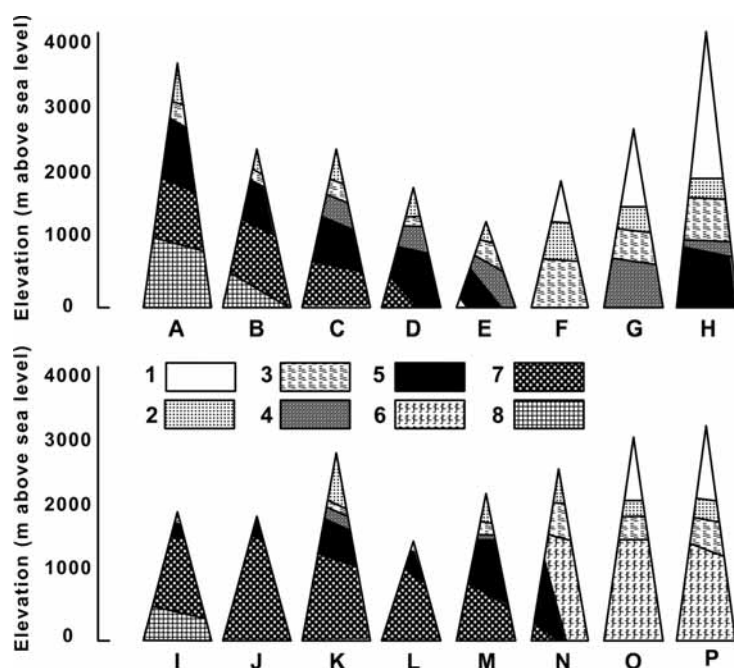


Fig. 5.2. Vertical zones in (top) subarctic-maritime and (bottom) continental sectors of the northeast Asian temperate zone. The diagram for each mountain has the southern slope to the left, the northern slope to the right. A: Fuji-san (135°N 139°E) [Northern slope, 600(summer-green)–1550(coniferous)–2200 m; Southern slope, 850(summer-green)–1800(coniferous)–2450 m]; B: Iwate-san (40°N 141°E) [Northern slope, summer-green 1100 m (coniferous); Southern slope, summer-green 1250 m (coniferous)]; C: Taisetsu-san (44°N 143°E) [Northern slope, summer-green 700 m (coniferous); Southern slope, summer-green 900 m (coniferous)]; D: Kunashir island (44°N 146°E); E: Iturup island (45°N 148°E); F: Paramushir island (50°N 156°E); G: Southern Kamchatka (52°N 158°E); H: Central Kamchatka (55°N 161°E); I: Halla-san (33°N 127°E); J: Jiri (35°N 127°E); K: Changbai range (42°N 128°E); L: Southern Sikhote Alin range (44°N 134°E); M: Central Sikhote Alin range (48°N 138°E); N: Badzhal'skiy range (53°N 135°E); O: Mus-Haya (62°N 141°E); P: Cherskiy range (65°N 146°E). Vegetation belts: (1) nival zone without plants, (2) alpine tundra, (3) subalpine dwarf pine and dwarf alder thickets, (4) subalpine stone-birch forests, (5) boreal dark-conifer (spruce) forests, (6) boreal light-conifer (larch) forests, (7) cool and cold temperate summer-green broadleaved forests, (8) warm temperate evergreen broadleaved forests.

The flora of the Sikhote Alin range includes over 100 endemic species (Qian et al., 2003). On the other hand, there are common circumboreal elements in the herb and moss layers, such as the cryptogams *Dicranum majus*⁶, *Dryopteris expansa*, *Hylocomium splendens*, *Lycopodium annotinum*, *L. complanatum*, *Phegopteris connectilis*, *Pleurozium schreberi* and *Rhytidiadelphus triquetrus*, and the orchids *Goodyera repens* and *Listera cordata*. These species have small and light anemochore diaspores, resulting in effective dispersal.

Peculiarities of conifer-forest distribution in the temperate zone of Eastern Asia

The main feature of the northern temperate zone of Asia is the presence and great importance of conifer species. Their distribution is generally restricted to

the temperate zone, while summer-green broadleaved species are dominant over the whole territory. Because of high fire sensitivity, the nemoral conifers can easily disappear from the communities leaving a great question for researchers; whether the pure broadleaved forests in densely populated and severely deforested regions were originally summer-green broadleaved or whether they used to be mixed with conifers before human influence. Conifer forests in those regions occur in very small areas, as a rule – not comparable in size with the areas of broadleaved forests.

On the other hand, many conifer species are adapted to extreme edaphic conditions within the temperate zone, such as water deficit, wind exposure, nutritionally poor soils, slope processes and others. Table 5.2 lists the conifer forests which are the focus of this chapter, stratified according the scheme of zonality.

⁶ Nomenclature of bryophytes follows Savich-Liubitskaia and Smirnova (1970).

Table 5.2
Zonal and azonal conifer forests in the temperate zone of Far East Asia

Phytogeographical units and main vegetation types	Dominant conifer species	
	Zonal sites	Azonal sites
Cold Temperate Zone		
Daurian Continental Area of <i>Quercus mongolica</i> forest	No conifers	<i>Pinus densiflora</i> , <i>P. sylvestris</i>
Manchurian Submaritime and Maritime Area of broadleaved– <i>Pinus koraiensis</i> and <i>Abies holophylla</i> forests	<i>Abies holophylla</i> , <i>Pinus koraiensis</i>	<i>Larix dahurica</i> , <i>Picea koraiensis</i>
Japanese Maritime and Suboceanic Area of Broadleaved– <i>Abies sachalinensis</i> forest	<i>Abies sachalinensis</i> , <i>Picea jezoensis</i>	<i>Picea glehnii</i>
Cool Temperate Zone and temperate belt in Warm Temperate Zone		
Japanese Broadleaved Suboceanic Area	No conifers	<i>Abies firma</i> , <i>A. homolepis</i> , <i>Chamaecyparis obtusa</i> , <i>Ch. pisifera</i> , <i>Cryptomeria japonica</i> , <i>Picea polita</i> , <i>Pinus densiflora</i> , <i>P. koraiensis</i> , <i>P. parviflora</i> , <i>Pseudotsuga japonica</i> , <i>Sciadopitys verticillata</i> , <i>Thuja standishii</i> , <i>Thujopsis dolabrata</i>
Boreal belt in the Cold Temperate zone		
Belt of mixed <i>Abies nephrolepis</i> – <i>Picea jezoensis</i> and <i>Abies sachalinensis</i> – <i>Picea jezoensis</i> forests	<i>Abies nephrolepis</i> , <i>A. sachalinensis</i> , <i>Picea jezoensis</i>	<i>Picea glehnii</i>
Boreal belt in the Cool Temperate zone		
Belt of mixed <i>Picea jezoensis</i> var. <i>hondoensis</i> – <i>Abies veitchii</i> – <i>Abies mariesii</i> forests	<i>Abies mariesii</i> , <i>A. veitchii</i> , <i>Picea bicolor</i> , <i>P. jezoensis</i> var. <i>hondoensis</i> , <i>P. koyamae</i> , <i>P. maximowiczii</i> , <i>Tsuga diversifolia</i>	<i>Larix kaempferi</i> , <i>Pinus koraiensis</i> , <i>Tsuga diversifolia</i>
Subalpine belt in the temperate zone		
Belt of <i>Pinus pumila</i> thickets in the temperate zone	<i>Juniperus communis</i> var. <i>hondoensis</i> , <i>Pinus pumila</i>	No conifers

CONIFER FORESTS OF THE TEMPERATE ZONE AND THE OROTEMPERATE BELT

Dauriyan broadleaved forests and woodlands

Most of the Dauriyan broadleaved forests lie in the northeast of China extending in the west to northeastern Mongolia. In the Russian Far East they appear in the upper part of the Amur River basin, called Dauriya, and in the basin of Ozero Khanka (Kolesnikov, 1956a). For the past 10–12 centuries, these areas have been

strongly influenced by human activity, which partly explains the state of vegetation in the area today. The vegetation cover now includes meadows, bogs, and forests in nearly equal proportions. Most of the meadows and part of the bogs were converted into agricultural land. The basic forest type is *Quercus mongolica*, either in pure stands or mixed with *Betula davurica*. All components of the forest communities are drought-tolerant and fire-resistant. Fire is the most important factor selecting the species combination in these communities.

⁷ *Pinus densiflora* and *P. sylvestris* are also treated in Chapter 4.

Conifer forests dominated by *Pinus densiflora*⁷ near Ozero Khanka and *P. sylvestris* in the upper Amur occur only as rare communities in azonal sites on the hill slopes and ridges (Krestov and Verkholat, 2003).

Although the climate of this area is humid – that is, precipitation exceeds evapotranspiration – the present-day moisture regime can be characterized as extreme for forest vegetation.

Although *Pinus koraiensis* can tolerate this climate, it has in fact a very restricted distribution in the area, occupying only the most fire-protected sites. The lack of this species on zonal sites is explained by extensive human activity from the Middle Ages to the present day. High anthropogenic pressure affects the present distribution of *P. sylvestris* in the northwest and that of *P. densiflora* in the southeast of the area. The latter species is considered as vulnerable in the Russian Far East and is protected by law.

Manchurian broadleaved–Korean pine forests

Distribution

The broadleaved–Korean pine forest is a zonal vegetation type in the subarctic sector of the northern temperate subzone. It occurs in the Far East of Russia in the Sikhote Alin mountain range and in northeast China in the Changbai Shan, LaoYe and Lesser Hingan mountains. Relatively isolated areas of forests with *Pinus koraiensis* are found in southern Korea (Song, 1988; Kim and Manko, 1994) and on the island of Honshu in Japan (Miki, 1956; Okitsu, 1997), where they are associated with different vegetation types.

The broadleaved–Korean pine forests form the lower vegetation belt from the sea level up to altitudes of 800–900 m. In the southern part of the range they occur up to an elevation of 1100–1200 m (Chun, 1994), coexisting and closely interacting with spruce, larch, and oak forests. The rather wide distribution of this forest type from the seacoast inland, where there is a sharp transition from an oceanic monsoon to a continental climate, have led to marked heterogeneity of vegetation within the zone. It is reflected in mapping of geobotanical districts and vegetation cover (Kolesnikov, 1956b, 1963; Sochava, 1969a,b). The area remained unglaciated during Pleistocene and Holocene times (Grichuk, 1984), although at present it borders

on permafrost areas in the north. The present climatic contrasts, marine transgressions, and the long period of uninterrupted development of vegetation cause a great mixture of northern and southern as well as maritime and steppe elements in the flora and vegetation of the region.

The occurrence of this vegetation type between clearly distinguishable boreal and temperate zones is a subject of disagreement among phytogeographers. However, the dilemma of whether it should be regarded as boreal or temperate, has in recent decades been settled in favour of temperate. Tatewaki (1958) related it to a special Pan Mixed forest zone, temperate in its nature, which includes also climatically and physiognomically similar vegetation of central Europe, for instance in the Carpathian and Tatra mountain systems, and in the eastern part of North America including the northern Appalachian mountains and the surroundings of the Great Lakes, though interrupted towards the interior of the continent by steppes or deserts. Hämet-Ahti et al. (1974) treated this vegetation as the northern subzone of the temperate zone; Sochava (1969b) and Kolesnikov (1963) treated it as belonging to the nemoral and temperate zones, respectively. Russian authors traditionally classified this part of the vegetation cover as a special vegetation area, the so-called “Far Eastern coniferous-broadleaved forest area”. (Y.Y. Vasiliev, 1947; Kolesnikov, 1961; Lavrenko, 1950). Kolesnikov (1956a) suggested naming it the “Eastern Asian area of mixed coniferous–broadleaved forests”, and related it to the temperate zone (Fig. 5.3). The boundaries of the area generally coincident with those of the Manchurian floristic area⁸.

At altitudes of 1100–1200 m in Changbai Shan, 800–900 m in Sikhote Alin and 500–600 m on the southern spurs of the Tukuringra-Dzhagdy and Badzhal’skiy ranges, broadleaved–Korean pine forests gradually give way in the altitude range from 500–1200 to 1500–2000 m to evergreen conifer *Abies nephrolepis*–*Picea jezoensis* forests representing the orotemperate belt.

The range of *Abies*–*Picea* forests extends north to the latitude of 55–57°N. In the northern temperate zone they constitute the zonal vegetation of the subarctic sector of the southern and middle boreal zone bordering on *Larix dahurica* forests in the north and west.

⁸ This area was defined by Komarov (1901), and is widely understood in geobotany to include northeastern China, North Korea, and the southernmost part of the Russian Far East (Sikhote Alin) (Komarov, 1934–64; V.N. Vasiliev, 1958; Kharkevich, 1985–96).



Fig. 5.3. The interior of a *Pinus koraiensis* forest (45.26°N, 136.57°E, elevation 60 m). Photo P.V. Krestov.

Although the forests in the orotemperate belt are similar in structure and species composition to the zonal forests, they are enriched with temperate species, some of which (*Oplopanax elatus*) do not occur in the lower belts.

Ecology

The climatic features of the broadleaved–Korean pine forest area are determined by the monsoon circulation of air masses. In winter the territory is under the influence of cold and dry air masses, formed in the region where the powerful Asian anticyclone develops. With the summer monsoon, southeastern winds carry cool and moist marine air during the first half of the summer, and very moist warm air in the second half. The coldest month is January; minimum temperature varies from -22°C to -26°C in the more continental part on the western slopes of Sikhote Alin, and from -17°C to -21°C on the eastern slope, exposed to the sea. The average summer temperature is $+15$ – 17.5°C on the coast up to $+18.5$ – 20°C in continental regions (Table 5.1). The warmest month in the continental regions is July, in coastal regions August. The day-degree temperature sums $[\sum \max(0, T_i - 10)]$, where T_i is the mean temperature in $^{\circ}\text{C}$ of the i th day] in continental regions range from 2400° to 2600° in the southernmost part of the Russian Far East and from 1600° to 1800° in the northern part of the subzone. Kira's warmth index ranges from 45 in the north to 60 in the south of the lower belt (Grishin, 1995) and from 25 to 45 in the orotemperate belt.

Within the northern temperate zone, both conifer and mixed broadleaved–Korean pine forests occur on a wide spectrum of sites, with different characteristics of

bedrocks and geomorphological attributes, but mostly on forest brown soils and podzols.

Change in forest area

The maps of potential vegetation (Kolesnikov 1956b, 1961) and bioclimatic indices (Grishin, 1995) assume a wide distribution of broadleaved–Korean pine forests on edaphically suitable sites in the subarctic sector of the northern temperate zone. However, the area of this vegetation type has considerably decreased in China and adjacent parts of Russia west of the Sikhote Alin mountains. Most authors ascribe this decrease to human activity by the Dzhurzhen (Juchen, Jürchen) population between 500 and 800 AD. During that period, forests were decreasing in area due to clearing for agriculture. Since then the area has remained relatively densely populated, and regular fires have supported the development of vegetation without conifers.

In the beginning of the 19th century the basin of the Ussuri river was settled by Russians. The first forest records appeared in the second half of that century (Budishchev, 1898), but more extensive forest records from China and Russia date from the time when local and international forest companies started to operate at the beginning of the 20th century. According to records from the 1890s, the broadleaved–Korean pine forests on Sikhote Alin covered an area of about $65\,000\text{ km}^2$ and *Abies–Picea* forests about $30\,000\text{ km}^2$. Nowadays the areas have decreased by $33\,000\text{ km}^2$ and $4\,000\text{ km}^2$, respectively (Petropavlovskiy et al., 1985). The major reasons for the decrease of forest area are extensive logging and fires. The area formerly covered with broadleaved–Korean pine forests is now occupied by secondary *Betula platyphylla* and *Larix dahurica* forests (3500 km^2) formed mainly after logging and/or single fires, secondary *Quercus mongolica* forests ($12\,000\text{ km}^2$) formed after logging and regularly repeated fires, especially around settlements, and by agricultural land (about $15\,000\text{ km}^2$). The area of *Abies–Picea* forests decreased only by $4\,000\text{ km}^2$; they were replaced mostly by secondary forests of *Betula platyphylla* and *Larix dahurica*. The relatively small decrease may be explained by the lack of land suitable for agricultural use and the sparse human population.

Decrease in forest area, however, does not reflect the decline of the quality of forests as a consequence of the disturbance regimes and the features of post-disturbance succession in different vegetation types.

Over seventeen years, changes in forest cover (10^3 ha) in Primorskiy Krai (Anonymous, 1990) were:

	1966	1983	change (%)
scrub	25.1	38.1	+51.8
oak forests	2301.2	3126.8	+35.8
other broadleaved forests	2123.6	1733.4	-18.4
larch forests	1090.1	1136.7	+4.3
broadleaved Korean-pine forests	2439.4	2181.9	-10.6
total forest area	10778.0	11146.1	+3.4

The potential forest area in the northeast of China extends north from the latitude of $40^{\circ}45'N$ and covers the provinces of Heilongjiang, Jilin and Liaoning. According to FAO data (Anonymous, 1982), the percentage of forest cover in these provinces is at present 30–40%, 23–30% and 10–20%, respectively. Large areas of natural forest in northeastern China are to be found only in inaccessible high-elevation regions on the Lesser Hingan and Changbai Shan mountain ranges, while the plains are intensively cultivated and densely populated.

Historical effects

Many authors explain the species richness and high diversity of Manchurian broadleaved–Korean pine forests by the fact that these areas have been unaffected by glaciation throughout the Pleistocene, or indeed since the high temperatures reached during the Pliocene optimum (Grichuk, 1984). Most of the present species constituting the broadleaved–Korean pine communities had ancestor taxa in the Tertiary palaeofloras of the Late Miocene and Pliocene. During the Pleistocene Ice Age the rich mesophytic flora in this area lost most of its mesothermic species. The vegetation of the maximum stage during the last glacial period consisted of drought-tolerant meadows and larch woodlands on the plains and dark-conifer taiga in the lower mountain belts. During the following warming, broadleaved temperate species invaded this territory from warmer and wetter regions in the south. However, some of them had survived in refugia in the montane belt, and spread out widely with the warming (V.N. Vasiliev, 1958). This is indirectly proved by the great number of endemic species in the Manchurian nemoral vegetation (Qian et al., 2003).

Zonal forest types

The syntaxonomy of the broadleaved–Korean pine forests is poorly developed and needs further study. Song (1988) described the Class *Quercetea mongolicae* at the southernmost point of the distribution area of this forest type. Studies carried out in the Russian Far East (Gumarova, 1995) were based on a small number of relevés collected from a limited area, and are insufficient for both assessment of forest diversity and determination of the phytogeographical positions of the units recognized.

According to the traditional, dominant-based, concept the broadleaved–Korean pine forests are subdivided into southern, middle and northern units. In terms of Sukachev's geobotanical school these units correspond to the following associations, respectively: *Nemoreto–Pinetum carpinosium* (with *Carpinus cordata*), *Nemoreto–Pinetum typicum* and *Nemoreto–Pinetum piceetosium* (with *Picea jezoensis*) (Krestov, 1997, 2003).

The southern broadleaved–Korean pine forests occur from the southernmost points of the Russian Far East at $42^{\circ}40'N$ (Vasiliev and Kolesnikov, 1962), and from $40^{\circ}15'N$ in northeastern China (Chun, 1994), northwards to a latitude of $44^{\circ}N$. In the southern spurs of the Sikhote Alin mountain range, on the Chiorniye Gory and on the Shuphan plateau they occupy gentle slopes of low mountains or hills within the altitude range from 50 to 600 m. These forests have a very rich species composition and a complex phytocoenotic structure (Fig. 5.4). They are usually dominated by two species of nemoral conifers *Abies holophylla* and *Pinus koraiensis*, which reach 45 m in height, as well as by nemoral broadleaved trees. *Carpinus cordata* always forms the lower tree layer on mesic sites. The shrub layer includes nemoral shrubs with southern and typical Manchurian ranges. The herb layer consists mostly of nemoral mesic herbs, ferns and sedges. Less significant are xeromesic herbs and sedges. Their ecological range is from xeromesic to hygromesic, and nutritionally from medium to very rich⁹.

Overall, the species composition of southern mixed forests includes 565 species of vascular plants. The species with Manchurian distribution have an affinity to geo-elements in the Korean–South Manchurian and the Japanese–South Manchurian areas.

Typical or middle broadleaved–Korean pine forests, the *Nemoreto–Pinetum typicum*, usually form the

⁹ The terminology for site regimes follows Pojar et al. (1987).

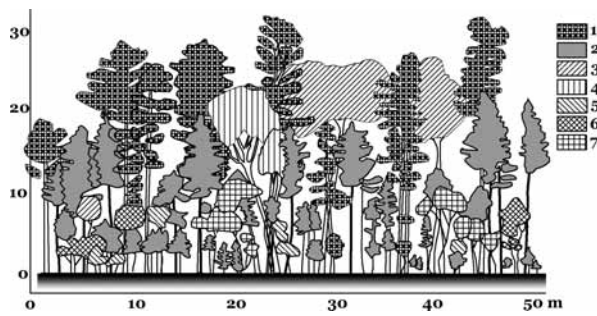


Fig. 5.4. Profile diagram of a typical stand of broadleaved-Korean pine forest on the Sikhote Alin range. The depth is 10 m and the length of strip is 50 m. Species are 1: *Pinus koraiensis*, 2: *Abies nephrolepis*, 3: *Betula costata*, 4: *Tilia amurensis*, 5: *Acer mono*, 6: *Acer ukurunduense*, 7: *Acer tegmentosum*.

lowest altitudinal vegetation zone in southern and middle Sikhote Alin range. *Pinus koraiensis* and broadleaved nemoral trees with typical Manchurian and Japanese-Manchurian distribution form the dominant layer. These forests generally contain 445 vascular plant species, mainly of the Manchurian geo-element, but with more Okhotsk-Manchurian species than the southern forests. The ecological range of the forests is xeromesic to mesic, and nutritionally medium to very rich. The typical broadleaved-Korean pine forests were considerably disturbed by clear-cutting in the past 80 years. Most of the conserved stands of these forests lie on the west slope of the Sikhote Alin range, along the big rivers (water-protective belts), and in the Bikin and Iman river basins. In addition to clear-cutting, frequent fires cause great damage to the forests. About 30% of the distribution area is today occupied by stable secondary oak forests of low productivity with *Quercus mongolica* replacing the typical Broadleaved-Korean Pine forests.

Northern broadleaved-Korean pine forests occur in all parts of the distribution area of *Pinus koraiensis*. In the southern Sikhote Alin they occupy the upper part of the broadleaved-Korean pine zone, while in the north they dominate completely. The flora of this forest type includes 394 species of vascular plants. The role of Manchurian nemoral species in the phytocoenoses decreases in comparison to the other vegetation classes discussed. The role of taiga and deciduous boreal forest species increases. The canopy is dominated by both nemoral and taiga species. The ecological range differs from typical broadleaved-Korean pine forests in that the main phytocoenoses are concentrated on mesic medium sites. On poor sites mosses and small herb types of the taiga occur. Hygric sites are occupied

by poor *Fraxinus mandshurica* and *Picea ajanensis* phytocoenoses with the boreal hygric sedges *Carex appendiculata* and *C. schmidtii*.

At present, the northern broadleaved-Korean pine forests are strongly affected by clear-cutting and by subsequent fires, and have been changed into persistent derivative *Betula platyphylla* and *Larix dahurica* forests.

Pure *Pinus koraiensis* forests have a narrow range on the eastern slopes of the Sikhote Alin range. The canopy is absolutely dominated by *Pinus koraiensis* reaching its maximum size in pure pine forests: 40–45 m high and about 1.2 m in diameter. The sub-tree layers are not clearly expressed. The shrub layer usually consists of *Lespedeza bicolor*, *Rhododendron mucronulatum*, *Ribes horridum* and *R. maximoviczianum*.

In the herb layer single individuals or small groups of oligomesotrophic, xeromesic and mesic herbs and dwarf shrubs may be present. The ecological range of this class is xeromesic to mesic, growing on poor to medium brown forest soils and podzols. The present distribution of this forest is very local because of a unique climatic condition on the eastern marine slope with low temperatures and high humidity on the one hand, and a strong disturbance regime, mainly clear-cutting, on the other hand.

Stand structure: The communities can be generally stratified into three layers. The tree layer normally includes three sublayers, formed by species of different growth forms and different life strategies. Because of high diversity in dominant species, complex interspecies relationships take place in the phytocoenoses. The shrub layer may include two sublayers, which often gradually replace the lowest tree sublayer. The herb layer is normally well developed. A dense cover of mosses and/or lichens usually indicates extremely cold or extremely dry sites. At the northern and upper limits of the mixed-forest range this is common. However, mosses can also form small patches in gaps of the herb layer and around stem bases in typical stands throughout the whole range of broadleaved-Korean pine forests.

The dominants of broadleaved-conifer forest ecosystems differ in growth forms and life strategies. Up to 12 tree species growing together can be found in the upper sublayer of one forest stand. The main species forming the dominant layer are *Abies holophylla*, *Betula costata*, *Fraxinus mandshurica*, *F. rhynchophylla*,

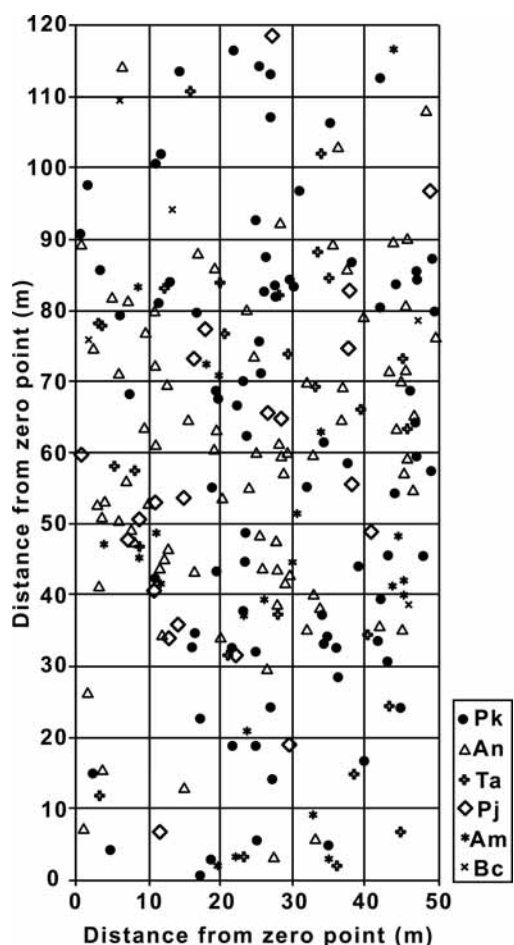


Fig. 5.5. Tree groupings on a permanent plot 50×120 m established in the southern Sikhote Alin. Species abbreviations: Am, *Acer mono*; An, *Abies nephrolepis*; Bc, *Betula costata*; Pj, *Picea jezoensis*; Pk, *Pinus koraiensis*; Ta, *Tilia amurensis*.

Juglans mandshurica, *Kalopanax septemlobus*, *Phellodendron amurense*, *Pinus koraiensis*, *Quercus mongolica*, *Tilia amurensis*, *T. mandshurica* and *Ulmus japonica*. Their usual height is 25–35 m, but on rich sites *Abies holophylla* and *Pinus koraiensis* may reach a height of 45 m, exceeding the height of other tree species and forming a sparse layer above the canopy. Uneven age structure is a characteristic feature of old-growth broadleaved–Korean pine forest. Trees in such stands grow in cohorts reflecting the gap character of stand dynamics (Fig. 5.5).

Lower sublayers normally occur in all communities of mixed forests. The main species in the second sublayer are *Acer mandshuricum*, *A. mono*, *Maackia amurensis*, *Micromeles alnifolia*, *Padus maximowiczii*,

Sorbus amurensis, *Taxus cuspidata* and *Ulmus laciniata*. Their crowns occupy a space from 12 to 20 m above the ground, without a visible boundary separating them from the crowns of the upper layer. In almost all undisturbed phytocoenoses a third layer is clearly expressed. *Acer pseudosieboldianum*, *A. ukurunduense*, *Carpinus cordata*, *Ligustrina amurensis* and *Padus avium* form a sublayer 6–10 m in height. They are all shade-tolerant species, but they differ in ecology and growth form.

The shrubs in the broadleaved–Korean pine forests are diverse and abundant. Commonly the shrub layer is sparse under the canopy and sometimes very dense in the gaps. It may include some sublayers, because of differences in the height of the shrubs. Whereas *Berberis amurensis*, *Lonicera chrysantha* and *Ribes maximowiczianum* normally do not exceed 1 m in height, *Acer barbinerve* and *Corylus mandshurica* may reach 6–7 m. The shrub layer is a valuable regulating factor for the development of tree saplings, especially in the early stages of secondary succession.

A special feature of this kind of forest is the presence of woody vines. The most common are *Actinidia arguta*, *A. kolomikta*, *A. polygama*, *Celastrus flagellaris*, *C. orbiculatus*, *Parthenocissus tricuspidata*, *Pueraria lobata*, *Schisandra chinensis* and *Vitis amurensis*. Some of them are significant successional species on account of their ability for intensive sprouting.

The herb layer is usually very well developed and characteristic in broadleaved–Korean pine forests; however, the driest sites on steep slopes and ridges may be free of herbs. Usually herbs of different species are grouped in patches of different size occupying certain ecological niches. The most important factors affecting plant distribution are light conditions, ground fires, presence of stronger competitors, and grazing. (Krylov, 1984). Because of light deficit, almost all herbs are shade-tolerant, with intensive vegetative reproduction. The herbs differ very greatly in growth forms and life strategies. The nemoral wide-leaved forbs – herbs with wide leaves oriented in the same horizontal plane – are more competitive. The average number of plants for one phytocoenosis may vary between 20 and 100 species. The total number of herbaceous species growing under the forest canopy in broadleaved–Korean pine forests exceeds 500.

A moss and lichen layer is not characteristic of the nemoral vegetation. However, the quantity of

mosses may increase in the northern part of the range of Korean pine forests. A moss layer is often formed of common boreal species such as *Hylocomium splendens*, *Pleurozium schreberi* and *Ptilium crista-castrensis*. As small patches, the nemoral mosses *Climacium dendroides*, *Pleuroziopsis ruthenica* and *Rhytidiadelphus triquetrus* also can be found.

Species combination: 645 species of vascular plants have been recorded in broadleaved–Korean pine forests (Krestov, 1997). The distribution of some species within the mixed-forests zone is heterogeneous. Many species, including some main dominants, have the northern limit of their distribution at about 44°N.

Temperate conifers are represented by *Abies holophylla* and *Pinus koraiensis*. In the central part of the Sikhote Alin range, *Pinus koraiensis* is a dominant or co-dominant of forest stands up to altitude of 800–900 m. On the eastern slopes it may form monodominant stands, because the low local temperatures make it more competitive in comparison with the broadleaved species.

The group of nemoral broadleaved tall trees consists of 11 species with a Manchurian distribution range: *Acer mono*, *Betula costata*, *Fraxinus mandshurica*, *Juglans mandshurica*, *Phellodendron amurense*, *Populus maximowiczii*, *Tilia amurensis* *T. mandshurica*, *T. taquetii*, *Ulmus japonica* and *U. laciniata*. They all create a canopy together with the conifers. In southern forests the number of tall broadleaved trees with a southern Manchurian distribution, such as *Fraxinus rhynchophylla* and *Kalopanax septemlobus*, is increasing.

Among the major components of the broadleaved–Korean pine forests are nemoral shrubs. The group totals 21 species in the middle and northern forests, and 28 species in the south. The most significant of them are *Corylus mandshurica*, *Eleutherococcus senticosus*, *Lonicera chrysantha* and *Philadelphus tenuifolius*.

In the herb layer of intact forests, nemoral herbs of various life forms occur. The most significant in different ecological conditions include the nemoral tall herbs *Filipendula glaberrima*, *Rabdosia excisa* and *R. glaucocalyx*; the nemoral ferns *Coniogramme intermedia*, *Cornopteris crenulatoserrulata* and *Dryopteris crassirhizoma*; the nemoral herbs *Arisaema amurense*, *Carpesium triste*, *Caulophyllum robustum* and *Lilium distichum*; the nemoral sedges *Carex campylorhina*, *C. quadriflora*, *C. siderosticta*, *C. ussuriensis*; and many other less significant groups.

Disturbance regime and dynamics: Having many potential strong competitors, a broadleaved–Korean pine phytocoenosis is characterized by complex dynamics even during the lifespan of one generation of Korean pine. This is controlled by different ecological factors, and by the disturbance regime. In a phytocoenosis-oriented approach a scheme of nemoral forest dynamics was elaborated by Ivashkevich (1933), and later added to and improved by Kolesnikov (1956a). Since that time no new ideas or special research concerning phytocoenosis dynamics have been proposed, despite intensive development of the gap-dynamics concept (Pickett and White, 1985) and the introduction of this topic into Russian forest ecology (Krestov and Ishikawa, 2000).

According to the scheme of Ivashkevich and Kolesnikov the normal development of a mixed phytocoenoses goes through a sequence of eight stages replacing one another. The first stage starts when the new surviving generation of Korean pine is appearing under the canopy of the mother generation (Table 5.3). Then the development of Korean pine normally encounters two periods of suppression as a minimum – the first in the youngest years (Stage 1), and the second when it starts forming a canopy (Stage 3). These periods are indicated by analysis of growth patterns. At 160–200 years (Stage 5) the Korean pine generation reaches maturity.

Figure 5.6 shows clusters of *Pinus koraiensis* trees regenerated at the same time, while the other species show a rather uniform pattern. The existence of these clusters is caused by the propensity of Korean pine to intensive regeneration every 35–40 years – the so-called explosions of regeneration mentioned by Ivashkevich (1933) and Solovyov (1958) – and by a complex patch structure of a phytocoenosis. In fact, Korean pine has an evident tendency to regenerate under the canopy, but only gap formation gives the saplings the possibility of developing. This was shown by investigations in China (Wang, 1961).

Normally the patch structure of the phytocoenosis reflects the gap character of regeneration. Gap formation in broadleaved–Korean pine forests depends mainly on natural death of old trees, and rarely, but over large areas, on natural disturbances such as winds and storms. The size of gaps ranges from 20 m (crown diameter size) to 40–50 m in diameter. Usually crowns of broadleaved trees, which are sufficiently transparent to light for a new generation of Korean pine to develop, close the gaps formed by Korean pine. Korean pine

Table 5.3

Kolesnikov's (1956a) hypothesis on the development of stands of Korean pine (*Pinus koraiensis*) in the middle part of its range during the life cycle of one generation

Stage ¹	Duration, years	The state of main phytocoenotic components
1 (6)	1–40	Appearance and early development of a new Korean pine generation, with the preceding generation causing a deficit of light and nutrition.
2 (7)	41–80	Development of Korean pine saplings within a subordinate layer.
3 (8)	81–120	Maximum increment in height and inclusion in the canopy. Canopy density is increasing. Role of broadleaved trees of older generations in canopy composition is important.
4	121–160	Fast increment in diameter of young Korean pines and dominance in the upper canopy. Old broadleaved trees and oldest trees of Korean pine die and fall. Density of young generation of Korean pine increases.
5	161–200	Mature canopy stage. Maximum proportion of Korean pine in canopy (up to 80–90%) while proportion of broadleaved trees is minimal. Increment rates of Korean pine are small. New pine seedlings die quickly. Lower layers are badly suppressed.
6 (1)	201–240	Fast death of trees of older generation (older than 300 years). Canopy density and proportion of Korean pine decrease (to 50–60%). Appearance of new Korean pine generation (future dominant generation) as suppressed saplings. Shrub and herb layers grow up. Tree layer becomes susceptible to insects, droughts and wind impact.
7 (2)	241–280	Over-mature stage. Almost all older Korean pines, and most broadleaved trees associated with the dominant generation of Korean pine have died. Minimum proportion of Korean pine in canopy (30–50%), minimum canopy density. Maximum development of lower layers, vines and saplings of broadleaved trees. No seedlings of Korean pine. Destruction of the canopy.
8 (3)	≥281	Place of older generation is occupied by young generation of Korean pine and broadleaved trees. Slow increase of young pine proportion in biomass and canopy density. Death of shade-intolerant shrubs and herbs.

¹ The numbers in parentheses indicate the stage of the preceding and following generations of Korean pine.

increases in biomass as well as in basal area, but at the same time biomass and basal area for broadleaved species remain relatively stable. With increasing age there is a tendency for the number of stems to decrease. The basal area and total volume increase up to an age of 300 years, and then decrease.

The relatively high diversity in the nemoral phytocoenoses is caused by the abundance of different ecological niches which replace one another in time and space. The study of age structure in the phytocoenoses led to confirmation of the cyclic pattern of development and to its connection with natural patch structure (Ishikawa et al., 1999). The earliest trees of a new generation of Korean pine appear before gaps have been formed under the canopy of the mature broadleaved–Korean pine forest. During the first 80 years their growth is suppressed by deficiency of light and nutrients. This is the time shade-tolerant nemoral herbs with stress-tolerant life strategies develop best. The species richness is optimal; the herb layer includes the typical representatives of the nemoral flora.

During the next 40 years the young trees of Korean pine reach the canopy, which at this time attains its highest density. The species richness does not decrease,

but the bulk of species do not form patches. Herbs now have the lowest cover.

When the youngest generation of Korean pine reaches 120 years of age, the process of natural formation of gaps is initiated because both broadleaved and coniferous trees of older generations start to die. In the first stages of this process the small initial gaps are closed by crowns of the young Korean pine generation, especially the trees with the highest increment in diameter and height. The shrubs increase their cover, the herb layer continues to be suppressed. Seral species (*Betula platyphylla*, *Populus tremula*, etc.) appear. Species richness increases slightly following invasion by these species. This process continues until the young generation of Korean pine reaches an age of about 200 years. Up to this moment the cover by young Korean pines and broadleaved species in the canopy increases up to 60–70%, but the number of over-mature trees is decreasing rapidly. The annual increment of Korean pine is small. Seedlings which appear soon die. The lower layers are suppressed.

In the next phase the oldest trees disappear completely. The percentage of Korean pine in the canopy decreases to 40–60%. The next generation of Korean

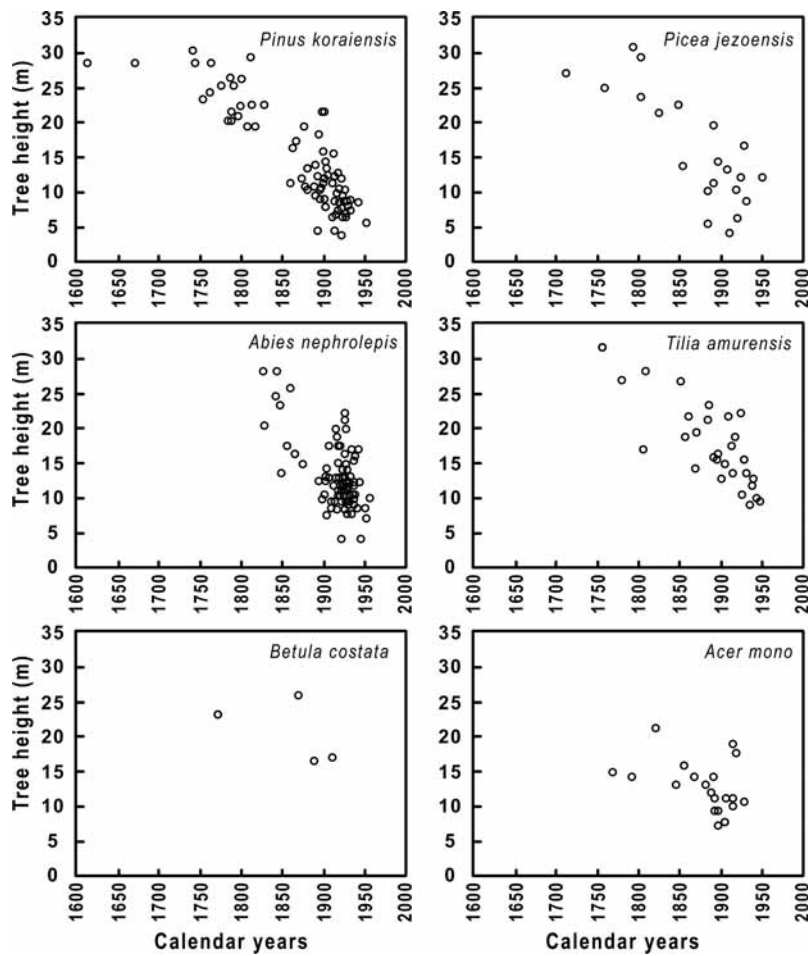


Fig. 5.6. Age–height relationships in mixed broadleaf–Korean pine forests of the southern Sikhote Alin (after Ishikawa et al. 1999).

pine appears as suppressed seedlings under the canopy. The cover of the shrub and herb layers increases. The tree layer becomes accessible to insects, and sensitive to the impact of drought and wind. In most large gaps the seral species develop intensively. The nemoral species common in mixed forests are suppressed by shade-intolerant species with a more rapid growth. As a result of increasing dominance of shade-intolerant species the diversity in the whole phytocoenosis increases. This stage continues for about 40 years; meanwhile the new generation begins to close the gaps. At the same time the common nemoral species form patches in small gaps, and branches of neighbouring broadleaved trees close the gaps.

Thus, during the cyclic dynamics of forest stands the shade-tolerant nemoral species, as well as shade-intolerant ones, are able to complete their life cycles. Because normally in old-growth forests the cycles do

not coincide, diversity within a forest community with stable edapho-climatic conditions is maintained.

Normally in old-growth forests different cycles are taking place in the different gaps within the same forest ecosystem. Because these cycles are not synchronous, a complicated dynamic mosaic is created, allowing the coexistence of species of different growth forms and life strategies.

Human impacts: The most important disturbance factors determining the pathway of recovery in nemoral forests are wood harvesting and human-initiated fires. The pattern of community development after cutting is similar to that of natural dynamics. Most nemoral species continue to be present in the ecosystem but decrease sharply in biomass because of the appearance of seral gap-dependent species (*Actinidia kolomikta*, *Aralia elata*, *Betula platyphylla*, *Padus maackii* etc.).

During the first years of succession the diversity of nemoral species decreases only slightly, as a result of strong competition from gap-dependent species for nutrients and space. Following this invasion, the number of species in the community reaches a maximum at this time. With the formation of a forest environment the recovery of the former diversity may take 20–30 years. The recovery of community structure requires a longer time, equal to the life span of the dominant trees.

Fires affect diversity in different ways, but always decrease it for a long time. Wildfires are rare events in the nemoral forest zone because the decomposition of debris is relatively fast and no great amount of flammable material accumulates. However, a wild fire occasionally takes place in the driest years. Post-fire succession may continue for some hundreds of years, and may never reach the climatic climax stage because of the formation of stable secondary phytocoenoses dominated by self-regenerated long-lived species such as *Larix dahurica*, especially in the northern part of the nemoral forest range. In this case the original nemoral flora changes to one consisting of species with wide ranges which may have Holarctic, boreal, Euroasiatic, Siberian and Far Eastern affinities.

Ground fires are very common in nemoral ecosystems. Rarely do they significantly affect species diversity, because most nemoral species are relatively fire-tolerant. Spring ground fires initiate seed germination of some gap-dependent species (*Betula platyphylla*, *Chamaenerion angustifolium*, *Chelidonium majus* var. *asiaticum*), which can take prominent positions in early post-fire succession (Komarova, 1992). If cover by the tree canopy remains the same, the nemoral species may quickly recover. However, the conifer seedlings are seriously damaged and usually die. If ground fires are repeated regularly every one to three years, the species of the nemoral ecosystems gradually give place to fire-tolerant forms. The nemoral species, in the first instant the nemoral trees, decrease in abundance and diversity. Fire-tolerant species of all growth forms become more competitive in the community and take the leading position in all layers. Usually regular fires become a most important factor in inter-community competition; this may be even more important than the transformation of site properties by fire. The community changes into a more stable state, which in the nemoral forest zone is a pure oak forest. Oak forests (Formation *Betuleto dahuricae–Querceta mongolicae*) are monotonous in community and floristic diversity, and simple in structure. They are

relatively rich in species composition – alpha diversity is 70–75 species per relevé. On the other hand, they are quite poor in community diversity and have low values of beta-diversity. They are widespread and occur mainly in areas with high human populations, where fire regularity is maintained by man.

Animals: Korean pine and Mongolian oak are the basis for the major food chains in this vegetation zone. The longest food chains from seeds and acorns include several species of small rodents (*Sciurus vulgaris mantschuricus*, *Clethrionomys rufocanus irkutensis*, *Eutamias sibiricus*), wild boar (*Sus scrofa continentalis*) and black bear (*Ursus tibetanus*), and continue in predators, which include abundant representatives of the mink family (*Martes zibellina schantaricus*, *Mustela sibirica*) specializing in small rodents, and big cats [the Amur leopard (*Panthera pardus orientalis*) and Amur tiger (*P. tigris altaica*)] specializing in big artiodactyls. Also closely connected with the ecosystem are a number of deer [*Cervus elaphus xanthopygus*, *C. nippon*, roe deer (*Capreolus capreolus*) etc.]. The population of wolves (*Canis lupus*) is controlled mainly by tigers, because the ecological niches of these species are very similar. The forest avifauna is rich. The birds include *Eurystomus orientalis*, *Falcipecten falcipecten* (a rare species) and *Tetrastes bonasia sibiricus*. *Nucifraga caryocatactes macrorhynchos* specializes in the seeds of Korean pine, but it is not as abundant as in ecosystems with *Pinus pumila* or *P. sibirica*.

Azonal forest types

The vegetation of azonal sites is formed under the firm control of zonal vegetation. Dry and wind-exposed ridges and the upper parts of slopes are covered by pure or mixed stands dominated by *Pinus koraiensis* or *Quercus mongolica*, or both together. River valleys with a thick layer of well-drained alluvial deposits are covered with very species-rich broadleaved or mixed broadleaved–Korean pine forests. Depending on the successional stage, these may be stands of *Chosenia arbutifolia* (the first forest community appearing on pure alluvium and existing only during the lifespan of one generation, 70–90 years), pure *Populus koreana* and/or *P. maximowiczii*, mixed *Ulmus japonica–Fraxinus mandshurica*, and finally, mixed broadleaved–Korean pine stands.

In cold valleys with well-developed temperature inversions, boreal stands of *Picea koraiensis* (well-drained valleys) and *Larix dahurica* (poorly-drained

valleys) occur. These vegetation types are described in detail in Chapter 2.

Insular northern cold temperate broadleaved–conifer forests

Distribution

The bioclimatic conditions of the Japanese Archipelago are those of the subtropical, warm temperate and cool temperate zones. The cool temperate zone includes the northern part of Honshu and most of Hokkaido. Hämet-Ahti et al. (1974) distinguished three subzones in the temperate zone of Japan: southern, middle and northern. The northern part of Hokkaido, Kunashir and the southern part of Sakhalin (the Kril'on peninsula at 47°N) were recognized as a hemiboreal zone.

The cool temperate zone in Japan is characterized by mean annual temperatures from 6°C to 13°C, and Kira's warmth index between 45 and 85 (Kira, 1948). The annual precipitation exceeds 1000 mm. The climatic climax vegetation of this zone is summer-green broadleaved forest including two major types: beech and oak forests.

Quercus crispula–*Abies sachalinensis* forests occur on most of Hokkaido and extend to the southern part of Sakhalin. Analogous broadleaved–conifer forest occur in the Primor'ye region on the continent. Kolesnikov (1961) and Hämet-Ahti et al. (1974) considered this vegetation type as a northern temperate forest. The area to the south is recognized as a middle temperate zone, which is similar to the Atlantic European summer-green forests of *Quercus-Fagetea* and *Quercetia robori-petraeae* (Pott, 1992) or *Quercetalia robori-petraeae* (Oberdorfer, 1992).

In contrast to the continental broadleaved–Korean pine forests in Primor'ye, the mixed broadleaved–*Abies sachalinensis* forests of Hokkaido have many features of a boreal-nemoral ecotone, as expressed by the concept of a Pan-Mixed forest zone, rather than true nemoral vegetation (Tatewaki, 1958; Hämet-Ahti et al., 1974; Walter and Breckle, 1987). The boreal dominant *Abies sachalinensis* takes an important place in the canopy structure, with characteristics intermediate between those of nemoral and boreal forests in all its ecosystem components. This explains the differences between two maps of potential natural vegetation of Hokkaido. One is based on the diagnostic species of vegetation alliances (Miyawaki et al., 1988), which differentiates the boreo-nemoral *Carpino-Quercion grosseserratae* region from the

nemoral *Saso-Fagion crenatae* region on Hokkaido, reflecting a larger proportion of boreal vegetation. The other, based on bioclimatic characteristics (Kojima, 1979), differentiates the boreal montane *Abies sachalinensis* zone and the nemoral *Acer mono* zone within nemoral vegetation. Here the insular northern temperate zone is accepted as the distribution area of mixed *Abies sachalinensis*, *Acer mono*, *Quercus crispula* and *Tilia japonica* forests belonging to the association *Abieti sachalinensis-Quercetum grosseserratae* and the *Dryopterido-Abietetum mayrianae* of the *Fagetea crenatae* (Suzuki, 1988).

The existing cool temperate zone may be divided into two regional zones on the basis of climate and vegetation types. Boreo-nemoral Hokkaido is considered to be in the cold temperate zone rather than in the cool temperate zone as at present. The boundary between cool and cold temperate zones is located in the Kuromatsunai lowland in southern Hokkaido.

Ecology

The climate of the region is suboceanic with cold winters and cool summers on Sakhalin and the Kurils, and essentially more continental with cold winters and warm summers in Hokkaido, although there too it is to some degree altered by an oceanic influence. The interior region of Hokkaido, where continentality prevails, can have an extreme minimum temperature of –40°C. At low elevations there are 4–6 months with mean monthly temperature above 10°C. Annual precipitation ranges from 700 to 2200 mm. September is usually the wettest month. The value of Kira's warmth index in the cool and cold temperate zones varies between 35 and 70. The climatic climax vegetation occupies a wide spectrum of ecologically different habitats, mainly on the mountain slopes.

Change in forest area

The natural stands of mixed broadleaved–conifer forests have tended to decrease because of human impact since the colonization of Hokkaido by the Japanese at the beginning of the 19th century. Before that time, Ainu people inhabited the whole of Hokkaido. They mainly used natural products, without changing the natural ecosystems for agricultural purposes. Therefore most of the original forests still existed in Hokkaido. Japanese pioneers logged forests along the coastline and cut down oak species for furniture making. At present, wind-exposed *Sasa* meadows near the seacoast

occupy areas formerly under oak forests. Human impacts increased in Hokkaido about 200 years ago, as indicated by a 40–50% dominance of *Pteridium aquilinum* in pollen spectra (Tsukada and Nakamura, 1988).

Historical effects

Floristically Hokkaido is more related to Sakhalin than to Honshu. The reason for this is that Hokkaido was connected with Sakhalin during the last glacial periods, and northern elements came down to Hokkaido. In postglacial periods Hokkaido was covered with wetlands and sparse woodland tundra (Tsukada, 1984). From the periglacial region of that age, there are traces of glacial cirques on the Hidaka mountains, at an altitude of 1600–1800 m. (Hashimoto and Minato, 1955). Northern elements invaded Hokkaido by two routes: North-America–Aleutians–Kamtschatka–Kurils, and Siberia–Sakhalin. Hydrophytic series such as snow-patch and raised-bog communities were mostly influenced by the North-American flora, and xerophytic series such as alpine semidesert communities were mostly influenced by the Siberian flora. Northern coniferous forests appeared on northern Honshu during the last ice age. However after the Jomon Transgression (5000–6000 BP) the temperature increased about 5°C in comparison with the present conditions (Matsushima and Ohshima, 1974). The boundary of the subalpine belt was higher than at present at about 300–400 m. Hokkaido represents the northern temperate zone with an oceanic influence. *Quercus–Abies* forests developed over the whole of Hokkaido as a climax temperate forest. Most of the conifer forests such as the *Picea jezoensis–Abies sachalinensis* community remained as an oroboreal belt. Beech forest earlier occupied the south of Hokkaido (the Oshima peninsula) forming the boundary between northern temperate and middle temperate zones. The northern boundary of beech forest today is located on the Kuromatsunai lowland (Miyabe, 1935).

Zonal forest types – mixed broadleaved–*Abies sachalinensis* forest (*Abieti sachalinensis–Quercetum grosseserratae*, *Dryopterido–Abietetum mayrianae*).

Distribution: Mixed broadleaved–*Abies sachalinensis* forest, the so-called Pan-Mixed forest, constitutes the zonal vegetation in the montane belt (from sea level

to an altitude of 600(750) m) in the northern part of the Kuromatsunai lowland, where it replaces the pure *Fagus crenata* forest. Vicarious vegetation develops in southern Sakhalin, especially on the Kril'on peninsula, and in the southern Kurils (Kunashir island). These mixed forests may be related to the *Carpinus cordata–Quercus crispula* deciduous forest in the lower montane belt and the *Abies sachalinensis–Picea jezoensis* conifer forest in the higher montane belt.

Stand structure: Typical stands of the mixed broadleaved–*Abies sachalinensis* forest are composed of well-developed tree, shrub and herb layers. The canopy is dominated by *Abies sachalinensis*, *Acer mono*, *Betula ermanii*, *Quercus crispula*, *Picea jezoensis* and *Tilia japonica*. Lower tree layers include *Acer palmatum* var. *matsumurae*, *Cornus controversa*, *Kalopanax septemlobus*, *Magnolia kobus* var. *borealis*, *Ostrya japonica* and *Prunus sargentii*. The density of conifers varies within a wide range depending on site conditions: from dominance on cold and moist sites to sparse presence on warm and dry sites (Ishikawa et al., 1986; Okitsu, 1995).

The presence of woody vines is a remarkable feature of this forest type. The most common species are *Actinidia arguta*, *Rhus ambigua*, *Schizophragma hydrangioides* and *Vitis coignetiae*. The shrub layer is composed of many species, and may be well or poorly developed depending on canopy cover and the ecological features of the site.

One of the most remarkable features of the insular mixed broadleaved–conifer forests is the high significance of small monocarpic bamboos of the genus *Sasa* in the understorey. *Sasa kurilensis* and *S. senanensis* are the main species on sites with deep snow cover, for instance along the coast of the Sea of Japan and on higher elevations, and *Sasa chartacea* and *S. nipponica* dominate on sites with shallow snow cover along the Pacific coast, surviving winter freezing by the development of over-wintering buds under the ground.

Species combination: Unlike the oroboreal coniferous forests, the *Fagetea crenatae* communities include many differential species such as the summer-green broadleaved *Acanthopanax sciadophylloides*, *Magnolia obovata*, *Prunus maximowiczii*, *Schizophragma hydrangioides* and *Viburnum furcatum*, and the conifer *Taxus cuspidata*.

Disturbance regime and dynamics: Since there are marked differences in ecology, especially in light

requirements, between the conifers *Abies sachalinensis* and *Picea jezoensis* and the broadleaved species *Acer mono*, *Quercus crispula* and *Tilia japonica*, the regeneration of Hokkaido mixed forests is assumed to be gap-dependent. However, a number of studies performed to clarify the relation of species to canopy openings and to find regularity in the species turnover (Namikawa and Ito, 1987; Namikawa, 1996; Namikawa et al., 1997) have shown no clear regeneration pattern among either broadleaved or conifer species, nor any clear alternation of shade-intolerant and shade-tolerant species in different stages of regeneration (Okitsu, 1995). Still the study of Namikawa (1996), based on observations of a 7-hectare permanent plot on mount Moiwa, southeastern Hokkaido, over a period of 12 years, showed that *Acer mono* regenerates successfully under a closed canopy; *Tilia japonica* depends on sprouts from stumps in new gaps; and *Magnolia kobus* var. *borealis* requires a gap for regeneration. Although *Quercus crispula*, one of the main dominants of Hokkaido mixed broadleaved–coniferous forests, is considered as a late-successional species (Kikuzawa, 1983), many authors point to its ability to form pure stands shortly after large-scale disturbances caused by storms, typhoons or volcanic eruptions (Namikawa et al., 1997).

Abies sachalinensis, a shade-tolerant species, commonly has a large number of seedlings and saplings under a closed canopy (Ishikawa, 1990). Under unfavourable light conditions it shows very slow growth, but after a disturbance of the canopy it grows rapidly in height. Synchronous regeneration of *Abies sachalinensis* in the extensive gaps formed after large disturbances, such as typhoons, is based mainly on the sapling and seedling bank formed under the closed canopy. On the other hand, *A. sachalinensis* regenerates continuously in small gaps and under light broadleaved canopies (Sano, 1988). Ishikawa (1993) showed that *A. sachalinensis* on Hokkaido is maintained by both synchronous large-scale and continuous small-scale regeneration.

The regeneration pattern in the mixed forests on Hokkaido is also regulated by the undergrowth vegetation, particularly *Sasa* spp. These bamboos, monocarpics with a lifespan of 10–15 years, have been observed to die off over areas of several square kilometres (Numata, 1970). The removal of suppressive factors causes a synchronous regeneration of early and mid-successional species in the area. Although the mass dying-off of *Sasa* over large areas is rather a

rare event, even at a small scale its growth dynamics affects the regeneration of dominants, especially the broadleaved species.

Human impacts: Mixed broadleaved–*Abies sachalinensis* forests occur from level to hilly belts below 600(750) m, and *Abies sachalinensis*, *Picea jezoensis* and *Larix kaempferi* are often subject to clear-cutting for the purpose of creating agricultural land. This human impact increased after 1800 AD, with the increasing immigration from Honshu. *Pteridium aquilinum*, which is an indicator of human impact, increases its presence in pollen spectra in this period (Tsukada and Nakamura, 1988). The secondary forests consist of stands of *Betula platyphylla* and *Quercus crispula* in the lower belt, and of *Betula ermanii* in the higher belt. *Betula platyphylla* forests are expanding their range, mainly as a result of forest fires.

With the development of agriculture, fields of *Beta vulgaris* var. *rapa* (beet), *Solanum tuberosum* (potato) and *Zea mays* (corn), plantations of *Larix kaempferi* and *Abies sachalinensis*, coppices of *Carpinus cordata* and *Quercus crispula*, and wind-exposed *Sasa* meadows along the seacoast have extended their distribution. The *Elsholtzia ciliata*–*Sonchus brachyotus* community composed of the therophytes *Chenopodium album*, *Commelina communis*, *Elsholtzia ciliata*, *Polygonum longisetum*, *P. nepalense* and *Sonchus brachyotus* develops in the pastures. Tall-herb communities composed of the perennial species *Aralia cordata*, *Artemisia montana*, *Cirsium setosum*, *Geum macrophyllum* var. *sachalinense* and *Petasites japonicus* var. *giganteus*, and climber-shrub communities composed of *Actinidia arguta*, *A. polygama*, *Hydrangea paniculata*, *Morus bombycis*, *Rubus idaeus* var. *aculeatissimus*, *Sambucus sieboldiana* var. *miquelii*, *Sorbaria sorbifolia* var. *stellipila*, *Spiraea salicifolia*, *Viburnum sargentii* and *Vitis coignetiae* appear in the afforested areas.

Animals: The Japanese Yezo deer (*Cervus yezoensis*) lives on the Pacific side of Hokkaido. Earlier, the population was controlled by losses of young deer through snow-fall. However, at the end of the 19th century they were brought near to extinction by over-exploitation. The population recovered through protection by law in 1890, and remained stable until 1920, but decreased from then until 1956 because of heavy snow. The brown bear (*Ursus arctos yezoensis*) is found throughout Hokkaido, but is decreasing as

a result of the replacement of natural habitats by managed lands. The large predators are the raccoon dog (*Nyctereutes procyonoides albus*) and the red fox (*Vulpes vulpes*). The gray wolf (*Canis lupus hattai*), which populated Hokkaido in the past, is considered extinct since 1890 because of the extremely decreased population of sika deer. Native small predators are *Martes melampus* (Japanese marten), *M. zibellina brachyura* (sable), *Mustela erminea orientalis* (stoat), *M. sibirica itatsi* (Japanese weasel), and *M. vison* (American mink). Because of the increasing human population and decreasing areas of natural habitats, the food chains of some large predators have been shifted towards the inclusion of anthropogenic links. Many predators have become human-dependent.

The first consumers in the food chains are six species of small rodents (*Apodemus argenteus*, *A. peninsulae*, *A. speciosus ainu*, *Clethrionomys rex*, *C. rufocanus bedfordiae* and *C. rutilus rutilus mikado*) and three species of squirrels (*Pteromys volans orii*, *Sciurus vulgaris orientalis* and *Tamias sibiricus lineatus*). There are 17 species of bats and 5 species of insectivorous small reptiles and amphibians.

Azonal forest types

Swamps, river-beds and valleys within the cool temperate zone were originally occupied by rich forests of *Alnus japonica*, *Fraxinus mandshurica*, *Salix rorida*, *Toisusu urbaniana* and *Ulmus japonica*, with *Cercidiphyllum japonicum*. *Abies sachalinensis* occasionally regenerates in these forests. However, at present the areas along the big rivers are largely used for agriculture. Relatively extensive areas of valley forests remain around the Kushiro mire and Yufutsu (=Yuhutsu) plain. In northern Hokkaido, Sakhalin, Kunashir and Iturup the boreal species *Picea glehnii* forms pure stands in cold river valleys. Detailed characteristics of *Picea glehnii* are given in the Appendix (p. 205).

Insular cool middle temperate forests of Honshu

Distribution

The insular cool middle temperate zone occurs in northern Honshu, with the latitude of 45°N as the southern limit. In the southern part of Japan evergreen broadleaved forests occur in the areas of warm temperate zone of Central Japan, from sea level

to an altitude of 600 m. The orotemperate belt occurs in the altitudinal range of 600–1650 m in central Honshu. The cool temperate zone and orotemperate belt are characterized by summer-green broadleaved forests with beeches (*Fagus crenata* and *F. japonica*) and oaks (*Quercus crispula* and *Q. serrata*) as dominants on fresh (mesic) and moist (hygro-mesic) brown forest soils. Most temperate conifer forests are on xeric sites. *Abies firma*, *Chamaecyparis obtusa*, *Pinus densiflora*, *P. parviflora*, *Thujopsis dolabrata*, *Thuja standishii* and *Tsuga sieboldii* make up the dominant canopy, mixed with the summer-green deciduous species (Miyawaki et al., 1964).

Ecology

The climatic climax *Fagus crenata* forest is found in regions with an annual mean temperature between 6°C and 13°C (Honda, 1912) or with a period of four to six months during which the monthly mean temperatures are above 10°C. Conifer forests occur as the edaphic climax on xeric, acidic soils on ridges. However, *Abies firma* and *Tsuga sieboldii* form climatic climax forests in the lower temperate belt on the Pacific side, where there is no summer drought, but where summer high temperature excludes *Fagus* and winter cold excludes such evergreen forest trees as *Castanopsis* and *Cyclobalanopsis*.

Change in forest area

The natural broadleaved deciduous forest region is better preserved than the evergreen broadleaved forest region, because the traditional uses of the former were for hunting, food gathering, and charcoal burning, rather than agriculture as in the evergreen forest region. At present traditional hunting villages remain around the Shiragami mountains as a World Heritage site representing the most common beech forests in Tohoku district. Natural coniferous forests are local and are found on xeric shallow soils around wet terrain. These sites are less suitable for agriculture than sites with deciduous forests such as *Fagus crenata* and *Quercus crispula*. Less changed coniferous forests remain on steep slopes and ridges, the sites with lower human impact. However, during and after World War II increases in plantations of *Chamaecyparis obtusa*, *Cryptomeria japonica* and *Larix kaempferi*, as well as sightseeing and skiing, have damaged the natural environment in the cool temperate zone. Nowadays

acid rain and increasing deer populations are the most important factors in the regression of beech forests.

Historical effects

At the beginning of the Pleistocene glacial period (75 000 years BP) boreal forest invaded Honshu through Hokkaido, and in the Late Glacial (15 000–20 000 years BP) boreal species remained the only dominants in northern Honshu (Igarashi, 1993). Fossils of *Abies sachalinensis* have been found in northern Honshu (Tsukada, 1983), and relic communities of *Picea glehnii* occur on serpentine rocks of the mountain Hayachine-san (Ishizuka, 1961). In the postglacial period the beech forest reached Hokkaido through Tohoku. During the Jomon Transgression about 6000 BP, *Cryptomeria japonica* formed forests on the Japanese seacoast in regions with heavy snow. Continental floristic elements, such as *Picea bicolor*, *P. maximowiczii* and *Pinus koraiensis*, remained in the subalpine belt of central Honshu where climatic conditions were more continental.

Zonal forest types – *Tsuga diversifolia* forest (*Maiantho-Tsugetum diversifoliae*)

Structure: *Tsuga diversifolia* forests occur on ridges in the lower belt of the coniferous forest zone. The forest is about 25 m high. Dominant species are *Picea jezoensis* var. *hondoensis* and *Tsuga diversifolia*. *Abies homolepis*, *Pinus koraiensis*, *P. parviflora* var. *pentaphylla* and *Thuja standishii* are also present. The lower tree layer is composed of coniferous species and *Sorbus commixta*. Cover of the shrub layer is 20–60%. *Viburnum furcatum*, *V. urceolatum* var. *procumbens*, and ericaceous species such as *Menziesia pentandra*, *Rhododendron brachycarpum* and *R. metternichii* var. *hondoense* are frequent. Evergreen species such as *Arachniodes mutica*, *Ilex rugosa*, *Plagiogyria matsumureana*, *Shortia soldanelloides*, *Skimmia japonica* var. *intermedia* f. *repens* are noteworthy and *Cornus canadensis*, *Oxalis acetosella*, *Phegopteris connectilis*, *Platanthera ophrydioides* and *Streptopus streptopoides* var. *japonicus* are common in the herb layer. The moss layer is poorly developed due to the moisture deficit on the convex sites.

Species combination: Differential species of this community are *Abies homolepis*, *Acer micranthum*, *Clethra barbinervis*, *Trochodendron aralioides* and *Tsuga diversifolia*. *Abies mariesii* and *A. veitchii* are absent.

Distribution: This forest type occurs on the Pacific side of Honshu and the Shikoku islands.

Human impacts: With few cutting areas, there is no human impact.

Animals: *Pinus koraiensis* has nutrient-rich seeds. *Nucifraga caryocatactes* (nutcracker) gathers these seeds and buries them in the soil. Other birds include *Erithacus akahige* (Japanese robin), *E. cyane* (Siberian blue robin), *Phylloscopus borealis* (Arctic warbler), *P. tenellipes* (pale-legged willow warbler) and *Tarsiger cyanurus* (Siberian bluetail). Mammals inhabiting the forest include *Apodemus argenteus* (small Japanese field mouse), *Clethrionomys rufocanus* (gray red-backed vole), *Glirulus japonicus* (Japanese dormouse), *Pteromys momonga* and *Sciurus lis*.

Azonal forest types – *Tsuga sieboldii* forest (*Carici-Tsugetum sieboldii*)

Distribution: *Tsuga sieboldii* forests occur on the Pacific side of Honshu and Shikoku islands in the lower belt of the orotemperate belt, on ridges in contact with *Fagus crenata* or *F. japonica* deciduous forests. The vertical distribution range is between 600 and 1200 m in central Honshu. The northern boundary is the northern part of Kanto district.

Stand structure: The height of the forest is 20–30 m. Dominant species are *Abies firma*, *Pinus densiflora*, *P. parviflora* and *Tsuga sieboldii*. Deciduous species, such as *Betula grossa*, *Carpinus laxiflora*, *Fagus japonica* and *Quercus crispula*, are commonly present. With increasing proportions of broadleaved species the canopy becomes light, and there is a well developed lower tree layer. It consists of young conifers and other deciduous species such as *Acer sieboldianum*, *Clethra barbinervis*, *Cornus kousa*, *Fraxinus sieboldiana*, *Ilex macropoda*, *Lyonia ovalifolia* var. *elliptica* and *Stewartia monadelphica*. The cover of the shrub layer is 20–40%. *Hydrangea hirta*, *Lindera umbellata*, *Pieris japonica*, *Viburnum wrightii*, and ericaceous species, such as *Rhododendron dilatatum*, *Rh. reticulatum*, *Tripetaleia paniculata*, *Vaccinium hirtum* and *V. japonicum* are common. The cover of the herb layer depends on the presence of *Sasamorpha borealis*. On thick acidic litter on drier sites *Arachniodes mutica*, *Athyrium rupestre*, *Dryopteris sabaiei*, *Skimmia japonica* and *Solidago virgaurea* are common.

Species combination: Differential species of this community are *Betula grossa*, *Fagus japonica*, *Hydrangea hirta*, *Rhododendron dilatatum*, *Tsuga sieboldii* and *Viburnum phlebotrichum*.

Disturbance regime and dynamics: The main disturbance factor is logging. Regional disturbances are caused by typhoons. The succession after logging starts with a plant community of annuals composed of the anemochore species *Macleaya cordata* and *Paraixeris denticulata*, and then continues with a sequence of *Rubus crataegifolius*–*Aralia elata* short shrub community, *Weigelia decora*–*Alnus firma* community of freely branching shrubs, *Lyonia ovalifolia* var. *elliptica*–*Carpinus laxiflora* secondary forest and, as the final stage, *Tsuga sieboldii* forest Cutting of *Quercus serrata* or *Q. crispula* coppices every 20–25 years maintains a continuous plagiosere community.

Human impacts: *Tsuga sieboldii* forests as the original natural vegetation in the foothill zone have been converted to coppice forests dominated by *Quercus crispula* and *Q. serrata*. After World War II many sites were afforested with *Chamaecyparis obtusa*, *Cryptomeria japonica* and *Pinus densiflora*. In particular, *Pinus densiflora* was widely planted because of its best performance on dry acidic sites. However, during the last 20 years *Pinus densiflora* plantations have been badly affected by the catastrophic pine disease caused by the nematode *Bursaphelenchus xylophilus*. After destruction of the plantation, the vegetation changes to summer-green deciduous forests such as pioneer stands of *Alnus firma*, and forests of *Carpinus laxiflora*, *Quercus crispula* or *Q. serrata*.

Animals: Mammals inhabiting the forest include *Cervus nippon* (Japanese deer), *Martes melampus* (Japanese marten), *Meles meles* (badger), *Mustela sibirica itatsi* (Japanese weasel), *Nyctereutes procyonoides viverrinus* (Japanese raccoon), *Pteromys momonga* (small Japanese flying squirrel), *Sciurus lis* (Japanese squirrel), *Sus leucomystax* (Japanese wild boar) and *Vulpes vulpes japonica* (Japanese fox). Birds include *Accipiter gentiles* (goshawk), *Aquila chrysaetos* (golden eagle), *Garrulus glandarius japonicus* (Japanese jay) and *Spizaetus nepalensis* (Hodgson's hawk eagle).

Azonal forest types – *Thuja standishii* forest (*Ilicio-Thujetum standishii*)

Distribution: *Thuja standishii* forests occur in the temperate and orotemperate summer-green deciduous forest zone of *Saso-Fagetalia* as edaphic climax vegetation on the steep spine of a range of mountains on the Sea of Japan side of central and northern Honshu, where the maximum snow depth exceeds 75 cm. Neighbouring communities are *Fagus crenata* forest on gentle slopes. The vertical distribution ranges between 1000 and 2000 m in central and northern Honshu (Fig. 5.7).

Stand structure: The height of the forest ranges from 5 up to 30 m. Dominant species are *Pinus parviflora*, *Thuja standishii* and *Thujopsis dolabrata*. In the canopy *Betula schmidtii*, *Chamaecyparis obtusa*, *Cryptomeria japonica*, *Quercus crispula* and *Tsuga diversifolia* are sometimes mixed with the dominant conifers. The cover in the lower tree layer is 20–40%. Here, young conifers and *Acanthopanax sciadophylloides*, *Acer micranthum*, *Evodiopanax innovans*, *Lyonia ovalifolia* var. *elliptica* and *Sorbus commixta* are most frequent. The cover of the shrub layer is 40–80%. It is dominated by evergreen shrubs *Ilex pedunculosa*, *I. sugerokii*, *Rhododendron metternichii* and young trees of *Thujopsis dolabrata*. Other common species are *Hamamelis japonica*, *Menziesia pentandra*, *Tripetaleia paniculata*, *Vaccinium smallii*, and *Viburnum urceolatum* var. *procumbens*. The herb layer is composed of evergreen species such as *Arachniodes mutica*, *Epigaea asiatica*, *Ilex rugosa*, *Mitchella undulata*, *Plagiogyria matsumureana*, *Schizocodon soldanelloides*, *S. soldanelloides* var. *magnus*, *Shortia uniflora*, *Struthiopteris niponica* and *Tripterispermum japonicum*, and few summer-green species such as *Solidago virgaurea* and *Vaccinium japonicum*.

Species combination: Characteristic species of the *Thuja standishii* forest are *Ilex sugerokii*, *Plagiogyria matsumureana*, *Thuja standishii*, *Thujopsis dolabrata* and *Viburnum urceolatum* var. *procumbens*.

Disturbance regime and dynamics: Gap formation results from felling and typhoons. The first successional stage in a gap consists of ericaceous shrubs such as *Menziesia pentandra*, *Rhododendron metternichii* and *Vaccinium smallii*. In wind-exposed sites a continuous shrub community may persist.



Fig. 5.7. The interior of a *Thuja standishii* forest (36.67°N, 138.51°E, ~1800 m). Photo P.V. Krestov.

Human impacts: The rocky steep slopes are not used by humans, except for the logging of some coniferous species suitable for house foundations, building material, wooden coffins and wooden bathtubs.

Animals: Mammals include *Capricornis crispus* (Japanese serow), *Cervus nippon* and *Selenarctos thibetanus* (Asiatic black bear); birds include *Accipiter gentiles* and *Aquila chrysaetos*.

BOREAL BELTS (OROTEMPERATE BELT) WITHIN THE NORTHERN TEMPERATE ZONE

Continental boreal belts

Distribution

The Yezo spruce, *Picea jezoensis*, occurs in the montane subarctic and maritime areas of northeastern Asia between latitudes 40°N and 56°N forming the zonal dark-conifer vegetation in the middle and southern boreal zone. Detailed characteristics of this zonal vegetation are given in Chapter 4 of this volume. Here we focus on those *Picea jezoensis* forests which lie within the northern temperate zone, for instance in the Sikhote Alin, Changbai Shan and Zhangguangcai Ling mountain ranges (Wang, 1961) in an elevation range from 600 to 1500 m in the north and from 1200 to

2000 m in the south (Fig. 5.8). The temperate vegetation in this area influences the forests of the oroboreal belt by enriching communities with nemoral species.

Ecology

The climate within the continental part of the dark-conifer forests is under the influence of marine and continental air masses characterized by monsoon circulation. The increasing continentality with distance from the seacoast causes marked heterogeneity in the local climates. On the whole, climate of these areas is much more severe in comparison with areas at the same latitude in western Eurasia (Ellenberg, 1980). The mean annual temperature in most of the continental part of area with Yezo spruce does not exceed zero. It tends to decrease with increasing latitude and elevation. Precipitation increases with elevation in the continental mountain systems up to 1000–1200 mm (Tarankov, 1974). On the Sikhote Alin mountain range the precipitation on seaward slopes is less than that on exposed interior slopes (Dmitrieva, 1960). The mean annual air humidity within the range of spruce does not fall below 60%, although this characteristic varies considerably from region to region (Anonymous, 1966–71).

Change in forest area

Since historical times the range of forests in the continental oroboreal belt has decreased to a much



Fig. 5.8. *Picea jezoensis* forest on a mesic site (54.10°N, 142.81°N, 70 m). Photo P.V. Krestov.

lesser degree than that of the temperate forests of the area, due to the fact that the former occur in inaccessible montane territories. Most was lost because of replacement by seral *Larix dahurica* communities, established between 100 and 500 years ago after devastating fires. The proportion of old-growth forests in the oroboreal belt has dramatically decreased over the last 100 years, because of logging. Most of the dark-conifer forests are at different stages of regeneration after logging. About 30% of them are now under seral *Betula platyphylla* and *Populus tremula* communities with a clear trend to regenerate to fir-spruce communities in a period of 50–100 years.

Historical effects

In the most severe Pleistocene glaciations 18–20 thousand years ago *Picea jezoensis* kept its dominant status in the lower montane belt of the Sikhote Alin range (Grichuk, 1984), which possibly was a refugium for a number of temperate species (V.N. Vasiliev, 1958). Within the Sikhote Alin oroboreal belt several species exist in isolated localities far from their main range. These species are *Ilex rugosa* (central Sikhote Alin, main range on the offshore islands) and *Rhododendron fauriei* (eastern slope of the central Sikhote Alin, main range in Korea and Japan). The nemoral species *Oplonanax elatus* occurs exclusively in the oroboreal

belt of the southern Sikhote Alin, and has never been found in temperate communities.

Zonal forest types *Abies nephrolepis*–*Picea jezoensis* forest (*Abieti nephrolepidis*–*Piceion jezoensis*)

Distribution: Mixed *Abies nephrolepis*–*Picea jezoensis* forests occur in the northern temperate zone as an oroboreal belt within the altitudinal interval from 1200 to 2000 m in the south and from 400 to 1300 m in the north.

Stand structure: *Picea jezoensis* usually forms stands with a simple structure, with one or two strata which are poorly differentiated. Where they are differentiated, *P. jezoensis* usually forms the first stratum and *A. nephrolepis* the second. The dense canopy in uneven-aged stands may be interrupted by gaps with abundant fir and spruce regeneration, as well as a well-developed herb layer. In the even-aged stands formed after disturbances, the amount of gaps in the canopy is always lower. The canopy in spruce forests can be simple monodominant with *Abies nephrolepis*, *Picea jezoensis* or *P. koraiensis*, or the same species in mixtures. *Picea jezoensis* also mixes with *Betula ermanii* at high elevations near the timber line.

In most stands the lower tree layer contains the same species as the uppermost layer, which here are

either suppressed or at younger developmental stages. Low-growing trees of *Acer ukurunduense* and *Sorbus amurensis* may form a lower layer in mountain spruce forests.

Usually in the dark-conifer forests the shrub layer cannot develop because of the low light intensity under the canopy. *Euonymus macropterus*, *Rosa acicularis*, *Spiraea beauverdiana*, *S. betulifolia* and shrubby *Acer ukurunduense* may form a sparse shrub layer on mesic sites. In contact with the temperate zone, nemoral shade-tolerant shrubs *Eletherococcus senticosus*, *Euonymus pauciflora*, *Oplopanax elatus* etc. may occur in the spruce communities. In subalpine spruce stands *Ledum palustre*, *Rhododendron aureum* and *Weigelia middendorffiana* form a well-developed layer. In wetter riverside stands the diversity of shrubs increases due to the presence of *Ribes triste*, *Sorbaria sorbifolia* var. *stellipila*, *Spiraea salicifolia* and *Swida alba*. However, all of these species form a relatively dense cover only in canopy openings.

The herb layer in the dark-conifer forests includes about 350 vascular plants with mainly boreal distributions. The patchy structure of the herb layer with clearly distinguishable dominance of certain species is a very characteristic feature of the spruce forests. The main patches of understorey vegetation occurring in Yezo spruce forests on mesic sites include the taiga herbs *Cornus canadensis* and *Maianthemum bifolium*; the taiga dwarf shrub *Vaccinium vitis-idaea*; the taiga sedges *Carex falcata* and *C. xyphioides*; and the taiga ferns *Diplazium sibiricum*, *Dryopteris expansa*, *Leptorumohra amurensis* and *Pseudocystopteris spinulosa*.

Mosses are always present in spruce phytocoenoses on mesic sites. On sites poor in nutrients they form a continuous cover with no vascular plants. The commonest species are *Dicranum* spp., *Hylocomium splendens*, *Pleurozium schreberi*, *Polytrichum commune*, *Ptilium crista-castrensis* and *Rhytidiadelphus triquetrus*. On the richer sites mosses occur in the gaps of the herb layer.

Species combination: The differential species of this community type, *Abies nephrolepis*, *Acer tegmentosum*, *Cacalia auriculata*, *Pinus koraiensis*, *Tilia amurensis*, *Trigonotis radicans* and *Valeriana fauriei*, reflect the great temperate influence on the vegetation in the oroboreal belt within the northern temperate zone.

Disturbance regime and dynamics: Fire is an important factor in the formation and dynamics of

Table 5.4
Periods and stages of ontogenesis of *Picea jezoensis* in even-aged stands¹

Period	Stage	Calendar age, years	
		Southern areas	Northern areas
Juvenile	Seedlings	1	1
	Saplings	2–25	2–40
Reproductive	Youth	25–60	40–80
	Prematurity	60–100	80–120
	Maturity	100–180	120–240
Senile	Overmaturity	180–220	240–300
	Dying	220–350	300–500

¹ After Manko (1987).

spruce forests as a result of the great amount of combustible material and the occurrence of dry periods in the summer. Most studies of dynamic processes consider fire or other disturbance as a reference point for spruce forest development. Most of the spruce stands in the Russian Far East are characterized by an even-age dominant layer, with the age of the trees indicating the time of disturbance. However, in some regions uneven-aged spruce ecosystems with cyclic dynamics are common (Shavnin, 1979; Kozin, 1981; Manko, 1987; Tatarinov et al., 1978).

Within a life-span reaching 500 years, the spruce individual passes through three stages from germination to death: juvenile, reproductive, and senile. The calendar age in different stages differs, depending on the location of the spruce stand: the duration of stages increases from south to north (Table 5.4). Though in even-aged stands the sequence of stages is predictable, this predictability disappears in uneven-aged stands because of the complex relationships between individuals. Trees in the juvenile and, partly, the reproductive stage may be found under the canopy of the mature generation.

The average length of a cycle has been estimated as 120–150 years (Manko, 1987). According to Manko, this cycle contains four stages, each characterized by a certain combination of dominant and subordinated generations.

In the stage of maturity, mature trees of different ages form a canopy, which has a maximum cover and a continuous distribution of assimilating organs along a stem. The proportion of diseased trees is minimal. There are no freshly fallen stems on the ground – all are well decomposed, covered by mosses. Saplings of

spruce and fir are suppressed. They have an umbrella-shaped crown, and minimal increment in diameter and height. The longer a stand stays in this stage the larger the proportion of fir in the undergrowth, because of its higher shade tolerance and ability to survive a long term under the canopy. Shrub and herb layers are poorly developed; their cover and diversity are minimal.

In the stage of over-maturity the trees in the canopy die off one by one. First the tallest but not necessarily oldest trees die. This stage starts when most of the canopy trees exceed an age of 220–240 years. The stand at the beginning of this stage has maximum stem volume; however, the proportion of diseased trees increases. The dying trees create favourable light conditions for the development of saplings. In the southern forests, fir predominates among the saplings. This state of stand development corresponds to a gap phase, except that saplings developing in the same gap are of uneven age. The shrub and herb layers increase their cover but not their diversity.

The stage of break-up follows the stage of over-maturity, and lasts several decades till the dominant canopy has been completely destroyed. The stem volume and crown cover tend to decrease. In fir–spruce forests the fir predominates in the stand because of rapid growth of saplings formerly dormant under the canopy (Manko, 1967; Mishkov, 1975). In a period of 10–20 years firs may close gaps which occur in the canopy. In subalpine forests the proportion of *Betula ermanii* in the canopy increases. The companion species increase their proportions, although they do not usually reach full dominance in the canopy because of the large number of very old trees still standing. Usually, in the life-span of the spruce there may be two generations of fir. During the break-up stage, a new generation of spruce is formed. Gaps formed in this canopy create favourable conditions for the development of herb and shrub layers. Many freshly fallen logs cover the ground. At the end of this stage the oldest spruce trees disappear completely from the canopy.

Formation of a new canopy starts with intensification of the break-up processes in the dominant fir generation and the initiation of growth of the spruce trees. The stand includes a large number of spruce saplings, a large number of fir stems of intermediate diameters, and few large stems of spruce from the previous generation. In several decades the young spruces replace the fir canopy. Self-thinning causes an abrupt decrease in the number of stems. Stem

volume gradually increases. Diseased trees are absent or few in number. This stage is characterized by poor light conditions under the canopy and by a minimal development of undergrowth. The development of the spruce canopy layer improves the light conditions and abundant fir and spruce saplings appear. This stage may last up to 50–80 years until the young spruce trees reach maturity.

Human impacts: Any post-fire succession in the dark-conifer forests results in the formation of spruce stands. However, a number of factors may cause a deviation from the standard successional scheme. These factors are: the degree of substrate mineralization (presence and development of humic horizons in the soils, humus form) and erosion rates, climatic conditions favourable to the growth of companion species or potential competitors (inhibitors), and the presence of seed sources. The fastest regeneration of spruce forests after wildfire occurs under the following conditions: (1) after fire the fine fractions are retained in the soil, and not blown away; (2) a seed source is nearby; and (3) seedlings are established in the first year(s) after fire. In this case the full regeneration cycle lasts 100–180 years, including several stages (Table 5.5).

In the first year after fire, herb and shrub communities appear on the burned sites. The first plants, *Chamaenerion angustifolium*, *Rubus sachalinensis* and *Sambucus racemosa*, form a sparse cover, creating favourable conditions (stabilization of substrate, protection from excessive evaporation on insolated sites) for the germination and growth of tree seeds. In the next year or two, grasses (*Calamagrostis langsdorffii*) and sedges (*Carex campylorhina*, *C. sordida*) form a dense herb cover inhibiting seed germination. Delay in seedling establishment in the first year caused by unfavourable weather conditions may considerably postpone the formation of a spruce stand.

In the next stage *Betula platyphylla* or *Larix dahurica* forms a closed forest stand, with spruce normally developing under their canopy, reflecting its shade tolerance. In further development both birch and spruce tend to grow normally until the break-up, the birch reaching the age of 100–120 years, and forming mono-dominant spruce or bidominant fir–spruce forest stands.

Post-fire development of spruce forests through a larch stage has been poorly investigated in the Russian Far East. A seral pure stand of larch without spruce saplings may be formed in the first years after fire,

Table 5.5
General scheme of after-fire dynamics of fir–spruce (*Abies nephrolepis*–*Picea jezoensis*) forests

Time after fire	State of main community components
0–10 years	Formation of herb and shrub community with simultaneous seed-set by birch, larch and spruce.
10–40 years	Formation of young birch or larch stand with spruce and/or fir under canopy. Exclusion of shade-intolerant species from the herb and shrub layers.
40–60 years	Spruce and fir form a subcanopy, gradually invading a canopy of birch or larch. Formation of species composition characteristic for spruce forests.
60–100 years	Break-up of the birch canopy. Increase in the role of spruce and fir in the major canopy.
100–180 years	Further increase in the role of spruce in the canopy, disappearance of birch from the canopy. Formation of structure and species composition typical for even-aged spruce forests.
180–220 years	First deaths of the first after-fire generation of spruce. The appearance of new generations in the canopy. Appearance of evidence of uneven-aged stand.

¹ After Manko (1987).

if there is no seed source for spruce. The lack of spruce may be explained by unsuccessful self-sowing of a site after formation of a dense grass cover. Transformation of the grass cover into a dense sub-shrub cover (*Ledum palustre*, *Vaccinium vitis-idaea*) under the larch canopy may inhibit successful establishment of a viable spruce generation, and thus lead to long-term persistence of a seral larch stand. The simultaneous establishment of spruce and larch saplings in most cases “guarantees” the formation of a spruce subcanopy, and full replacement of larch by spruce after the canopy generation of larch breaks up.

Animals: Despite the spatial proximity of boreal and temperate vegetation in the mountains of Sikhote Alin, the fauna is strongly differentiated. Animal species diversity in the *Abies*–*Picea* boreal forest is much poorer, because of the limited ability of the ecosystem to provide food sources for the primary consumers in the food chains; the chains are generally very short, the first link being the small rodents (*Mus* spp., *Sorex* spp.) and hares (*Lepus timidus*) and the final links the small predators, represented mainly by types of mink (*Martes zibellina*, *Mustela sibirica*) and lynx (*Lynx vulgaris*). The brown bear (*Ursus arctos lasiotus*) is very abundant; its high population, however, depends on its low food specialization on the one hand, and on contributions from other ecosystem types, like fish in rivers and berries from the alpine tundra. The commonest artiodactyls are *Moschus moschiferus parvipes*, specializing on herbal sources of food in summer and on lichens from branches of conifers (*Alectoria* spp., *Usnea* spp.), bark and young twigs

and buds in winter; and *Capreolus pygargus bedfordi*, specializing in winter on bark and young twigs.

Azonal forest types

In the Sikhote Alin mountains *Abies nephrolepis* and *Picea jezoensis* form stands on the mountain ridges and very dry steep slopes, avoiding only excessively moist, poorly drained sites, and early stages of succession on the fresh alluvial deposits along the big rivers. Succession on the well-drained alluvial deposits starts with stands of *Chosenia arbutifolia* and goes through the stages of *Salix rorida* and *Populus maximowiczii* to the highly productive *Picea jezoensis*–*Picea koraiensis* communities, with the proportion of *P. koraiensis* varying between 10 and 60% (Krestov, 1997). In the upper parts of rivers the narrow valleys are occupied by *Toisusu cardiophylla* communities.

Poorly drained sites on the river banks with cold air drainage are occupied by *Larix dahurica* forests and woodlands. However, they only occur in the river valleys of the northern half of Sikhote Alin. The sparse to dense canopy is formed by *Larix dahurica* with a mix of *Betula platyphylla*. The shrub layer includes *Ledum hypoleucum*, *L. palustre*, *Lonicera edulis* and *Vaccinium uliginosum* in varying density depending on the site ecology. Most nutritionally poor wet sites are occupied by larch woodlands with well-developed pillows of *Sphagnum*, which include *S. palustre*, *S. squarrosum*, *S. fuscum*, *S. compactum*, etc. The herb layer depends on the development of shrubs and bryophytes. The warmer and drier sites (but even these are wet) are occupied by *Angelica cincta*, *Calamagrostis langsdorffii*, *Ophelia chinensis*, *Thalictrum contortum*

Table 5.6

Mean temperature and precipitation in the insular oroboreal belt (Maeda and Miyakawa, 1967).

Climatic stations	Monthly values ¹												Annual	Warmth index (month/degree)
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec		
Mean temperature (°C)														
Tsurugi-san, Shikoku (1945 m)	-7.2	-6.2	-3	3.4	7.6	11.3	15.1	15.5	12.2	6.4	1.5	-4	4.4	38.1
Fuji-san, Tokai (1700 m)	-6.9	-6.6	-2.7	4.9	7.4	12.1	16.6	17.2	13.6	7.6	3	-3.7	5.2	44.5
Ozegahara moor, northern Kanto (1665 m)	-9.5	-9.1	-5.5	1.4	6.8	11.8	17.2	17.6	13	5.8	0.1	-6	3.6	42.2
Mean precipitation (mm)														
Tsurugi-san	NA	NA	NA	NA	258	450	462	530	548	224	NA	NA	NA	
Fuji	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	2000	
Ozegahara moor	180	125	120	86.1	93	163	210	179	195	145	79.5	130	1705.9	
Snow depth (cm)														
Tsurugi-san	78	98	66	12	0	NA	NA	NA	NA	0	11	36		

¹ NA: no data available or measurements not applicable.

and other herb species. Along the gradient of increasing moisture and decreasing temperature, the dominant herbs in the stands change in the following order: *Carex appendiculata*, *C. cryptocarpa*, *C. schmidtii* (on extremely wet sites with moving water), *Carex gmelinii*, *Oxycoccus palustris* and *Rubus chamaemorus* (wet and cold sites only in the northern Sikhote Alin).

Insular oroboreal belt

Distribution

In the northern temperate zone in Hokkaido, Kunashir and Sakhalin, dark-conifer forests form the oroboreal belt above 600–800 m on all mountains exceeding 800 m in elevation. Most Japanese conifer forests belonging to the *Vaccinio-Piceetea* and characterized by *Picea*, *Abies*, *Larix*, *Pinus* and *Tsuga* species occur in montane and subalpine belts of the warm temperate and cool temperate zones. Dark-conifer forests of central Honshu occur above 1650 m in the Japanese Alps as climatic-climax forests isolated from the main range of the type, and are rather different in structure and species composition.

The orotemperate and oroboreal conifer forests are divided clearly by having different dominant species,

and also belong to different vegetation classes, *Fagetea crenatae* and *Vaccinio-Piceetea*, respectively. The differentiation of these vegetation types between Honshu, Hokkaido and Sakhalin appears to have been caused by their different history. The conifer forest of Honshu developed independently, being isolated in the island of Honshu; on the other hand, the conifer forests of Hokkaido were influenced by the northern boreal forests of Sakhalin, Siberia and Kamchatka during the last Glacial period.

Ecology

Japanese coniferous forests mainly occur as climatic climax vegetation in the subalpine belt on mountain slopes. The precipitation in these areas reaches 1600–5000 mm per year. The climatic data of the southernmost location, Tsurugi-san in Shikoku, of Fuji-san, and of Ozegahara moor in the northern Kanto sanchi are shown in Table 5.6. The soil types¹⁰ of these forests are respectively dry brown forest soil (Bb), dry podzol (Pd), and wet podzol (Pw). The soil types of the *Abies mariesii* forest at Oze, on the Sea of Japan side, are all podzols in any topographic situation, from Pw on slopes to Pd on narrow ridges (Maeda and

¹⁰ For Japanese forest soil types see Forestry Agency (1983).

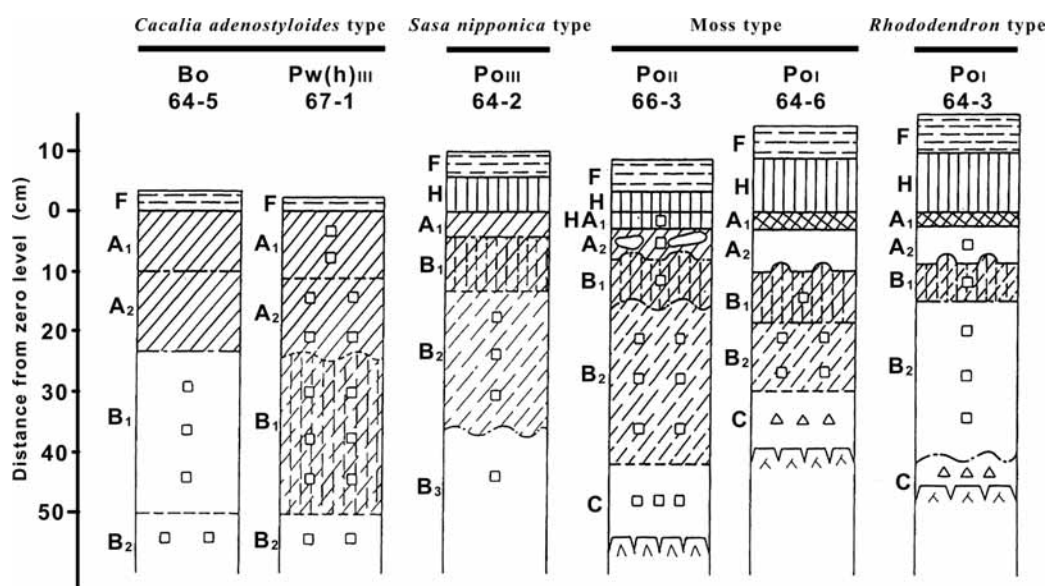


Fig. 5.9. Understorey and soil types of *Abies mariesii* and *Tsuga diversifolia* forests on Yatsuga-take (Miyakawa, 1983).

Table 5.7
Biomass and other properties of fir forests on Fuji-san¹

Properties measured	Plot number			
	Plot 11	Plot 14	Plot 21	Plot 22
No. of trees (ha ⁻¹)	3179	9700	19500	10000000
Mean tree height (m)	14.6	6.8	4.5	0.46
Mean DBH (cm)	15.5	7.6	4.3	0.66*
Basal area (m ² ha ⁻¹)	64.77	56.84	33.65	36.95*
Stem volume (m ³ ha ⁻¹)	515.55	284.99	113.67	12.18
Stem dry weight (tha ⁻¹)	190.24	107.63	45.73	4.9
Total branch dry weight (tha ⁻¹)	15.69	15.48	8.67	1.8
Current twig dry weight (tha ⁻¹)	0.77	0.78	0.59	0.4
Total needle dry weight (tha ⁻¹)	16.7	17.61	13.95	5.5
Current needle dry weight (tha ⁻¹)	3.29	3.43	2.86	1.6
Root dry weight (tha ⁻¹)	61.78	36.93	16.32	4.3
Whole plant dry weight (tha ⁻¹)	284.4	177.65	84.65	16.5
Total needle area (ha ha ⁻¹)	8.2	9.7	8.1	5.5
Current needle area (ha ha ⁻¹)	1.6	1.9	1.9	1.5

¹ Tadaki et al. (1967).

Miyakawa, 1967). For the *Abies veitchii*-*Abies mariesii* forest on the Pacific side, however, humic brown forest soil (Bd) is common, and Pd and Pw soil types are also present on Yatsuga-take (Forestry Agency, 1983; Miyakawa, 1983). There is a relationship between forest-floor composition and soil types (Fig. 5.9). A

herb layer with *Cacalia adenostyloides* indicates Bd and Pw soil types. A herb layer with *Sasa nipponica* indicates a slightly dry Pd soil type. Abundant ground moss indicates a Pd soil type, and a *Rhododendron brachycarpum* understorey indicates a drier Pd soil type.

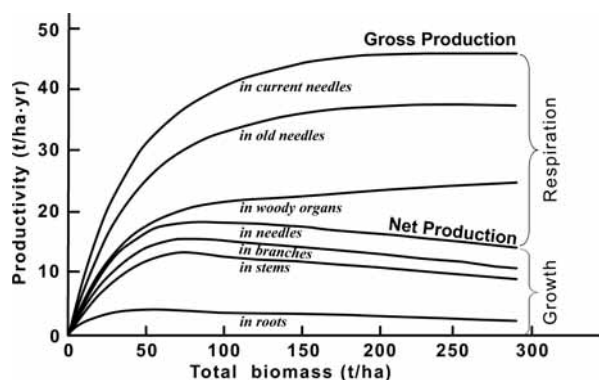


Fig. 5.10. Dry matter production of *Abies veitchii* in the full-density stages on Fuji-san (Tadaki et al., 1967).

The biomass of four plots of *Abies veitchii* forest on Fuji-san is shown in Table 5.7, and the change of productivity in *Abies veitchii* forests, as related to increase in total biomass, is shown in Fig. 5.10 (Tadaki et al., 1967).

The *Abies mariesii* forest occurs in the heavy-snow region at the Sea of Japan side of Honshu. The crowns of these forests are not very dense, enabling many summer-green shrubs to appear under the canopy of tall trees. There is heavy snow damage in *Abies mariesii*, both by the weight of the snow in the crown and by avalanches down the slopes (Ishizuka, 1981). Sugita (1987) showed that there was a positive relationship between accumulated snow depth and the development of coniferous forests in the Joetsu mountains (Fig. 5.11,

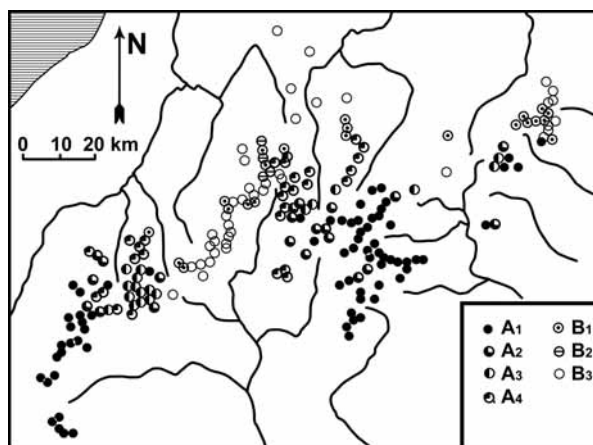


Fig. 5.11. Geographical distribution of mountains within the study area in the Joetsu mountains, classified according to the development of subalpine coniferous forests (Sugita, 1987). (A1–A4): Coniferous forests are continuous. A1 to A4 show cover decreasing from extensive to local. (B1–B3): Coniferous forests are discontinuous. B1 to B3 show cover decreasing from local to none.

Table 5.8 Relationship between snow depth and types of subalpine coniferous forest in the Joetsu mountains¹

Class of snow depth (m)	Number of mountains with different forest types ²						
	A1	A2	A3	A4	B1	B2	B3
1–2	2	–	–	–	–	–	–
2–3	8	2	1	–	1	1	–
3–4	–	1	3	3	–	–	–
4–5	–	–	1	7	1	–	2
5–6	–	–	–	3	6	1	4
6–7	–	–	–	–	1	3	–

¹ From Sugita (1987).

² Crown density is used to classify the stands into forest types. A1 dense and B3 open stand.

Table 5.8). Figure 5.12 shows a vegetation profile of the upper limit of the *Abies mariesii* forest on Hakkoda-san (Saito and Saito, 1981). Another regional association is the isolated *Abies veitchii* forest, which only occurs on mountain tops. This association has few characteristic species, in spite of the many summer-green species established from the temperate zone. *Tsuga diversifolia* forms the climatically dominant forests at the lower limit of the inland subalpine zone, as well as forests depending on local edaphic conditions.

Two communities of conifer forests, the *Picea jezoensis*–*Abies sachalinensis* and *Picea glehnii* communities, occur in the subalpine zone in Hokkaido. The

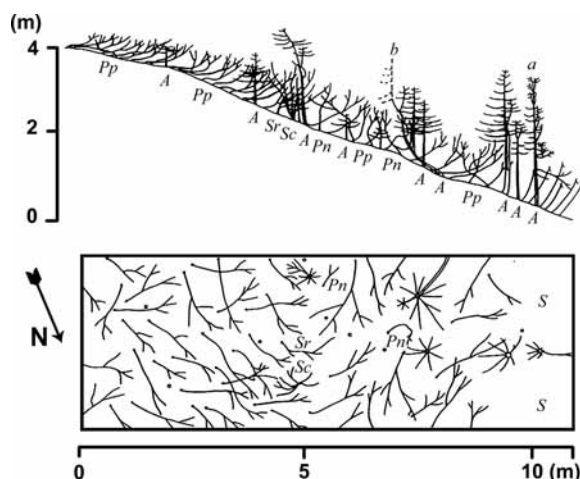


Fig. 5.12. An upper-limit fir forest at 1440m on Hakkoda-san, northern Honshu (Saito and Saito, 1981). A: *Abies mariesii*; Pn: *Prunus nipponica*; Pp: *Pinus pumila*; S: *Sasa kurilensis*; Sc: *Sorbus commixta*; and Sr: *Salix reinii*.

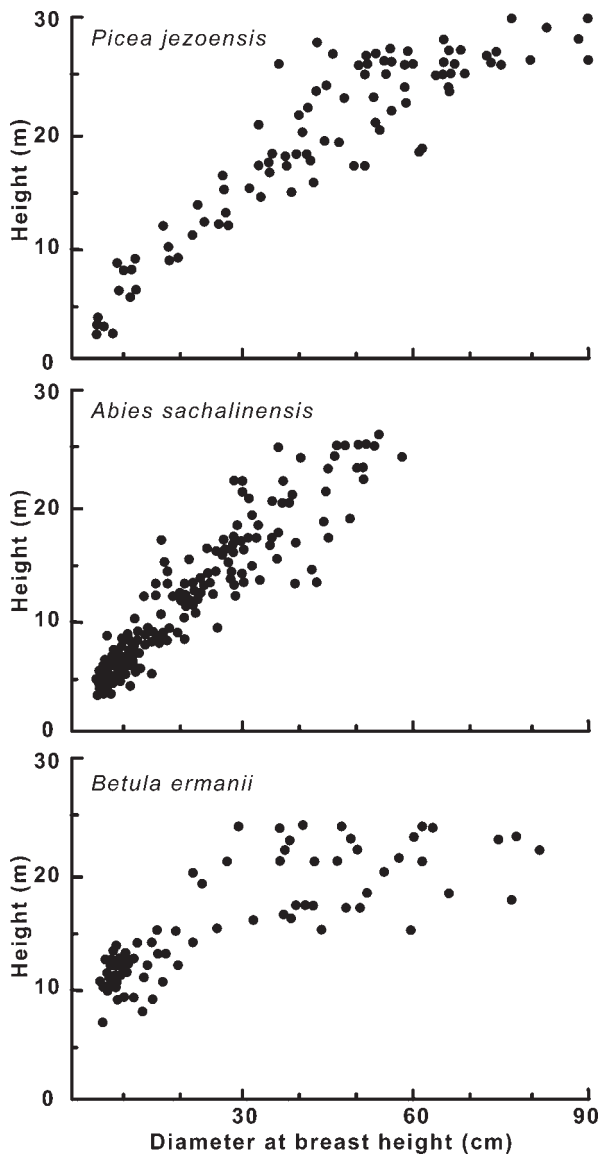


Fig. 5.13. Relationship between height and trunk diameter of three major canopy species on Tokachi-dake, Hokkaido (Okitsu et al. 1982).

average number of trees, basal area and volume per hectare were measured in a mature *Picea jezoensis*–*Abies sachalinensis* forest stand on Tokachi-dake (Okitsu et al., 1982). *Picea jezoensis* lives longer than *Abies sachalinensis* and probably forms the final overstorey of the forest, as may be concluded from the relationship between conifer height and diameter (Fig. 5.13). Suzuki et al. (1987) measured basal areas, as well as age and tree height of the important species, in Plot 1 (*Abies sachalinensis* forest at an altitude of

Table 5.9
Composition of fir and spruce forests in Naka-gawa Experimental Forest in northern Hokkaido¹

Species	Plot 1 (<i>Abies</i> forest)		Plot 2 (<i>Picea</i> forest)			
	Stems ha ⁻¹		Basal area (m ² ha ⁻¹)	Stems ha ⁻¹		Basal area (m ² ha ⁻¹)
	H ≥ 1.3 m	H < 1.3 m		H ≥ 1.3 m	H < 1.3 m	
<i>Abies sachalinensis</i>	391	735	27.1	161	951	2.4
<i>Picea glehnii</i>	5	0	0.2	122	590	19.0
<i>Picea jezoensis</i>	0	11				
<i>Taxus cuspidata</i>	32	32	0.0	43	336	0.0
Total conifers	428	778	27.3	326	1877	21.4
<i>Betula ermanii</i>	27	0	2.9	19	35	0.6
<i>Quercus mongolica</i> var. <i>grosseserrata</i>	16	11	2.8	46	60	0.9
<i>Sorbus commixta</i>	1105	219	1.1	217	1414	0.4
<i>Acer mono</i>	783	27	1.0	106	68	0.0
Total broadleaved	1931	257	4.9	369	1577	1.9
Total others	493	69	0.7	143	337	0.2
Total	2853	1104	35.8	859	3789	23.5

¹ From Suzuki et al. (1987).

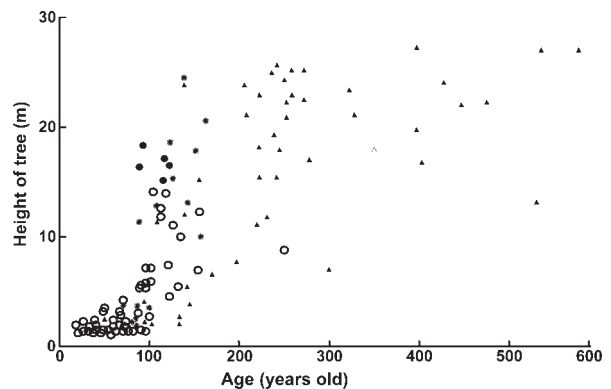


Fig. 5.14. Relationships between age and tree height of *Abies sachalinensis*, *Betula ermanii* and *Picea glehnii* in the Naka-gawa Experimental Forest in northern Hokkaido (Suzuki et al. 1987).

200 m) and Plot 2 (*Picea glehnii* forest at an altitude of 1300 m on a site with serpentine soil) in the Naka-gawa Experimental Forest in northern Hokkaido (Table 5.9; Fig. 5.14). *Picea glehnii* also lives longer than *Abies sachalinensis*; the oldest spruce was about 600 years old. *Picea glehnii* forests not only occur in the upper subalpine belt but also on dry sites, on serpentine rocks

and around bogs. In particular, *Picea glehnii* propagates vegetatively around the bog and solfatara Kawayu.

Change in forest area

In the subalpine conifer belt there have not been any marked anthropogenic effects yet. Sightseeing roads cause only insignificant local disturbances. Natural events, such as typhoons, snow avalanches or natural dying-off, damage coniferous forests over larger areas. There are several successional series, determined by forest structure and gap size (Kohyama, 1983; Tohda and Kikuchi, 1981). In the most common successional series, *Calamagrostis* meadows or tall herb communities develop first, accompanied by young conifers and sometimes *Ribes* and *Rubus* species. After that, summer-green shrubs of *Alnus maximowiczii*, *Betula ermanii* and others occupy these sites, because they grow more rapidly than young conifers. However, the young conifers grow steadily under the summer-green canopy. In high mountain areas such as Shimagare in Yatsuga-take, above 2300 m, where there are no summer-green shrubs or tall herb communities because of the high density of fir seedlings and the more continental climate, there is an additional dynamic effect called “dead tree strips” (“fir waves” or “Shimagare phenomenon”) (Ohshima et al., 1958). The forest forms successive bands of different ages, including over-mature and dying, merging into one another, and repeated across the landscape. There is no secondary community composed of broadleaved species. Only *Abies* species form the monodominant initial, mature and degenerate stages in the fir-wave sequence (Fig. 5.15). These fir waves occur not only on Shimagare but also in the Kii peninsula, on the Chichibu mountains in Kanto sanchi, and on Hakkodasan in Tohoku (Yato, 1964; Tohda and Kikuchi, 1981). Tadaki et al. (1977) showed the common environmental and morphological characters of this phenomenon:

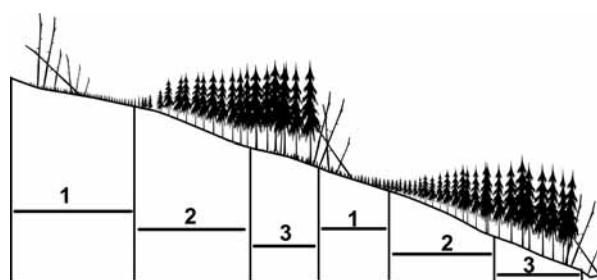


Fig. 5.15. Schematic dynamics of the Shimagare phenomenon in fir forests at Shimagare, central Japan (Nakamura, 1985). 1: initial phase; 2: optimal phase; 3: degeneration phase.

wind-exposed southerly slopes, podzolic soils, pure and dense *Abies* forests, and the turnover of one wave from 100 to 130 years. The biomass in the different parts of the “wave” in an *Abies veitchii* forest with dead tree strips is shown in Tables 5.10 and 5.11. Rapid increase of the needle biomass reached a maximum about 40 years after emergence of the seedlings, and was followed by a gradual decline and a relatively long stable stage, after which the needle biomass decreased remarkably after the trees reached the age of 100 years (Tadaki et al., 1977; Fig. 5.16).

A *Larix kaempferi* community develops as a pioneer stage on volcanoes. On Asama-yama, Chubu, larch seedlings are primarily established on heath sites, and need about 30 years to reach a height of 20–40 cm. In

Table 5.10
Basal area and biomass structure of 7 plots among the fir waves on Asahi-dake, Chubu¹

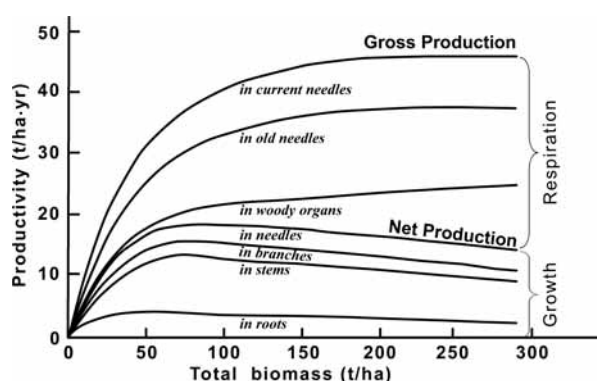
Variable	Plot number						
	1	2	3	4	5	6	7
No. of trees sampled	7	7	7	7	8	10	20
Basal area (m ² ha ⁻¹)							
– at breast height	52.2	66.9	62.2	9.7			
– at stem base				96.1	61.1	31.6	5.3
Stem volume (m ³ ha ⁻¹)	232	307	230	179	55	7.8	
Stem biomass (t ha ⁻¹)	92.2	130.3	97.2	74.9	29.2	6.4	1
Branch biomass (t ha ⁻¹)	11.3	15.7	12.2	10.6	8.1	2.6	0.4
– current	0.3	0.4	0.4	0.5	0.5	0.4	0.2
– old	11	15.3	11.8	10.1	7.6	2.2	0.2
Needle biomass (t ha ⁻¹)	8.3	14.3	13.6	17.1	13.6	4.6	2.3
– current	1.7	2	2.2	3	2.2	1.3	0.6
– old	6.6	12.3	11.4	14.1	11.4	3.3	1.7
Cone biomass (t ha ⁻¹)	0.2	1.1	1.4	0.9			
Above-ground biomass (t ha ⁻¹)	112	161.4	124.4	103.5	50.9	13.6	3.7
Root biomass (t ha ⁻¹)	31.1	43.8	32.8	25.7	11.2	2.7	0.9
Leaf area (ha ha ⁻¹)	2.8	5.4	5.9	6.8	6.5	2.8	1.4
– current	0.8	0.9	0.8	1.4	1.1	0.9	0.4
– old	2	4.5	5.1	5.4	5.4	1.9	1
Undergrowth biomass (t ha ⁻¹)	4.5	2.7	0.4	0.7	0.2	1.3	
– moss	2.8	1.9	0.4	0.7	0.2	1.3	
– herb	0.2	0.4	0			0	
– woody plant	1.5	0.4					

¹ From Tadaki et al. (1977).

Table 5.11

Biomass production of 7 plots among the fir waves on Asahi-dake, Chubu¹

Current production (t ha ⁻¹ yr ⁻¹)	Plot number					
	1	2	3	4	5	6
Stem	1.2	3.7	3.6	4.7	3.8	1.3
Branch	0.4	1.6	1.5	1.5	1.4	0.8
Needle	1.7	2.0	2.2	3.0	2.2	1.3
Cone	0.2	1.1	1.4	0.9	–	–
Root	0.5	1.6	1.5	1.8	1.5	0.6
Total (net production)	4.0	10.0	10.2	11.9	8.9	4.0

¹ From Tadaki et al. (1977).Fig. 5.16. Change of net production and its components in *Abies veitchii* forest in relation to increasing stand age on Asahi-dake (Tadaki et al., 1977).

the mature larch forest, seedlings of *Abies veitchii*, a canopy tree of the potential natural vegetation, develop in the understorey, and after they reach the canopy and the larch trees die off, the fir becomes a dominant (Maeda et al., 1978).

Historical effects

The subalpine coniferous forests of Honshu and Shikoku have many more local endemic species than the subalpine communities of Hokkaido (Table 5.12). This suggests that the *Abietion mariesii* developed particularly on the Japanese Islands. The basic community is considered to be the *Abies veitchii*–*Abies mariesii* forest, which subsequently diverged into two regional associations under changing climatic conditions (Morita, 1984). In the Quaternary, the island of Hokkaido was frequently connected by a land bridge with the Asian mainland and the northern islands Sakhalin, Kunashir and Habomai (Grichuk, 1984). At the times of connection *Picea jezoensis* and *Picea*

Table 5.12

Local endemic and circumpolar species of the forests in Honshu¹

Local endemic species	Circumpolar species
<i>Abies mariesii</i>	<i>Coptis trifolia</i>
<i>Abies sachalinensis</i>	<i>Dicranum majus</i>
<i>Abies veitchii</i>	<i>Dryopteris austriaca</i>
<i>Cacalia adenostyloides</i>	<i>Goodyera repens</i>
<i>Chiogenes japonica</i>	<i>Hylocomium splendens</i>
<i>Coptis quinquefolia</i>	<i>Linnaea borealis</i>
<i>Dactyloctenium ringens</i>	<i>Listera cordata</i>
<i>Menziesia pentandra</i>	<i>Listera pinetorum</i>
<i>Pedicularis keiskei</i>	<i>Lobaria linita</i>
<i>Picea jezoensis</i> var. <i>hondoensis</i>	<i>Oxalis acetosella</i>
<i>Picea koyamae</i>	<i>Phegopteris connectilis</i>
<i>Picea shirasawae</i>	<i>Platanthera ophrydioides</i>
<i>Pseudobryum speciosum</i>	<i>Pleurozium schreberi</i>
<i>Pteridophyllum racemosum</i>	<i>Pogonatum japonicum</i>
<i>Pyrola alpina</i> **	<i>Pyrola secunda</i>
<i>Rubus ikenoensis</i>	<i>Rhytidadelphus triquetrus</i>
<i>Tsuga diversifolia</i>	<i>Sphagnum girgensohnii</i>
<i>Vaccinium smallii</i> *	<i>Trientalis europaea</i>
<i>Vaccinium yatabei</i>	<i>Vaccinium vitis-idaea</i>

¹ From Miyawaki and Nakamura (1988).

glehnii, as well as a great number of companion species, were able to spread from the southern Japanese regions up to the north.

Zonal forest types – *Abies sachalinensis*–*Picea jezoensis* forest (*Piceo*–*Abietetum sachalinensis*)

Structure: *Abies sachalinensis* is the commonest coniferous species in Hokkaido. It occurs in the temperate summer-green deciduous forest, the so-called “Pan Mixed forest”. It is also an important oroboreal coniferous forest species. The *Quercus crispula*–*Abies sachalinensis* forest was classified as *Abieti sachalinensis*–*Quercetum grosseserratae*. This association occurs often as zonal natural vegetation in the lowlands of the temperate zone.

The *Abies sachalinensis*–*Picea jezoensis* forest in oroboreal montane and subalpine belts belongs to the *Piceo*–*Abietetum sachalinensis* (Nakamura, 1988). The height of the forest is 16–32 m and crown cover is 40–95%. The lower tree layer, 10–20 m high, has a cover of 10–50%. The shrub layer, 1.8–5 m high, has



Fig. 5.17. *Abies sachalinensis*–*Picea jezoensis* forest in the oroboreal belt of Hokkaido at 1000 m. Photo Y. Nakamura.

a cover of 10–70%. The cover of the herb layer, 0.3–2.0 m tall, is 20–100%.

Species combination: High-frequency species in the tree layer are *Abies sachalinensis*, *Picea jezoensis* and *Sorbus commixta*; in the shrub layer, *Acer ukurunduense*, *Euonymus macropterus*, *Hydrangea petiolaris*, *Menziesia pentandra*, *Vaccinium smallii* and *Viburnum furcatum*; the herb layer includes *Arachniodes mutica*, *Carex sachalinensis*, *Dryopteris expansa*, *Galium kamtschaticum*, *Huperzia serrata*, *Ilex rugosa*, *Maianthemum dilatatum*, *Oxalis acetosella*, *Phegopteris connectilis*, *Sasa kurilensis* and *S. senanensis*. Characteristic species of this community are *Actinidia kolomikta*, *Carex sachalinensis*, *Galium kamtschaticum*, *Hydrangea petiolaris*, *Phegopteris connectilis*, *Picea jezoensis*, *Ribes sachalinense*, *Sasa senanensis*, *Schizophragma hydrangeoides*, *Skimmia japonica* var. *intermedia* f. *repens* and *Viola selkirkii*.

Distribution: The *Abies sachalinensis*–*Picea jezoensis* forest is distributed over Hokkaido and in the southern part of Sakhalin (Fig. 5.17).

Human impacts: Cutting and plantation have increased since World War II.

Animals: Mammals include *Apodemus argenteus* (small Japanese field mouse), *Cervus yezoensis* (Yezo deer), *Clethrionomys rufocanus*, *Sciurus vulgaris orientalis* (Yezo squirrel), *Tamias sibiricus* (Siberian chipmunk), *Ursus arctos* (brown bear) and *Vulpes vulpes schrencki* (red fox), and the birds *Dryocopus martius* (black woodpecker), *Erithacus akahige*, *Prunella rubida* (Japanese accentor), *Pyrrhula pyrrhula* (bullfinch), *Regulus regulus* (gold crest) and *Tarsiger cyanurus* (Siberian bluetail). The Japanese wolf (*Canis hondophlax*) is extinct. With global warming the population of *Cervus yezoensis* is increasing.



Fig. 5.18. The interior of an *Abies mariesii*–*Abies veitchii* forest on the main island of Japan, at 2150 m. Photo Y. Nakamura.

Zonal forest types – *Abies mariesii*–*Abies veitchii* forest (*Abietetum veitchio-mariesii*)

Structure: *Abies mariesii*–*Abies veitchii* forests occur on montane and subalpine belts on the Pacific side of central Honshu, where the snow depth does not exceed 75 cm (Nakamura, 1986). It borders on *Tsuga diversifolia* forest at lower levels (at 1700 m in the Kiso mountains), and on *Pinus pumila* krummholz at higher levels (2600 m). *Abies mariesii*, *A. veitchii* and *Tsuga diversifolia* are dominants in the canopy. Another high-frequency species is *Picea jezoensis* var. *hondoensis*. The stand height is about 32 m. In the lower oroboreal montane belt this forest type also includes *Pinus koraiensis*, *P. parviflora* var. *pentaphylla* and *Thuja standishii*. Common in the lower tree layer are the coniferous species and the deciduous *Betula ermanii* and *Sorbus commixta*. The cover of the shrub layer, consisting largely of shrubs and saplings

of young conifers, is 10–90%. Other high-frequency species are *Acer tschonoskii*, *Menziesia pentandra*, *Sorbus commixta* and *Vaccinium smallii*. Common herb and dwarf-shrub species are *Arachniodes mutica*, *Cornus canadensis*, *Maianthemum dilatatum*, *Ilex rugosa*, *Oplopanax japonicus*, *Rubus pedatus*, *Oxalis acetosella*, *Shortia soldanelloides*, *Streptopus streptopoides* var. *japonicus* and *S. streptopoides*. Cover of the moss layer on the forest floor usually exceeds 60%. Small herbs such as *Goodyera repens*, *Listera cordata*, *L. nipponica*, *Orthilia secunda*, *Platanthera ophrydioides* and *Pyrola alpina* are spread over the moss cover. (Fig. 5.18).

Species combination: Characteristic species of this community are endemics of the islands of Honshu and Shikoku: *Abies mariesii*, *A. veitchii*, *Chiogenes japonica*, *Coptis japonica* var. *dissecta*, *C. quinque-*

folia, *Pedicularis keiskei*, *Pteridophyllum racemosum*, *Rubus ikenoensis*, *Smilacina hondoensis*, *Streptopus streptopoides* var. *japonicus* and *Vaccinium yatabei*.

Distribution: The Pacific side of central Honshu. The southern boundary lies in the southern part of the Akaishi mountains (35°08'N, 138°E). The northern boundary reaches the northern part of Tochigi prefecture, at 37°05'N and 139°56'E.

Human impact: Large-scale destruction, such as clear-cutting, occasionally occurs; small-scale destruction occurs along sightseeing roads. The interior of the forest stand may be damaged by light and wind coming from the road, as happened on Fuji-san at an altitude of 2400 m. Regrowth of the edge communities of *Alnus*, *Betula* and *Salix* species is slower on windward dry sites.

Animals: Mammals include *Apodemus argenteus*, *Capricornis crispus*, *Clethrionomys rufocanus*, *Glirulus japonicus* and *Pteromys momonga*; birds include *Erithacus akahige*, *E. cyane*, *Nucifraga caryocatactes*, *Phylloscopus borealis*, *P. tenellipes*, *Pyrrhula pyrrhula*, *Regulus regulus* and *Tarsiger cyanurus*.

Zonal forest types: *Abies mariesii* forest (*Abietetum mariesii*)

Structure: *Abies mariesii* forest is distributed on the Sea of Japan side of Honshu, where snow depth exceeds 75 cm, on gentle slopes and/or ridges, where the snow damage is not so grave (Nakamura, 1986). The limiting factor is snow damage from sticking, pressure and moving. *Abies veitchii* cannot survive in these conditions (Fig. 5.19).

Abies mariesii forms stands mixed with *Betula ermanii*. The shrub layer is composed of the summer-green *Acer tschonoskii*, *A. ukurunduense*, *Rhododendron albrechtii* and *Viburnum furcatum*, each represented by a tussock form adapted to the snow pressure. *Sasamorpha borealis* is common, and sometimes dominates the understorey. Frequent species in the herb layer are *Coptis trifolia*, *Maianthemum dilatatum* and *Plagiogyria matsumureana*. Common mosses are *Dicranum majus*, *Pleurozium schreberi*, *Pseudobryum speciosum* and *Sphagnum girgensohnii*.

Species combination: The *Abies mariesii* forest is characterized by *Epigaea asiatica*, *Heloniopsis orientalis*, *Ilex leucoclada*, *Rhododendron albrechtii*



Fig. 5.19. *Abies sachalinensis* surviving under snow and forming a unidominant forest in the subalpine belt of Oze, central Japan, at an altitude of 1740 m. Photo Y. Nakamura.

and *Sasamorpha borealis*, the so-called 'Sea of Japan elements'.

Distribution: The *Abies mariesii* forest is distributed on Honshu at the Sea of Japan side. The southern boundary is Haku-san, located at 36°10'N and 136°50'E. The northern boundary is Hakkoda-san (40°40'N, 140°50'E).

Human impacts: Sightseeing roads have impact on the forests. Although there are many ski grounds in the deep snow area, damaging effects on nature have not been recorded.

Animals: Mammals inhabiting the forests include *Apodemus argenteus*, *Capricornis crispus*, *Clethrionomys rufocanus* and *Glirulus japonicus*; birds include *Erithacus akahige*, *E. cyane*, *Nucifraga caryocatactes*, *Phylloscopus borealis*, *P. tenellipes*, *Pyrrhula pyrrhula*, *Regulus regulus* and *Tarsiger cyanurus*.

Zonal forest types – *Abies veitchii* forest (*Abietetum veitchii*)

Structure: The height of stands varies from 13 up to 24 m. Dominant species are *Abies veitchii* and *Tsuga diversifolia*. *Picea jezoensis* var. *hondoensis* is also common in the canopy. The lower tree layer is composed of *Acer australe*, *Betula ermanii* and *Sorbus commixta*. Dominant species of the shrub layer are *Menziesia pentandra* and *Abies* saplings. Other common species are *Magnolia sieboldii* and *Sorbus commixta*. The herb layer is composed of *Cacalia*

adenostyloides, *Carex fernaldiana*, *C. hakkodensis*, *Dryopteris expansa*, *Luzula plumosa*, *Oplopanax japonicus* and *Oxalis acetosella*. In the moss layer *Bazzania yoshinagana*, *Dicranum majus*, *Hylocomium splendens*, *Pleurozium schreberi* and *Pogonatum japonicum* are common.

Abies veitchii forests occur on summits over 1800 m, in small areas as relic stands from the Ice Age (Nakamura, 1986; Yamanaka, 1981).

Species combination: Differential species distinguishing *Abies veitchii* forest from *Abies veitchii*–*A. mariesii* forest are *Acer australe*, *Carex fernaldiana*, *Luzula plumosa*, *Rubus pseudoacer* and *Viburnum urceolatum*. *Abies mariesii* is absent.

Distribution: This community occurs on Misen mountain on the Kii peninsula, and on Tsurugi-san and Ishizuchi-san in Shikoku. Ishizuchi-san is the southernmost limit of subalpine coniferous forest in Japan.

Human impacts: Relic vegetation from the Ice Age survived sparsely on the summits of the mountains Tsurugi-san and Ishizuchi-san in Shikoku. These areas must be preserved against recreation pressure such as the skiing area in Tsurugi-san and the trail up to the summit of Ishizuchi-san. *Sasa tsuboiana* forms a continuous meadow community as a degeneration phase, in which *Abies veitchii* forest cannot regenerate.

Animals: The increasing population of Japanese deer will lead to a catastrophic situation. The deer scrape the bark off the trunks of coniferous species such as *Picea jezoensis* var. *hondoensis*. This causes the forest communities to degenerate to the shrub or herb stages. The main mammals are *Capricornis crispus*, *Glirulus japonicus* and *Pteromys momonga*; a prominent bird is *Erithacus akahige*.

Azonal forest types – *Picea glehnii* forest (*Piceetum glehnii*)

Structure: *Picea glehnii* is dominant in the canopy. The height of stands is 15–30 m, and crown cover is 60–90%. The lower tree layer, 7–15 m high, has a cover of 20–40%, the shrub layer, 1.5–6 m high, has 10–70%, and the herb layer, 0.4–1.7 m tall, has 20–90%. The moss layer usually has a 20–90% cover.

Picea glehnii forests occur on volcanic areas, swamps, ridges and the upper part of the subalpine belt. In the cool temperate belt, *Picea glehnii* forests

are confined to specific edaphic conditions, such as volcanic rocks, ultrabasic rocks, swamps, sand dunes, and sites around solfataras. The vertical range is from sea level to 1460 m in Hokkaido, Sakhalin, and Kunashir.

Species combination: *Picea glehnii* dominates in the canopy. The canopy may also include *Abies sachalinensis*, *Betula ermanii* and *Picea jezoensis*, but they never dominate. Dominant species in the shrub layer are *Menziesia pentandra*, with saplings of *Picea* and *Abies*. Other high-frequency species are *Acer tschonoskii*, *A. ukurunduense*, *Euonymus macropterus*, *Rhododendron brachycarpum*, *Sorbus commixta*, *Vaccinium ovalifolium* and *V. smallii*. The dominant species in the herb layer is *Sasa kurilensis*. Other common species are *Coptis trifolia*, *Cornus canadensis*, *Ilex rugosa*, *Maianthemum dilatatum*, *Oxalis acetosella* and *Streptopus streptopoides*. The moss layer is composed of *Dicranum majus*, *Hylocomium splendens*, *Pleurozium schreberi*, *Pogonatum japonicum* and *Rhytidiadelphus triquetrus*.

Distribution: This forest type is found in most of Hokkaido south of the Ishikari lowland, the island of Rishiri-to, southernmost Sakhalin and Kunashir.

Human impacts: The damage by forestry cuttings on Hokkaido and Kunashir is not very serious, however the lowland communities on southernmost Sakhalin were almost completely eliminated at the beginning of the 20th century.

Animals: A wide spectrum of site conditions gives rise to a high diversity of ecosystems. However, there are no characteristic animals. Most of the species are also found in *Abies sachalinensis*–*Picea jezoensis* forest. These include, among mammals, *Cervus yesoensis*, *Sciurus vulgaris orientalis*, *Tamias sibiricus*, *Ursus arctos* (brown bear), and *Vulpes vulpes schrencki* (red fox); birds include *Erithacus akahige*, *Prunella rubida*, *Pyrrhula pyrrhula*, *Regulus regulus* and *Tarsiger cyanurus*.

Azonal forest types – *Larix kaempferi* forest (*Larix kaempferi* community)

Structure: *Larix kaempferi* forests occur on volcanoes, avalanche tracks and swamps as a pioneer or edaphic community (Nakamura, 1986). The stand structure and species combination of the forests depend

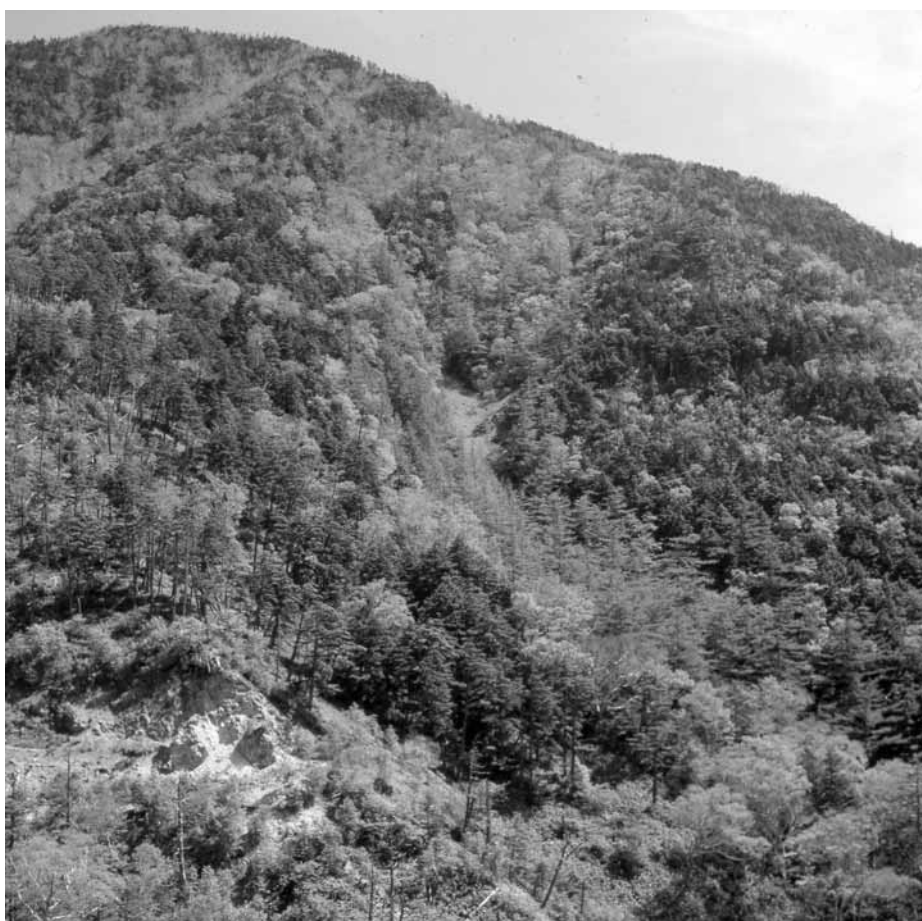


Fig. 5.20. *Larix kaempferi* forest on an unstable site within *Abies mariesii*–*Abies veitchii* forest, Tochigi, at 1900 m. Photo Y. Nakamura.

on site conditions. *Larix kaempferi* forms an open canopy varying in height from 1 to 25 m. In forests of pioneer stages of succession the understorey is composed out of tall herbs: *Aster glehnii* var. *hondoensis* and *Senecio nemorensis*. Forests on volcanic gravel soil include the alpine species *Empetrum nigrum*, *Lerchenfeldia flexuosa* and *Vaccinium uliginosum*.

Larix kaempferi can germinate only in sunny open places. For regeneration, it needs canopy openings, which usually appear after substantial damage. During succession without disturbance the larch community changes to the climatic climax *Abies veitchii*–*Abies mariesii* forest (Fig. 5.20).

Species combination: Larch forest forms heterogeneous stands with various combinations of species. The most characteristic species of the community is *Larix kaempferi* itself.

Distribution: This forest type is found in central Honshu. Large areas of larch forests are found on the volcanoes Fuji-san and Asama-yama. It also occurs on swamps in Ozegahara moor in north Kanto sanchi.

Human impacts: In the montane belt of central Honshu the establishment of plantations of *Larix kaempferi* after World War II caused slope erosion over extensive areas.

SUBALPINE KRUMMHOLZ BELT (CRYOROTEMPERATE BELT) WITHIN THE NORTHERN TEMPERATE ZONE

Distribution

The upper limit of woody vegetation on high mountains within the northern temperate zone, above the *Betula ermanii* belt, is formed by a well-developed belt of

Pinus pumila krummholz, occurring at about 2600–3200 m in Honshu, 1900–2100 m in Hokkaido, 1000–1500 m in Kunashir, 2000–2500 m on Changbai Shan, 1500–2000 m in the central Sikhote Alin and above 1100 m on the southern spurs of the Badzhal'skiy mountains. Below these elevation marks, krummholz may occur in windward habitats such as the summits and ridges of high mountains, especially on western and southwestern slopes. *Pinus pumila* krummholz needs sufficient snow protection during the winter, but if the layer of snow is too heavy it retards development on the site, especially in areas with relatively high winter temperatures. *Pinus pumila* reproduces vegetatively and forms extensive stands on ridges. *Pinus pumila* krummholz also occurs near steam vents, and is then accompanied by *Ledum palustre* var. *diversipilosum*.

On the continent within the northern temperate zone *Pinus pumila* has its southern boundary of distribution. On Sikhote Alin it can be found on all mountains exceeding an elevation of 1200 m, which climatically corresponds to the fir–spruce forests. *Pinus pumila* sometimes occurs at low elevations, which may be interpreted as a lowering of the vertical zonation (Grishin et al., 1996); this occurrence is mainly caused by wind affecting the snow distribution on the mountain ridges. Snow accumulation, with late melting, is the main factor stopping the development of forest vegetation and favouring the development of *Pinus pumila* scrub. However, the distribution pattern of *Pinus pumila* on mountains reaching 2000 m is mainly determined by climatic factors.

Ecology

Pinus pumila krummholz occurs climatically where the values of Kira's warmth index are around 15. Its vertical extent, however, depends on topographic conditions. *Pinus pumila* krummholz must always be protected by a sufficient snow cover during the winter (Suzuki and Umezu, 1965, Fig. 5.21). The soil type is iron podzol in the case of the mountain Kurobe, middle Honshu (Suzuki, 1964). Biomass and litterfall of krummholz were measured in the Kiso mountains in central Japan at altitudes of 2600 and 2665 m (Tables 5.13 and 5.14). Kajimoto (1989) compared these values with the pine krummholz biomass of other regions (Fig. 5.22). The pine krummholz biomass in Hokkaido is high and comparable to that of forest vegetation

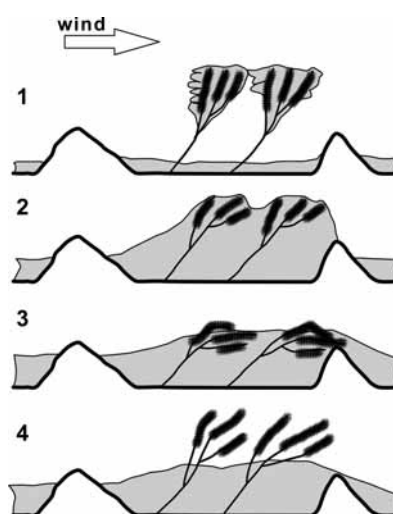


Fig. 5.21. Snow depth in the *Pinus pumila* community at different times of year in the Taisetsu Massif, central Hokkaido (Okitsu and Ito, 1983).

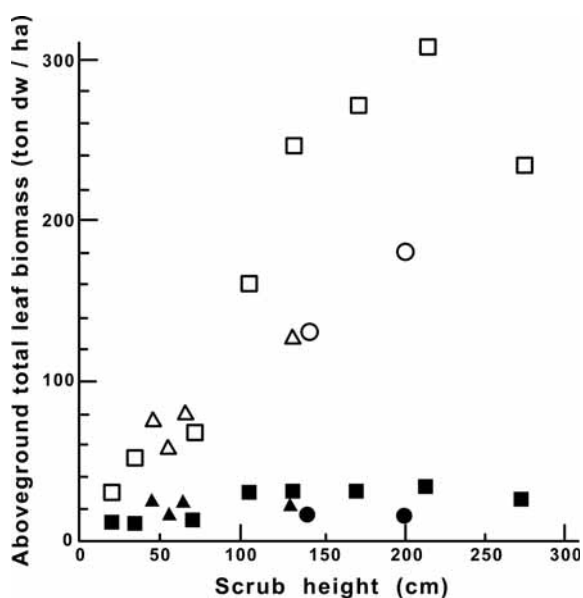


Fig. 5.22. Biomass of above-ground parts (open symbols) and leaves (full symbols) in *Pinus pumila* scrub on three mountains in Japan (Kajimoto 1989): triangles, Tatesyama; squares, Taisetsu; circles, Shogigashira.

(Okitsu, 1981). The biomass on the Taisetsu Massif is shown in Table 5.14.

Change in forest area

The mean rate of stem elongation on the Taisetsu Massif is 30–45 mm per year (Fig. 5.23). The leaves

Table 5.13

Rates of litter fall in *Pinus pumila* krummholz in the Kiso mountains in central Japan¹

Component	Plot 1					Annual rates kg ha ⁻¹ y ⁻¹	Plot 2					Annual rates kg ha ⁻¹ y ⁻¹
	Rates by time intervals ² (kg d.m. ha ⁻¹ d ⁻¹)						Rates by time intervals (kg d.m. ha ⁻¹ d ⁻¹)					
	[1]	[2]	[3]	[4]	[5]		[1]	[2]	[3]	[4]	[5]	
Leaves of <i>Pinus pumila</i>	31.26	1.58	2.79	2.27	44.89	2.01	9.73	2.21	14.62	10.97	32.85	1.96
Bud scales of <i>Pinus pumila</i>	4.95	0.33	0.72	0.2	2.93	0.34	2.81	0.22	0.35	0.2	2.14	0.2
Branches of <i>Pinus pumila</i>	0.28	0.06	0	0.14	0.67	0.03	0.41	0.23	0.4	0.7	1.15	0.12
Bark of <i>Pinus pumila</i>	0.58	0.18	0.18	0.15	0.17	0.08	0.18	0.09	0.21	0.05	0.1	0.04
Sexual organs of <i>Pinus pumila</i>	0.54	0.03	0.08	28.69	2.2	1.07	0.01	0	0	0.25	2.05	0.01
Insect bodies and faeces	0.07	0	0.03	0.05	0.04	0.01	0.04	0	0.03	0.05	0.03	0.01
Organs of other plants	0.61	0.11	0.07	0	0.57	0.06	0.73	0.05	0.03	0	0.29	0.05
Total	38.29	2.29	3.87	31.5	50.86	3.6	13.91	2.8	15.64	12.22	37.29	2.39

¹ From Kajimoto (1989).² Intervals: [1] from Aug. 31, 1984 to Oct. 15, 1984; [2] from Oct. 16, 1984 to June 14, 1985; [3] from June 15, 1985 to July 24, 1985; [4] from July 25, 1985 to Aug. 29, 1985; [5] from Aug. 30, 1985 to Oct. 18, 1985.

Table 5.14

Morphological character and biomass of the *Pinus pumila* community on Taisetsu, Hokkaido¹

Morphological character and biomass	Site type				
	Wind exposure	Upper slope	Middle slope	Lower slope	Around snow patches
Height (cm)	20	34	70	130	213
Mean stem diameter (cm)	0.78	2.18	2.33	5.79	7.47
Mean stem length (cm)	34.66	82.31	125.18	247.6	338
Density (stems ha ⁻¹)	880 000	130 000	110 000	50 000	32 500
Density of dead trees (stems ha ⁻¹)	0	20 000	50 000	0	5 000
Basal area (m ² ha ⁻¹)	46.7	51.87	106.55	127.91	102.07
Basal area of dead trees (m ² ha ⁻¹)	0	4.76	5.77	0	6.38
Leaf dry weight (WL, ton)	12.56	12.06	14.35	32.03	34.64
Stem dry weight (WS, ton)	18.44	39.63	53.96	214.92	277.36
Total dry weight (WT, ton)	31	51.69	68.31	246.95	308
WL/WT	0.41	0.23	0.21	0.13	0.11
Dry weight of dead trees (t ha ⁻¹)	0	4.08	6.01	0	13.45
Volume increment (m ³ ha ⁻¹)	15.45	71.12	98.26	399.74	509.12
Volume increment of dead trees (m ³ ha ⁻¹)	0	7.17	10.13	0	25.05

¹ From Okitsu (1981).

fall every 6–7 years on Kitadake and in middle Honshu. The stems of *Pinus pumila* develop adventitious roots and reproduce vegetatively.

Extensive stands on ridges, so-called “dwarf-pine seas”, are formed by vegetative reproduction. Seedlings are not found in the understorey.

Historical effects

Species in the dwarf-pine scrub communities include a few local endemics, but most occur more widely around Siberia or beyond, some having circumpolar distribution. It is suggested that most species of dwarf-

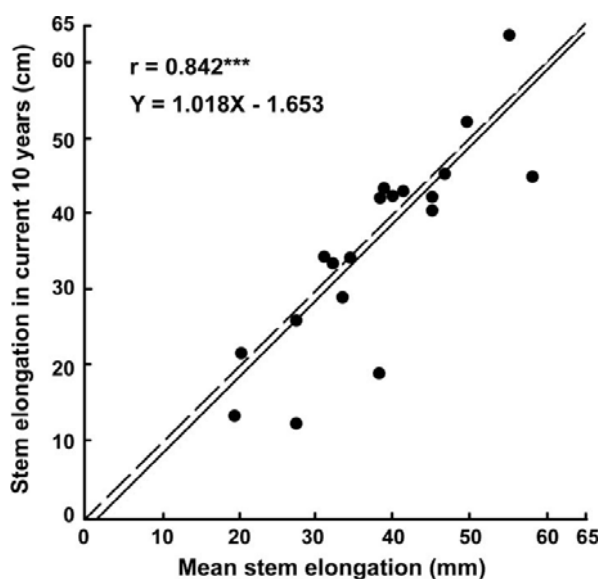


Fig. 5.23. *Pinus pumila* on the Taisetsu Massif: correlation between mean stem elongation in the current year and stem elongation during the last 10 years (Okitsu and Ito, 1983).

pine scrub came from the northern Holarctic region to Japan at several times during the Glacial period (Okitsu, 1985).

Zonal sites – *Pinus pumila* scrub (*Vaccinio–Pinetum pumilae*)

Distribution

The southern boundary is at Haku-san in eastern Honshu. The vertical distribution ranges from 2400 m to 3050 m in central Honshu, over 1400 m in central Hokkaido, 2000–2500 m on Changbai Shan, 1500–2000 m in the central Sikhote Alin and above 1100 m on the southern spurs of the Badzhal'skiy mountains.

The *Pinus pumila* scrub community occurs in the upper belt of the subalpine zone, in habitats exposed to strong winds, such as western and northwestern slopes along high mountain ridges. The height of the vegetation varies with exposure to wind – from 30 cm to 5 m (Grishin et al., 1996).

Structure

The height of *Pinus pumila* krummholz at tree line may reach 5 metres, but in the alpine belt the more wind-exposed mat form, in small hollows, may be only 5 cm high. The canopy layer is composed of the dominant *Pinus pumila*. In the taller communities the shrubs *Rhododendron brachycarpum*, *Vaccinium ovalifolium* and *V. smallii*, with *Prunus nipponica*

var. *kurilensis* in the island part of the range and *Rhododendron mucronulatum* and *Sorbus sambucifolia* in the continental part of the range form a well-developed shrub layer, which in low-growing stands may be a part of the canopy. In the herb layer there are many evergreen dwarf-shrubs and herbs such as *Coptis trifolia*, *Empetrum nigrum* var. *japonicum*, *Ledum palustre* var. *decumbens*, *Lycopodium annotinum*, *Rhododendron aureum*, *Shortia soldanelloides* and *Vaccinium vitis-idaea*. The moss layer is well developed, including *Dicranum fuscescens*, *Dicranum majus*, *Hylocomium splendens*, *Pleurozium schreberi* and *Ptilium crista-castrensis*. In sunny, dry habitats, lichens such as *Cladina mitis*, *C. rangiferina* and *C. stellaris* appear in the moss layer.

Species combination

Characteristic species are *Pinus pumila*, *Ptilium crista-castrensis*, *Rhododendron aureum* and *Rubus pedatus*.

Human impacts

Pinus pumila scrub is protected by law in Japan. The main source of damage in Hokkaido is recreational activity; however, elsewhere in the *Pinus pumila* range the main disturbance factor is fire.

Animals

Pinus pumila has a symbiotic relationship with *Nucifraga caryocatactes*, which carries the seeds of dwarf pine to sunny, open places such as *Vaccinium–Empetrum* heath, and stores them there. Then 10–15 seeds from the storage may germinate together (Nakagoshi and Soga, 1981; Wilmanns et al., 1985). Small rodents, such as *Eutamias sibiricus*, also play a high dispersal role by creating storages of *Pinus pumila* seeds in soil. The accentor (*Prunella collaris*) and (in Honshu) the Japanese ptarmigan (*Lagopus mutus japonicus*) live in dwarf-scrub areas. *Mustela erminea orientalis* and *Ochotona alpina* in Hokkaido, and *Mustela erminea nippon* in Honshu, are found in open places around dwarf-pine thickets.

Azonal sites – Summer-green scrub and tall herb meadows

Distribution

The summer-green scrub and tall herb communities have similar developmental areas throughout the northern temperate zone of Far Eastern Asia. These

correspond to the potential natural vegetation areas of subalpine coniferous forest in the south of the range, and to subalpine dwarf-pine thickets in the middle and northern Sikhote Alin. The southern limit occurs on Ishizuchi-san (1982 m) in Shikoku. Summer-green scrub and tall forbs occur above 1800 m in Shikoku, above 1650 m in Chubu, above 1100 m in middle Tohoku and above 700 m in Hokkaido. The most extensively developed communities occur on the Sea of Japan side, where there is no subalpine coniferous forest.

Subalpine summer-green scrub and tall herb meadows occur azonally on steep slopes, landslide tracks, sites with deep snow, and around snow patches and bogs. Heavy snow brings physical disturbance, such as snowslides and pressure, and physiological disturbance by delaying the growing season. The melting snow does, however, insure a constant water supply. The most extensively developed regions of this vegetation are on the Sea of Japan side. The summer-green scrub and tall herb meadows also occur as substitute communities instead of coniferous forests.

Physiognomy

Summer-green scrub communities vary from 1 to 13 m in height and may have 1–4 layers, depending mainly on altitude and slope aspect. Dominant species in the tree layer are *Alnus matsumurae*, *A. maximowiczii* and *Betula ermanii*. *Betula ermanii* scrub occurs mostly in the subalpine coniferous forest zone. *Alnus maximowiczii* dominates in the upper subalpine, where dwarf-pine scrub develops.

In the four main subareas of the range of this forest type [Honshu (H), Hokkaido (K), Sakhalin (S) and Sikhote Alin (A)], and in the Kurilskiye islands (Ku), the most prominent species in the summer-green scrub are:

- Shrubs:
 - *Alnus maximowiczii* (H, K, A, S, Ku)
 - *Euonymus tricuspidatus* (H, K)
 - *Lonicera tschonoskii* (H)
 - *Sorbus matsumurana* (H, K)
 - *Weigelia middendorffiana* (H, K, S, A, Ku)
- Herbs:
 - *Angelica matsumurae* (H)
 - *Athyrium sinense* (H)
 - *Conioselinum filicinum* (H, K, Ku)
 - *Diphylleia grayi* (H)
 - *Glaucidium palmatum* (H, K)

- *Pedicularis chamissonis* var. *japonica* (H)
- *Peucedanum multivittatum* (H, K)
- *Streptopus amplexifolius* var. *papillatus* (H, K)
- *Trautvetteria japonica* (H, K, S, A)

Tall herb communities are 40–150 cm high and are usually composed of just one layer. When composed of two layers, the species of the lower layer begin to bloom first and then the species of the higher layer grow up and flower. On the mountain Chogatake, *Anemone debilis*, *Angelica matsumurae*, *Heloniopsis orientalis*, *Primula jesoana*, *Saxifraga fusca* var. *kikubuki*, *Shortia soldanelloides* and *Viola brevistipulata* var. *acuminata* come into flower soon after the snow melts. Then *Aconitum hakusanense*, *Ranunculus acris* var. *nipponicus*, *Saussurea nikoensis* var. *sessiliflora*, *Thalictrum aquilifolium* var. *intermedium* and *Trautvetteria japonica* grow up and flower. In the continental part of the range, the tall forb communities are composed of *Angelica cincta*, *Pleurospermum uralense*, *Sanguisorba stipulata*, *Veratrum alpestre*, etc.

Ecology

Summer-green scrub and tall forb communities occur not only as substitute vegetation on coniferous forest sites but also as permanent communities on steep slopes, sites with deep snow, and around snow patches and bogs, especially in large areas on the Sea of Japan side of the islands, and on all mountain tops on the mainland within the cool temperate zone exceeding 1800 m in the north and 2500 m in the south. Woody plants such as *Alnus* and *Betula* have somewhat flexible trunks and withstand the pressure from snow creep and snow slides. The soil is mesic or wet, especially for several weeks in spring after the snow melts. In some years, however, the snow does not melt completely and the vegetation remains at least partly under the snow cover. In such situations the understorey cannot produce new leaves.

Dynamics

One type of summer-green scrub develops as a substitute for coniferous forest, with structure and species combination depending on site conditions, especially gap size. To give an example, in a new 5×10 m gap in the *Abietetum veitchio-mariesii* community at Miike, in the Akaishi mountains, *Betula ermanii* seedlings appeared, with *Acer ukurunduense*, *Aster glehnii* var. *hondoensis*, *Chamaenerion angustifolium*, *Rubus yabei*, *R. yabei* f. *marmoratus*, *Sambucus sieboldiana*,

Senecio nemorensis and other summer-green species. Near this stand was a young *Abies*–*Betula* mixed forest, about 12 m high and with trees about 5–10 cm in diameter. The *Abies* trees were taller than those of *Betula*, some of which were weak or dead. The species combination corresponded to that of the *Abietetum veitchio-mariesii*.

Animals

In Hokkaido, the brown bear (*Ursus arctos*) digs up the roots of *Peucedanum multivittatum* in early spring. In Honshu, *Capricornis crispus* and *Lagopus mutus japonicus* browse on young leaves of forbs.

CONCLUDING REMARKS

In Far East Asia temperate coniferous species and their vegetation types are distributed according to latitudinal ranges reflecting climatic gradients. They occur in the cold temperate zone, the cool temperate zone and the orotemperate belt in the warm temperate zone, and the oroboreal belt in the temperate zone. The forests may also be subdivided according to continentality from suboceanic to ultra-continental. The natural vegetation of the northern temperate zone is well conserved in its natural environments compared with the summer-green broadleaved forest zone, which is the sphere of most human habitation.

The Cold temperate zone is the largest area, and is characterized by *Abies holophylla*, *A. sachalinensis*, *Larix dahurica*, *Picea jezoensis*, *P. koraiensis*, *P. glehnii* and *Pinus koraiensis*, mixed with deciduous *Quercus crispula* and *Q. mongolica*. In the middle temperate zone, the so-called cool temperate zone and the orotemperate belt of suboceanic Japan are characterized by endemic coniferous species such as *Abies homolepis*, *A. firma*, *Pinus densiflora*, *P. parviflora*, *Thujopsis dolabrata*, *Thuja standishii* and *Tsuga sieboldii* mixed with deciduous *Quercus crispula*, and in the oroboreal belt of the temperate zone of the Russian Far East *Abies nephrolepis*, *Larix dahurica* and *Picea jezoensis*, mixed with deciduous *Betula costata* are found, while in this belt in Japan *Abies mariesii*, *A. veitchii*, *Picea jezoensis* var. *hondoensis* and *Tsuga diversifolia*, occur mixed with deciduous *Betula ermanii*.

These coniferous species and their habitats have been conserved in good condition because land use by native people like the Ainu was light and adapted to nature. They used the natural resource by hunting and gather-

ing. The function of forest ecosystems in preserving large animals such as deer, the Amur tiger, Amur leopard, lynx, wild boar, black bear, brown bear and gray wolf in Far East Asia has been stabilized till lately. However, forest ecosystems are threatened by logging, fires caused by smoking, sightseeing and acid rain. A large area may disappear within a short time as a result of fire, as exemplified by the *Larix dahurica* forests in Sakhalin. There is a tendency to increase logging in the forest areas of the Russian Far East, to supply timber exports to Japan. The logging of conifer forests risks melting the permafrost. Wetland develops in the area where trees are cut, and methane will evolve, which is a factor responsible for global warming. Sightseeing activities and ski resorts have been developed in the temperate and orotemperate areas of Japan during the last 30 years; however, acid rain and the fogs caused by air pollution are slowly but steadily killing the conifer forests. Acid rain caused by the dispersal of air pollutants from China affects a wide area. The westerly winds bring the acid rain to the Sea of Japan side especially; the average pH is 5.3–5.6, higher than on the Pacific side. Acid mist is a more local phenomenon. Nitrogen oxides from metropolitan Tokyo drift to the mountains surrounding the city, gain altitude and cool down. The acid fog in which air pollutants have accumulated adheres to trees such as *Abies veitchii* and *Abies mariesii* for a long time, and causes damage.

The effect of global warming is severe in the eastern part of Eurasia. A sudden rise in temperature of 1°C in 100 years has been calculated for Japan. There are concerns about the impact on vegetation. In particular, effects for coniferous species and the vegetation of the temperate zone have been pointed out as follows:

- (1) In the southern temperate region, relic vegetation from the Ice Age and endemic species on the summits of mountains will disappear;
- (2) Corresponding with the warming, organisms living in warm climates bring disease and damage.
- (3) Rapid climatic change, such as heavy snow and aridity, may destroy the forest ecosystems. In Japan the most southerly oroboreal forest is located in Shikoku, at 34°N on a summit ~1800 m above sea level. *Abies veitchii* and *Tsuga diversifolia* have difficulty in re-establishment. Seedlings can only survive on rocks or fallen trees. A small bamboo like *Sasa tsuboiana* occupies the understorey. In accordance with the warming trend, species of deciduous beech forests are taking over the habitats of coniferous species.

ACKNOWLEDGEMENTS

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APPENDIX: MAIN DOMINANT CONIFERS

The coniferous species of the temperate zone and the oroboreal belt in far-eastern Asia are here described in succession. They occur in temperate broadleaved deciduous forests or subalpine coniferous forests. Each species is described in terms of structure and morphology, reproduction, habitat, soil conditions, tolerance, distribution pattern and climate.

Abies holophylla Maxim

Structure and morphology: Dominating canopy tree. Height: 35–40(55)m. Diameter at breast height (DBH): 50–80(170) cm. Chromosome number: $2n = 24$.

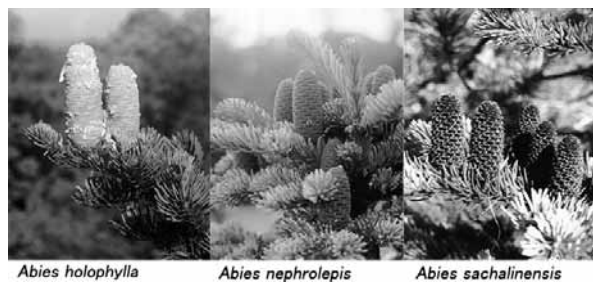


Fig. 5.24. Cones of *Abies holophylla*, *A. nephrolepis* (both photographed in August) and *A. sachalinensis* (photographed in early June). Photos P.V. Krestov.

Reproduction: Monoecious. Flowering stage: 20th May to 10th June (Fig. 5.24). Ripening time: mid-September to October. Large crops are repeated at intervals of 2–3 years. Anemochore. Weight of 1000 seeds: 32 g. Seed number per kilogram: about 25 000–35 000 (Kabanov, 1977).

Habitat: Dominant or present in mixed canopy of climatic climax broadleaved–conifer forest in the northern temperate zone.

Soil conditions: brown forest soils developed on mesic sites of mountain slopes. Mother rocks composed of andesite, sandstone and conglomeratic rock.

Tolerances: Low light: high (it grows under a closed canopy of broadleaved trees). Frost: low (many

trees with frost cracks on trunks). Heat: medium. Water deficit: low (occasionally it grows on water-deficient sites). Water surplus: low (it never grows on waterlogged sites).



Fig. 5.25. Distribution range of *Abies holophylla*.

Distribution pattern: The range is of the Manchurian type. The northern limit is at 44°N in the Razdolnaya (Suifen He) river basin. The southernmost point is on the island of Cheju Do in the south of Korea at approximately 33°N (Fig. 5.25). The main range covers the southern Sikhotealin and Changbai mountain ranges. Relatively isolated occurrences of *Abies holophylla* west of the main range occur on the mountain range Dunlin in central China.

Climate: The climate is that of the cool temperate zone. Humid monsoon climate with annual precipitation of 600–800 mm and annual temperature from +2° to +7°C.

Abies mariesii Masters

Structure and morphology: Height: 20–25(40)m. DBH: 40–60 cm. The trunks and branches are flexible under snow pressure. Chromosome number: $2n = 24$.

Reproduction: Monoecious. Flowering stage: June. Ripening time: September–October. Anemochore. Seed number per kilogram: about 55 000–57 000 (Hayashi, 1969).

Habitat: *Abies mariesii* dominates in the canopy of oroboreal climatic-climax conifer forests in Honshu (particularly on the Sea of Japan side) and Shikoku. It

occurs on mesic and humid sites on mountain slopes and around bogs where the soil is deep, and occurs also at high wind-exposed sites. Saplings survive in the understorey; however, the photoenvironment is not as dark as under *Abies veitchii*.

Soil conditions: Acidic and humid brown forest soil, and also on peat soils around bogs. Mother rocks are andesite, quartz porphyry, liparite and granite.

Tolerances: Low light: high (but less than *Abies veitchii*). Frost: high (but damage through snow fall and horizontal movement is high). Heat: low. Water deficit: low. Water surplus: high (occasionally grows on waterlogged sites).

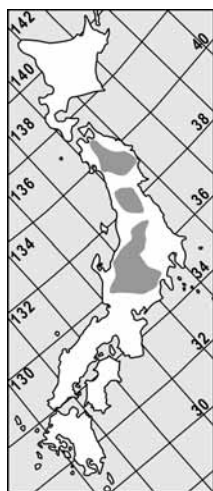


Fig. 5.26. Distribution range of *Abies mariesii*.

Distribution pattern: Endemic to Honshu. Distribution pattern is from central Honshu to the northern part of Honshu (Fig. 5.26). Pure *Abies mariesii* forests occur on the Sea of Japan side, where snow exceeds 50 cm in depth. The northern limit is Hakkoda-san in the Tohoku district (40°42'N). The southern limit is Akaishi-dake (35°13'N). The vertical distribution is from 1800 to 2500 m in central Japan.

Climate: Humid monsoon climate. Mean annual precipitation: 1500–3000 mm, with most deposited as snowfall during winter. Warmth indices: 15–45.

Abies nephrolepis (Trautv.) Maxim

Structure and morphology: Subordinate canopy tree. Height: 20–25(30) m. DBH: 30–50(80) cm. Chromosome number: $2n=24$.

Reproduction: Monoecious. Flowering stage: 10 May–5 June (Fig. 5.24). Ripening time: September.

Large crops occur at intervals of 2–3 years. Anemochore. Seed number per kilogram: about 100 000–110 000, weight of 1000 seeds: 9–10 g (Kabanov, 1977).

Habitat: Subordinate canopy tree of edaphic-climax conifer forest in the oroboreal belt in the northern temperate zone, and of climatic-climax conifer forest in the southern boreal zone.

Soil conditions: Brown forest soils developed on mesic sites of mountain slopes. Mother rocks composed of andesite, basalt, sandstone and conglomeratic rock.

Tolerances: Low light: very high (grows under closed canopy). Frost: medium (many trees have frost cracks on trunks). Heat: low. Water deficit: low (occasionally grows on water-deficient sites). Water surplus: low (occasionally grows on waterlogged sites).

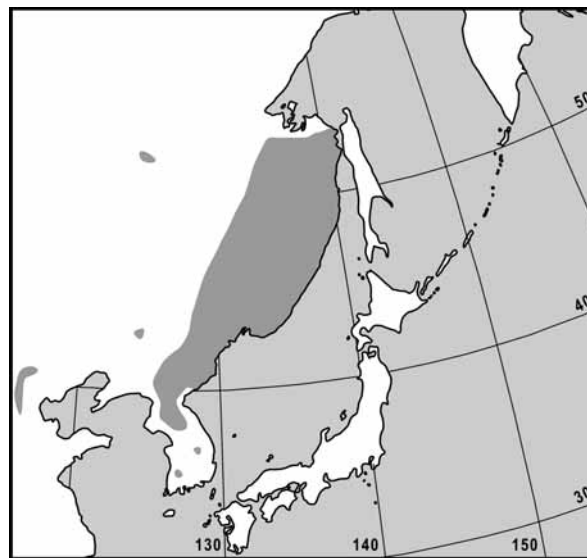


Fig. 5.27. Distribution range of *Abies nephrolepis*.

Distribution pattern: The range is of the Okhotian type. The northern limit is 54°30'N in the Zeya river basin. The southernmost point is in Korea at approximately 35°N. The main range includes the Sikhote Alin and Badzhal'skiy ranges, and the southern spurs of the Stanovoy and Changbai ranges (Fig. 5.27). Relatively isolated occurrences west of the main range of this species can be found on the mountain ranges Zhangguangcai Ling in central China and the Lesser Hingan in northern China.

Climate: The bioclimate is that of the northern temperate to middle boreal zone. Humid monsoon climate with annual precipitation 600–1200 mm and annual mean temperature from -6°C to $+4^{\circ}\text{C}$.

Soil conditions: Podzols, brown forest soils, gleyosols and peats on a variety of mother rock.

Tolerances: Low light: very low (saplings cannot survive under the mother canopy). Frost: very high. Heat: very high. Water deficit: medium. Water surplus: very high.

Abies sachalinensis (Fr. Schm.) Masters

Structure and morphology: Height: 20–25(30) m. DBH: 30–50(80) cm. Chromosome number: $2n=24$.

Reproduction: Monoecious. Flowering stage: June (Fig. 5.24). Ripening time: September–October. Anemochore. Seed number per kilogram: about 118 000 (Hayashi, 1969).

Habitat: Dominating canopy tree of edaphic-climax conifer forest on convex sites in the northern temperate zone and of climatic-climax conifer forest in the southern boreal zone.

Soil conditions: rich organic brown forest soil. Mother rocks composed of andesite, slate, sandstone and conglomeratic rock.

Tolerances: Low light: high [grows under small bamboos (*Sasa* spp.) and under very closed canopies]; Frost: medium. Heat: low. Water deficit: medium (grows on water-deficient sites). Water surplus: low (occasionally grows on waterlogged sites).

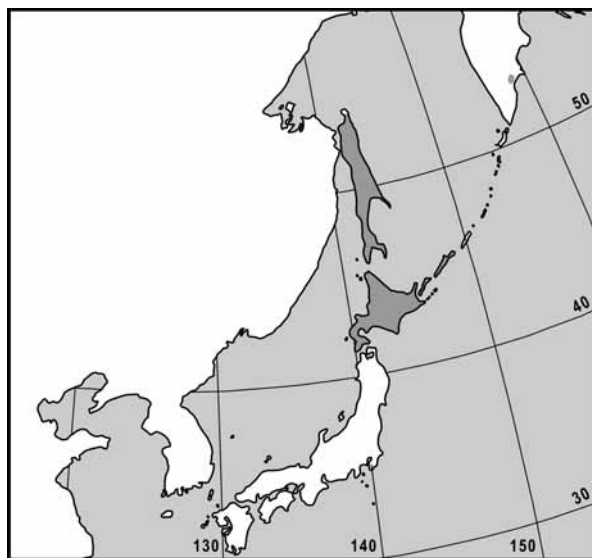


Fig. 5.28. Distribution range of *Abies sachalinensis*.

Distribution pattern: The northern limit in Japan is Soya misaki, Hokkaido (45°32'N). It abounds over the whole of Sakhalin except the northernmost part

of Shmidta Poluostrov. The northernmost point in the Kurils is the island of Iturup (~55°N.) The southern limit is Hidaka (41°58'N) in Hokkaido (Fig. 5.28). The vertical distribution in central Hokkaido is from 20 to 1650 m. There is one isolated occurrence of unknown origin, probably of the same species, nearly 1000 km away from the main range, on southern Kamchatka (Neshataeva and Fet 1994). The species was originally described by Komarov (1901) as *Abies gracilis* Kom. Karpachevskiy (1968), and Bobrov (1978) treated the fir from Kamchatka as *Abies sachalinensis*, assuming that it was introduced by native tribes.

Climate: The bioclimate is that of the northern temperate to southern boreal zone. Humid monsoon climate with mean annual precipitation 1000–1500 mm and mean annual temperature from –2°C to +7°C.

Abies veitchii Lindley

Structure and morphology: Height: 20–25(35) m. DBH: 30–50 cm. Chromosome number: $2n=24$. *Abies veitchii* is the dominant canopy species of montane and subalpine coniferous forest in Honshu.

Reproduction: Monoecious. Flowering stage: June. Ripening time: September–October. Anemochore. Seed number per kilogram: about 138 000–140 000 (Hayashi, 1969).

Habitat: Mesic sites of mountain slopes.

Soil conditions: Mesic and humid brown forest soil. Mother rocks are andesite, quartz porphyry, liparite and granite.

Tolerances: Low light: high (saplings survive in a dark understorey under dense canopy, better than *Abies mariesii*). Frost: high (snow damage has been reported). Heat: low. Water deficit: medium. Water surplus: medium.

Distribution pattern: Endemic species in Honshu. Its distribution pattern in Honshu is predominantly on the Pacific Ocean side, where snowfall during the winter season is light, and the maximum snow depth 45–50 cm. The northern boundary is at the mountain Azuma in the Tohoku district, Japan (37°46'N). The southern limit is the mountain Ishizuchi-san in Shikoku, Japan (33°44'N) (Fig. 5.29). *Abies veitchii* in Shikoku is distinguished as the variety var. *sikokiana* Kusaka because of its thick leaves and rather small and round cones. Vertical distribution is from 1650 to 2500 m in central Japan.

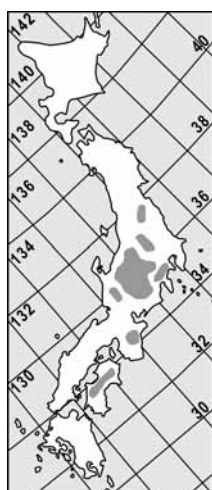


Fig. 5.29. Distribution range of *Abies veitchii*.

Climate: Humid monsoon climate with most precipitation falling in the summer season. Winter season is fair and dry. Warmth indices: 15–45. Mean annual precipitation: 1000–1500 mm; however, the precipitation in the Kii peninsula is over 3000 mm annually.

Larix dahurica Lewis

Taxonomical note: Since there is no agreement between taxonomists in relation to the taxonomy of Far Eastern larches, we accept the widest concept suggested by Tzveliov (1994).

Structure and morphology: Height: 20–30(50) m. DBH: 60–80(250) cm. Chromosome number: $2n = 24$.

Reproduction: Monoecious. Flowering stage: May. Ripening time: October. Anemochore. Weight of 1000 seeds: 2–4 g (Kabanov, 1977). Large crops occur at intervals of 5–6 years.

Habitat: Within the cool temperate zone *Larix dahurica* forms exclusively seral stands on areas where native forests have been destroyed and near the northern limit of the cool temperate zone, and edaphic-climax stands in poorly drained valleys with cold air drainage.

Soil conditions: Podzols, brown forest soils, gleysoils and peats on a variety of mother rocks.

Distribution pattern: *Larix dahurica* has one of the widest ranges among conifer species, covering the whole of the Far East and Eastern Siberia, northwards as far as latitude 72°N, and forming the Arctic tree-line in continental Asia (Fig. 5.30). The southern boundary of the range is in Korea approximately at latitude 39°N.

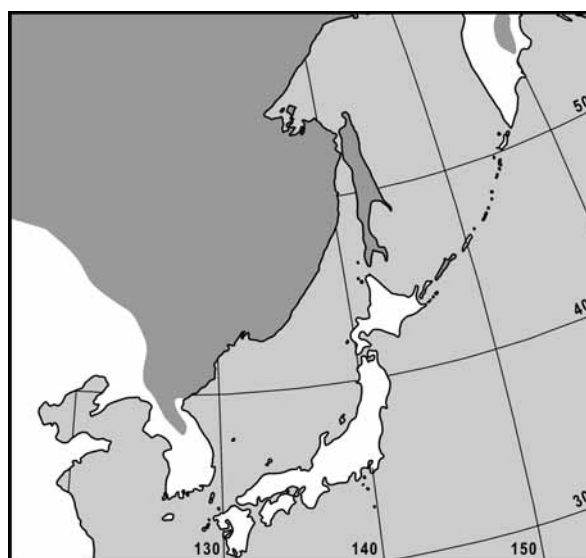


Fig. 5.30. Distribution range of *Larix dahurica*.

Climate: The bioclimatic range is that of the boreal zone and oroboreal belt. Monsoon climate, with mean annual precipitation 600–1200 mm and mean annual temperature from -6°C to $+4^{\circ}\text{C}$.

Larix kaempferi (Lamb.) Carr.

Structure and morphology: Height: 25(30) m. DBH: 30–60(90) cm. Chromosome number: $2n = 24$.

Reproduction: Monoecious. Flowering stage: April–May. Ripening time: August–September. Anemochore.

Habitat: *Larix kaempferi* is not a climatic-climax species; it grows in open places such as new volcanic lavas, where there has been stream erosion in headwaters, and in snow ravines. It also forms continuous stands around moors. Naturally-grown trees of *Larix* have hard wood; however, the quality of planted *Larix* is not good for saw timber because growth is so fast.

Soil conditions: *Larix kaempferi* can grow on poor and shallow soils on dry habitats.

Tolerances: Low light: very low (saplings cannot survive under the mother canopy). Frost: very high. Heat: high. Water deficit: high. Water surplus: high.

Distribution pattern: *Larix kaempferi* is endemic in central Honshu (Fig. 5.31). The vertical distribution in Chubu is from 1200 m to 2650 m. It forms the timber line on the highest peak of Japan, Fuji-san. The northern boundary is the mountain Zao-san at 38°05'N, and the southern boundary is in the Akaishi mountains at 35°08'N.

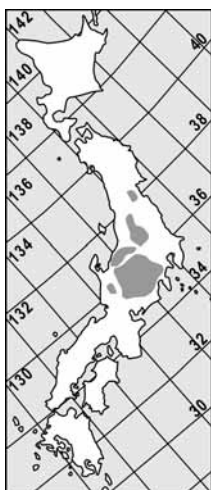


Fig. 5.31. Distribution range of *Larix kaempferi*.

Climate: The bioclimatic range is that of the orotemperate and oroboreal belts.

Picea glehnii (Fr. Schm.) Masters

Structure and morphology: Height: 20–30(40) m. DBH: 50–60(150) cm. Chromosome number: $2n=24$. Seed can germinate on dead trunks and moss. It is difficult to find seedlings in an understory dominated by *Sasa*.

Reproduction: Monoecious. Flowering stage: May–June. Ripening time: October. Anemochore. Seed number per kilogram: about 326 000–340 000 (Hayashi, 1969). Vegetative propagation has been recorded (Shafraunskiy, 1987).

Habitat: *Picea glehnii* occurs in extreme edaphic habitats such as dry or wet acidic sites around swamps, on wet podzols and volcanic material, and at high elevations in the subalpine belt. Its vertical distribution zone ranges from sea level to 1650 m (Hayashi, 1969); dominant forests of this species occur between 5 and 1460 m. There is a relict of this species on Hayachine-san in northern Honshu, on avalanches of ultrabasic rocks.

Soil conditions: Wet or dry podzol, gleyosol or peat. Mother rocks are andesite, granite, basaltic lava, liparite, slate, sandstone, conglomerate and crystalline schist.

Tolerances: Low light: very high. Frost: high. Heat: medium. Water deficit: high. Water surplus: very high (often grows on waterlogged sites).

Distribution pattern: Over the whole of Hokkaido except the Oshima peninsula, at the southernmost point



Fig. 5.32. Distribution range of *Picea glehnii*.

of Sakhalin, and on Kunashir and Iturup (Fig. 5.32). An isolated site where this species can be found is in Honshu on Hayachine-san (1914 m); however, many fossils have been discovered in diluvial sediments in the Aomori and Iwate prefectures.

Climate: Mean annual temperature: 5–8.5°C. Warmth indices: 15–55. Mean annual precipitation: 1000–1500 mm.

Picea jezoensis (Siebold & Zucc.) Carr

Taxonomic notes: In Russian taxonomy, *Picea jezoensis* was long treated as *Picea ajanensis* (Lindl. et Gord.) Fisch. ex Carr., on account of the assumption by leading Russian taxonomists Bobrov (1978) and V.N. Vasiliev (1950) that *Picea jezoensis* is a garden form of spruce, while many taxonomists consider that a single species is referred to by these two names. Although the priority rule has regulated this situation in favour of the name *Picea jezoensis*, in modern Russian literature the name *Picea ajanensis* is widely used. In this chapter the name *Picea jezoensis* is accepted for both the continental and the island parts of the range of this species.

Structure and morphology: Height: 20–30(40) m. DBH: 70–80(100) cm. Chromosome number: $2n=24$. Life span: over 300 years; the maximum age reported in the north of the range is 520 years (Starikov, 1961).

Reproduction: Monoecious. Flowering stage: June on islands, 20 May to 10 June on the continent. Ripen-

ing time: September–October on islands, August–September on the continent. Large crops occur at intervals of 3–4 years. Anemochore. Seed number per kilogram: about 450 000–460 000 (Hayashi, 1969). Weight of 1000 seeds: 2–3 g (Kabanov, 1977). Natural “layering” has been described on Kamchatka (Manko and Voroshilov, 1978).

Habitat: Dominant in the canopy of oroboreal climatic-climax conifer forest in Hokkaido, and on the Sikhote Alin and Changbai mountain ranges. Occurs on mesic and humid sites of gentle mountain slopes. For saplings the best habitat for survival is on moss-covered fallen trunks; survival is difficult in an understorey dominated by *Sasa*.

Soil conditions: Mesic to moist podzols and brown forest soils (on Sikhote Alin). Mother rocks are andesite, liparite, slate, sandstone, conglomerate and tuff.

Tolerances: Low light: high (grows under closed canopy). Frost: high. Heat: low. Water deficit: low (on water-deficient sites, saplings can survive on fallen decomposed trunks). Water surplus: medium (sometimes grows on waterlogged sites).

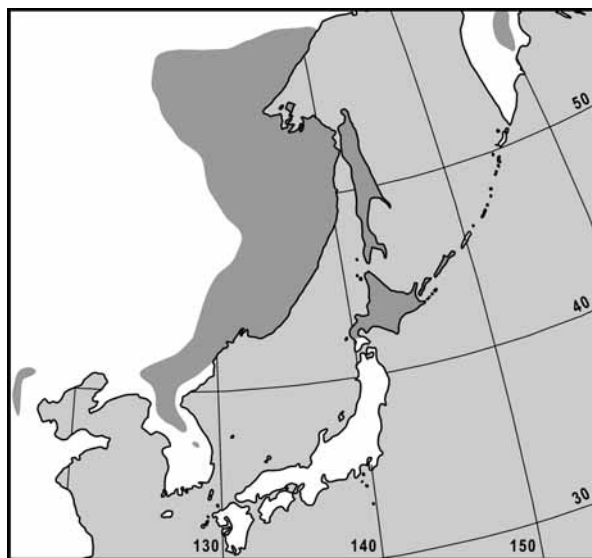


Fig. 5.33. Distribution range of *Picea jezoensis*.

Distribution pattern: *Picea jezoensis* is distributed all over Hokkaido except for the Oshima peninsula, on the southern Kurils (north to the island Iturup), on the Sikhote Alin and Changbai mountains, on Pektusan and the island of Sakhalin (Fig. 5.33). Isolated occurrences can be found in central Kamchatka and the mountain range Taihang Shan. The southern boundary

in Hokkaido lies at 42°02'N, in Korea at approximately 38°N; the northern boundary lies in southern Yakutia at a latitude of 59°N.

Climate: Mean annual temperature: +5–8°C in Hokkaido, –4°C to +5°C on the continent. Warmth indices: 45–85 on Hokkaido, 25–55 on the continent (Grishin, 1995). Mean annual precipitation: 1000–1500 mm on Hokkaido, 500–1000 mm on the continent. Maximum snow depth: below 30 cm. In the southern part of its range *P. jezoensis* occurs more on northern and eastern slopes where humidity is high; in the north of the range it occurs exclusively in the most insolated parts of southern slopes with the warmest microclimate.

Picea jezoensis var. *hondoensis* (Mayr) Rehder

Structure and morphology: Height: 20–25(40) m. DBH: 50–60(100) cm. Chromosome number: $2n = 24$. Life span: over 300 years.

Reproduction: Monoecious. Flowering stage: May to June. Ripening time: October. Anemochore. Seed number per kilogram: about 530 000–540 000 (Hayashi, 1969).

Habitat: It is found in oroboreal climatic climax conifer forest in Honshu, however dominated forest is limited in Kii peninsula. It occurs on mesic and humic sites of mountain slopes. For saplings the best habitat for survival is on moss-covered fallen trunks, but they also occur on mineral soils of dryer habitats such as southern slopes.

Soil conditions: Mesic to moist podzols. Mother rocks are andesite, granite, liparite, slate, sandstone, conglomerate and tuff.

Tolerances: Low light: high (grows under closed canopy). Frost: high. Heat: low. Water deficit: low (on water deficient sites saplings can survive on fallen decomposed trunks). Water surplus: medium (sometimes grows on waterlogged sites).

Distribution pattern: Endemic species in Honshu. It can be found in central Honshu and the Kii peninsula (Fig. 5.34). The northern limit is Tochigi prefecture in Kanto district (37°05'N). The southern limit is the Kii peninsula (34°05'N). Vertical distribution ranges from 1100 to 2650 m in central Japan and from 1450 to 1900 m on the Kii peninsula.

Climate: Annual temperature is +5–9°C. Warmth indices: 15–45. Annual precipitation is 1000–3000 mm and over 4000 mm on the Kii peninsula, where the local

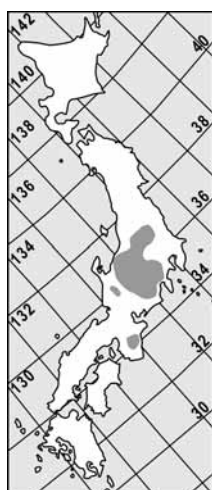


Fig. 5.34. Distribution range of *Picea jezoensis* var. *hondoensis*.

topographic conditions such as northern and eastern slopes bring high precipitation and humidity.

Picea koraiensis Nakai

Taxonomic notes: The species is currently accepted by Russian, Korean and Chinese taxonomists under this name, however, there are no clear morphological differences between this species and *Picea obovata*, distributed in Siberia, and *Picea abies*, distributed in Europe; consequently the exact range boundaries are unclear. Voroshilov (1982) used the taxonomic combination of *Picea obovata* ssp. *koraiensis* (Nakai) Worosch.

Structure and morphology: Height: 25–30 m. DBH: 70–80(100) cm. Chromosome number: $2n=24$. Life span: over 300 years.

Reproduction: Monoecious. Flowering stage: June on islands, 20 May–10 June on the continent. Ripening time: August–September. Large crops occur at intervals of 2–3 years. Anemochore. Weight of 1000 seeds: 6–7 g (Kabanov, 1977).

Habitat: Dominant in the canopy of edaphic-climax conifer forests in the valleys of Sikhote Alin. Occurs on mesic and moist sites of alluvium valleys and gentle slopes.

Soil conditions: Mesic to moist podzols and brown forest soils. Mother rocks are andesite, liparite, slate, sandstone, conglomerate and alluvial deposits.

Tolerances: Low light: high (grows under closed canopy). Frost: medium. Heat: medium. Water deficit: low. Water surplus: high (sometimes grows on water-logged sites).

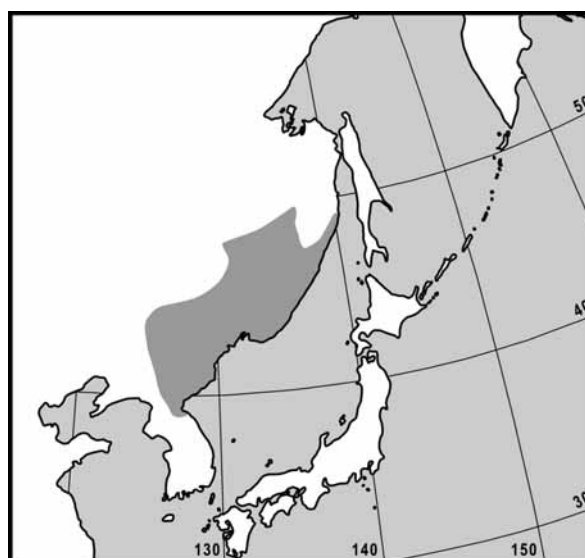


Fig. 5.35. Distribution range of *Picea koraiensis*.

Distribution pattern: *Picea koraiensis* occurs on the mountain ranges of Sikhote Alin, Changbai and Pektusan (Fig. 5.35). The location of the northern boundary is unclear, because of the difficulties in differentiating this species from *Picea obovata*. The southern boundary crosses the Korean peninsula at approximately 38°N.

Climate: Mean annual temperature: 0–6°C. Mean annual precipitation: 700–900 mm.

Pinus densiflora Siebold & Zucc.

Taxonomic notes: Plants in the continental part of the population combine features of both *Pinus sylvestris* and *P. densiflora*, and appear to be closer to *P. sylvestris* (Nedoluzhko, 1995). An intermediate species was described in northeastern China as *Pinus ussuriensis* (Liu et Wang) Chew et Y.W. Law and in Russia as *P. funebris* Kom.

Structure and morphology: Height: 15–25(30) m. DBH: 40–60 cm. Chromosome number: $2n=24$.

Reproduction: Monoecious. Flowering stage: from the end April to the beginning of May. Ripening time: October of the following year. Anemochore. Seed number per kilogram: 100 000.

Habitat: Extremes in water condition. Edaphical species on dry mountain ridges or on wet sandy soil of riverbeds. It occurs in secondary forest at an early successional stage.

Soil conditions: acidic shallow soil. Mother rocks are granite, serpentine and other sedimentary rocks

such as sandy stone, mudstone and shale. Limestone is uncommon.

Tolerances: Low light: very low. Frost: medium. Heat: high (common in the warm temperate zone). Water deficit: high (sometimes grows on rocky substrates). Water surplus: high (sometimes grows on waterlogged sites along river beds).

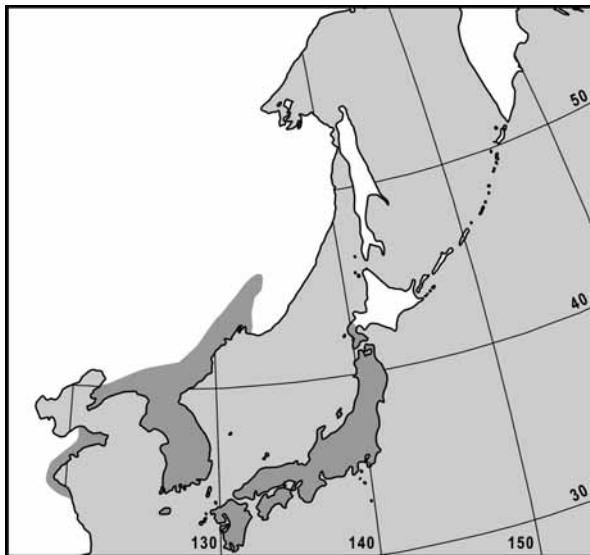


Fig. 5.36. Distribution range of *Pinus densiflora*.

Distribution pattern: Warm temperate and lower part of the montane belt. Northeastern China, Korean peninsula, southern part of Hokkaido, Honshu, Shikoku and Kyushu (Fig. 5.36).

Climate: Warmth indices: 60–160. Mean annual temperature: 7.5–18.7°C. Annual precipitation: 900–2000(4000) mm.

Pinus koraiensis Siebold & Zucc.

Structure and morphology: Five-needle pine. Height: 25–30(45) m. DBH: 60–80(150) cm. Chromosome number: $2n=24$. Life span: 400–500(600) years.

Reproduction: Monoecious. Flowering stage: June (May in Japanese Alps). Ripening time: October–November of the second year (October of the following year in the Japanese Alps). Synzoochore by *Nucifraga caryocatactes*, small mammals and wild boar. Seed is 25–30 mm long and 25–28 mm wide (Hayashi, 1969). Weight of 1000 seeds: 500–700 g. Seed number per kilogram: about 2010 (Kabanov, 1977). Large crops are repeated at intervals of 3–4 years.

Habitat: Within the main part of its range in the cool temperate zone *Pinus koraiensis* occurs on a

wide spectrum of slope gradients, aspects and shapes from sea level to an elevation of 900 m in Sikhote Alin and 1500 m in Changbai. In an isolated locality in the Japanese Alps it occurs on gentle slopes of orotemperate and oroboreal belts between 1050 and 2600 m in Honshu, and edaphically along the riverbeds.

Soil conditions: Brown forest soils and podzols. Mother rocks are andesite, basalt, granite, liparite, slate, sandstone, and tuff.

Tolerances: Low light: medium (saplings perform best under 70% shade). Frost: medium. Heat: high. Water deficit: high. Water surplus: low.

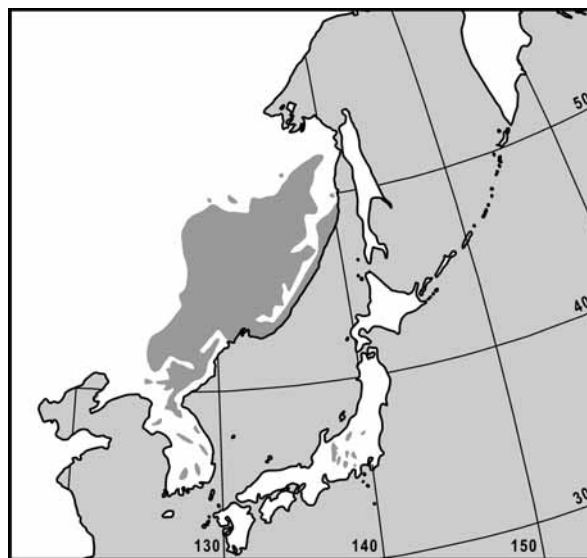


Fig. 5.37. Distribution range of *Pinus koraiensis*.

Distribution pattern: *Pinus koraiensis* is widespread mixed with *Acer* spp., *Betula* spp., *Fraxinus* spp., *Quercus mongolica* and *Tilia* spp. in the northern temperate zone of the Sikhote Alin, Changbai and Lesser Hingan ranges and on the southern spurs of the Badzhal'skiy range (Fig. 5.37). The most remote isolated tract of *Pinus koraiensis* is found on the northern, central and southern Japanese Alps in central Honshu around the latitude of 37°00'N, and in a remote and isolated tract at 33°50'N on serpentine rocks in Shikoku.

Climate: Mean annual precipitation is 600–900 mm and the mean annual temperature is 0–5°C. On Honshu it occurs in the interior of the central part of the island, with a subcontinental climate – where annual precipitation is below 1000 mm, and the mean annual temperature 5–10°C.

***Pinus parviflora* Siebold & Zucc.**

Taxonomic notes: *Pinus parviflora*, Japanese white pine, has two varieties. The seed of *Pinus parviflora* sp. has a short adnate wing. The seed of var. *pentaphylla* has a wing as long as the seed. The variety *laevis* is a serpentine plant on the mountain Apoi in Hokkaido. Hybrids with *Pinus pumila* occur, the so-called *Pinus hakkodensis*, in northern Honshu and Hokkaido.

Structure and morphology: Five-needle pine. Height: 20–30 m. DBH: 60–100 cm. Chromosome number: $2n=24$. *Pinus parviflora* does not form a monodominant forest, but rather occurs in mixtures with *Pinus koraiensis*, *Thuja standishii* and *Tsuga sieboldii*.

Reproduction: Monoecious. Flowering stage: the beginning of May. Ripening time: October of the second year. Seed is 10 mm long.

Habitat: *Pinus parviflora* occurs on ridges on xerophytic acidic sites in the cool temperate zone.

Soil conditions: Shallow podzols. Mother rocks are andesite, basalt, granite, metamorphic rock, sandstone and tuff.

Tolerances: Low light: medium (saplings can survive in understorey under half shade). Frost: low. Heat: high. Water deficit: high (saplings survive in insolated places such as forest edges and rock outcrops). Water surplus: low.

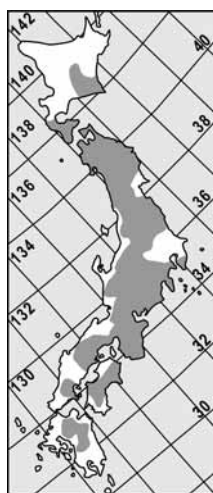


Fig. 5.38. Distribution range of *Pinus parviflora*.

Distribution pattern: *Pinus parviflora* sp. is distributed in Honshu, Shikoku and Kyushu. The northern boundary is the Kanto district. The variety *pentaphylla*

is distributed in northern Honshu and Hokkaido (Fig. 5.38).

Climate: Within the range of *Pinus parviflora* the mean temperature of the coldest month varies widely, with the lowest values -16°C at the northern boundary on Hokkaido and -14.7°C at the highest point of Fuji-san in Honshu (Hayashi, 1969). Annual precipitation ranges from 1000 to 3000 mm.

***Pinus pumila* (Pallas) Regel**

Taxonomic notes: In the upper subalpine belt on Honshu, some trees of *Pinus pumila* are shorter with shorter leaves and smaller cones. These are often referred to as var. *yezoalpina* Ishii et Kusaka.

Structure and morphology: Five-needle trailing dwarf coniferous tree. Height of branches in summer is 1.5–2.5(6) m. DBH: 12–16(28) cm. Chromosome number: $2n=24$.

Reproduction: Monoecious. Flowering stage: June and July in the island part of the range, first half of June on the continent. Ripening time: August and September of the next year on the islands and in the northern continental part of the range, September–November in the southern continental part of the range. Synzoochore by *Nucifraga caryocatactes*. Seeds are 8–10 mm long and 5–7 mm wide. Seed number per kilogram: about 24000. Weight of 1000 seeds: 100–130 g (Kabanov, 1977). Vegetative propagation by trunks and branches is the main reproductive strategy in the dense thickets. Seeds germinate successfully in canopy openings and on disturbed areas, for instance after fire, or on newly formed substrates.

Habitat: Within the cool temperate zone, *Pinus pumila* climatically occurs in the upper oroboreal (subalpine) belt, and edaphically around solfataras, on moors and on ancient marine dunes. The distribution range in central Honshu is between 1400 and 3180 m, usually between 2650 and 3000 m as the climatic climax. In Hokkaido it occurs between 50 and 2240 m. On the continent, within the cool temperate zone as well as the southern and middle boreal zones, the elevation of the *Pinus pumila* belt varies from 1100–1300 to 1800–2000 m. In the northern temperate and subarctic zones, *Pinus pumila* forms communities from the sea level to altitudes of 600–800 m. The sites have wind-exposed mesic and dry habitats on mountain ridges and the upper parts of slopes; however, dwarf pine needs protection by snow cover against drought and cold due to strong gales

from the temperate westerlies. Saplings cannot survive in the understorey; however, *Nucifraga caryocatactes* gathers seeds and buries them in open places such as alpine tundra.

Soil conditions: The soil is dry in convex sites in the island part of the range, and dry to mesic on different slope shapes on the continent. Mother rocks are andesite, basalt, granite, liparite, slate, sandstone, conglomerate, rhyolite, crystalline schist and ultrabasic rock.

Tolerances: Low light: low (saplings cannot survive under the mother canopy). Frost: very high. Heat: very high. Water deficit: high. Water surplus: low.

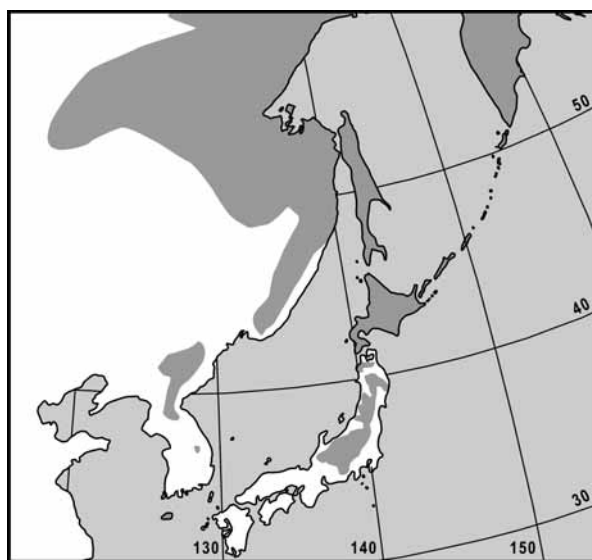


Fig. 5.39. Distribution range of *Pinus pumila*.

Distribution pattern: The southern boundary line of dwarf pine is the mountain Tekari located in central Honshu at approximately 35°20'N. On the continent the southern boundary crosses Korea at approximately 38°N. The range of *Pinus pumila* extends far to the north, and includes the whole island of Sakhalin, the Kuril islands, the Far East and eastern Siberia up to the latitude 69–70°N (Fig. 5.39).

Climate: The mean temperature of the coldest month within the range of *Pinus pumila* varies from –25.6°C at the highest point of Hokkaido and –21.5°C in Honshu (Hayashi, 1969) to –50°C in Oymyakon (Yakutia). The mean annual precipitation ranges from 1000–3000 mm on the Japanese mountains to 200 mm in the interior of the Magadan region.

Thuja standishii (Gord.) Carrière

Structure and morphology: Height: 15–30(35) m. DBH: 40–60(100) cm. Chromosome number: $n = 11$. The thick stem carries a cone-shaped crown. The trees are resistant against snow pressure.

Reproduction: Monoecious. Flowering stage: May. Anemochore. Seed number per kilogram: about 935 000–940 000 (Hayashi, 1969).

Habitat: *Thuja standishii* constitutes an edaphic climax forest mixed with *Pinus parviflora* var. *penta-phylla* and *Thujopsis dolabrata* in the temperate montane belt on insolated convex sites exposed to winds.

Soil conditions: Acidic shallow podzols. Mother rocks are andesite, basalt, granite and various sediments. However, one isolated site in Shikoku shows the high tolerance of this species to ultrabasic minerals such as olivine.

Tolerances: Low light: high (saplings can survive in a shaded understorey). Frost: medium (branches tolerate heavy snow pressure). Heat: low. Water deficit: high (saplings survive in insolated places such as ridges and rock outcrops). Water surplus: low.

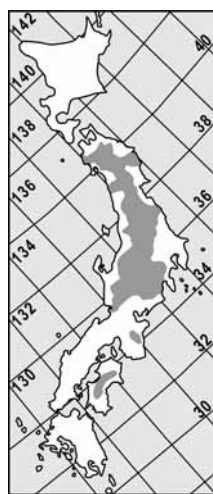


Fig. 5.40. Distribution range of *Thuja standishii*.

Distribution pattern: The species is common in beech-forest areas on the Sea of Japan side of northern Honshu. The northern boundary is 40°36'N, and the southern boundary is the mountain Aozare, 33°47'N (Fig. 5.40).

Climate: The range of biotemperature is wide. Mean annual precipitation: 1000–2500 mm.

***Thujopsis dolabrata* Siebold & Zucc.**

Structure and morphology: Height: 20–30(40) m. DBH: 60–80(100) cm. The stems and trunks tolerate snow pressure.

Reproduction: Monoecious. Flowering stage: May. Ripening time: October. Anemochore. Seed number per kilogram: about 230 000–240 000 (Hayashi, 1969).

Habitat: *Thujopsis dolabrata* occurs in the montane belt of the cool temperate zone. Site conditions are mesic-dry to moist. It forms pure forests and/or mixed forests with *Fagus crenata*, *Pinus parviflora* and *Thuja standishii* forests. It occurs in northern Honshu in the elevation range of 250–1700 m.

Soil conditions: Moist podzols are common. However, the seedlings are often found on dry podzols.

Tolerances: Low light: extremely high (saplings can survive in a shaded understorey). Frost: medium (branches tolerate heavy snow pressure). Heat: low. Water deficit: medium. Water surplus: high (sometimes grows on waterlogged sites).

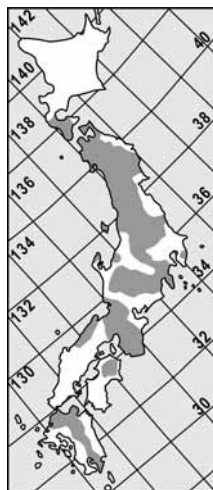


Fig. 5.41. Distribution range of *Thujopsis dolabrata*.

Distribution pattern: The northern boundary is 40°53'N, and the southern boundary is the mountain Takakuma in Kyushu, 31°30'N (Fig. 5.41).

Climate: The range of biotemperature is wide. Annual precipitation: 1500–3000 mm.

***Tsuga diversifolia* (Maxim.) Masters (Fig. 5.25)**

Taxonomic notes: *Tsuga diversifolia* is endemic to the islands of Kyushu, Shikoku and Honshu. The closely related species *Tsuga longibracteata* Cheng occurs on

mountains of southeastern China, and an Oligocene fossil of it has been found in Japan (Kitamura and Murata, 1979).

Structure and morphology: Height: 15–20(25) m. DBH: 40–60(150) cm. Chromosome number: $2n=24$. The stem and trunks are weak under snow pressure; in consequence, few individuals are found on the Sea of Japan side, where deep snow is common.

Reproduction: Monoecious. Flowering stage: June. Ripening time: October. Anemochore. Seed number per kilogram: about 430 000 (Hayashi, 1969).

Habitat: *Tsuga diversifolia* occurs in the upper part of the orotemperate belt and the lower part of the oroboreal belt on central Honshu at altitudes between 1100 and 2750 m, and is common between 1650 and 2200 m. Habitats are dry to mesic-dry on mountain slopes.

Soil conditions: Dry to extremely dry podzol on shallow soil and rocks. Mother rocks are andesite, granite, liparite, slate, sandstone, conglomerate and tuff.

Tolerances: Low light: medium (saplings can survive in an understorey with half shade). Frost: medium. Heat: low. Water deficit: high (saplings survive in isolated places such as forest edges and rock outcrops). Water surplus: low.

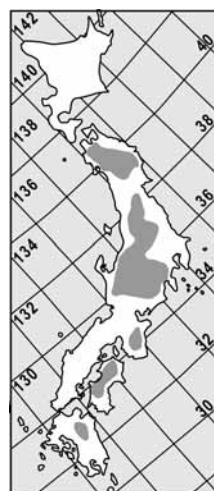


Fig. 5.42. Distribution range of *Tsuga diversifolia*.

Distribution pattern: On the Pacific side of Honshu, particularly in the Japanese Alps, Shikoku, and on Kyushu only on the mountain Sobo-san in a beech forest (Fig. 5.42).

Climate: Warmth indices: 18–35. Annual precipitation: 1000–2500 mm.

Tsuga sieboldii Carrière

Structure and morphology: Height: 15–25(30) m. DBH: 40–100 cm. Chromosome number: $2n=24$. The tree has an umbrella-shaped crown.

Reproduction: Monoecious. Flowering stage: April to June. Ripening time: October. Anemochore. Seed number per kilogram: 290 000–300 000.

Habitat: *Tsuga sieboldii* occurs on ridges on xerophytic acidic sites in the warm temperate and cool temperate zones. It forms mixed forests with *Abies firma*, *Carpinus laxiflora*, *Fagus japonica*, *Pinus parviflora* and *Quercus crispula*.

Soil conditions: Podzolic shallow soil with thick litter inhabited by various fungi. Mother rocks are andesite, granite, metamorphic rock, sandstone and tuff.

Tolerances: Low light: medium (saplings can survive in an understorey under half shade). Frost: low. Heat: high. Water deficit: high (saplings survive in insolated places such as forest edges and on rock outcrops). Water surplus: low.

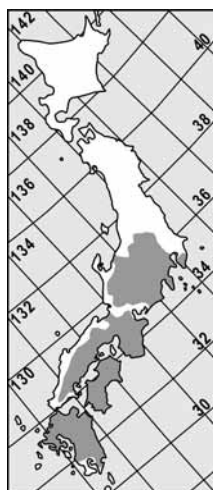


Fig. 5.43. Distribution range of *Tsuga sieboldii*.

Distribution pattern: The northern boundary is the mountain Yamizo-san in the Fukushima prefecture at 36°58'N (Fig. 5.43).

Climate: Warmth indices: 55–120. Mean annual temperature: 12–18°C. Mean annual precipitation: 1000–4000 mm.

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