Chapter 5

Forest Vegetation of Easternmost Russia (Russian Far East)

Pavel V. KRESTOV
Institute of Biology and Soil Science, Vladivostok, 690022, Russia, e-mail: krestov@ibss.dvo.ru

Abstract: The forest vegetation of the Russian Far East, an area of more than 3 million square kilometers in northeastern Asia, has been well studied by Russians but has remained unknown to most vegetation scientists outside Russia. The region is important because it represents natural vegetation processes and their environmental relationships over a huge territory, from polar deserts to cool-temperate forests, from the Pacific coast to the continental interior. These landscapes are among the best preserved forest ecosystems in the world. This chapter includes the first overview in English of eastern Siberian forest vegetation in its basic types, with a focus on phytogeography, ecosystem structure and dynamics, and developmental trends. Special attention is paid to the zonal forest types, including mixed broadleaf-*Pinus koraiensis* forests, dark-conifer (evergreen) forests of *Picea ajanensis*, deciduous light-conifer forests of *Larix dahurica*, broad-leaved deciduous forests of *Betula ermanii*, and the unique dwarf forests of *Pinus pumila* and *Alnus fruticosa*.

Key words: Eastern Siberia, Russian Far East, Manchuria, *Pinus koraiensis*, *Picea ajanensis*, *Betula ermanii*, *Larix dahurica*, *Pinus pumila*, *Alnus fruticosa*, vegetation zone, continentality sector, forest dynamics, Sukachov approach, vegetation classification, Russian-language literature

1. INTRODUCTION

1.1 Russian Far East

Easternmost Russia, well known in Russia as the Russian Far East and known elsewhere as eastern Siberia, represents the northeastern edge of the Asian continent, at the northwestern edge of the Pacific Ocean. The whole area covers approximately 3,125,000 km^2, ranging from 42°15’N to 71°30'N latitude and from 122°E to 169°W longitiude. This includes the area east of the Kolyma River, including its tributaries the Anuy, Omolon and upper Kolyma Rivers (above the Chubukulakh range), the upper Indigirka River (upper half of its tributary the Nera), the east side of the Yudoma River basin and Maya River (Lena River basin) and the Amur River basin from the confluence of the Shilka and Argun’ Rivers (see Fig. 5.1). The territory represents the Far East Federal Territory of the Russian Federation and includes its eight of nine administrative units (krai and oblast’): the Chukotian Autonomous Region, Magadanskaya oblast’ (Magadan Region), Khabarovskiy krai, Amurskaya oblast’, Jewish Autonomous Region, Primorskiy krai, Kamchatskaya oblast’ and Sakhalinskaya oblast’. The land is bordered on the north by the Eastern-Siberian and Chukotian Seas (Arctic Ocean basin) and on the east by the Bering Sea, Sea of Okhotsk and Sea of Japan (Pacific Ocean basin).

The vegetation of this territory changes from polar deserts with scattered or no plants at all

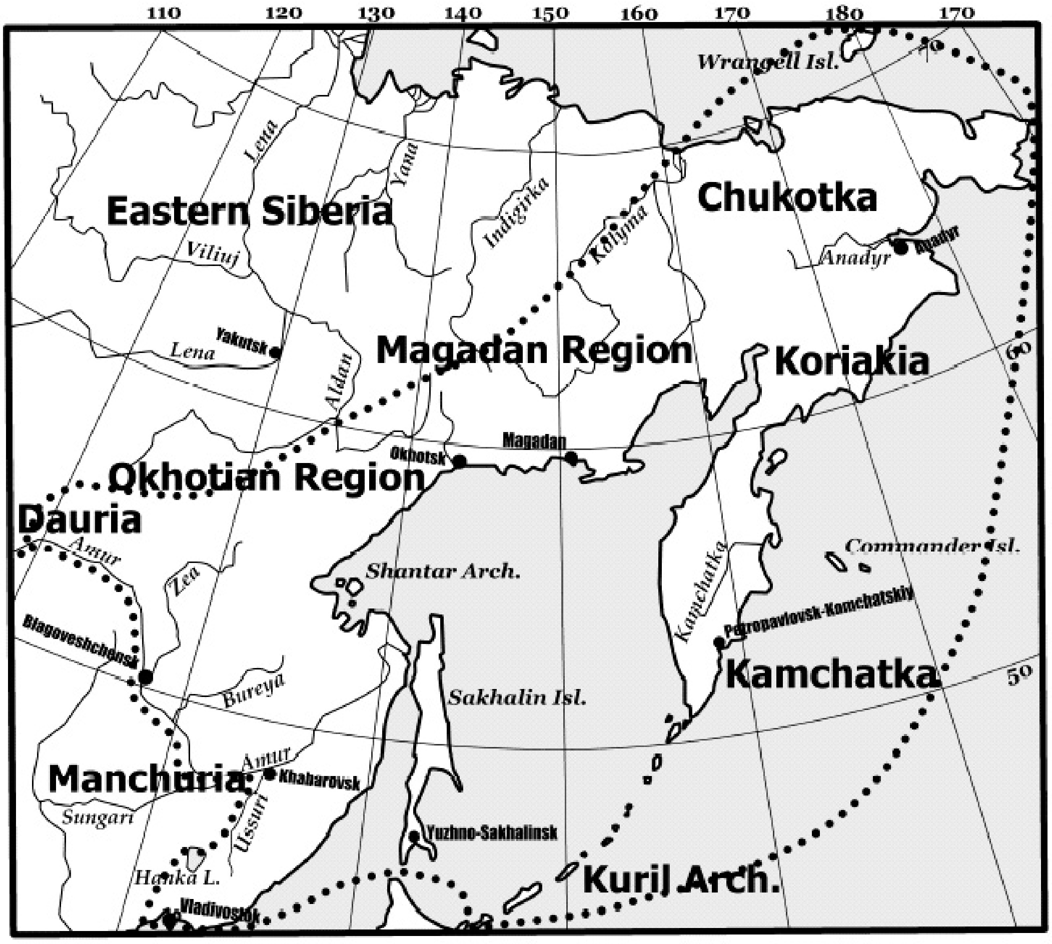

Figure 5.1. Northeastern Asia, with the area traditionally called the Russian Far East (dotted line).

(northernmost Wrangell Island) to diverse mixed forests of broad-leaved trees and Korean pine in the south. Five broad vegetation zones replace each other from north to south (Fig. 5.2). The Arctic deserts, occurring on Wrangell and Gerald Islands, are replaced southward by a tundra zone along the Arctic coast, including the whole Chukotka Peninsula. East of the Kolymskiy range is the zone of Beringian woodlands, very specific to northeasternmost Asia. The main vegetation type of this zone is low (6 m) dwarf-pine forest. The boreal zone occurs from 43°N (southern mountains) to almost 70°N, occupying nearly 75% of the Russian Far East. The dominant vegetation type is larch forest, replaced only in the south by spruce (lower Amur basin) or by *Betula ermanii* on the Kamchatka Peninsula. At about 46–50°N the boreal zone gradually changes to the temperate zone, represented by mixed hardwood-conifer forests.

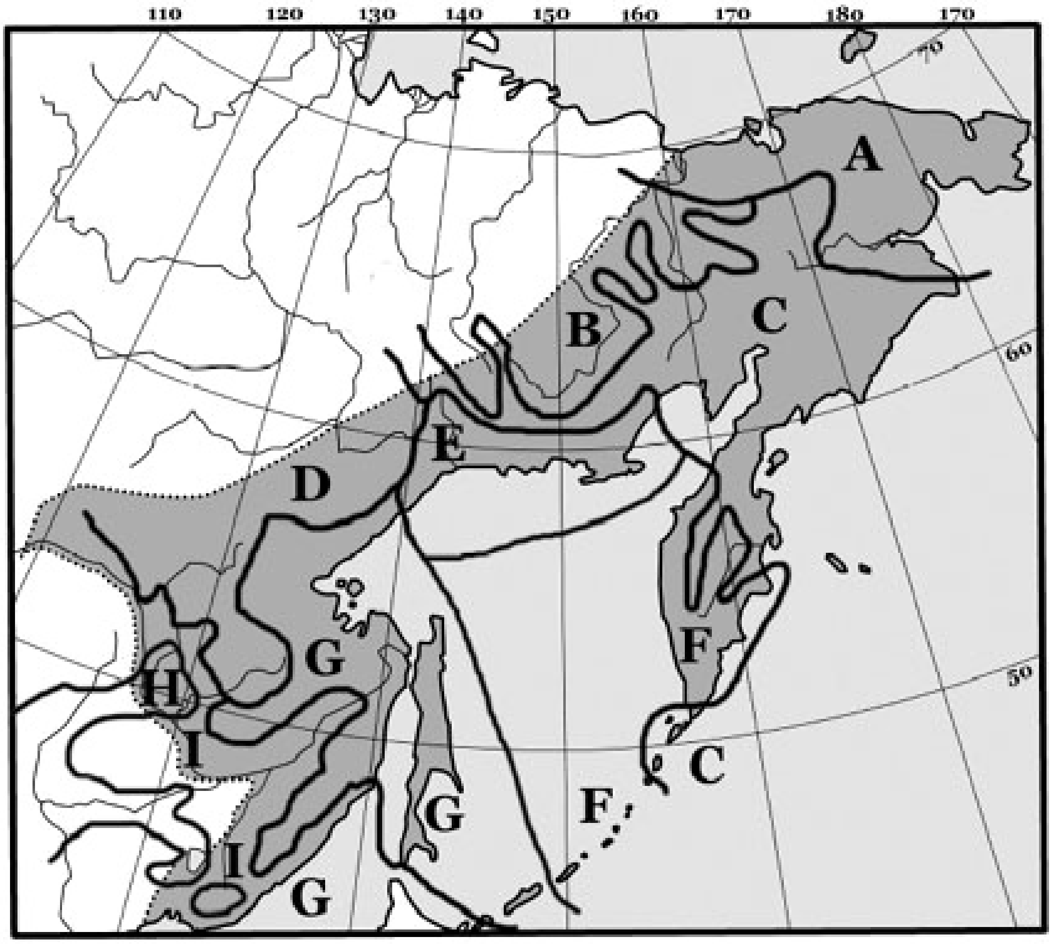

Figure 5.2. Vegetation zones and areas recognized in the Russian Far East (Kolesnikov 1961). A = Arctic tundra, B = northern East Siberian larch region, C = Beringian woodland, D = middle East Siberian larch region, E = North Okhotsk area of East Siberian larch region, F = North Pacific meadow-stonebirch area, G = western Okhotsk dark conifer area, H = Dauria-Hanka steppe-woodland, I – Manchurian-North Japanese mixed (broadleaf+conifer) forest area.

1.2 History of vegetation study in easternmost Russia

Before the 17th century no information on the vegetation of northeastern Eurasia was known in Europe. This large area was sparsely populated by about 15 indigenous tribes: the Chuktchi, Eskimo, Koriak, Itelmen, Aleutian, Even, Evenk, Nanai, Ulchi, Nivkh, and others. According to 1959 data, the number of native people was estimated at 50,000, which was less than 1% of the current population of the region.

Russians reached the eastern edge of the Asian continent in the 17th century. The expedition of Ivan Moskvitin reached the Sea of Okhotsk in 1639. The search party of Vasiliy Poiarkov reached the Amur basin in 1644. In 1648 the party of Semion Dezhniov went down the Kolyma River and circled the Chukotka

Peninsula. In 1697 the party of Vladimir Atlasov crossed Kamchatka from north to south.

Attempts to study the vegetation of the region followed two basic strategies, descriptive (by expedition) and experimental (stationary). Extensive data on the vegetation cover were obtained from expeditions before the 1960s. All expeditions were organized in Russian capitals, Moscow and St. Petersburg, at that time the main scientific centers. There were no scientific centers nor professional botanists or foresters in the Russian Far East at that time.

Stepan Krasheninnikov was the first professional naturalist, working on Kamchatka in 1737–1741 during the 2nd Kamchatka expedition, sent by Peter the Great for exploring the farthest reaches of the Russian Empire. His book "Description of the Land Kamchatka" written in 1755 (Krasheninnikov 1949) remained for a long time the only source of information about the nature and vegetation of Kamchatka. George Steller, working in that expedition as a physician, collected the first herbarium from Kamchatka and adjacent areas.

The first systematic botanical and zoological information was obtained in the mid-19th century: by A. Middendorf from the coast of the Sea of Okhotsk and Shantar Islands, by Maximowicz from the Ussuri and Amur basin, by Maack in 1855 from the Amur basin, and by Schmidt from Sakhalin, Ussuri and the Amur basin.

At the end of the 19th century the Russian Government, interested in colonizing Far Eastern regions, created a special Ministry for regulation of interior immigration, with the intent of settling the Amur basin and huge areas to the north with Russians. This Ministry initiated a series of expeditions to obtain information about lands suitable for colonization. Research was conducted in 1895–1917, mainly in the southern part of the region. One main focus of the research was the vegetation cover. The fundamental studies of Dokturovskiy in the Upper Amur region, of Korotkiy in the Zeya and Bureya River basins, and a series of studies by Komarov on flora and vegetation of southeasternmost Russia were conducted during that expedition. Until the 1950s, most of what we knew about the vegetation and major phytogeographical subdivisions of the Russian Far East was obtained from those early expeditions.

The establishment of Far Eastern Science began at the end of the 19th century with the foundation in 1899 of the Eastern Institute, which later was transformed into the Far East State University. In the 1930s the network of specialized scientific institutes belonging to the Academy of Science of the Soviet Union was established in the biggest cities of eastern Russia. Several nature reserves were created for preservation of the diversity of natural rarities. All those organizations focused on accumulating knowledge on the nature of the Russian Far East.

At the beginning of the 20th century, preliminary vegetation descriptions and forest resource estimates were obtained from all of eastern Russia. The data were summarized by the "Vegetation Cover of the USSR" (Lavrenko & Sochava 1956), which was the explanatory book for the first geobotanical map of the USSR (scale 1: 4,000,000). Another book "Outline of the Vegetation of the [Russian] Far East" (Kolesnikov 1955) remains the only description of the vegetation cover of this territory.

Since the 1960s research on the vegetation has intensified, due to the foundation of several large scientific institutes by the Academy of Sciences. The biggest scientific unit, focused on investigation of the vegetation cover, was the Laboratory of Geobotany, founded by Prof. N.G. Vasiliev in 1964, in the Institute of Biology and Soil Science in Vladivostok. This laboratory, in cooperation with geobotanists from Leningrad (St. Petersburg), prepared a map of the vegetation of the Amur basin, the most advanced work on vegetation cartography in southeastern Russia up to now.

The number of doctoral degrees granted reflects the increasing research on the vegetation cover: seven during 1935–1945, eight during 1946–1955, and 21 during 1956–1967 (Krylov & Salatova 1969). The vegetation cover was also the subject of study by geographers, foresters, and ecologists. The number of publications on flora and vegetation of the Far East increased from 1225 items in 1928 (Komarov 1928) to 7500 in 1969 (Gorovoi 1973).

Since 1950 the whole territory of eastern Russia was photographed from the air and covered by topographic maps at a scale 1: 100,000. The forests were inventoried every 10 years. In the 1970s satellite photographs became available for vegetation monitoring, and topographic maps at a scale 1: 25,000 were published for the whole territory. Nearly all remote points became accessible with helicopters.

A specific feature of Soviet science, especially in the Russian Far East, was that most papers were not published in refereed journals but in local sets of papers issued by different scientific organizations. Information on these papers did not go abroad, and they were absolutely inaccessible to foreign readers. Papers in European languages were published only occasionally.

In the 1990s the situation for science changed dramatically as Russia became open for information exchange. The political crisis in all states of the former Soviet Union caused a very deep crisis in science. Centralized funding for many scientific directions was stopped, including vegetation science. Because of the current freedom for information exchange, vegetation science in Russia is now slowly recovering from the crisis.

1.3 Current state of knowledge on forest vegetation of the Russian Far East

Intensive research on the vegetation of easternmost Russia in the 20th century enriched our knowledge of the flora and vegetation diversity. Publication of the “Flora of the USSR” (Komarov 1934–1964) initiated local floristic research, resulting in the appearance of several regional floristic manuals: “Guidebook to the Vascular Plants of Sakhalin and Kuril Islands” (Vorobiov *et al.* 1974), with 1528 species; “Guidebook to the vascular plants of Kamchatka” (Kharkevich & Cherepanov 1981), with 1168 species; “Guidebook to the vascular plants of Vladivostok and its suburbs” (Vorobiov 1982); and the “Flora of the Magadan Region” (Khokhriakov 1985). In 1985–1996 the most complete and reliable information on Far Eastern flora was published in the eight-volume series “Vascular plants of the Soviet Far East” (Kharkevich 1985–1996). These books contain information on taxonomy, morphology and distribution of 4350 vascular species, based exclusively on herbarium specimens collected in the territory.

Vegetation analyses appeared in many local descriptive studies focused mainly on important forest, meadow and tundra types. The material was generalized in several geobotanical maps, based on the principles of different cartographic schools (Aliokhin 1930, 1950, Lavrenko 1939, Lavrenko & Sochava 1954, Sochava 1969a, Sochava & Bayborodin 1977, etc.). Schemes for nature regionalization and for phytogeographical zonation were developed, for all of easternmost Russia, by Kolesnikov (1961, 1963).

In the boreal zone, the principles of vegetation classification developed by Sukachov (Sukachev & Dylis 1964) were generally used for distinguishing and ordering community types. For classification of mixed forests (broadleaved + Korean pine), an original approach was elaborated by Ivashkevich (1933) and developed by Kolesnikov (1956a). Not only static criteria (dominants, floristic composition, topography) but also dynamic (short-term successional) criteria were used for identifying the main classification units. This approach was called genetic (cf. Man’ko 1967) and was supported by several modern Far Eastern forest ecologists.

Despite the extensive classifications of vegetation of eastern Russia, numerous local classification schemes were also developed. No school was strong enough to coordinate classification work and convince others to use common classification principles. The Braun-Blanquet approach could not be used as an

Table 5.1. Areas (millions of hectares) occupied by the main tree species and total volumes of wood in the different administrative units (krai and oblast’ = district) of eastern Siberia (simplified from Anonymous 1990).

Dominant species	Primorskiy krai	Khabarovskiy krai	Amurskaya oblast’	Kamchatskaya oblast’	Magadanskaya oblast’	Sakhalinskaya oblast’	Total Far East	
							million hectares	million m^3
Pinus sylvestris	5.4	650.5	747.1	6.3	0.1	43.6	1453.3	97.9
Picea ajanensis	2666.1	9071.1	433.7	201.1	-	1414.3	13686.3	2594.7
Abies nephrolepis	248.1	456.1	52.7	-	-	804.5	1561.4	245.3
Larix dahurica	1136.7	23159.9	13281.5	951.3	7238.8	1656.2	47424.4	4892.1
Pinus koraiensis	2181.9	872.2	7.2	-	-	-	3061.3	711.4
Quercus mongolica	1920.9	615.4	428.3	-	-	24.9	2989.5	247.8
Fraxinus mandshurica	316.1	105.1	0.4	-	-	-	421.6	58.0
Acer mono	11.2	8.9	0.2	-	-	6.9	27.2	2.7
Ulmus japonica	128.2	35.7	1.2	-	-	1.1	166.2	22.4
Betula ermanii	750.2	763.7	62.2	5781.6	-	854.7	11784	731.8
Betula platyphylla	1003.8	3060.7	4195.1	641.7	13.7	140.6	9055.6	599.7
Populus tremula	179.7	575.8	161.4	19.8	0.1	21.7	958.5	92.1
Alnus hirsuta	32.1	2.5	6.8	-	0.6	3.4	45.4	2.1
Alnus fruticosa s.l.	6.1	85.3	0.4	167.6	0.7	79.9	340.0	16.0
Tilia amurensis	435.4	314.4	17.0	-	-	-	766.8	113.2
Populus suaveolens	61.6	216.4	30.3	168.3	132.7	13.2	622.5	91.5
Salix spp.	14.7	153.8	13.3	311.0	106.6	40.0	639.4	47.7
Pinus pumila	38.0	4432.5	1162.6	8062.1	9595.4	333.3	23623.9	745.8
Others	9.9	49.3	642.8	2727.1	416.9	0.8	3846.8	88.4
Total	11146.1	44629.6	21244.2	19037.9	17505.6	5306.5	118869.9	11400.6
Changes over the period 1965–1990	+3.4	+4.7	+9.4	+1.6	−15.6	+17.9	+1.8	

integrating basis for political reasons (Mirkin & Naumova 1998), so it was mainly the methodologies of Sukachov and Ivashkevich-Kolesnikov that were used for classification.

Forestry, faced with the necessity of using uniform classifications and methods, attempted to simplify existing schemes by using dominance only as the criterion for distinguishing forest formations and by using combined dominance-topography criteria for distinguishing forest types.

All forests of eastern Russia were inventoried before 1975 (Table 5.1), and several decisions were made for forest management. All forest formations were subdivided into management units (Solovyov & Sheingauz 1981), and detailed techniques were developed for practical silviculture; accurate data-bases allowed long-term forestry planning.

2. PRINCIPAL CONCEPTS

2.1 Units of phytocenotic classification

The problem of inventorying phytocenotic diversity is closely connected with problems of vegetation classification. In easternmost Russia the main units of classification are associations (in the phytosociological sense) and forest types (in the forestry sense), accepted by different authors in different volumes and reflecting accordingly the units of cenotic systems at various levels. This, in combination with the lack of original published relevés, made classification systems for the vegetation of this region very confusing.

The term ‘association’ was adopted in Russia from Scandinavian classification approaches (Trass & Malmer 1973, Frey 1973) and has a completely different meaning from the association of the Braun-Blanquet school (Braun-Blanquet 1951). It is more similar to Braun-Blanquet's variant and subvariant, but instead of indicating species abilities, the Russian association is based on potential to dominate in different layers or other plant groupings, such as synusiae, layers, growth form spectra, etc. Authors realized the advantages of the Braun-Blanquet nomenclature for ordering vegetation units but had no possibility to apply this nomenclature in easternmost Russia, because most vegetation studies were based on original approaches to vegetation classification. All references to associations and other vegetation units in this chapter will refer only to the Russian system of classification categories.

Despite the agreement of many authors to accept a main classification unit (the association, or the forest type in the sense of Sukachov 1928), such agreement is not found in the real associations defined by these authors. In the survey of the vegetation of eastern Sikhote-Alin, Kolesnikov (1938) described 19 association groups, grouped into five classes; Dylis & Vypper (1953) classified phytocenoses into 18 forest types, related to six subgroups and three groups of types; and Smagin (1965) described 16 types for middle Sikhote-Alin, related to nine series and to four geomorphologic complexes. These authors use different criteria for distinguishing associations in complex mixed (broad-leaved + Korean pine) forests of the Far East, though there is a tendency to base classification units on the dominants of various layers in the communities. Nearly the same situation characterizes the syntaxonomy of the other vegetation types.

Since the criteria used to classify different vegetation types may not be well known, those used herein are summarized in Table 5.2.

The terms ‘phytocenosis’ and ‘association’ are accepted in the sense of Sukachov (1957): “The phytocenose (phytocoenose), or plant community, is taken to mean any plot of vegetation on a given area, uniform in its composition, synusial structure, and the pattern of interactions among plants and between these and the environment”. The term “association

Table 5.2. Diagnostic criteria of identifying syntaxa.

Syntaxa (English and Latin names)	Diagnostic criteria			
	Floristic	Ecological and structural	Dynamics	Ecotope
Association (Associatio)	Homogeneity in species composition, certain species showing cenotic activity in same ways in all layers.	Homogeneity in synusial structure in analogous stages of stand development.	Changeability of phytocenoses in the scopes of stability of populations of significant species.	Homogeneity in ecological parameters.
Association group (Grex associationum)	Species of one cenogroup show cenotic activity.	Homogeneity in layer structure.	Same as for associations.	Same as for associations.
Association class (Classus associationum)	Characteristic group of species (sensu Dokhman 1960).	Phytocenoses have the same dominants and belong to the same life form.	Changeability in the scopes of stability of cenopopulations of dominants and subdominants of phytocenoses.	Homogeneity in regional climatic parameters.
Formation (Formatio)	Same as for associations.	The dominants are similar in the origin and in adaptations to the main directly acting natural factors.	Changeability in the scopes of stability of cenopopulations of dominants.	Homogeneity in zonal climatic parameters.

(or forest type) unites communities similar in organization and habitat adaptations, or alternately, identical in main species and layer structure on similar habitats." Thus, the association is an abstract unit, a product of the typification of phytocenoses based on structural attributes, unity of dynamic processes, and location in different vegetation gradients (Shennikov 1935).

We consider that associations consist of several developing phytocenoses incorporating all stages of normal ontogenetic development of all determinant species of the forest community on biologically similar habitats. Thus, to distinguish associations we employ the following criteria: similar sets of canopy dominants; similar cenotic activity by the same species, and as a consequence, similar synusial structure in the lower layers; and similar environmental conditions, as indicated through various groups of indicator species. These criteria are similar to those of Dokhman (1960) and Dolukhanov (1957) (see also Alexandrova 1973).

The term 'association group' (following Shennikov) refers to sets of associations characterized by uniform climatic and similar soil and hydrological conditions, by a similar composition in the tree layers, and by cenotic and biomorphological generality of the dominants of lower synusiae (Krylov 1984). This concept is closer to the variant or in some cases to the subassociation of the Braun-Blanquet approach. The term 'association class' means sets of associations united by generality of dominant species and similarity in features, reflecting adaptations to the regional climate (Krylov 1984). As far as the climate determines the differences in vegetation cover at this level, the association class corresponds somewhat to the zonal association of the Braun-Blanquet school.

'Formation' unites the associations based on criteria of the ecological similarity of the dominants (Dolukhanov 1957, Krylov 1984).

2.2 Methods of ecological ordination

The site typology of Pogrebnyak (1955), as interpreted by Krylov (1984), was used to display ecological ranges of the main association groups and their distributions on environmental gradients. An edaphic grid is constructed using qualitative axes for soil moisture and nutrient regimes. The soil-moisture axis includes six ranks (hygrotopes, sensu Pogrebnyak): 1) xeric (dry), 2) meso-xeric (slightly dry), 3) mesic (fresh), 4) meso-hygric (moist), 5) hygric (very moist), and 6) hydric (wet). The axis for soil nutrient level includes four ranks (trophotopes, sensu Pogrebnyak): A) oligotrophic (very poor), B) oligo-mesotrophic (poor), C) mesotrophic (medium), and D) megatrophic (rich). This yields 24 classes for site type (e.g. mesic oligotrophic, mesic mesotrophic, mesic megatrophic), similar to those of Cajander (1926), Krajina (1969) and Pojar *et al*. (1987).

The exact position of association groups in the edaphic grid was determined by analyzing the ecological optima of the indicator species composing the phytocenoses, using the ecological scales of Ramenskiy (1953), as adapted by Tsatsenkin (1978) and Seledetz (2000) for Far Eastern species.

2.3 Nomenclature

The vegetation syntaxa were named according to the traditions of the Russian geobotanical school (Sukachev & Dylis 1964, Alexandrova 1973). The naming of associations follows the binary principle, with the name of the dominant as the noun, plus the suffix '-etum', and the name of the subordinate (shrub, herb or moss) layer as the adjective, with suffix '-osum'. For example, *Pinetum caricosum* for a pine forest with *Carex* understorey. Latin species names may be added to genus names as an adjective in the genitive case, for example *Pinetum koraiensis caricosum sordidae*. In the case of two equal

Table 5.3. Distribution of dominant species and phytogeographic areas according to vegetation zones and climatic sectors.

Zone	Sectors			
	continental	submaritime	maritime	oceanic
Arctic deserts				Open lichen aggregations
				Arctic polar deserts
Tundra		dwarf-shrub tundra	lichen tundra	lichen tundra
		the Arctic area of tundra		
Dwarf-shrubs		*Pinus pumila*	*Alnus fruticosa*	*Alnus fruticosa*
		Beringian woodland area		
Northern boreal	*Larix dahurica, Pinus pumila*	*Larix dahurica, Pinus pumila*	*Picea ajanensis*	*Betula ermanii*
	Eastern Siberian larch area		Eastern Okhotsk dark-conifer area	Northern Pacific meadow-stonebirch Area
Middle boreal	*Larix dahurica*	*Larix dahurica*	*Larix dahurica, Picea ajanensis*	*Betula ermanii*
	Eastern Siberian larch area		Western-Okhotsk dark-conifer area	Northern Pacific meadow-stonebirch area
Southern boreal	*Larix dahurica*	*Larix dahurica*	*Picea ajanensis, Abies nephrolepis*	*Picea ajanensis, Abies sachalinensis*
	Eastern Siberian larch area		Western-Okhotsk dark-conifer area	Northern Pacific meadow-stonebirch area
Northern temperate	*Quercus mongolica, Betula davurica*	*Pinus koraiensis, Fraxinus* spp., *Tilia* spp., *Quercus mongolica, Pinus koraiensis*		*Abies sachalinensis Quercus crispula* (s.s.)
	Dauria-Hanka steppe woodland wrea	Manchurian Broadleaved Conifer Area		Northern Japanese Broad-leaved Conifer Area

co-dominants in the layer, both can be given, separated by a hyphen and placing the less significant species first, for example a *Fraxineto mandshuricae-Pinetum koraiensis cardaminoso leucanthae-caricosum sordidae*. The names of association groups and higher units are given by using plural Latin names of genera, species or their growth forms or other attributes, with the suffix '-osa' for association groups and '-osium' for association classes. Examples: *Pineta caricosa* and *Lariceta herbosa* are association groups; *Pineta carpinosium* and *Piceeta abietosium* are association classes (Alexandrova 1973).

The plant species nomenclature follows the Plantae Vasculares Orientis Extremi Sovetici (Kharkevich 1985–1996), with exclusions mentioned in the text.

3. VEGETATION ZONATION IN THE RUSSIAN FAR EAST

The vegetation cover of easternmost Russia is very heterogeneous, due to two basic climatic gradients characteristic for northeast Asia. The wide latitudinal range results in major climatic changes, from the Arctic zone in the north to the northern temperate zone in the south. The location near the Pacific Ocean causes another type of climatic gradient, that of continentality. The climate of the oceanic islands is suboceanic, with cold summers and mild winters. In the continental interior the climate is ultra-continental, with very cold winters (absolute minimum −72°C at Oymiakon) and warm summers (absolute maximum 43°C at the same location). The climatic differences cause changes in the vegetation, expressed from north to south as a sequence of phytogeographical zones: (1) polar deserts; (2) tundra; (3) dwarf-pine woodlands; (4) boreal forests; (5) temperate hardwood-conifer forests and (6) steppe-woodlands. This sequence of vegetation zones is commonly accepted in the Russian school of phytogeography, with east-west differentiation reflecting the continentality gradient (Komarov 1927, Grishin 1995). The Russian Far East is subdivided commonly into five continentality sectors: (1) suboceanic; (2) maritime; (3) sub-maritime; (4) continental; and (5) ultra-continental (Table 5.3). Vegetation in each continentality sector reflects the change from damp, relatively seasonal, even oceanic climates near the coast to dry, seasonally contrasting climates in the interior (Table 5.4).

The sectoral nature of the vegetation zonation is reflected by subdividing zones or subzones into phytogeographical areas with continentality-dependent features in the vegetation. The main characteristics of these phytogeographical areas are summarized briefly below.

Table 5.4. Climatic data for sites and phytogeographical areas.

Area and station	Latitude	Longitude	Mean temperature (°C)			Annual precipitation (mm)
			annual	coldest month	warmest month	
Arctic area of tundra						
Rauchua	69°N	166°E	−14	−31.9	4.9	-
Pevek	69°N	170°E	−10.4	−27.1	7.5	136
Cape Schmidt	68°N	179°W	−12.1	−27.3	3.6	254
Uelen	66°N	170°W	−8.2	−21.7	5.4	386
Anadyr	65°N	176°E	−7.4	−22.7	10.5	312
Kresta Bay	66°N	179°W	−7.1	−20.1	8.3	530
Providenia	64°N	174°W	−4.9	−15.9	7.6	494
Cape Navarin	62°N	178°E	−4.1	−13.4	8.0	540
Beringian woodland area						
Ostrovnoe	67°N	167°E	−12.0	−36.4	13.3	182
Eropol	68°N	162°E	−12.0	−34.2	13.4	340
Bilibino	66°N	158°E	−11.1	−30.8	13.8	210
Markovo	65°N	170°E	−9.2	−28.4	13.4	334
Khatyrka	62°N	176°E	−4.6	−16.5	8.6	-
Kamenskoye	62°N	166°E	−6.5	−23.0	13.1	-
Apuka	61°N	170°E	−2.6	−13.2	10.4	-
Palana	59°N	160°E	−2.8	−15.9	10.3	450
Ossora	59°N	163°E	−2.4	−14.9	12.1	550
Nikolskoye	55°N	166°E	2.1	−4.0	10.5	-
Cape Lopatka	51°N	157°E	1.1	−6.9	9.4	-
Shumshu	51°N	156°E	1.6	−6.8	10.8	1245
East-Siberian larch area						
Oymiakon	63°N	143°E	−12.3	−50.4	22.0	313
Gizhiga	62°N	160°E	−6.1	−22.2	12.0	321
Magadan	60°N	151°E	−4.7	−21.0	12.6	434
Okhotsk	59°N	144°E	−5.0	−23.0	13.0	364
Nelkan	58°N	137°E	−7.5	−37.3	17.1	390
Tynda	55°N	125°E	−6.5	−31.7	17.1	525
Ignashino	53°N	121°E	−4.8	−31.3	19.0	417
Skovorodino	54°N	124°E	−4.7	−29.1	18.0	434
Ust’-Njukzha	57°N	122°E	−6.4	−32.8	17.6	407
Chekunda	50°N	132°E	−4.6	−34.3	19.0	652
Eastern Okhotsk dark conifer area						
Kozyrevsk	56°N	160°W	−1.8	−19.2	15.1	512

Area and station	Latitude	Longitude	Mean temperature (°C) annual	coldest month	warmest month	Annual precipitation (mm)
Milkovo	55°N	159°E	−2.7	−21.8	15.0	540
Northern Pacific meadow − stone birch area						
Sobolevo	55°N	156°E	−1.3	−14.8	12.1	789
Storozh Bay	55°N	162°E	0.6	−8.5	11.7	1020
Bolsheretsk	52°N	156°E	−0.4	−12.6	11.4	880
Petropavlovsk	53°N	159°E	1.7	−8.6	13.7	1335
Matua	48°N	153°E	1.5	−6.3	10.9	1223
Simushir	47°N	152°E	2.5	−5.8	11.0	1610
Western Okhotsk dark conifer area						
Ayan	57°N	138°E	−3.3	−19.7	13.2	791
Cape Enkan	57°N	139°E	−3.4	−20.2	13.3	521
Poliny Osipenko	52°N	136°E	−3.3	−29.3	17.8	410
Chumikan	55°N	135°E	−3.9	−23.7	14.5	681
Belogorsk	51°N	128°E	−2.0	−28.8	20.7	480
Bolon’	50°N	136°E	−1.7	−28.3	19.7	650
Nikolayevsk-na-Amure	53°N	141°E	−2.4	−23.9	16.5	513
Okha	54°N	143°E	−2.4	−19.9	14.0	546
Nogliki	52°N	143°E	−2.0	−20.2	14.4	613
Poronaisk	49°N	143°E	0.0	−17.7	15.8	747
Dauria-Hanka steppe-woodland area						
Ilyinka	45°N	132°E	3.0	−18.4	20.7	498
Manchurian mixed broadleaf-conifer area						
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
Sovgavan’	49°N	140°E	−0.4	−19.4	16.5	742
Dalnerechensk	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
Olga	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
Riazanovka	43°N	131°E	5.2	−11.4	20.5	961
Northern Japanese mixed broadleaf-conifer area						
Yuzhno-Sakhalinsk	47°N	143°E	2.1	−13.8	17.3	753
Uglegorsk	49°N	142°E	1.6	−14.8	17.0	600
Cape Krilion	46°N	142°E	3.8	−7.6	15.9	960
Kurilsk	45°N	148°E	4.3	−7.2	16.0	1040

3.1 Arctic zone

3.1.1 Arctic deserts

In northeastern Asia only Wrangell and Gerald Islands are in the zone of Arctic Deserts (Kolesnikov 1961, 1963), which are characterized by the lack of a closed vegetation cover. Large areas on the islands are covered by talus or rock outcrops. Crustose and foliose lichens (species of *Gyrophora*, *Lecidea*, and *Rhizocarpon*) are most abundant on the stony substrates. On the sites with accumulations of fine soil, fruticose lichens (*Alectoria*, *Cetraria* and *Cladonia*) and mosses (mainly *Andraea papillosa*, *Pogonatum capillare*, *Rhacomitrium lanuginosum* and *Tetraplodon mnioides*) form the sparse cover. The vascular plants are represented by *Douglasia ochotensis*, *Artemisia glomerata*, *Papaver polare*, *Saussurea tilesii*, *Saxifraga funstonii*, etc. The bryophytes and flowering plants are scattered and not numerous (Gorodkov 1958a, b).

3.1.2 Arctic tundra

The coast of the Arctic Ocean and all of the Chukotka Peninsula north of 65°N are covered by tundra vegetation (Fig. 5.3). The Tundra Zone is subdivided into two subzones: typical Arctic tundra along the Arctic coast and lichen tundra as the main zonal vegetation on the Chukotka Peninsula and lower Anadyr River basin (Kozhevnikov 1996).

The Far Eastern sectors of the Arctic Polar Desert and Tundra are differentiated from the rest of the circum-Arctic zone by the presence of so-called Beringian plant species, which are also common to Alaskan and eastern-Canadian sectors of the Arctic zone (Yurtsev *et al*. 1978).

Tundra vegetation is characterized by a closed, one-layer cover composed mainly of perennial plants, especially dwarf-shrubs, mosses and lichens, and by a lack of larger shrubs and trees. Most typical tundra plants have their renewal buds no higher than 20–30 cm above the ground and reproduce mainly vegetatively. All tundra plants are adapted to the short vegetative season with its long period of daylight (Kozhevnikov 1996).

Tundra communities vary in composition depending on site edaphic and climatic conditions. Regions along the Arctic coast are characterized by predominance of sedge and heath communities with *Carex* spp., *Eriophorum vaginatum*, *Vaccinium uliginosum*, *Betula exilis* and leafy mosses. On the Chukotka Peninsula sedge communities are also important, but lichen communities with *Cladina* spp. and some ericaceous dwarf-shrubs increase.

Figure 5.3. Tundra vegetation on the Chukotka Peninsula (photo by A. Belikovich).

3.2 Subarctic zone

3.2.1 Beringian woodland

This area is characterized by the dominance of dwarf trees, the conifer *Pinus pumila* (Fig. 5.4) and broad-leaved *Alnus fruticosa* s.l. (Fig. 5.5). This vegetation occurs widely in the basins of the Anadyr and Penzhina Rivers, on the Koriakskiy mountain range, northern half of Kamchatka, southernmost Kamchatka (Lopatka Cape), and on the Commander Islands and northern Kuril Islands. The dwarf-pine zone does not occur in continental areas (Kolyma River), where the arctic zone borders the boreal larch zone. Kolesnikov (1955) proposed that the presence of more or less extensive tundra patches on 'plakors' (zonal sites, or 'eu-climatopes') should be a criterion for distinguishing the Beringian woodland area. By this criterion the Beringian woodland area extends due south along the coast of the Sea of Okhotsk to Magadan, including the northern Koni Peninsula.

Although the Beringian woodland occurs only in the submaritime, maritime and suboceanic sectors, the vegetation does gradually change from mainly *Pinus pumila* thickets inland to mainly *Alnus fruticosa* thickets in coastal areas. Scattered *Larix dahurica* trees are a stable component of the vegetation, increasing inland. These can form

Figure 5.4. Dwarf-pine thickets in Northern Kamchatka: 1 = *Pinus pumila* communities, 2 = inversion communities of *Betula ermanii* on the warmest slope positions, 3 = inversion communities of tall herbs on snow-accumulation sites (photo by P. Krestov).

Figure 5.5. Alnus fruticosa thickets on Paramushir (Northern Kurils). The snow patches remaining through the summer are characteristic of the maritime and suboceanic sectors of the Subarctic zone (photo by P. Krestov).

small forest patches in river valleys and on southern slopes. Mires with *Carex appendiculata*, *Eriophorum* spp. and *Sphagnum* spp. occur widely in areas on permafrost. Small patches of forest dominated by *Populus suaveolens* and *Chosenia arbutifolia* occur in river valleys, in combination with wet grass meadows (Yurtsev *et al*. 1978).

3.3 Boreal zone

3.3.1 Eastern Siberian larch area

The larch area is one of the largest homogeneous phytogeographical areas in the whole circum-boreal zone. It stretches from the tundra (continental regions) and Beringian woodlands (maritime regions) in the north to the coast of the Sea of Okhotsk (northern boreal zone) and Amur basin in the south. Larch forests extend westward to the Yenisey River, where they are replaced by spruce (*Picea obovata*) forests (Sochava 1956). The main feature of the area is the dominance of *Larix dahurica* s.l. on zonal sites (Fig. 5.6).

Despite the great variety of ecological regimes and climatic conditions in larch communities, the species composition remains surprisingly homogeneous over the whole range from south to north and from west to east. Several seral species, mainly *Betula platyphylla*, *Populus suaveolens* and *Alnus hirsuta*, may accompany *Larix dahurica* on zonal sites. River valleys are occupied by forests of *Populus suaveolens*, *Salix udensis*, *S. rorida* and *Chosenia arbutifolia*.

The dominance of shade-intolerant larch over such a large territory is caused by the severe climatic conditions and permafrost, which can be tolerated only by *Larix dahurica*.

Figure 5.6. Larch taiga in Magadan. *Larix dahurica* covers all parts of the relief: slopes, valleys and ridges. A *Pinus pumila* shrub is in the foreground (photo by P. Krestov).

3.3.2 Eastern Okhotsk dark-conifer forests

This area lies in the middle of the Kamchatka Peninsula, between the Sredinniy and Vostochniy mountain ranges. Larch and spruce (*Picea ajanensis*) form the forest here, in the locally submaritime climate made possible by the mountains that block both Okhotsk and Pacific air masses (Man’ko & Voroshilov 1973). The area is surrounded by Beringian woodlands to the north, with *Alnus fruticosa* as a dominant, and by birch (*Betula ermanii*) forests plus tall-herb meadows to the south, east and west.

Spruce and larch forests represent zonal vegetation in the area. Although this is not the northernmost extent of spruce, it is the coldest part of the geographical range of *Picea ajanensis*. The spruce forests of the area are characterized by the predominance of circumboreal or Pacific-boreal species in all layers.

Larix dahurica forests in this area dominate mainly on sites with intensive disturbance regimes caused by fires or volcanic activity, or in areas with a locally subcontinental climate lying to the south of the “conifer island”. The structure and floristic composition of the larch forests are similar to those in the continental part of eastern Siberia.

Populus suaveolens, *Chosenia arbutifolia* and *Salix udensis* forests represent the valley vegetation of the area. Grass meadows are typical for the floodplain of the Kamchatka River.

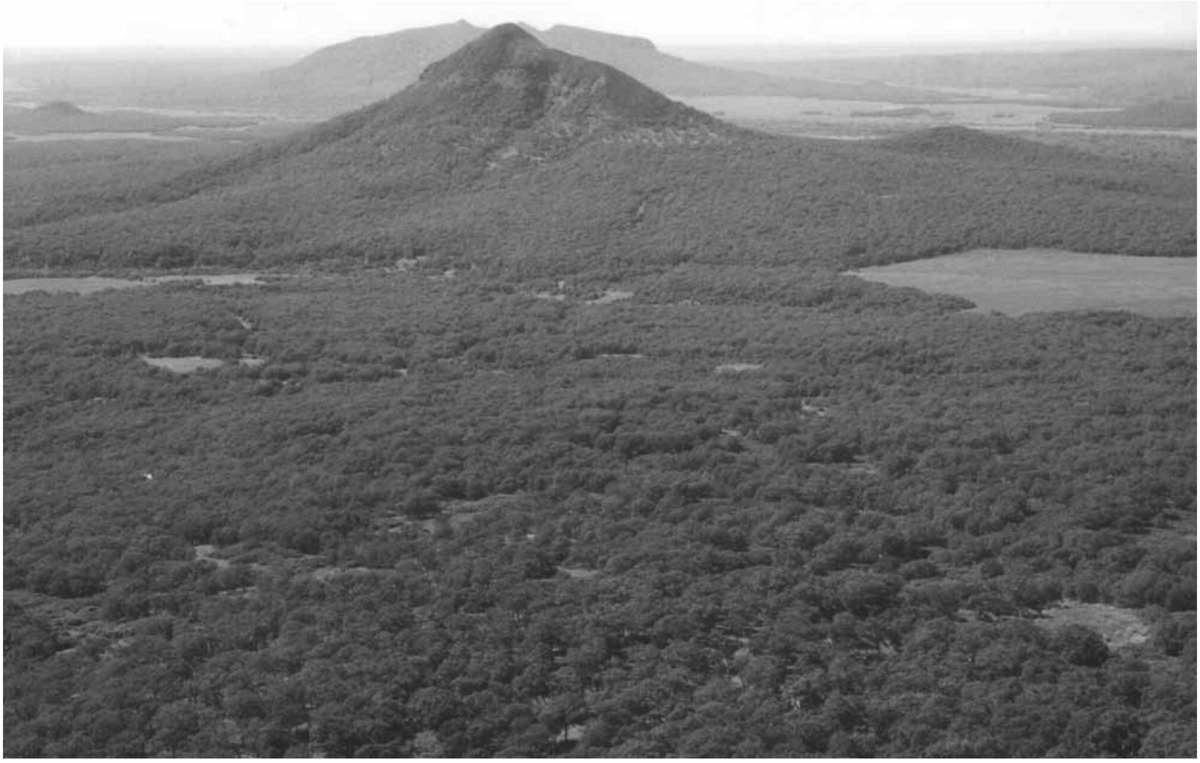

Figure 5.7. Stone birch forests on Kamchatka (photo by V. Yakubov).

3.3.3 Northern Pacific meadow-birchwood area

Stone birch (*Betula ermanii*) forms forests on zonal sites in southern Kamchatka and the middle Kuril Islands (Iturup, Urup), in a severe sub-oceanic climate with cold summers, mild winters, and nearly equal distribution of precipitation throughout the year (Fig. 5.7). Another important zonal vegetation type, the tall-herb meadow, develops on areas of snow accumulation. Both vegetation types characterize the cold, wet, sub-oceanic climate within the northern boreal zone (Shamshin 1999).

The main, most widespread community type in the area is the stone-birch forest with tall herbs (*Senecio cannabifolius*, *Filipendula camtschatica*). On well-drained sites the proportion of mesophytic herbs increases (e.g. *Geranium erianthum*, *Saussurea pseudotilesii*, *Artemisia opulenta*). Tall herbs, in combination with *Calamagrostis purpurea*, form subalpine-like meadows in wetlands on extensive areas mostly in the southern and eastern parts of the area.

Populus suaveolens, *Chosenia arbutifolia* and *Salix udensis* forests represent the valley vegetation. Their characteristic features are dominance by tall herbs in the herb layer.

3.3.4 Western Okhotsk dark-conifer forests

Picea ajanensis is the dominant species in the Western Okhotsk Dark-Conifer Area (Fig. 5.8), occurring in the submaritime and maritime climates in the middle and southern parts of the boreal zone. Spruce forests within this area cover the southern Dzhugdzhur Range, eastern Stanovoy Range, the area between the Amur and Uda Rivers, the northern Sikhote-Alin Range, all of Sakhalin, Iturup (southern Kurils), and the Pacific side of Hokkaido (Man'ko 1987). On the north and west, this area borders the eastern Siberian Larch area. On the south it contacts the northern-temperate mixed-forest area.

The main vegetation type is pure spruce forest in the north or mixed with firs (*Abies nephrolepis* or closely related *A. sachalinensis*) in the south. *Abies sachalinensis*, however, can form pure stands in southern Sakhalin and in the southern Kuril Islands. Several other spruce species also form communities within this area. *Picea koraiensis* (close to *Picea obovata* and *Picea abies*) forms stands in well-drained river valleys in continental areas, and *Picea glehnii* forms stands in wetlands at a few places in southernmost Sakhalin and on Kunashir, Shikotan and Iturup (southern Kurils).

Extensive fires decreased the modern range of spruce forests, with secondary larch forests replacing them. Larch forests are the second important vegetation formation in the area. If seed sources are present and wildfires do not recur, spruce can replace larch on zonal sites within 100–300 years after fire.

The basic vegetation types in river valleys are larch forests and woodlands, *Populus suaveolens* and *P. maximowiczii* forests, and *Chosenia arbutifolia*, *Salix udensis* and *S. rorida* forests. Grass meadows with *Calamagrostis purpurea* develop in the lowest areas. Sedge (*Carex appendiculata*) and sphagnum bogs occur widely across the zone, in depressions with cool-air drainage over permafrost and on poorly drained sites.

Figure 5.8. Western-Okhotsk Ajan Spruce taiga: *Abies nephrolepis-Picea ajanensis* forest on the Miaochan range, north of the Amur River (photo by P. Krestov).]

3.4 Northern temperate zone

This zone lies in the basin of the Amur River and on the spurs of the Sikhote-Alin, Badzhal, Lesser Hingan and Chyornye Gory mountain ranges (Krestov 1997). The Amur valley permits oceanic air masses to penetrate deeply into the interior, shifting the eastern boundary of the continental climate considerably further inland. In addition, the continental cold air masses continue building over the winter, creating a strong contrast between summer and winter. Winter temperatures are extremely low for a maritime region at 40° latitude (−20°C mean for January), and summer temperatures are relatively high (August means to +22°C), with high humidity. The high mean annual temperatures (+2 to +5°C), with the strong seasonal contrast, permit occurrence of a great variety of vegetation types on zonal sites. The continentality gradient causes a change in vegetation that ranges from drought-tolerant oak forests in the interior to species-rich mixed broadleaf-conifer forests in coastal areas. Three areas are recognized in this northern temperate zone.

3.4.1 Daurian broad-leaved forests

Most of this area lies in northeastern China, reaching northeastern Mongolia in the west (Fig. 5.9). On the Russian territory it appears in the upper Amur basin, called Dauria, and in the basin of Lake Hanka (Kolesnikov 1956a). These areas have been strongly influenced by human activity for many centuries, which partly explains the current state of vegetation in the area. The modern vegetation cover contains meadows, bogs and forests in nearly equal proportions. Most meadows and some bogs areas were transformed into agri-

Figure 5.9. Mongolian oak forests on southern spurs of the Sikhote-Alin Range. *Quercus mongolica* forms patches on northern slopes in combination with meadows of *Arundinella anomala* (photo by V. Verkholat).

cultural lands. The basic forest type is Mongolian oak (*Quercus mongolica*), forming 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 influencing natural selection in the oak forests. Meadows in the zone occur on sunny, well-drained slopes (steppe-like meadows) and in lowlands next to boggy vegetation. The characteristic feature of the meadows is the presence of xeric and xero-mesic herbs and grasses (*Cleistogenes kitagawae*, *Stipa baicalensis*, *Arundinella anomala*, different species of *Astragalus*, *Galium*, *Scabiosa*, *Allium*, and *Artemisia*, etc.). Mesic and hygric meadows dominated by *Miscanthus sacchariflorus* and *Calamagrostis langsdorffii* occur in lowlands.

Pinus densiflora (near Lake Hanka), *P. sylvestris* (in the upper Amur), *Armeniaca sibirica*, and *Ulmus macrocarpa* form small patchy stands on hill slopes and ridges.

3.4.2 Manchurian mixed forests

This area of temperate mixed forests (broad-leaved trees plus five-needled Korean pine) lies on the spurs of the Sikhote-Alin range and the southern spurs of the Lesser Hingan, Bureinskiy and Badzhalskiy ranges (Fig. 5.10). The main vegetation type is mixed forests co-dominated by *Pinus koraiensis* and various broad-leaved tree species: *Tilia amurensis*, *T. mandshurica*, *Fraxinus mandshurica*, *Quercus mongolica*, *Betula costata*, *Abies holophylla* (only south of 44°N), *Kalopanax septemlobus*, *Phellodendron amurense*, *Ulmus japonica* (Kolesnikov 1956a, Krestov 1997). In most communities the number of tree co-dominants is 3–5 species. At 600–800 m above sea level, the temperate communities may be enriched by boreal dominants *Picea ajanensis* and *Abies nephrolepis*.

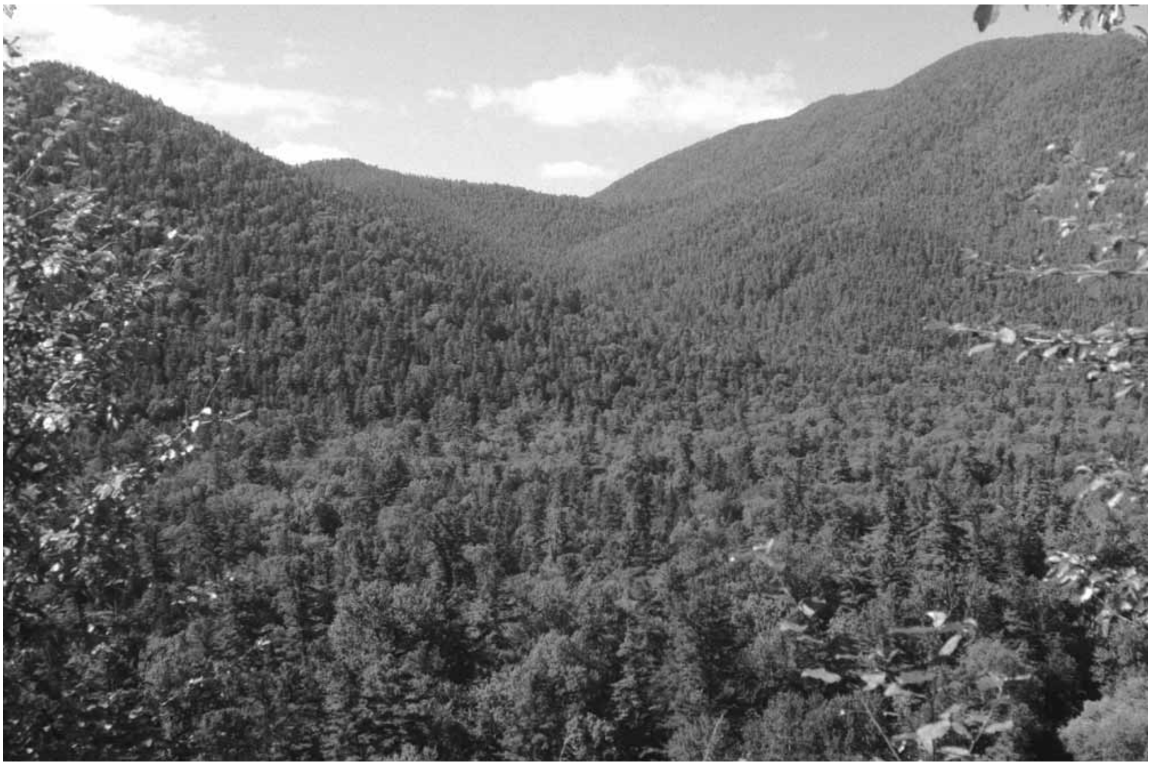

Figure 5.10. Mixed broadleaf + Korean Pine forests on the Sikhote-Alin Range (photo by P. Krestov).

Other vegetation types in the area include broad-leaved valley forests of *Ulmus japonica* and *Fraxinus mandshurica* on old, stable parts of river valleys; *Populus maximowiczii* and *Populus koreana* (in fact close species) on younger parts of river valleys; and *Chosenia arbutifolia* on fresh alluvial deposits. Poorly drained parts of the Ussuri valley are occupied by grass meadows.

Old-growth forests in the area have been drastically reduced in the 20th century as a result of forest exploitation and fires. Secondary forests are represented by mixed broad-leaved forests with no conifers, *Betula platyphylla* and *Populus tremula* forests, and *Quercus mongolica* forests with no conifers, depending on site ecological conditions and kind of damage.

3.4.3 Northern Japanese mixed forests

The temperate vegetation in suboceanic southern Sakhalin and the southernmost Kurils (Kunashir, Shikotan, Zelioniy, Tanfilieva) differs from the temperate vegetation on the mainland, in terms of dominants and species composition, due to the influence of the Japanese flora (Fig. 5.11). The main vegetation type is mixed *Abies sachalinensis-Quercus crispula* forest with sasa (short, fruticose broad-leaved bamboo). Most of the area lies on Hokkaido, north of the Kuromatsunai Lowlands, where it borders the area of *Fagus crenata* forests (Miyawaki & Nakamura 1988). The zonal vegetation in the area is mixed *Abies sachalinensis-Quercus crispula* forest with an admixture of broad-leaved species such as *Kalopanax septemlobus*, *Tilia maximowicziana*, and *Fraxinus mandshurica*.

Figure 5.11. Mixed broadleaf + Sakhalin fir forests on Kunashir (southern Kurils). The moist lowlands are occupied by wet meadows of *Carex thunbergii, Calamagrostis langsdorffii,* and *Myrica tomentosa,* fringed by *Alnus japonica-Fraxinus mandshurica* forests. *Ulmus japonica* and *Fraxinus mandshurica* form forests with *Lysichiton camtschatcense, Symplocarpus renifolius, Trillium camschatcense* and *Dryopteris crassirhizoma* in the understorey (photo by P. Krestov).

4. VERTICAL VEGETATION BELTS

Easternmost Russia is a mountanous area, with mountain systems that vary greatly in origin, age, height, modern geological processes, and orientation of the main ranges. Climatic changes with elevation cause changes in the vegetation. Traditionally, in Russian geobotany, a vegetation belt formed by climate differentiation with elevation is considered a vertical zone, or belt, and analyzed as a secondary zonation within the framework of the horizontal zones (Krylov 1984). The (horizontal) areas described are characterized by a definite sequence of vertical belts and by the altitudinal position of each belt. This last may vary depending on geomorphologic factors, especially the aspect (directional exposition) of the slopes. Belts occur higher on south-facing and lower on north-facing slopes.

The general sequence of vertical belts in the submaritime sector of southeastern Russia repeats the sequence of horizontal zonation. From bottom to top this includes mixed (broadleaf-Korean pine) forests, fir-spruce forests, *Betula ermanii* forests, dwarf-pine thickets and alpine tundra (Rosenberg & Vasiliev 1967). The vertical belts in most cases may be considered as analogs of the horizontal zones in terms of physiognomy as well as species composition. Depending on the region, however, the species composition of a belt may be enriched by species from belts directly above or below (Krestov 1999).

The upper limits of the vertical vegetation belts vary with the changing latitude and continentality. Fig. 5.12 shows the average upper limits of the vegetation belts in various continentality sectors.

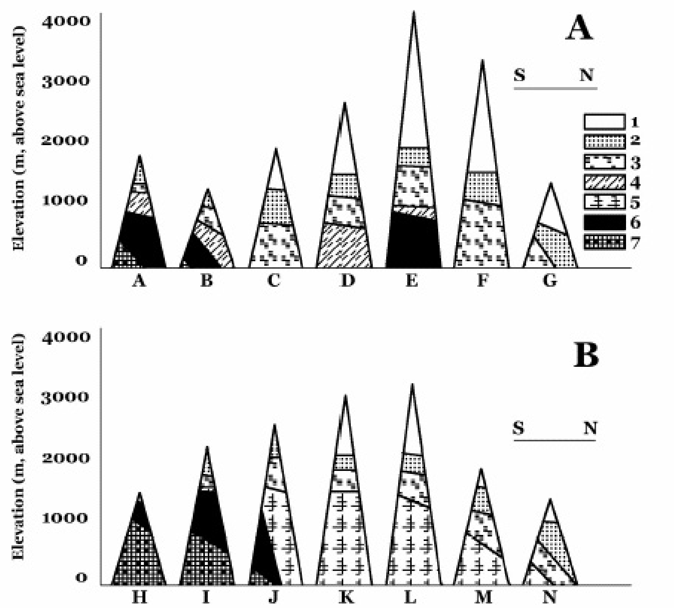

Figure 5.12. Vertical vegetation belts in submaritime-maritime (A) and continental (B) sectors of the Russian Far East. Name and coordinates of montane regions: A - Kunashir Isl. (44°N 146°E), B - Iturup Isl. (45°N 148°E), C - Paramushir Isl. (50°N 156°E), D - Southern Kamchatka (52°N 158°E), E - Central Kamchatka (55°N 161°E), F - Koriakia (62°N 171°E), G - Chukotka (68°N 178°E), H - Southern Sikhote-Alin (44°N 134°E), I - Central Sikhote-Alin (48°N 138°E), J - Badzhalskiy Mt. Range (53°N 135°E), K - Mt. Mus-Haya (62°N 141°E), L - Cherskiy Mt. range (65°N 146°E), M - Momskiy Mt. Range (67°N 145°E), N - northern Yakutia (70°N 150°E). Vegetation belts: 1 - no plant zone, 2 - alpine tundra, 3 - subalpine dwarf pine and dwarf alder thickets, 4 - subalpine stone birch forests, 5 - boreal light conifer (larch) forests, 6 - boreal dark-conifer (spruce) forests, 7 - cool and cold temperate deciduous forests.

5. MIXED (BROADLEAF - KOREAN PINE) FORESTS (NORTHERN TEMPERATE ZONE)

The mixed forests (various broad-leaved trees + Korean pine) of southeastern Siberia are a vegetation complex combining some peculiarities of both nemoral and boreal vegetation (Fig. 5.13). The mixed forest is the zonal vegetation type in the submaritime sector in the northern temperate subzone. These forests occur in the Russian Sikhote-Alin range and in northeastern China (Changbai, Lao-ye and Lesser Hingan mountains). Relatively isolated tracts of forest with Korean pine (*Pinus koraiensis*) are found also in southern Korea (Song 1988, Kim & Man'ko 1994) and on Honshu island of Japan (Miki 1956, Miyawaki & Nakamura 1988), but these stands with Korean pine belong to different vegetation types.

The mixed broadleaf-Korean pine forests form lower and middle vegetation belts from sea level to 800–900 m, extending in the south as high as 1100–1200 m (Chun 1994), coexisting and closely interacting with spruce, larch, and oak forests. The rather large north-south range of this forest type and sharp transition from oceanic monsoonal to continental climate have resulted in quite diverse vegetation within the mixed-forest zone. This has been reflected in various schemes of geobotanical districts and on vegetation maps (Kolesnikov 1956b, 1963, Sochava 1969a, b). This region was not glaciated during the Pleistocene or Holocene (Grichuk 1984), although it currently does border the permafrost area to the north. The strong modern climatic gradients, past marine transgressions, and long period of uninterrupted vegetation development have permitted much mixing of northern and southern as well as maritime and steppe elements in the regional flora and vegetation.

The occurrence of the mixed forest between clearly distinguishable boreal and temperate zones has posed the question whether the mixed forest is temperate or boreal. In recent decades, phytogeographers seem to have favored the idea that it is temperate. In 1958 M. Tatewaki related it to the special “Pan Mixed Forest Zone,” temperate in nature, which also includes climatically and physiognomically similar vegetation of central Europe (Carpathian and Tatra mountains) and of eastern North America (northern Appalachians and around of the Great Lakes), interrupted in continental interiors by steppes or deserts. Hämet-Ahti *et al.* (1974) treated this vegetation as a northern subzone of the temperate zone; Sochava (1969b) treated it as nemoral and Kolesnikov (1963) as temperate. Russian authors have traditionally placed this forest in a special so-called ‘Far Eastern coniferous-broadleaf forest area’ (Ya. Vasiliev 1947, Kolesnikov 1961, Lavrenko 1950). In 1956 Kolesnikov suggested naming it the East Asian area of mixed coniferous-broadleaf forests and related it to the temperate zone. The boundaries of the area coincide generally with those of the Manchurian floristic area distinguished by Komarov in 1901 and still used by botanists (Komarov 1934–1964, Kharkevich 1985–1996).

5.1 Physiography

5.1.1 Terrain

Much of the range of the mixed broadleaf-Korean pine forest in Russia occurs in the Sikhote-Alin range, extending from southwest to northeast over about 1200 km. The Sikhote-Alin was formed in the late Cretaceous by a combination of folding and volcanic activity (Ivashinnikov 1999). The western slope faces the Ussuri River valley, the eastern slope faces the Sea of Japan. The system is formed by a set of more or less parallel, north-south mountain ranges, the altitude of which frequently exceeds the height of the main dividing range in the middle.

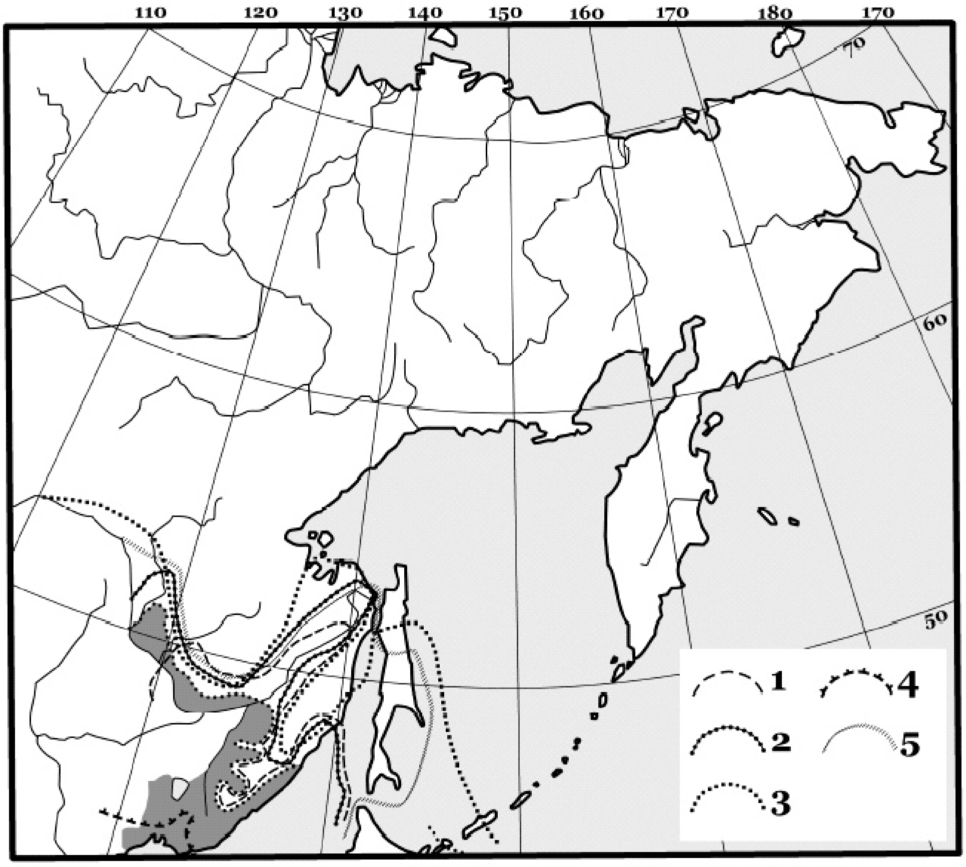

Figure 5.13. Distribution of mixed broadleaf-conifer forests in the Russian Far East and northern range limits of main dominants: 1 = *Pinus koraiensis*, 2 = *Tilia amurensis*, 3 = *Quercus mongolica*, 4 = *Abies holophylla*, 5 = *Fraxinus mandshurica*.

The average height of the dividing range is 1500–1700 m, and only separate peaks exceed 2000 m (Tardoki-Yani at 2090 m and Mt. Ko at 2004 m). The eastern slope of the Sikhote-Alin is more deeply dissected by erosion and steeper than the western slope. The highest areas are often extensive plateaus, cut by the large rivers Khor, Bikin, and Bolshaya Ussurka, with valleys up to 7–8 km wide in the middle parts of their basins, on the western slope.

The southern part of the mixed-forest area also occupies the low Pogranichniy and Chorniye Gory ranges and the Shufanskoye Plateau (average 600–700 m), and the foothill of the Lao-ye-ling (mountains) in northeastern China. In the north the mixed forests occur on the west side of the Amur River, northern foothills of the Greater Hingan mountains and southern foothills of the Badzhalskiy range. Most of the range of nemoral vegetation lies in northeastern China, where it occupies mainly lower and middle elevations (up to 700–800 m) of the Changbai-shan, the eastern Lao-ye-ling, and the Lesser Hingan range.

5.1.2 Climate

The climate of the mixed-forest area is controlled by the monsoon circulation. In the winter the region is under the effect of cold, dry air masses formed in interior East Asia by the powerful Asian anticyclone. Summer monsoon winds from the southeast bring cool, damp maritime air in early summer and very damp warm air later in the summer. The coldest month is January, with minimum temperatures −22 to −26°C on the western slope of the Sikhote-Alin and −17 to −21°C on the eastern slope, closer to the sea. Average summer temperature is 15 to 17.5°C on the coast and 18.5 to 20°C in the continental interior (Anonymous 1966–1971). The warmest month is July in the interior, August near the coast. Biotemperature sums (>10°C) in continental regions are 2400–2600° in south and 1600–1800° in the north of this subzone. Biotemperature sums are generally 100–200° lower on the coast facing slopes of the Sikhote-Alin.

5.2 Structure and composition

5.2.1 Structure of phytocenoses

All early explorers of the Russian Far East noted the complexity and unusual richness of the mixed forests (Maximowicz 1859, Komarov 1917, Budishchev 1898, etc.). Many explorers experienced with boreal vegetation met with nemoral vegetation for the first time in this part of Russia. They found the diversity of the broad-leaved forests and their structure to be really complex, caused not only by their climatic position but also their non-glaciated history.

These forests can usually be stratified into three layers. The tree layer normally includes three sublayers, formed by species of different growth forms and different life strategies. Because of the high diversity in co-dominant species, complex inter-species relationships occur.

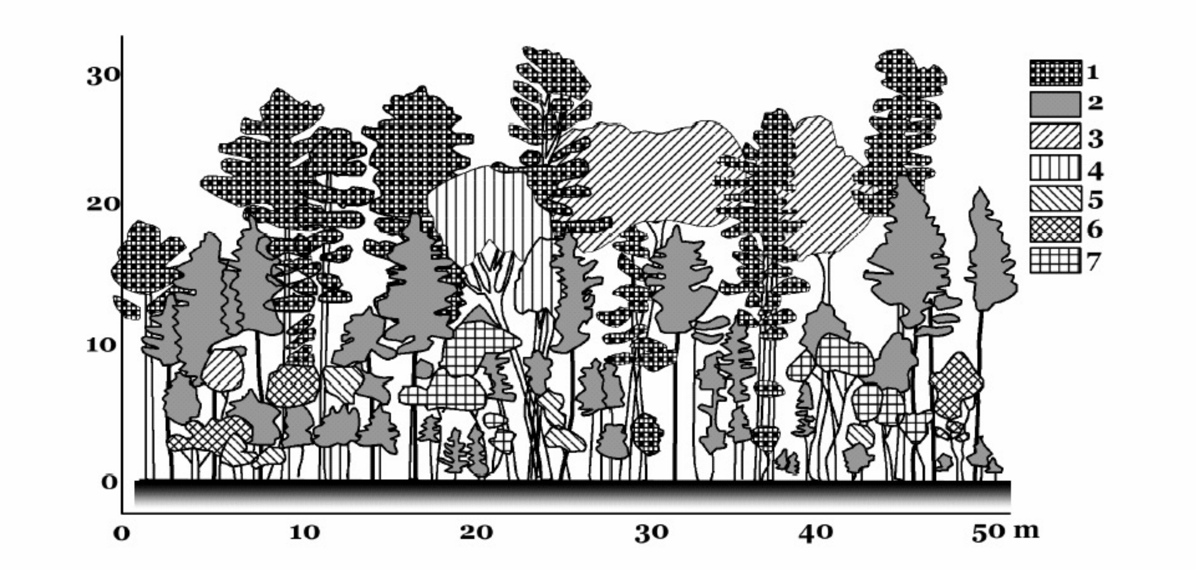

Figure 5.14. Profile of a typical stand of mixed broadleaf + Korean pine forest on the Sikhote-Alin Range (10 m x 50 m): 1 = *Pinus koraiensis*, 2 = *Abies nephrolepis*, 3 = *Betula costata*, 4 = *Tilia amurensis*, 5 = *Acer mono*, 6 = *Acer ukurunduense*, 7 = *Acer tegmentosum* (simplified from Krylov 1984).

The shrub layer may include two sublayers, which often gradually replace the lowest tree sublayer. The herb layer is normally very well developed. A dense cover of mosses or lichens is usually uncommon in forests except on extremely cold or dry sites. In typical broadleaf-Korean pine forests mosses can form small patches in herb-layer gaps and around the base of stems.

Important structural features of this community are 1) that the assimilation organs of different species are located vertically throughout the entire forest profile (Fig. 5.14); and 2) that trees of some species form clumps of different sizes, caused by both gap dynamics and competition for light (Krestov & Ishikawa 2000).

5.2.1.1 The canopy

The dominants in the mixed-forest ecosystems have different growth forms and life strategies. Up to 12 tree species can be found growing together in the canopy (upper sublayer) of a forest stand. The main canopy species are *Pinus koraiensis*, *Betula costata*, *Tilia amurensis*, *T. mandshurica*, *Fraxinus mandshurica*, *F. rhynchophylla*, *Juglans mandshurica*, *Quercus mongolica*, *Ulmus japonica*, *Kalopanax septemlobus*, *Abies holophylla*, and *Phellodendron amurense*. Their usual height is 25–35 m, but on rich sites *Pinus koraiensis* and *Abies holophylla* can reach 45 m, exceeding the height of all other canopy trees and forming a sparse cover above the canopy. An uneven age structure is characteristic of old-growth mixed forests with Korean pine. Trees in such stands grow in cohorts reflecting the gap character of stand dynamics (Fig. 5.15).

Depending on site properties and dynamic stage, those species of similar ecology, growth form and life strategy may form a synusia and represent a specific structural part of the canopy. *Pinus koraiensis*, *Betula costata*, *Tilia amurensis*, *Fraxinus mandshurica*, *Quercus mongolica*, *Ulmus japonica*, and *Abies holophylla* are able to form pure synusiae, but mixed synusiae are more typical. For example, in stands on sunny 15° slopes, synusiae of *Pinus koraiensis* + *Tilia amurensis* + *Quercus mongolica* and *Quercus mongolica* can be distinguished. In river-valley stands the main synusiae can be *Pinus koraiensis*, *Ulmus japonica*, and *Ulmus japonica* + *Fraxinus mandshurica* + *Juglans mandshurica*. The synusial structure of the canopy is determined mainly by stand dynamics and is discussed below in detail.

5.2.1.2 The middle tree layer

A middle tree layer (sub-canopy, middle sublayer of tree layer) normally occurs in mixed forests. The main species are *Acer mono*, *A. mandshuricum*, *Ulmus laciniata*, *Padus maximowiczii*, *Maackia amurensis*, *Sorbus amurensis*, *Taxus cuspidata*, and *Micromeles alnifolia*. Their crowns occupy a space 12–20 m above the ground, without a visible separation from the true canopy layer.

The development of this middle tree layer is determined mainly by the gap structure of the canopy and by site parameters such as soil nutrient and moisture regimes, slope aspect and steepness, etc. After severe disturbance (fire) some trees usually growing under the canopy can form a dominant synusia, as in pure stands of *Acer mono*.

5.2.1.3 The lower tree layer

A third tree layer also occurs in almost all undisturbed mixed forests, consisting mainly of *Carpinus cordata*, *Acer ukurunduense*, *A. pseudosieboldianum*, *Ligustrina amurensis*, and *Padus avium*, reaching about 6–10 m in height. All these are shade-tolerant species, but they differ in ecology and growth form. It is usually difficult to distinguish a clear boundary between this layer and the secondary trees and shrub layer. These trees are typical “patient species” (Ramenskiy 1932) or stress tolerators (Grime 1979), and are not able to form even temporary stands.

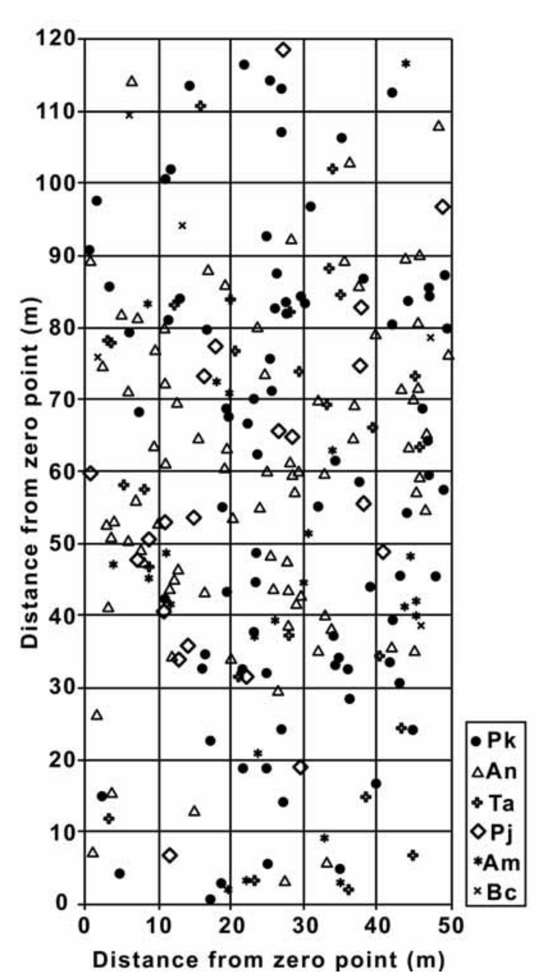

Figure 5.15. Tree groupings on a permanent plot 100 × 100 m in the southern Sikhote-Alin. The average sizes of groups are: *Pinus koraiensis* (Pk) - 144 m^2, *Abies nephrolepis* (An) - 576 m^2, *Tilia amurensis* (Ta) - 18 m^2, *Picea jezoensis* (Pa) - 36 m^2, *Acer mono* (Am) and *Betula costata* (Bc) - no groupings found (after Ishikawa *et al*. 1999, Krestov & Ishikawa 2000).

5.2.1.4 Secondary trees

In addition to the above tree species, there are some that normally do not occur in stable phytocenoses but appear only after disturbances. In the mixed-forest area these are *Betula platyphylla*, *Populus tremula*, *P. koreana*, *Padus maackii* and *Alnus hirsuta*. The first three are light-demanding, while the last two also require mineral soil. These species usually appear in canopy gaps but also form pure stands after large wildfires and clear-cuts, maintaining a forest environment on disturbance sites. The positive effect of fire on the germination of various secondary species was described by Komarova (1992).

5.2.1.5 The shrub layer

Shrubs are diverse and abundant in the mixed broadleaf-Korean pine forests. Commonly the shrub layer is sparse under the canopy but sometimes very dense in gaps. The shrub layer may merge with other layers due to differences in plant height. If *Lonicera chrysantha*, *Ribes maximoviczianum*, and *Berberis amurensis* do not exceed 1 m, then *Corylus mandshurica* and *Acer barbinerve* can reach 6–7 m in height. The shrub layer is valuable for sapling development, especially in the early stages of post-disturbance succession.

5.2.1.6 The herb and dwarf-shrub layer

An herb layer is usually very well developed and characteristic for the mixed forests, but the driest sites on steep slopes and ridges may be free of herbs. Usually different herb species are grouped in synusiae occupying certain ecological niches. The most important factors affecting their development are light, ground fires, presence of stronger competitors, and influence of herbivores (Krylov 1984). Because of low light levels in the forest understorey, almost all herbs are shade-tolerant, and capable of intensive vegetative reproduction. The herbs are quite different in growth form and life strategy; most competitive are the nemoral broad-leaved herbs with leaves oriented horizontally. The average number of species in a phytocenosis may vary between 20 and 100. The total number of herbaceous understorey species in the mixed forests exceeds 600.

5.2.1.7 The moss and lichen cover

A moss-lichen layer is not characteristic for nemoral vegetation, but mosses may indeed increase toward the northern limit of Korean pine forests. Moss ground synusiae are formed by common boreal species such as

Pleurozium schreberi, *Hylocomium splendens*, and *Ptilium crista-castrensis*. Small patches of nemoral mosses can also be found: *Rhytidiadelphus triquetrus*, *Pleuroziopsis ruthenica*, *Climacium dendroides*.

5.2.1.8 Inter-layer plants

A special feature of this type of forest is the presence of woody vines, especially *Vitis amurensis*, *Actinidia arguta*, *A. kolomikta*, *A. polygama*, *Schisandra chinensis*, *Celastrus flagellaris*, *Celastrus orbiculata*, *Pueraria lobata*, and *Parthenocissus tricuspidata*. Some are significant successional species due to their intensive sprouting ability.

5.2.2 Floristic composition of the mixed-forest phytocenoses

Some 645 vascular species have been found in the mixed broadleaf-Korean pine forests (Krestov 1997). The term ‘cenoflora’ has been applied here to identify the number and combinations of species in communities of the same type. The distribution of some species within the mixed-forest zone is heterogeneous. Many species, including some major dominants, have northern distributional limits near 44°N.

Geographical analysis permitted assigning the vascular species to eight geoelement types (Table 5.5). Most species have a Manchurian type of range. As a whole, the spectrum of cenoflora geoelements is Manchurian, plus Far Eastern, Eurasian and boreal species groups. South-Manchurian species have a rather weak position in forests of the classes *Nemoreto-Pineta typicum* and *piceetosium*, characterized by a colder climate (95 species versus 162 in more southern forests); the group of Okhotsk-Manchurian species is more diverse (mean of 43 species versus 36 in southern forests).

Dauro-Manchurian species connect the nemoral-forest cenoflora with the continental vegetation types, such as steppes and dry meadows. Plants of this group have some xeromorphic traits.

The Far Eastern geoelements (66 and 64 species in the two classes) are basically characteristic of azonal vegetation and are consistently present in valley broad-leaved forests, *Chosenia arbutifolia* forests and in valley meadows.

Siberian, Eurasian, and Boreal geoelements are generally represented by species cenotically not active in mixed forest (*Polemonium chinense*, *Calamagrostis langsdorffii*, *Vaccinium vitis-idaea*); some (*Calamagrostis langsdorffii*, *Chamerion angustifolium*, *Chelidonium asiaticum*), however, considerably strengthen their position in derivative communities.

Table 5.5. Occurrence of major geoelements in the cenofloras of the middle and southern mixed broadleaf-Korean pine forests, including the main Manchurian geoelements.

Types of geoelements	Association Classes	
	Nemoreto-Pineta typicum and *piceetosium*	*Nemoreto-Pineta carpinosium*
Multi-regional	1	1
Holarctic	20	20
Boreal	30	30
Disjunct*	31	34
Euroasiatic	16	16
Siberian	15	15
Far Eastern	66	64
Manchurian*	288	385
- Manchurian typical	75	80
- transitional Japanese-Korean-South Manchurian	95	162
- transitional Okhotsk-Manchurian	43	36
- transitional Dauro-Manchurian	56	78
- Ussurian endemics	19	28
Total	467	565

Table 5.6. Life forms represented by the types of cenoelements in the middle and northern (above line) and southern (below line) mixed broadleaf-Korean pine forests. Life forms: Tn - tall needle-leaf tree, Tlh - tall broad-leaf tree, Tll - low broad-leaf tree, Shr - shrub, SSh - subshrub, Fn - fern, Ht - horsetail, Gr - graminoid, Th - tall herb, Fb - medium herb, Sh - small herb, Vn - liana, Eph - ephemeroid.

Type of cenoelement	Life forms												
	Tn	Tlh	Tll	Shr	SSh	Fn	Ht	Gr	Th	Fb	Sh	Vn	Eph
Nemoral	2	11	18	21	1	15	1	15	19	65	23	6	9
	4	15	26	28	1	18	1	16	24	75	28	12	12
Taiga	3	-	1	12	2	8	-	2	2	4	22	1	-
	2	-	1	12	2	8	-	2	2	4	22	1	-
Deciduous boreal forest	1	3	4	10	-	6	3	5	9	17	5	-	-
	2	3	5	10	-	6	3	5	9	17	5	-	-
Valley forest	-	2	1	3	-	-	1	10	4	7	-	-	-
	-	2	1	3	-	-	1	10	5	8	-	-	-
Meadow	-	-	-	-	-	-	-	13	8	31	1	-	-
	-	-	-	-	-	-	-	15	15	46	4	-	-
Oak forest	-	2	-	4	-	-	-	7	1	34	3	-	-
	-	3	-	5	-	1	-	8	2	37	3	-	-
Xeric pine forest	-	-	-	3	2	-	-	-	-	-	-	-	-
	2	-	-	3	2	-	-	-	-	-	-	-	-
Swamp	-	-	1	3	-	-	-	1	-	-	-	-	-
	-	-	1	3	-	-	-	1	-	-	-	-	-
Total	6	18	25	56	5	29	4	53	42	158	51	7	9
	10	23	34	64	5	33	5	57	57	187	66	13	12

5.2.2.1 Cenotic analysis of the flora

As shown in Table 5.6, the cenoflora of the mixed broadleaf-Korean pine forests is characterized by nemoral species (206 species in middle and northern, 260 species in southern forests), with admixtures of boreal deciduous-forest, taiga and meadow species. The numbers of species by main life form are: 10 conifer trees, 59 broad-leaved trees, 67 shrubs, 5 dwarf-shrubs, and 504 herbs. Nemoral cenoelements include essentially all main life forms and constitute all of the phytocenotic structure. Nemoral needle-leaved trees are represented by *Pinus koraiensis* and *Taxus cuspidata* in middle and northern mixed forests; in southern forests *Abies holophylla* and *Pinus densiflora* also appear. *P. koraiensis* is a dominant or co-dominant of forest stands in the middle Sikhote-Alin up to 800–900 m; it may form mono-dominant stands on the eastern slopes because the lower temperatures make it more competitive with the broad-leaved species.

Usually a canopy synusia of *Pinus koraiensis* coexists with synusiae of nemoral broad-leaved trees and, in the north, with synusiae of taiga conifers. *Pinus koraiensis* occurs over a wide range of soil moisture and nutrient regimes, but its role in the canopy increases in more extreme conditions on dry sites. *Abies holophylla*, another principal tree of mixed forests, occurs in the southern part of the mixed-forest range, usually forming phytocenoses with Korean pine and broad-leaved nemoral species. The geographical ranges of species of this group (Fig. 5.16A) show the typical Manchurian distribution.

The group of tall broad-leaved nemoral trees consists of 11 species with Manchurian ranges: *Acer mono*, *Fraxinus mandshurica*, *Juglans mandshurica*, *Phellodendron amurense*, *Populus maximowiczii*, *Tilia amurensis*, *T. mandshurica*, *T. taquetii*, *Ulmus laciniata*, *U. japonica* and *Betula costata*. They all can occur in the canopy, together with conifers. In southern forests, the number of tall broad-leaved trees is increased by the addition

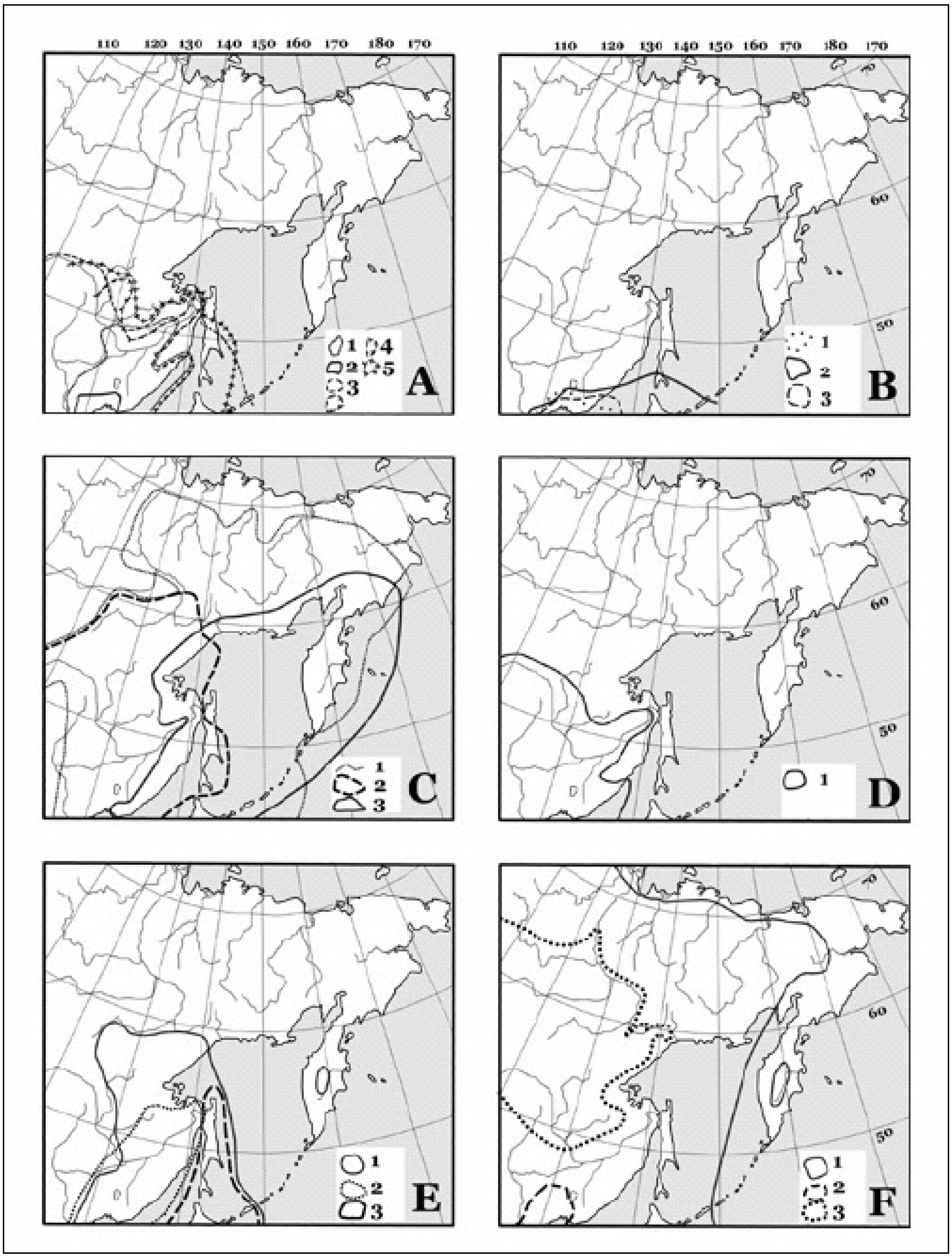

Figure 5.16. Ranges of the dominant species of the main cenotic groups in the vegetation of the Russian Far East. A. Manchurian element: 1 = *Pinus koraiensis*, 2 = *Abies holophylla*, 3 = *Quercus mongolica*, 4 = *Tilia amurensis*, 5 = *Fraxinus mandshurica*; B. southern Manchurian element: 1 = *Fraxinus rhynchophylla*, 2 = *Kalopanax septemlobus*, 3 = *Acer mandshuricum*; C. Far Eastern element: 1 = *Chosenia arbutifolia*, 2 = *Toisusu cardiophylla*, 3 = *Populus maximowiczii*, 4 = *Salix schwerinii*; D. *Daurian element*: 1 = *Betula davurica*, E. boreal dark-conifer taiga element: 1 = *Picea ajanensis*, 2 = *Abies nephrolepis*, 3 = *Abies sachalinensis*; F. boreal light-conifer taiga element: 1 = *Larix dahurica*, 2 = *Pinus sylvestris*, 3 = *Pinus densiflora*.

of southern-Manchurian species such as *Fraxinus rhynchophylla* and *Kalopanax septemlobus*. Their geographical ranges (Fig. 5.16B) are largely similar to those of nemoral conifers.

A major component of the mixed forests is the nemoral shrubs, which include 21 species in middle and northern forests and 28 species in southern forests. The most significant are *Eleutherococcus senticocus*, *Lonicera chrysantha*, *Philadelphus tenuifolius*, and *Corylus mandshurica*.

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

The valley-forest cenoelement groups 28 species characteristic of northern and southern valley forests and topographically bound to thick deposits of river alluvium. All these species have wide north-south ranges (Far Eastern geoelements), or Manchurian ranges but with taxonomically related species in more northern regions (Fig. 5.16C). A classic example of this cenoelement is *Chosenia arbutifolia* (Moskalyuk 1988), which initiates the establishment of broad-leaved floodplain forests on pure river alluvium (Kolesnikov 1937). This cenoelement also includes, in addition to *Chosenia arbutifolia*, some other trees (*Toisusu cardiophylla*, *Salix schwerinii*, *S. rorida*, *Populus maximowiczii*, *Alnus hirsuta*), shrubs (*Sorbaria sorbifolia*, *Spiraea salicifolia*, *Swida alba*), tall herbs (*Urtica angustifolia*), and graminoids (*Carex dispalata*, *C. sordida*, *C. drymophila*, *C. egena*).Those species related to *Quercus mongolica*-*Betula davurica* and *Quercus dentata* stands belong to the oak-forest cenoelement. The oak forests in eastern Siberia have mostly arisen after fire degraded the mixed broadleaf-Korean pine forests (V. Vasiliev 1958, Kurentsova 1973, Dobrynin 2000). Even so, ecological features of xeromesic species (Verkholat & Krylov 1982) and their fire resistance led us to relate these species to the oak-forest cenoelement. These species are the tree *Betula davurica*, shrubs *Lespedeza bicolor* and *Corylus heterophylla*, and herbs *Doellingeria scabra*, *Artemisia keiskeana*, *Dictamnus dasycarpus*, *Atractylodes ovata*, etc. The ranges of these species go far into the continental climates to the west (Fig. 5.16D). Most species of this group show xeromorphic features.

Taiga species usually are common components of fir-spruce forests and are present also in the mixed broadleaf-Korean pine forests. Their cenotic activity varies from extremely low (sole species) at low altitudes and on sunny slopes to domination of subordinate synusiae in shaded habitats and in the ecotone between the nemoral and boreal zones. The most widespread species of the taiga cenoelement are dark-coniferous trees with submaritime boreal ranges (Fig. 5.16E), i.e. *Picea ajanensis* and *Abies nephrolepis*; ferns *Leptorumohra amurensis* and *Dryopteris expansa*; small herbs *Maianthemum bifolium*, *Chamaepericlymenum canadense*, etc.; and green mosses *Rhytidiadelphus triquetrus*, *Hylocomium splendens*, *Pleurozium schreberi*, etc.

Xeric pine-forest species are represented by five oligotrophic and oligomesotrophic xeric species (e.g. *Festuca ovina*, *Antennaria dioica*, *Rhododendron mucronulatum*) in the southern Far East, cenotically connected with xeric *Pinus densiflora* communities (Verkholat & Krylov 1982). On the middle and northern Sikhote-Alin, essentially the whole complex of xeric pine-forest species occurs in dry larch forests and *Juniperus sibirica* thickets. *Rhododendron mucronulatum* can form synusiae in dry mixed broadleaf-Korean pine forests.

The deciduous-boreal cenoelement unites species characteristic for boreal white-birch (*Betula platyphylla*, *B. pendula*) and larch (*Larix dahurica*) forests, having rather wide ranges in the boreal zone (Fig. 5.16F). In mixed broadleaf-Korean pine forest, 84 species belonging to this cenoelement were noted. Of them, 23 have circumboreal ranges, 14 belong to the boreal zone of Eurasia, 20 to the boreal and oroboreal areas of the Russian Far East, and the others are connected with boreal formations of northeastern China and the Ussuri floristic region.

A special place in this cenoelement is occupied by *Larix dahurica*, a boreal summergreen needle-leaved tree. The role of larch on the Sikhote-Alin is not significant in undisturbed vegetation. Virgin larch forests do occur on wide, less-drained river terraces, especially in the Khor, Bikin and Anuy basins. Secondary larch forests are common, however, on the middle and northern Sikhote-Alin and on the east side of the Amur River. Other groups in this cenoelement are the herbs (*Saussurea triangulata*, *Hieracium virosum*, *Truellum thunbergii*, *Galium boreale*, etc.) and shrubs (*Lonicera edulis*, *Ledum hypoleucum* and others).

Meadow cenoelements in forests occur as suppressed understorey individuals but are much more abundant in canopy gaps (*Calamagrostis langsdorffii*, *Trisetum sibiricum*) and at forest edges (*Chamerion angustifolium*, *Vicia amoena*). Some meadow species are consistently present in nemoral forests (*Cimicifuga simplex*, *Ligularia fischeri*, etc.) and on forest edges, where meadow communities directly affect forest regeneration (*Lilium pensylvanicum*, *Lycopus lucidus*).

Other cenoelements occur on specific ecotopes (rocks, bogs) or show cenotic activity only during or after strong disturbances (ruderal cenoelements).

5.3 Phytocenotic diversity

Traditionally, the mixed broadleaf-Korean pine forests are subdivided into southern, typical (middle) and northern subtypes. These divisions correspond geobotanically to the following classes of associations: *Nemoreto-Pineta carpinosium* in the south, *Nemoreto-Pineta typicum* in the middle and *Nemoreto-Pineta piceetosium* in the north (Krestov 1997). The major classification units (formatio, classus associationum and grex associationum) are presented in Table 5.7.

Table 5.7. Classification of mixed broadleaf + Korean pine forests, with indicator species, ecology, topographical position of association groups. Abbreviations for edatope here and after are for the gradient of soil moisture regime: dry – D, slightly dry – SD, fresh – F, moist – M, very moist – VM, wet – W; for the soil nutrient regime: very poor – VP, poor – P, medium – MN, rich – R. Soil moisture and soil nutrient regimes are showed as intervals following each other.

Grex associationum	Indicator plants	Edatope	Topography, aspect
Formatio: *Nemoreto-Pineta koraiensis*			
Classus associationum: *Nemoreto-Pineta carpinosium*			
Nemoreto-Pineta caricosa nemoretae	*Carex ussuriensis, C. lanceolata, C. reventa, Lespedeza bicolor, Weigela praecox*	SD, P–MN	Upper concave slopes and ridges: S, W, E
Nemoreto-Pineta herbosa nemoretae	*Carex campylorhina, C. pallida, Thalictrum filamentosum, Arisaema amurense, Osmorhiza aristata, Cacalia protermissa, Asarum sieboldii*	SD–F, MN–R	Mid-slopes, all aspects
Nemoreto-Pineta fruticosa nemoretae	*Corylus mandshurica, Philadelphus tenuifolius, Deutzia amurensis, Lonicera praeflorens, Actinidia arguta*	SD–F, R	Middle and lower slopes, all aspects
Nemoreto-Pineta grandifilicosa nemoretae	*Cornopteris crenulatoserrulata, Athyrium monomachii, Dryopteris goeringiana, Polystichum tripteron*	F–M, MN–R	Lower concave slopes and upper river terraces
Nemoreto-Pineta grandifilicosa vallisae	*Matteuccia struthiopteris, Osmundastrum asiaticum, O. claytonianum, Symplocarpus renifolius, Urtica laetevirens*	F–M, R	River terraces

Grex associationum	Indicator plants	Edatope	Topography, aspect
Classus associationum: *Nemoreto-Pineta typicum*			
Querceto-Pineta nanocaricosa taigae	*Carex callitrichos, Rhododendron sichotense, Orthilia secunda*	SD, P–MN	Steep (>30°) convex slopes, N, E
Nemoreto-Pineta nanocaricosa nemoretae	*Carex nanella, C. reventa, Rhododendron mucronulatum, Iris uniflora*	SD, MN–R	Steep convex slopes and ridges: S, W,
Nemoreto-Pineta herbosa nemoretae	*Waldsteinia ternata, Thalictrum filamentosum, Caulophyllum robustum, Uraspermum aristatum*	SD–F, MN–R	Gentle mid-slopes, wide saddles: S, W, E
Nemoreto-Pineta fruticosa nemoretae	*Corylus mandshurica, Philadelphus tenuifolius, Lonicera chrysantha, Eleutherococcus senticocus*	SD–F, MN–R	Gentle lower concave slopes, all aspects
Nemoreto-Pineta fruticosa vallisae	*Sorbaria sorbifolia, Spiraea salicifolia, Swida alba*	F–M, R	River lower terraces, alluvial deposits
Nemoreto-Pineta grandifilicosa nemoretae	*Cornopteris crenulatoserrulatae, Dryopteris crassirhizoma, D. goeringiana, Athyrium sinense, Coniogramme intermedia*	F–M, MN–R	River upper terraces, lower concave slopes, alluvial and deluvial deposits
Nemoreto-Pineta grandifilicosa vallisae	*Matteuccia struthiopteris, Osmundastrum asiaticum*	F–M, R	River lower terraces, alluvial deposits
Nemoreto-Pineta grandicaricosa	*Carex sordida, C. drymophylla, C. egena, C. dispalata*	M, MN–R	River terraces poorly drained terraces
Querceto-Pineta festucosa	*Festuca pseudosulcata, Schizachne callosa*	D–SD, P	Steep slopes with marine exposures
Classus associationum: *Nemoreto-Pineta piceetosium*			
Piceeto-Pineta nanocaricosa taigae	*Picea ajanensis, Carex callitrichos, Pyrola minor, Vaccinium vitis-idaea, Linnaea borealis*	D–SD, P–MN	Steep upper slopes and ridges, above 700 m
Piceeto-Pineta herbosa nemoretae	*Waldsteinia ternata, Thalictrum tuberiferum*	SD–F, MN–R	Gentle mid-slopes, S aspect
Nemoreto-Piceeto-Pineta fruticosa taigae	*Acer ukurunduensis*	F, MN	Steep slopes with narrow valley exposure
Nemoreto-Piceeto-Pineta filicosa taigae	*Leptorumohra amurensis, Dryopteris expansa, Diplazium sibiricum*	SD–F, MN	Gentle slopes, all aspects above 700 m
Nemoreto-Piceeto-Pineta grandifilicosa nemoretae	*Dryopteris crassirhizoma Coniogramme intermedia, Clintonia udensis*	F–M, MN–R	Gentle convex lower slopes
Nemoreto-Piceeto-Pineta herbosa taigae	*Aconitum kirinense, Maianthemum bifolium, M. dilatatum, Carex falcata, C. xyphium*	SD–F, P–MN	Gentle slopes: S, E aspects above 700 m
Nemoreto-Piceeto-Pineta fruticosa boreale	*Ledum hypoleucum, Lonicera edulis, Sphagnum girgensohnii, S. nemerosum*	F–M, P–MN	Poorly drained upper river terraces
Classus associationum: *Pineta purum*			
Pineta purum herbosa taigae	*Maianthemum bifolium, M. dilatatum, Clintonia udensis, Linnaea borealis*	SD–F, P–MN	Gentle slopes, E-N
Pineta purum filicosa nemoretae	*Pseudocystopteris spinulosa, Dryopteris crassirhizoma*	SD–F, MN	Same, S, W
Pineta purum caricosa taigae	*Carex xyphium*	D–SD, P–MN	Steep slopes, E Sikhote-Alin, S, W
Pineta purum muscosa	*Rhytidiadelphus triquetrus, Hylocomium splendens, Pleurozium schreberi*	F, P–MN	Steep slopes, E Sikhote-Alin, N

The southern mixed forests occur from 42°40’N in eastern Russia (Vasiliev & Kolesnikov 1962), or from 40°15’N in NE China (Chun 1994), north to 44°N. They occupy gentle slopes at 50–600 m on the southern foothills of the Sikhote-Alin, on the Chorniye Gory, and on the Shufan plateau. These forests are very species-rich and have complex phytocenotic structure (Fig. 5.17). They are usually co-dominated by two nemoral coniferous trees *Pinus koraiensis* and *Abies holophylla*, reaching 45 m in height, and by nemoral broad-leaved 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 mesic nemoral megatrophic herbs, ferns and sedges. Less significant are xeromesic herbs, sedges and many others. Their ecological range is xeromesic-hygromesic mesotrophic and megatrophic. The cenoflora of the southern mixed forests contains 565 vascular species in all. Species with Manchurian distributions prevail, especially those with Korean-South Manchurian or Japanese-South Manchurian links.

The first Russian settlers exterminated most of the southern mixed forest before the end of the 19th century, but large tracts of intact southern forest were preserved in the Ussuriyskiy reserve and in the Chorniye Gory.

Typical (middle-subzone) mixed forests, *Nemoreto-Pineta typicum*, usually form the lowest altitudinal belt on the southern and middle Sikhote-Alin. *Pinus koraiensis* and broad-leaved nemoral trees with typical Manchurian and Japanese-Manchurian ranges form the dominant layer (Fig. 5.18). The mean species richness of these typical forests is 445 vascular species; most represent the Manchurian geoelement, but the number of Okhotsk-Manchurian species is higher than in the southern forests. The phytocenotic diversity was classified into 25 associations united into 9 groups (Table 5.7). Their ecological range as a whole is xeromesic-mesic meso-megatrophic. The driest sites are occupied by xeromesic associations belonging to groups *Querceto-Pineta caricosa taigae* (*Carex callitrichos*) and *Querceto-Pineta caricosa nemoretae* (*Carex ussuriensis*, *C. reventa*, *C. lanceolata*). A *Querceto-Pinetum festucosum* occurs on xeric oligomesotrophic sites. Hygric sites, mostly in river valleys, are occupied by mixed broadleaf-Korean pine forests with hygric sedges (*Carex sordida*, *C. dispalata*) and hygric ferns (*Osmundastrum asiaticum*, *Matteuccia struthiopteris*).

The typical mixed broadleaf-Korean pine forests were greatly reduced by clear-cutting over the past 80 years. Most of the typical forests remaining are on the west slope of the Sikhote-Alin, along the big rivers (water-protective belts) and in the Bikin and Iman River basins. In addition to clear-cutting, frequent fires damage these forests greatly around the settlements. On about 30% of the area, less productive secondary oak forests with *Quercus mongolica* replaced the typical mixed forests.

The northern mixed forests occur throughout the range of *Pinus koraiensis*. In the southern Sikhote-Alin they occur only in the upper mixed-forest belt, but in the north the mixed-forest belt is composed completely of northern-type forests. The northern mixed forests involve 394 vascular species. The role of Manchurian nemoral species in these phytocenoses gradually decreases northward, while the role of taiga and deciduous boreal-forest species increases. The canopy is dominated by both nemoral and taiga species, of which the latter can be quite significant (Fig. 5.19).

Figure 5.17. Typical stand of *Nemoreto-Pineta carpinosium* (photo by V. Yakubov).

Figure 5.18. Typical stand of *Nemoreto-Pineta typicum* (photo by P. Krestov).

Figure 5.19. Typical stand of *Nemoreto-Pineta piceetosium* (photo by S. Grishin).

The phytocenotic diversity within this class in the middle and southern Sikhote-Alin was classified into 15 associations united into 7 groups (Table 5.7). Their ecological range differs from that of the typical (middle) mixed forests by its concentration of the main association groups on mesic mesotrophic sites. Phytocenoses with green mosses and small taiga herbs occur on poor sites. The hygric sites are occupied by poor *Fraxinus mandshurica* and *Picea ajanensis* phytocenoses with boreal hygric sedges *Carex schmidtii* and *C. appendiculata*. The northern mixed forests have been reduced greatly by clear-cutting and by subsequent fires, and have largely been replaced by derivative *Betula platyphylla* and *Larix dahurica* forests.

The class *Pineta purum* has a narrow range on the eastern Sikhote-Alin. The canopy is dominated absolutely by *Pinus koraiensis*, reaching its maximum size (40–45 m high and about 1.2 m in breast-height diameter) in pure pine forests. The admixture of *Picea ajanensis* and *Quercus mongolica* and other broad-leaved trees is insignificant (Fig. 5.20). Average basal area of *Pinus koraiensis* reaches 40–60 m^2/ha, while no other species exceeds 4–5 m^2/ha. The lower tree layers are not clearly developed. The shrub layer usually involves only *Rhododendron mucronulatum*, *Lespedeza bicolor*, *Ribes horridum* and *Ribes maximoviczianum*. In the herb layer single individuals or small groups of oligo-mesotrophic, xeromesic, and mesic herbs and dwarf-shrubs, or semi-shrubs may be present.

The species richness is much poorer (<100 species) in these communities than in any of the above forest classes. Some phytocenoses may have a dense cover of green mosses. All phytocenoses have a thick litter layer that decomposes slowly over a period of several years.

Figure 5.20. Typical stand of *Nemoreto-Pineta purum* (photo by P. Krestov).

The phytocenotic diversity of pure Korean pine forests was studied insufficiently. Five associations of four groups were distinguished (Table 5.7). The ecological range of this class is xeromesic to mesic oligomeso- to mesotrophic.

This forest occurs only locally, because of the unique climatic conditions on maritime eastern slopes (low temperature, high humidity) on the one hand and the strong disturbance regime (mainly clear-cutting) on the other.

5.4 Community dynamics

5.4.1 Natural dynamics

Having many strong competitors, the mixed broadleaf-Korean pine phytocenosis is characterized by very complex dynamics, even over the lifespan of one generation of Korean pine. The dynamics are controlled by different ecological factors and by disturbance regimes. In a phytocenosis-oriented approach, the dynamics of nemoral forests was elaborated by Ivashkevich (1933) and later expanded and improved by Kolesnikov (1956a). From that time no new original ideas or special research concerning phytocenosis dynamics have been proposed, despite the interest in gap dynamics (Pickett & White 1985) introduced into Russian forest ecology by various authors.

According to the Ivashkevich-Kolesnikov scheme, the normal development of mixed phytocenoses goes through eight sequential stages. The first stage starts with the appearance of the new generation of Korean pine under the canopy of the mother generation (Table 5.8). Korean pine normally goes through at least two periods of suppression, the first while very young (stage 1) and the second when it reaches the canopy (stage 3). These periods are indicated by analysis of growth patterns. At 160–200 years (stage 5) the Korean pine generation reaches maturity.

Table 5.8. Development of Korean pine stands over the life cycle of one generation, according to Kolesnikov (1956a). Stage refers to the developing Korean-pine generation, with the stage of the older generation shown in parentheses.

Stage	Ages (years)	State of the main phytocenotic components
1 (6)	1–40	Appearance and early development of new Korean pine generation, under light and nutrition deficit due to of older generation.
2 (7)	41–80	Development of Korean pine saplings within subordinate layer.
3 (8)	81–120	Maximum height increment, also in the canopy. Canopy density is increasing, with broad-leaved canopy trees of older generations important.
4	121–160	Fast diameter increment of young Korean pine trees and their dominance in upper canopy. Old broad-leaved trees and the oldest Korean pines are dying and fall; increasing density of young Korean pine generation.
5	161–200	Mature canopy stage. Maximum proportion of Korean pine in the canopy (up to 80–90%), with minimal proportion of broad-leaved trees. Small increments of Korean pine. Newly appearing pine seedlings are dying quickly; lower layers badly suppressed.
6 (1)	201–240	Older-generation trees (older than 300 years) rapidly dying. Canopy density and proportion of Korean pine decreasing (to 50–60%). New Korean-pine generation (future dominants) appearing as suppressed saplings. Shrub and herb layers growing up. Tree layer becoming susceptible to insects, drought and wind damage.
7 (2)	241–280	Stand over-mature. Most older Korean pines and most broad-leaved trees growing with the dominant pine generation falling out. Minimum proportion of Korean pine in canopy (30–50%), minimum canopy density. Maximum development of lower layers, vines and saplings of broad-leaved trees. No seedlings of Korean pine. Destruction of canopy.
8 (3)	281 and more	Young Korean pines and broad-leaved trees becoming coherent current generations. Young pines slowly increasing in biomass and canopy density. Shade-intolerant shrubs and herbs dying.

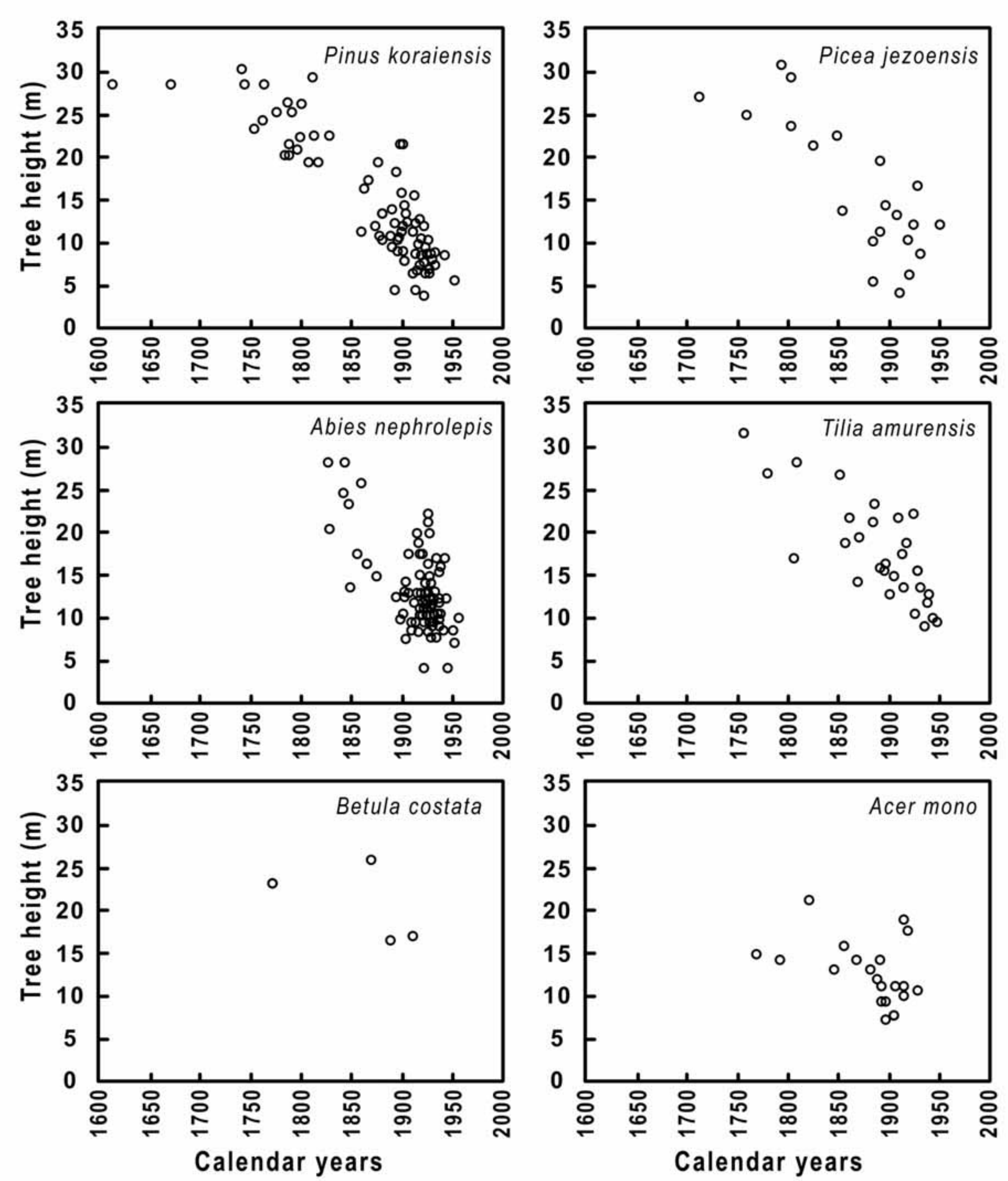

Figure 5.21. Age-height relationships in the mixed hardwood-Korean pine forests of the southern Sikhote-Alin (after Ishikawa *et al*. 1999).

Table 5.9. Growth pattern of the northern and middle mixed broadleaf+Korean pine forest stands, as exemplified by phytocenoses of *Piceeta-Pineta herbosa nemoretae* (from Anonymous 1990). Pk – *Pinus koraiensis*, dc – dark conifers *Picea ajanensis* + *Abies nephrolepis*, bl – broad-leaved, DBH – diameter at breast height and H – total height of trees.

Age of Korean pine	Layer	Tree-layer composition (% cover)	Average for pine		Number of stems		Basal area (m^2)	
			DBH (cm)	H (m)	Total	Korean pine	Total	Korean pine
110	I	37Pk; 83bl	17.4	14.7	512	226	25.4	8.4
130	I	43Pk; 57bl	22.3	17.7	472	201	26.5	10.2
160	I	52Pk; 48bl	27.2	19.9	237	170	23.2	11.0
	II	6Pk; 30dc; 64bl	16.0	13.9	200	9	4.0	0.2
170	I	55Pk; 45bl	32.1	21.8	204	145	23.2	11.7
	II	7Pk; 30dc; 63bl	17.0	14.5	202	13	4.8	0.3
190	I	58Pk; 42bl	36.9	23.9	172	117	23.0	12.5
	II	8Pk; 30dc; 62bl	18.0	15.1	208	16	5.7	0.4
210	I	61Pk; 39bl	41.8	25.2	151	95	22.6	13.0
	II	9Pk; 30c; 61bl	18.0	15.1	204	19	6.4	0.5
230	I	63Pk; 37bl	46.6	26.5	126	77	22.1	13.1
	II	9Pk; 30dc; 61bl	19.0	15.6	204	20	6.9	0.6
250	I	65Pk; 35bl	51.5	27.7	108	64	21.6	13.3
	II	9Pk; 30c; 61bl	20.0	16.2	202	21	7.4	0.6
270	I	65Pk; 35bl	56.3	28.8	100	54	21.4	13.3
	II	9Pk; 30dc; 61bl	20.0	16.2	196	22	7.7	0.7
290	I	64Pk; 36bl	60.9	29.7	96	44	21.3	12.9
	II	11Pk; 30dc; 59bl	21.0	16.7	202	22	7.8	0.8
310	I	63Pk; 37bl	65.0	30.4	96	39	21.6	12.6
	II	11Pk; 30dc; 59bl	22.0	17.3	204	22	7.9	0.8
330	I	62Pk; 38bl	68.3	30.8	95	33	22.0	12.2
	II	11Pk; 30c; 59bl	22.0	17.3	215	22	7.9	0.8
350	I	61Pk; 39bl	71.0	31.4	93	30	22.5	11.9
	II	12Pk; 30dc; 58bl	23.0	17.8	227	22	7.9	0.9

Fig. 5.21 shows clusters of *Pinus koraiensis* trees regenerating at the same time, while the other species show rather smooth patterns. These clusters are caused by the ability of Korean pine to regenerate intensively every 35–40 years (so-called explosive regeneration), as mentioned by Ivashkevich (1933) and Solovyov (1958), and by the complex patch structure of the phytocenosis. In fact Korean pine has an evident tendency to regenerate under the canopy, but only gap formation permits the saplings to develop further, as was shown by studies in the Chinese part of the range (Wang 1961).

Normally the patchy structure of the phytocenosis reflects the gap character of regeneration. Gap formation in mixed broadleaf-Korean pine forests depends mainly on the natural death of old trees and only more rarely (but over large areas) on natural disturbances (wind and other storms). The diameter of gaps ranges from 20 m (crown diameter of one tree) to 40–50 m. Usually the crowns of broad-leaved trees, which permit more light penetration (enough for new Korean pine development), close the gaps formed by Korean pine. Korean pine increases its biomass and basal area, while the biomass and basal area of broad-leaved trees remain relatively stable (Table 5.9). With increasing age the number of stems decreases. Basal area and total volume increase up to 300 years and then decrease.

The relatively high diversity in the nemoral phytocenoses is caused by the many different ecological niches that replace each other in time and space. The study of age structure in the phytocenoses confirmed a cyclic pattern of development connected with a naturally caused patch structure (Ishikawa *et al.* 1999).

The first trees in the new generation of Korean pine appear before gap formation, under the canopy of mature mixed forest. During the first 80 years the growth of these new trees is suppressed because of low light and nutrient levels. This is the time of the best development of shade-tolerant nemoral herbs with “patient” (stress-tolerant) life strategies (Ramenskiy 1932). Species richness is highest, with the herb layer including typical representatives of the nemoral cenoflora. The plants form the normal forest synusiae, common in mixed forest.

Over the next 40 years the young Korean pine trees reach the canopy, which then becomes densest. Species richness does not decrease, but most species are not able to form synusiae; herbs have their lowest cover.

When the young generation of Korean pine reaches 120 years old, the process of natural gap formation is starting, as both old broad-leaved and coniferous trees begin to die. In the first stages of this process, small initial gaps are closed by the crowns of young Korean pines, which are growing fastest in diameter and height. Shrub cover increases, but herbs continue to be suppressed. Seral species (*Populus tremula*, *Betula platyphylla*, etc.) begin to appear, increasing the species richness slightly. This process continues until the young generation of Korean pine reaches about 200 years old. During this time the cover of young Korean pines and broad-leaved species in the canopy increases to 60–70%, but the number of overly mature trees decreases rapidly. The increment of Korean pine is smallest, with new seedlings dying quickly. The lower layers are badly suppressed, and synusial structure in the undergrowth is scarcely visible.

Next the oldest trees disappear completely. Canopy density and the proportion of Korean pines decrease to 40–60%. The new Korean pine generation (future dominant generation) appears as suppressed saplings under the canopy. Cover in the shrub and herb layers increases. The tree layer becomes susceptible to damage by insects and sensitive to desiccation and wind impact. In most large gaps the synusiae of ruderal and seral species develop intensely. The nemoral species common to mixed forests are suppressed by light-demanding species with more rapid growth. The activity of the light-demanding species, however, increases the diversity of the whole phytocenosis. This stage continues about 40 years, during which the new generation begins to close the gaps and the usual nemoral species form the normal synusiae in small gaps. Branches of broad-leaved species with crown deformations close the gaps.

Thus, over the cyclic dynamics of forest stands, the shade-tolerant nemoral species as well as the light-demanding species have the possibility to complete their life cycles. Because these cycles normally do not coincide in old-growth forests, diversity within a phytocenosis with stable edapho-climatic conditions is maintained at a certain level.

In old-growth forests, different cycles normally take place in the same phytocenoses on the area of each gap. Since the stages do not occur simultaneously, they create a complicated dynamic mosaic, allowing the coexistence of species of different growth forms and life strategies.

5.5 Dynamics after disturbances

The most important disturbance factors that constrain the recovery of nemoral forests are wood harvesting and fires. The pattern of community development after cutting is similar to that of the natural dynamics. Most nemoral species remain in the phytocenosis but sharply decrease their biomass, due to the appearance of seral gap-dependent species (*Betula platyphylla*, *Padus maackii*, *Aralia elata*, *Actinidia kolomikta*, etc.). During the first years of succession, nemoral-species diversity shows only small decreases due to competition from gap-dependent species (for nutrients and space), so community species richness 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 diversity requires more time, equal to the lifespan of the dominant trees.

Fire is a complicating factor that affects diversity in different ways but always decreases it over the long term. Wildfires are rare events in the nemoral forest zone because litter decomposition is relatively fast and there is no large accumulation of flammable material. Wildfire does occasionally occur in the driest years. Post-fire succession can continue for several hundred years and may not reach the climatic climax stage if a stable secondary phytocenosis develops, dominated by self-regenerating long-living species (e.g. *Larix dahurica*), especially in the northern nemoral forest subzone. In this case the original nemoral cenoflora changes to one composed of species with wide ranges (Holarctic, Boreal, Eurasian, Siberian, Far Eastern geoelements). This, as a whole, decreases diversity.

Ground fires are very common in nemoral ecosystems but seldom affect species diversity greatly because most nemoral species are relatively fire tolerant. Spring ground fires stimulate germination by seeds of some gap-dependent species (*Chelidonium asiaticum*, *Betula platyphylla*, *Chamerion angustifolium*), which can take a leading position in early post-fire succession (Komarova 1992). If canopy cover remains the same, the growth ability of the nemoral species may recover quickly. Conifer seedlings, however, are badly damaged by fire and usually die. If ground fires recur regularly every 1–3 years, the nemoral phytocenoses are gradually transformed into fire-tolerant forms. Nemoral species decrease their abundance and diversity, first of all the nemoral trees. Fire-tolerant species of all growth forms become more competitive and take the leading position in all layers. Regular fires usually affect intra-community competition even more than they change site properties. The community changes into a more stable state, which in the nemoral forest zone means into a pure oak forest. Oak forests (Formation *Betuleto dahuricae-Querceta mongolicae*) are monotonous in community and floristic diversity and simple in structure. Relatively rich in species composition (alpha diversity of 70–75 species per phytocenosis), they are quite poor in community diversity and have very low beta-diversity. They are widespread mainly in more populated areas where human activity insures regular fires.

The increasing biodiversity after artificial canopy disturbances in the mixed broadleaf-Korean pine forests, declared by several authors (Seledetz 1992, Dobrynin 2000), is no more than an illusion from the ecosystem point of view. The species entering the phytocenosis after disturbance often turn out to be strong competitors in open forests, especially if the disturbance factor is recurrent. Because the nemoral plants are the main components of the phytocenoses, with considerable biomass, reducing their reproductive capacity reduces the number of ecological niches, which are needed for the normal development of climax species. Under optimal climatic conditions (middle and southern forests), strong disturbances result in long-term succession tending to the climax type. If disturbances recur (fires becoming an important stabilizing factor), monotonous oak forests replace the diverse nemoral vegetation; and if disturbances are too strong, forests may be replaced by shrub or meadow vegetation. With low temperatures, the mixed broadleaf-Korean pine forests can be replaced by monotonous larch forests, even after a single disturbance. This process was well illustrated by data from the Russian Forest Service. From 1966 to 1983 the forested area in the Primorskiy krai increased by 3.4%. The proportion of Korean pine forest decreased by 10.6% and that of predominately broad-leaved forest by 18.4%. At the same time, shrub areas increased by 51.8%, oak forests by 35.8%, and larch forests by 4.3% (Anonymous 1990).

6. SPRUCE-FIR FORESTS

Ayan spruce (or Yezo spruce), *Picea ajanensis* (=*Picea jezoensis*) occurs in the montane submaritime and maritime areas of northeastern Asia between latitudes 40°N and 56°N (Fig. 5.22). Due to its great shade tolerance, this species forms dense forest stands over most of its range. This range includes the northern Sikhote-Alin, western coast of the Sea of Okhotsk, the Changbai-shan, Shantar Islands, Sakhalin, the southern Kurils (Iturup and Kunashir) and Hokkaido. Outlying areas are also found in central Honshu (Numata 1972), in middle Kamchatka (Man'ko & Voroshilov 1973, 1978) and on the Dunlin range of northeastern China (Wang 1961).

Within its range Ayan spruce forests occur irregularly, along with other local forest types, in different proportions. Spruce forests can be considered a zonal vegetation type in the lower Amur basin, on Sakhalin, and on the southern Kurils (Iturup) and northeastern Hokkaido. Ayan spruce forms stands in the lowest vegetation belt, from sea level to timberline or to the *Betula ermanii* forest belt. Spruce forests occupy almost the whole range of ecologically different sites in this belt, except only in mires and on rock outcrops (Rosenberg 1959, Man'ko 1967). *Abies nephrolepis* (continental areas) and *A. sachalinensis* (island areas) are important companion species in the stands. In northern areas, however, including Kamchatka, the northernmost Schmidt Peninsula (Sakhalin), and the Maya River basin (continental), spruce forms pure stands without fir.

In addition to fir, other species of dark conifer may be admixed in Ayan spruce stands. In southern areas, *Picea koraiensis* (vicariant of *P. obovata* = *P. abies* var.

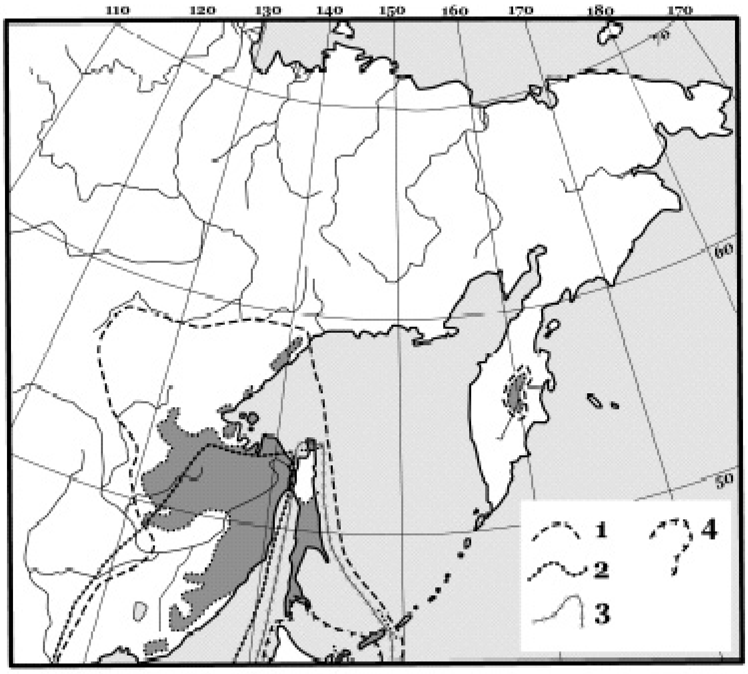

Figure 5.22. Distribution of boreal dark-coniferous forests and ranges of main dominants in the Russian Far East: 1 = *Picea ajanensis*, 2 = *Abies nephrolepis*, 3 = *Abies sachalinensis*, and 4 = *Picea glehnii* (compiled from Sokolov *et al*. 1977).

obovata, Schmidt-Vogt 1974, 1977) sometimes forms pure stands, usually in river valleys or gentle lower or middle slopes (Kurentsova 1960, 1968). It occurs also mixed with Ayan spruce on such sites. The ranges of *P. obovata* and *P. ajanensis* overlap in the Okhotsk part of the *P. ajanensis* range, although *P. obovata* occasionally forms pure stands across all its range, mainly in river valleys. *P. glehnii* occurs on southern Sakhalin (Tatewaki 1958, Tolmachov 1959), in the southern Kurils (Vorobiov 1963, Ishizuka 1974) and on Hokkaido (Numata 1972). Unlike *P. ajanensis*, the edaphic optimum of *P. glehnii* is on saturated sites with groundwater at or above ground level at some time during the growing season. These species form mixed stands where their ranges overlap on slope–mires ecotones (Man'ko 1987). In Hokkaido *P. glehnii* occupies the wide range of azonal sites, such as volcanic deposits, and forms stands near timberline (Miyawaki & Nakamura 1988).

Different aspects of *Picea ajanensis* and its stands in eastern Russia were thoroughly studied by Tolmachov (1954, 1955, 1956), Rosenberg (1959, 1961, 1963, 1967, 1971), and Man'ko (1961, 1965, 1967, 1974, 1980, 1987). It is commonly accepted that spruce-fir forests represent the vegetation of the southern and middle boreal subzones in the submaritime and maritime sectors (Kolesnikov 1961, Hämet-Ahti *et al*. 1974, Grishin 1995, Krestov 2000). Spruce forests, as a zonal vegetation type, are characteristic for the western coast of the Sea of Okhotsk (extending west into the continent for about 1500 km) and for the "conifer island" of central Kamchatka. The first area is called the Western Okhotsk Area and the second the Eastern Okhotsk Area of dark conifer forests (Kolesnikov 1961).

6.1 Physiography

6.1.1 Terrain

Picea ajanensis forms mono-dominant or fir-mixed stands from sea level to 1500–2000 m, depending on latitude. The upper limit of spruce forests exceeds 2000 m only in the Japanese Alps (Central Honshu), outside the boreal zone.

The range of Ayan spruce lies in deeply dissected montane territory. Most ranges, especially those along the Sea of Okhotsk and Sea of Japan, are oriented north-south. The main ranges are the Sikhote-Alin and Dzhugdzhur on the continent, Sredinniy and Vostochniy on Kamchatka, and Vostochno-Sakhalinskiy and Zapadno-Sakhalinskiy on Sakhalin. The mountain ranges along the coast produce a sharp continentality gradient toward the continental interior, blocking the moist maritime air masses in summer but not, blocking the very cold continental air masses in winter.

The mountain systems differ in time of origin and orogeny. The oldest part of the Ayan spruce range, the Aldan shield at the edge of the East-Siberian Platform, was formed in Pre-Cambrian time; most of the territory, however, is related to the zone of Mesozoic folded mountains. The eastern edge of the continent was formed in the Cenozoic period, by folding accompanied with intensive volcanism (Nikolskaya 1974). The youngest range, the Sikhote-Alin, was formed in the late Cretaceous.

The coastline changed shape in the different geological epochs, with several important land bridges temporarily connecting presently isolated islands. At the last glacial maximum (ca. 18,000 years ago), northern Sakhalin and the Shantar Archipelago were united with the continent (Grichuk 1984) and Hokkaido was united with southern Sakhalin. Sakhalin separated from the continent at the end of the Pleistocene. Land bridges served as important routes for species migrations that partly explain the known similarity in species composition of spruce forests of northern Sakhalin and the Amgu basin, or southern Sakhalin and Hokkaido. In regions of modern volcanism, on Kamchatka and the Kuril Islands, different forms of volcanic activity influenced the processes of orogeny. Characteristic features of this volcanic terrain are the presence of cone-shaped mountains, lava fields, tephra fields and the very high speed of modern orogenic processes.

6.1.2 Climate

Climate within the area of dark conifer forests is controlled by the seasonally alternating maritime and continental air masses brought by the monsoon circulation. The sharp continentality gradient inland produces quite diverse local climates, which as a whole, are much more severe than at the same latitude in Europe (Ellenberg 1980). Mean annual temperature over most of the range of Ayan spruce is not above zero; it decreases with latitude and elevation, though less rapidly along the coast than in the interior. Mean annual precipitation varies from 460 mm (lower Amur, central Kamchatka) to 1250 mm (southern Kurils). Precipitation increases with elevation on the continental mountains, up to 1000–1200 mm (Tarankov 1974), and is more on seaward slopes of the Sikhote-Alin than on slopes exposed to the interior (Dmitrieva 1960). Mean annual air humidity within the range of spruce does not fall below 60%, although it does change considerably from region to region (Anonymous 1966–1971). The most characteristic feature of the climate in the area is high continentality. Even on islands (especially Shantar, northern Sakhalin and Hokkaido), the climate is rather continental (Ivanov 1959).

Summarizing climatic conditions in the areas where *Picea ajanensis* forms pure or fir-mixed stands, on all mesic well-drained sites, it is possible to conclude that the optimal climatic parameters for this species include mean annual temperature −1°C to 0°C, vegetative period 145–155 days, and mean summer precipitation 370–590 mm. The climatic optimum of *Picea ajanensis* is thus much more severe than that of *P. abies* (Schmidt-Vogt 1977, Man’ko 1987).

6.2 Structure and composition: community level

Despite the width of the circum-boreal zone and differences in dominant species, the structure and species composition of dark conifer forests appear to be similar across the zone. Common community features are: 1) the dense tree layer, composed of different species of spruce and fir; 2) the vertical continuum of photoassimilating organs, achieved by the tall monopodial tree forms, bearing living branches from top to bottom (cylindrical crowns); 3) the shade tolerance of the dominants, resulting in certain aspects of natural forest dynamics; 4) the relative species poverty, with most species characterized by circum-boreal or trans-continental ranges; 5) the presence of well-developed moss covers; and 6) the similar post-disturbance successional sequences (Fig. 5.23). The spruce forests of eastern Asia, however, show several specific features caused by the severe climatic conditions and development history.

6.2.1 Structure of phytocenoses

Picea ajanensis usually forms structurally simple one or two-layer stands with poorly differentiated strata. If layers are expressed, they may contain the same species, although fir occurs more frequently in the second layer. The dense canopy in uneven-aged stands may suddenly be interrupted by gaps, with abundant fir and spruce regeneration as well as a well-developed herb layer. In even-aged stands formed after disturbance, canopy gaps are always less frequent.

The main synusiae are simple in structure. Within the range of spruce forests, monodominant synusiae may be formed by each of the following species: *Picea ajanensis*, *Abies nephrolepis* (only on the mainland), *A. sachalinensis* (only on islands), *Picea glehnii*, *P. obovata*, and *P. koraiensis*. All these species can also form mixed synusiae, and *P. ajanensis* mixes with *Betula ermanii* at high elevations near timberline.

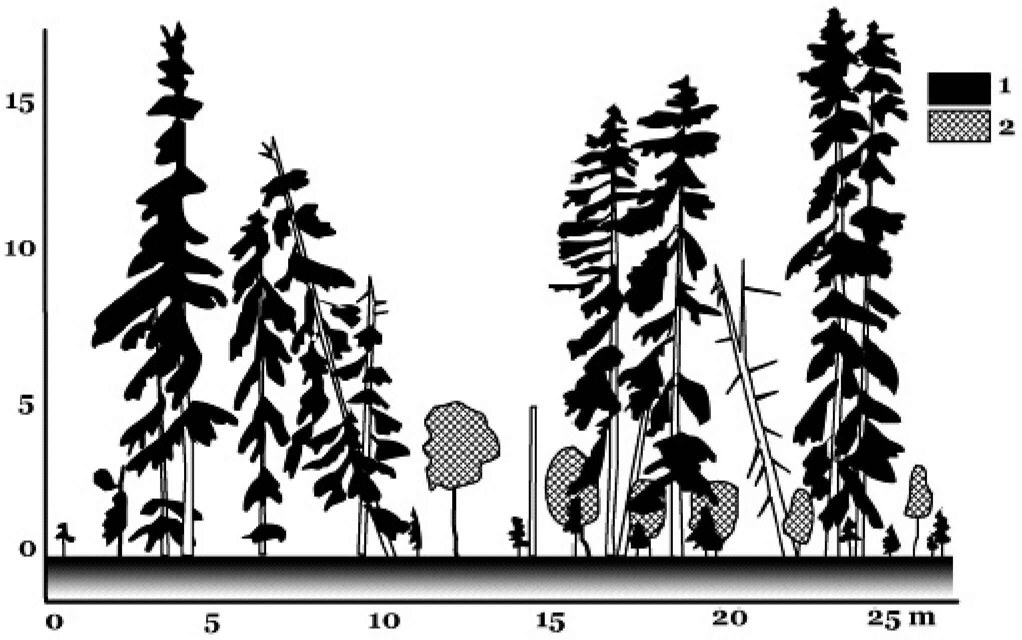

Figure 5.23. Profile of an Ayan spruce stand on the northern Sikhote-Alin Range (5 m x 25 m): 1 = *Picea ajanensis*, 2 = *Acer ukurunduense* (after Krylov 1984).

The shrub layer is generally sparse or poorly developed. The herb layer may be well expressed on richer, wetter sites, but its structure is rather simple. The moss cover is usually well developed. The undergrowth in spruce-fir forests is represented mainly by boreal species, except near the southern border, where invasion of temperate species is significant. In maritime and suboceanic areas, species with Far Eastern distribution may augment the species composition.

6.2.1.1 The upper tree layer

The main species in the dark-conifer forests is *Picea ajanensis*, forming dense canopies 20–25 m high with trees 50–60 cm in diameter. Maximum stand height varies from 30 m with 80–85 cm diameters in the north (Man'ko & Voroshilov 1971) to 37 m in the south, in the Ussuri reserve (Ya. Vasiliev 1938). Recorded maximum stand height on Kamchatka is 33.5 m with a diameter of 102 cm (Man'ko & Voroshilov 1978) and on Sakhalin 37 m with a diameter of 164 cm (Vlasov 1959).

In different parts of the area, different broad-leaved tree species may also be found in the canopy. In the north (Kamchatka) and near upper limits in mountains, spruce may mix with *Betula ermanii*. In the south, nemoral broad-leaved *B. costata* and *Fraxinus mandshurica* may form mixed stands with spruce.

On southern Sakhalin and the southern Kurils, the dominant layer may also be formed by *Abies sachalinensis*, with spruce present only as individuals. *Abies nephrolepis* may form pure stands on the mainland only after major disturbances remove big trees from the canopy and release the growth of understorey fir saplings.

Due to its high shade tolerance, spruce is less dependent on canopy gaps (Ishikawa *et al.* 1999). Horizontal stand structure is commonly random, but under moisture deficit spruce may regenerate successfully on decomposing fallen logs and stumps that serve as moisture reservoirs (Tolmachov 1954, Man'ko 1967, 1987, Chumin 1965, Nechaev 1975, Mayer 1978, etc.). In this case spruce trees may form small patches within a stand.

6.2.1.2 The lower tree layer

In most stands the lower tree layer contains the same species as in the upper layers, suppressed or simply younger. On the most productive sites, however, where spruce reaches its maximum size, common companion species such as *Abies nephrolepis* or *A. sachalinensis* may form a clear lower layer. Shorter trees *Sorbus amurensis* and *S. sibirica* (continental areas) as well as *S. commixta* (island areas) always occur individually in spruce-fir forests. In the south *Acer ukurunduense* may form a lower layer in mountain spruce forests.

6.2.1.3 Seral species

After extensive disturbances the spruce forest may be replaced by broad-leaved species with short lifespans, in particular *Betula platyphylla* and *Populus tremula*. In continental areas extensive *Larix dahurica* stands replace spruce forests after wildfires.

6.2.1.4 The shrub layer

The shrub layer usually cannot develop in dark-conifer forests due to the low light levels under the dense canopy. *Rosa acicularis*, *R. amblyotis*, *Euonymus macroptera*, *Spiraea beauverdiana*, *S. betulifolia* and shrubby *Acer ukurunduense* may form a sparse shrub layer on mesic sites. At the contact with the temperate zone, shade-tolerant nemoral shrubs such as *Eleutherococcus senticocus*, *Oplopanax elatus*, and *Euonymus pauciflora*. may occur in the spruce forests. *Weigela middendorffiana*, *Rhododendron aureum*, and *Ledum palustre* form a well-expressed layer in subalpine spruce stands. On islands, *Ilex rugosa*, *Skimmia repens*, *Vaccinium axillare*, and *V. hirtum* are significant components of the shrub layer in spruce forests. In floodplains, *Swida alba*, *Sorbaria sorbifolia*, *Ribes triste* and *Spiraea salicifolia* increase the shrub diversity. Nevertheless, all of these species form relatively dense cover only in canopy openings.

6.2.1.5 The herb layer

The herb layer in the dark-conifer forests may be composed of plants from a pool of about 250 mainly boreal vascular species. The patchy structure of the herb layer, with clearly distinguishable dominance by certain species in the synusiae, is a very characteristic feature for spruce forests.

The main synusiae occurring in the Ayan spruce forests on mesic sites are *Maianthemum bifolium* + *Chamaepericlymenum canadense*, *Vaccinium vitis-idaea*, *Carex falcata* or *C. xyphium*, *Leptorumohra amurensis* + *Dryopteris expansa* + *Diplazium sibiricum*, and *Pseudocystopteris spinulosa*.

6.2.1.6 The moss layer

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

6.3 Dynamics of phytocenoses

6.3.1 Natural dynamics

Fire is an important factor in the formation and dynamics of spruce forests due to the great amount of flammable material that accumulates and due to the occurrence of dry periods in summer. Most research on dynamics considers fire or other disturbance as a reference point for spruce forest development. Most spruce stands in easternmost Russia have an even-aged canopy with the age of the trees indicating the time of disturbance. Cyclic dynamics of uneven-aged spruce phytocenoses was also studied, however, in some continental areas and on Kamchatka (Shavnin

1979, Kozin 1981, Diukarev *et al*. 1971, Man’ko 1987, Tatarinov *et al*. 1978).

Over the course of a lifespan reaching 500 years, spruce individuals germinate, pass through juvenile, generative and senile stages, and then die. Actual age in the different stages differs with location, with the duration of the stages increasing from south to north (Table 5.10). These regular stages in even-aged stands disappear in uneven-aged stands, due to the complex relationships between individuals of different ages. The average longevity of a complete forest cycle was estimated at 120–150 years (Man’ko 1987), based on four stages per cycle, each characterized by certain dominant and subordinate generations.

In the mature stage, mature trees of different ages form the canopy, which has maximum cover and a continuous vertical distribution of assimilating organs along the boles. There are few diseased trees, and there are no freshly fallen trees on the ground; all are well decomposed, covered by mosses. Saplings of spruce and fir are suppressed; they have umbrella-shaped crowns and minimal increments in diameter and height. The longer the stand remains in this stage, the more fir is in the undergrowth, because of its higher shade tolerance and ability to survive long periods under the canopy. Shrub and herb layers are poorly developed, with minimal cover and diversity.

In the over-mature (senescent) stage, canopy trees die off one by one, first the tallest but not necessarily the oldest. This stage starts when most canopy trees reach 220–240 years or more. The stand has its maximum stem volume at the beginning of this stage, but the proportion of diseased trees increases. Tree death creates favorable light conditions for sapling development. In the south fir predominates among the saplings. This stage corresponds to a gap phase, with the exception that the saplings developing in a gap are of uneven age. The shrub and herb layers increase their cover but not their diversity.

A break-up stage follows the over-mature stage and lasts for several decades, until the former canopy is fully destroyed. Stem volume and crown cover tend to decrease. Fir predominates in these spruce-fir forests because the formerly suppressed saplings grow rapidly (Man’ko 1967, Mishkov 1975). Within 10–20 years fir may close the canopy gaps that had appeared. In subalpine forests, *Betula ermanii* increases in the canopy. Although such companion species increase their cover in the canopy, they usually cannot reach full canopy dominance because most old trees remain standing. The lifespan of spruce usually includes two generations of fir. The new spruce generation forms during the break-up stage. Gaps formed in this canopy create favorable conditions for development of the herb and shrub layers. Many freshly fallen logs cover the ground surface. The oldest spruce trees fully disappear from the canopy by the end of this stage.

Table 5.10. Periods and stages in the ontogenesis of spruce in even-aged stands (after Man’ko 1987).

Periods	Stages	Calendar age (years)	
		in southern part	in northern part
Juvenile	Seedling	1	1
	Sapling	2–25	2–40
Generative	Youth	25–60	40–80
	Pre-mature	60–100	80–120
	Mature	100–180	120–240
Senile	Over-mature	180–220	240–300
	Dying	220–350	300–500

The new canopy starts to form as the dominant fir generation breaks up more and the spruce saplings start to grow. At this point the stand includes many thin spruce saplings, many fir trees of intermediate size, and a few big spruces from the previous generation. In several decades the young spruce replaces the fir canopy. Self-thinning causes an abrupt decrease in stem number, but stem volume gradually increases. Diseased trees are few or absent. This stage has darker conditions under the canopy and minimal undergrowth development. The development of the spruce canopy improves the light conditions, and many fir and spruce saplings appear. This stage may last up to 50–80 years, until the young spruce trees become mature.

6.3.2 Post-fire dynamics

All post-fire succession in the areas of dark-conifer forest results in the formation of spruce stands, but various factors may deflect succession from the standard sequence: substrate mineralization and erosion rates, climatic advantages for companion species or potential competitors (inhibitors), and presence or absence of seed sources. The fastest regeneration of spruce forests after wildfire occurs when: 1) the soil is not eroded after fire and still contains its fine fraction, 2) seed sources are nearby, and 3) spruce seeds reach the site in the first year(s) after fire. In this case, complete regeneration requires 100–180 years, following the stages shown in Table 5.11.

Herb and shrub communities appear on the burned sites in the first year after a fire. The first plants, *Chamerion angustifolium*, *Rubus sachalinensis* and *Sambucus racemosa*, form a sparse cover creating favorable conditions (substrate stabilization, reduced evaporation from sunny sites) for germination and growth of tree species. In the next year or two, grasses (*Calamagrostis langsdorffii*) and sedges (*Carex campylorhina*, *C. sordida*) form a dense herb cover, inhibiting germination by woody species. If unfavorable weather conditions prevent the arrival or germination of spruce seeds in the first year (or two), the development of a spruce stand may be delayed considerably.

In the next stage, *Betula platyphylla* or *Larix dahurica* forms a closed forest stand with spruce developing under the canopy, due to its shade tolerance. Birch and spruce then tend to grow normally until the birch reaches its age limit of 100–120 years and begins to die. Then a pure spruce or a spruce-fir stand can develop.

Thus, in the area of spruce-fir forests, stands with mainly spruce form 90–100 years after fire, or perhaps as long as 150 years after fire in Kamchatka (Man’ko & Voroshilov 1978). Recovery of spruce forest under a larch canopy takes different amounts of time in different regions. Kozin *et al*. (1975), working in the middle Sikhote-Alin, found a closed spruce subcanopy under larch after 34 years; Baburin (1976) on the upper Bikin plateau after 50–60 years; and Kartashov (1984) on Sakhalin after 50 years. Glagolev (1984), however, described stands in the northern Sikhote-Alin in which larch continued to dominate 200–250 years after fire, with only individual spruce trees under the canopy.

The post-fire development of spruce forests through the larch stage remains poorly investigated in the Russian Far East. Seral pure larch stands without spruce saplings may be formed in the first years after fire due to lack of a spruce seed source or a bad crop of seeds. Absence of spruce may often be explained by arrival of spruce only after a dense grass cover had already formed. The grass cover may be transformed into a dense dwarf-shrub cover (*Vaccinium vitis-idaea*, *Ledum palustre*) peculiar to larch forests, but this also inhibits the successful establishment of viable spruce and results in long-lasting seral larch stands. The simultaneous establishment of spruce and larch saplings in most cases supports the formation of a spruce subcanopy and full replacement of larch by spruce, after the larch canopy breaks up.

Table 5.11. Post-fire dynamics of spruce-fir forests (after Man'ko 1987).

Time after fire	State of main phytocenotic components
0–10 years	Formation of herb-shrub community, with simultaneous arrival of birch, larch and spruce.
10–40 years	Formation of young birch or larch stand, with spruce 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 the canopy of birch or larch. Development of a species composition characteristic for spruce forests.
60–100 years	Break-up of the birch canopy; increasing canopy of role of spruce and fir.
100–180 years	Further increase of spruce in the canopy, with birch disappearing from the canopy. Development of structure and species composition typical for even-aged spruce forests.
180–220 years	First post-fire spruce generation starting to die, with appearance of new generations in the canopy. Characteristics of an uneven-aged stand appearing.

6.3.3 Spruce forest decline

Spruce-fir forests have a tendency to decline in the southern portion of their range on the Sikhote-Alin (Man’ko & Gladkova 2001). Several waves of decline occurred over extensive areas in the recent past, including the last, in 1970–1980, in the central Sikhote-Alin (Man’ko 1987, Man’ko & Gladkova 1993, 1995, Man’ko *et al.* 1998). Stand dieback started with the simultaneous death of several trees in 1972, not necessarily the oldest trees in the stand. After 1978 the area of dead stands increased, and the patches of dead trees merged. In 1983 the total area of dead forest was not considered a large-scale decline, but the subsequent merging of existing breakdown sites and appearance of new patches caused canopy degradation over an area of 140 km^2 (Kamibayashi *et al*. 1994).

According to Man’ko *et al.* (1998), forest decline is expressed as death of canopy trees preceded by appearance of dead branches along the mid-stem and yellowing needles on the whole stem. The authors discovered that stem death tended to increase with increasing diameter and that it was mainly fir that was dying. The dead trees ranged between 100 and 160 years old, and dying stands were uneven-aged. The young sub-canopy spruce generation did not suffer when the canopy trees disappeared but rather tended to grow better. Spruce and fir saplings successfully regenerated the stands with dead canopies.

Analyses and experiments carried out in dying or dead forests did not show a definite factor causing the forest decline. The authors hypothesize that drought during the growing season may play a crucial role, citing the complex mechanisms of forest response to water stress and various accompanying stresses. These include excesses of various elements (Zn, Li, Ni, Co, Pb, Ti) in the soil, fungal diseases in the dead centers, and consequent damage by insects (Man’ko *et al.* 1998, Man’ko & Gladkova 2001).

6.4 Phytocenotic diversity

Dark-conifer vegetation in the boreal zone of eastern Russia involves two basic types of spruce forest: Formation *Piceeta ajanensis,* widely occurring in continental as well as insular regions, and at high elevations in northeastern China; and Formation *Piceeta glehnii,* a rare vegetation type occurring locally on the islands (southernmost Sakhalin, Iturup and Kunashir). The largest mass of *Picea glehnii* forest occurs on Hokkaido (Tatewaki 1943). Classification of dark-conifer forests of easternmost Russia is shown in Table 5.12.

Table 5.12. Classification of dark-conifer forests, with indicator species, ecology, and topographical position of association groups. Abbreviations for edatopes as in table 5.7.

Grex associationum	Indicator plants	Edatope	Topography, aspect
Formatio: *Piceeta ajanensis*			
Classus associationum: *Piceeta purum*			
Piceeta purum fruticulosa	*Vaccinium vitis-idaea, Diphasiastrum complanatum, Gymnocarpium dryopteris*	SD, P–MN	Steep southern slopes
Piceeta purum nano-herbosa taigae	*Maianthemum bifolium, M. dilatatum, Linnaea borealis, Chamaepericlymenum canadense*	F, MN	Gentle slopes at different elevations
Piceeta purum hylocomiosa	*Hylocomium splendens, Pleurozium schreberii, Ptilium crista-castrensis*	SD–F, P–MN	Flats and gentle northern slopes
Piceeta purum filicosa	*Diplazium sibiricum*	M, MN	Small terraces on mountain slopes
Piceeta purum grandiherbosa	*Senecio cannabifolius, Calamagrostis langsdorffii, Athyrium felix-femina*	M–VM, MN–R	Moist river valleys
Piceeta purum sphagno-ledosa	*Ledum palustre, Sphagnum fuscum, Polytrichum commune*	VM, P–MN	Poorly drained valleys
Classus associationum: *Piceeta abietosium nephrolepis*			
Abieto-Piceeta fruticulosa	*Vaccinium vitis-idaea, Diphasiastrum complanatum, Orthilia secunda*	SD, P–MN	Northern steep slopes
Abieto-Piceeta nanocaricosa taigae	*Carex callitrichos, Pseudocystopteris spinulosa*	SD, MN–R	Insolated steep slopes
Nemoreto-Piceeta herbosa nemoretae	*Dryopteris crassirhizoma, Aconitum umbrosum, Thalictrum tuberiferum*	F–M, MN–R	Gentle (<20°) southern slopes and river valleys
Nemoreto-Piceeta filicosa	*Dryopteris expansa, Leptorumohra amurensis, Diplazium sibiricum, Phegopteris connectilis*	F, MN–R	Gentle (<20°) northern slopes
Nemoreto-Piceeta nano-herbosa taigae	*Maianthemum bifolium, Chamaepericlymenum canadense, Carex falcata, C. xyphium*	F, MN	Gentle slopes and terraces
Abieto-Piceeta hylocomiosa	*Hylocomium splendens, Pleurozium schreberii, Rhytidiadelphus triquetrus, Pleurosiopsis ruthenica*	SD–F, MN	Gentle and medium slopes and flats
Abieto-Piceeta oplopanaxosa elati	*Oplopanax elatus, Euonymus macroptera, Carex xyphium*	F–M, R	Micro-terraces on mountain slopes
Abieto-Piceeta grandi-filicosa	*Cornopteris crenulatoserrulata, Koniogramme intermedia, Athyrium filix-femina*	VM, MN–R	Well-drained river valleys
Abieto-Piceeta grandi-caricosa	*Carex appendiculata, Ledum palustre, Calamagrostis langsdorffii*	VM–W, MN–R	Poorly-drained valleys
Classus associationum: *Piceeta abietosium sachalinensis*			
Abieto sachalinensis-Piceeta sasosa	*Sasa kurilensis, S. senanensis, Ilex rugosa, Skimmia repens*	F–M, MN–R	Gentle slopes
Abieto sachalinensis-Piceeta hylocomiosa	*Hylocomium splendens, Pleurozium schreberi, Pleuroziopsis ruthenica*	F, P–MN	Gentle northern slopes
Abieto sachalinensis-Piceeta filicosa taigae	*Leptorumohra amurensis, Dryopteris expansa*	F–M, MN–R	Gentle concave slopes
Abieto sachalinensis-Piceeta nano-herbosa taigae	*Maianthemum dilatatim, Linnaea borealis, Vaccinium praestans*	F, MN	Gentle slopes and terraces
Abieto sachalinensis-Piceeta sphagno-ledosa	*Ledum palustre, Rubus chamaemorus, Sphagnum fuscum, Vaccinium uliginosum, Carex schmidtii*	VM–W, VP–MN	Poorly drained river valleys
Formatio: *Piceeta glehnii*			
Classus associationum: *Piceeta glehnii laricetosium dauricae*			
Lariceto-Piceeta glehnii sphagno-ledosa	*Ledum palustre, Sphagnum fuscum, Betula middendorffii, Rubus chamaemorus*	W, VP–P	Poorly drained valleys
Lariceto-Piceeta glehnii nano-herbosa taigae	*Maianthemum dilatatum, Ilex rugosa, Sphagnum girgensohnii*	M–VM, MN	Gentle slopes

6.4.1 *Piceeta ajanensis – Picea ajanensis* (=*Picea jezoensis*) forests

This whole formation is characterized by the presence of species with circumboreal or boreal trans-continental distribution, such as: *Hylocomium splendens*, *Pleurozium schreberi*, *Peltigera aphtosa*, *Oxalis acetosella*, *Diplazium sibiricum* and *Rosa acicularis*. Various climate-dependent types related to gradients of heat and continentality occur over the wide boreal range. Three association classes can be distinguished over the whole range: 1) *Piceeta purum*, pure spruce forests in the northern part of the range (north of 54°N and in Kamchatka's "conifer island"); 2) *Piceeta abietosium nephrolepis*, mixed spruce-fir forests on the mainland south of 54°N, plus the Shantar Islands; and 3) *Piceeta abietosium sachalinensis*, mixed spruce-fir forests on Sakhalin, Iturup and Hokkaido.

6.4.1.1 *Piceeta purum*

Forests of this association class have the simplest structure (Fig. 5.24) and poor species composition. The tree layer contains only *Picea ajanensis*, with some possible admixture of *Betula ermanii* at high elevations. Solitary individual trees of broad-leaved *Sorbus sibirica* occur under the main canopy. After severe fires these forests recover through a *Larix dahurica* stage. Occasionally admixtures of spruce, form the young canopy, and a canopy of larch can be found at different stages of breakdown.

On Kamchatka we noted 110 vascular species and 15 main species of ground mosses. Most vascular boreal geoelements occur widely across the circum-boreal zone. The most important cenobiogroups are taiga small herbs *Maianthemum bifolium*, *Chamaepericlymenum suecicum* etc.; ferns *Diplazium sibiricum*, *Dryopteris expansa* and *Phegopteris connectilis*; herbs *Streptopus strepto*

Figure 5.24. Typical stand of *Piceeta purum* (photo by P. Krestov).

poides, *Saussurea oxyodonta*, *S. pseudotilesii* (only on Kamchatka), *Solidago spiraeifolia* and *Veratrum alpestre*; the taiga dwarf-shrub *Vaccinium vitis-idaea*; and taiga shrubs *Rosa acicularis*, *Juniperus sibirica*, *Spiraea beauverdiana* and *Ribes triste*.

Chamaepericlymenum suecicum and *Lonicera chamissoi* characterize this association class. Common species for *Piceeta purum* and *Piceeta abietosium nephrolepis* not present in *Piceeta abietosium sachalinensis* are *Maianthemum bifolium* and *Mitella nuda*.

The basic, mostly widespread zonal community types in the *Piceeta purum* are the association groups *Piceeta purum hylocomiosa* occurring on middle or upper slopes and *Piceeta purum nano-herbosa taigae* occurring on flats and gentle slopes. Other association groups occupy a wide range of sites, with different soil moisture and soil nutrient regimes. Near upper belt limits in mountains, subalpine *Rhododendron aureum* and *Sorbus sambucifolia* may invade the spruce stands. These subalpine species, however, require extensive gaps to maintain their cenopopulations.

6.4.1.2 *Piceeta abietosium nephrolepis*

These stands normally involve at least two tree species, *Abies nephrolepis* and *Picea ajanensis*, forming a dense forest canopy (Fig. 5.25). *Picea obovata* (in the west) and *Picea koraiensis* (in the south) may also occasionally be present in the canopy. Differences in eco-biological characteristics of fir and spruce cause well-expressed cyclic dynamics of these spruce-fir forests, with dominance by different species in different stages of stand development. In addition to conifers, various broad-leaved species characterize this association class.

Figure 5.25. Typical stand of *Piceeta abietosium nephrolepis* (photo by P. Krestov).

The canopy of spruce-fir forests may contain individual trees or groups of *Sorbus amurensis* or *Betula ermanii* (at higher elevations). *Acer ukurunduense* occurs and occasionally forms a stratum under the canopy. In the south, spruce-fir forests may be enriched by temperate tree species such as *Acer mono*, *Betula costata*, *Fraxinus mandshurica*, *Pinus koraiensis*, or *Tilia amurensis*. Normally the tree layer shows only poor further stratification, if any; if differentiated, the second stratum contains the same species as the canopy but with greater amounts of *Abies nephrolepis*.

On the Sikhote-Alin we noted 250 vascular species in spruce-fir forests. In addition to common boreal species mentioned for the *Piceeta purum*, the cenoflora of *Piceeta abietosium nephrolepis* is characterized by the presence of species endemic to easternmost boreal Siberia, so-called Okhotsk and Manchurian species. These considerably enrich all cenobiogroups and include taiga small herbs *Huperzia serrata* and *H. chinensis*; taiga ferns *Leptorumohra amurensis* and *Pseudocystopteris spinulosa*; taiga sedges *Carex callitrichos* and *C. xyphium*; taiga herbs *Clintonia udensis*, *Smilacina davurica*, etc.; and the taiga dwarf-shrub *Chimaphila japonica*.

The association groups *Abieto-Piceeta filicosa taigae*, *Abieto-Piceeta hylocomiosa* and *Abieto-Piceeta nano-herbosa taigae* are the most widespread community types. Their ecological range involves mesic poor (hylocomiosa), medium (nano-herbosa) and rich (filicosa) sites. In the south the association group *Nemoreto-Piceeta herbosa nemoretae* can also be present on medium to rich mesic sites.

The *Abieto-Piceeta fruticulosa* and *Abieto-Piceeta nano-caricosa taigae* occur under drier conditions. On wetter sites the herb layer of spruce forests may contain the hygro-mesic ferns *Athyrium filix-femina*, *Coniogramme intermedia*, *Cornopteris crenulatoserrulata* and hygromesic sedges *Carex pallida*, *C. sordida*, and *C. schmidtii*. The performance of spruce and fir trees on wet sites is very poor.

6.4.1.3 *Piceeta abietosium sachalinensis*

This association class represents the spruce-fir forests on Sakhalin, in the southern Kurils and on Hokkaido, under maritime and oceanic climates. The main difference from *Piceeta abietosium nephrolepis* is the presence of *Abies sachalinensis* in the tree layer. In contrast to *A. nephrolepis*, *A. sachalinensis* can form normal self-regenerating monodominant stands, even without spruce in the south (Fig. 5.26). In these forests *Sorbus commixta* may occur as individuals in the canopy, and *Acer ukurunduense* usually occurs in the understorey as solitary trees or in groups. At high elevations *Betula ermanii* occurs in the canopy. In the south, on the Krilion Peninsula of Sakhalin, on Kunashur and on Hokkaido, temperate tree species such as *Kalopanax septemlobus*, *Fraxinus mandshurica*, and *Tilia japonica* occur as individuals in the canopy. The tree layer may be somewhat stratified into two strata with the same species composition.

We found 260 vascular species in the spruce-fir forests of Sakhalin. The cenoflora includes many species endemic to Japan and Sakhalin, such as shrubs *Hydrangea paniculata*, *Euonymus miniata*, *Viburnum furcatum*, *Vaccinium axillare*, and *V. hirtum*; smaller shrubs *Ilex rugosa*, *I. sugeroki*, *Skimmia repens*, and *Vaccinium praestans*; and herbs *Aralia cordata*, *Petasites amplus*, and *Lysichiton camtschatcense*. In southern Sakhalin, in the southern Kurils and on Hokkaido, short bamboos of the genus *Sasa*, represented by 12 species, characterize the spruce-fir forests of this class. Two species, *Sasa kurilensis* and *S. senanensis*, dominate the ground layer.

The main community types in northern Sakhalin are *Abieto sachalinensis-Piceeta hylocomiosa*, *filicosa taigae* and *nano-herbosa taigae*. In southern Sakhalin the association group *Abieto sachalinensis-Piceeta sasosa* prevails on medium to rich mesic sites. A well-developed shrub layer of *Vaccinium axillare*, *V. hirtum* and *Viburnum furcatum* represents the communities on rich wetter sites.

Figure 5.26. Typical stand of *Piceeta abietosium sachalinensis*, with understorey of *Sasa kurilensis* (photo by S. Grishin).

6.4.2 *Piceeta glehnii – Picea glehnii* forests

The range of *Picea glehnii* in Russia includes only Mereya basin and the Aniva Peninsula on southernmost Sakhalin. In this area *Picea glehnii* stands occur mainly in mires and on slopes, sharing these sites with *Larix dahurica* (Fig. 5.27). *Picea glehnii* also occurs on Iturup and Kunashir, where it forms monodominant communities in mires (Sugawara 1937, Tolmachov 1959, Vorobiov 1963, Shafranovskiy 1987). This differentiates the Sakhalin stands from the Hokkaido and Kuril stands, where spruce grows alone or together with solitary trees of *Abies sachalinensis*, *Betula ermanii* or *Acer mono* (Tatewaki 1958, Shafranovskiy 1987). The differences in structure and species composition of Japanese (including Kuril) *Picea glehnii* forests from Sakhalin forests allows us to distinguish two association classes: *Piceeta glehnii laricetosium* and *Piceeta glehnii typicum*.

On Sakhalin we described two association groups, contrasting in ecological conditions and species composition. *Lariceto-Piceeta glehnii sphagno-ledosa* occurs on saturated sites in floodplains. *Picea glehnii* forms stands with *Larix dahurica*. *Abies sachalinensis* and *Picea ajanensis* may occur solely, and trees are suppressed. *Ledum palustre* dominates in the understorey. *Sphagnum fuscum*, *S. palustre* and *S. nemoreum* form large ground cushions, with patches of *Polytrichum commune* between them. This association group is characterized by the presence of *Rubus chamaemorus* and *Betula middendorffii*.

Abieto-Piceeta glehnii nano-herbosa taigae occurs on 5 to 15° slopes. The canopy is much denser than in the previous association group. *Picea glehnii* is mixed with *Abies sachalinensis*. Small taiga herbs *Maianthemum dilatatum* and *Chamaeperi-clymenum canadense* prevail in the understorey, with a well-developed moss cover.

Figure 5.27. Typical stand of *Piceeta glehnii laricetosium dahuricae* (photo by P. Krestov).

7. LARICETA DAHURICAE

Larix dahurica Laws. is a complex species occurring over a huge area of northeastern Asia (Fig. 5.28). The great variability of its morphological features caused *Larix* taxonomy to be understood differently in different areas. Kolesnikov (1946) distinguished 11 main species of *Larix* in northeastern Asia: *L. leptolepis* Gord. on Hokkaido and Honshu; *L. komarovii* B. Kolesn. in montane areas of maritime eastern Russia; *L. middendorffii* B. Kolesn. in both continental and maritime regions; the Okhotsk species *L. ochotensis* B. Kolesn.; *L. olgensis* A. Henry, the characteristic species for maritime regions; *L. maritima* Suk. on maritime and suboceanic islands; *L. kurilensis* Mayr on the Kurils and in Kamchatka; *L. principis-rupprechtii* Mayr in northern China and the Greater Hingan Mountains; *L. lubarskii* in northeastern China, northern Korea and southeastern Russia; *L. dahurica* Turcz. in the Baikal area, Amur basin and Saha-Yakutia; and *L. cajanderi* Mayr in central and northern Yakutia and the Kolyma River basin. The ranges of these species are shown in Fig. 5.29.

Bobrov (1978) has explained larch polymorphism by the modern processes of introgressive hybridization between forms and species. He reduced the diversity of northeast Asian larches to four species: *Larix kamtschatica* (Rupr.) Carr., *L. olgensis* A. Henry, *L. gmelinii* (Rupr.) Rupr. (=*L. dahurica* Turcz. ex Trautv.), and *L. cajanderi* Mayr. The other species were considered to be hybrids. The last taxonomic survey by Koropachinskiy (1989) reduced larch diversity to three species: *Larix cajanderi* (including *L. kamtschatica*), *L. olgensis* and *L. gmelinii*. The morphological and eco-biological boundaries even among these three species, however, remain unclear. Thus, we accept the wider interpretation of Larix species in northeastern Asia, by Tsveliov (1994), relating all species mentioned to *L. dahurica* Laws. 1836, Agricult. Man.: 389; Turcz. ex Trautv. 1846, Fl. Imag. Descr. Fl. Russ. Ill.: 48, tab. 32. – *Larix gmelinii* (Rupr.) Rupr. – *Larix olgensis* A. Henry, – *Larix cajanderi* Mayr.

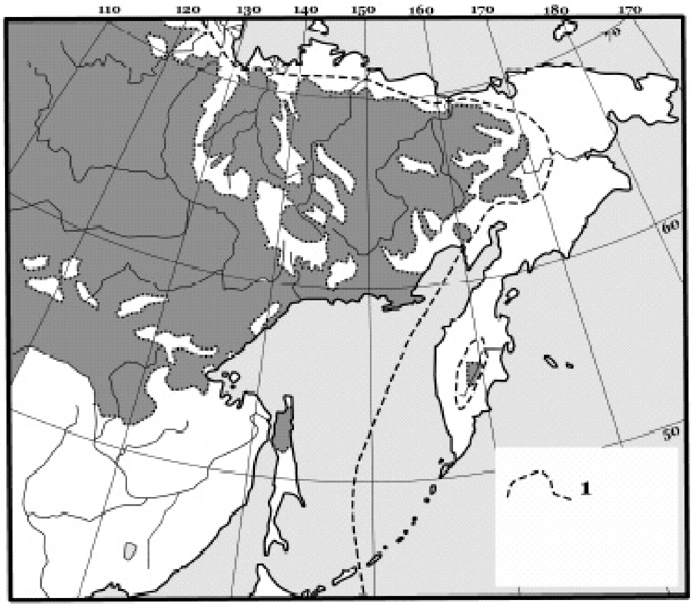

Figure 5.28. Distribution of boreal larch forests and range of dominant *Larix dahurica* s.l. (dashed line).

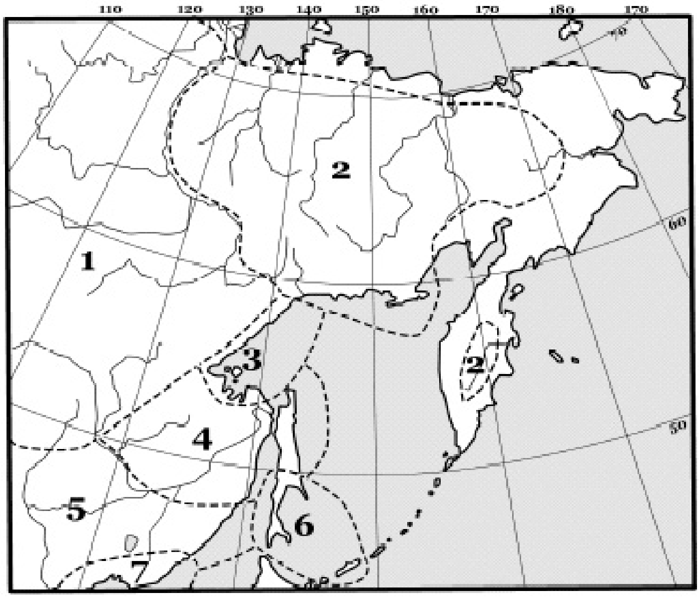

Figure 5.29. Ranges of larch species sensu stricto of section *Pauciseriale* recognized in this work as *Larix dahurica* Laws (after Bobrov 1978): 1 = *Larix gmelinii*, 2 = *Larix cajanderii*, 3 = *Larix cajanderi* × *kamtschatica*, 4 = *Larix* × *maritima* (*Larix gmelinii* × *kamtschatica*), 5 = *Larix* × *lubarskii* (*Larix gmelinii* × *kamtschatica* × *olgensis*), 6 = *Larix kamtschatica*, 7 = *Larix olgensis*.

7.1 Physiography in the larch-forest area

7.1.1 Terrain

Larix dahurica forests occupy a large area in northeastern Asia, on sites ranging from river valleys to mountain tops. In interior northeast Asia larch forms the subarctic treeline, reaching 72°N latitude. In many mountain areas larch is a main or the only species forming the alpine treeline, at elevations above 1000 m even at the Arctic Circle. Terrain within the range of *Larix dahurica* is very diverse. Larch forms mono-dominant stands on extensive plains (East Siberian Plain, Middle Amur Lowlands) just as successfully as on massive mountain ranges (Stanovoy, Tukuringra, Kolymskiy, and Anujskiy ranges).

7.1.2 Climate

Climate in the larch-forest area is continental to ultra-continental, despite proximity to the Sea of Okhotsk. The monsoon circulation, characteristic for all of easternmost Russia, determines the main climatic characteristics in the area.

The Sea of Okhotsk, covered with ice 8 months a year, strongly affects the climate in the narrow land strip (100–200 km) between the coast and the Dzhugdzhur Mountains. Winter lasts about 7 months here, from late October to late May. Strong northwest winds, bringing very cold air masses from the continental interior, result in sunny winter weather with humidity not exceeding 65%, very low for a coastal area. In the north temperatures remain below −20°C from December to February, and in the south from January to February. Extremes of −35 to −40°C are common along the Okhotsk coast. Because winter cyclones have almost no affect in the area, the snow cover is much lower than in Kamchatka and the lower Amur region. It disappears in late May, and by mid-June air temperature increases to the +5°C needed for plant activity.

From May to August the weather is determined by winds from the Sea of Okhotsk, where ice melts in June. Because seawater temperatures do not exceed 10–12°C, air temperatures remain cool all summer. Mean daytime temperatures are above 10°C only in July and August and do not reach 15°C. Summer precipitation ranges from 200 mm in the north to 600 mm in the south. Although precipitation amounts are low, rainy periods along the coast may be long.

Behind the Dzhugdzhur Range the climate becomes much more continental, with warmer summers and much colder winters. Winter lasts almost 8 months, from late September to the end of May. Winter temperatures are very low, with the January mean below −40°C and March mean lower than the January mean on the coast. Temperature inversions are common in all of this area, with lower air temperatures in valleys and lowlands than on slopes or in highlands. Under the anticyclonic conditions there is little snow, and the snow cover does not exceed 30 cm even in the highlands.

In the spring temperatures increase rapidly, reaching above freezing by mid-May and exceeding 5°C by the end of May. Summer is short, cool and dry. The period with daytime temperatures above 10°C lasts from mid-June to mid-August. Highest temperatures are July and can reach as high as 30°C, with relative humidity not above 50%.

The range of pure larch forests coincides with the area of continetal to ultra-continental climates, with cool summers and extremely cold winters (absolute minimum of −72°C in Oymiakon). Climatic dryness in winter, the short vegetative season, and the high insolation in spring, when soils are still frozen, have a crucial effect on vegetation development in the areas occupied by larch forests. Permafrost is the most important factor limiting all tree species except larch. The slow thawing of the permafrost, moderate summer air temperatures and consequent low evapotranspiration rates compensate for the climatic moisture deficit, even though drought does occur in July and August in the ultra-continental regions.

7.2 Eco-biological features of larch

The problems in larch taxonomy are caused by the great variety of ecological forms and races within the genus, especially in the series Pauciseriale (Bobrov 1978). Climatypes and ecotypes of larch are expressed much more clearly than morphotypes, as was confirmed in cultivation experiments showing inheritance of ecoforms but loss of morphological features (shape and size of cones) (Dylis 1961).

Larix dahurica is a long-living species that can live 500 years in northern regions. A maximum age of 526 years was recorded by Nedrigaylov (1932) in southern Yakutia. An important feature of larch limiting its distribution is its very low competitive ability, caused mostly by its intolerance of shade. On many sites optimal for larch growth, it can easily be replaced by several other species if site conditions favor them. In contrast, larch has the advantage when many species colonize an opening, due to its rapid growth at earlier ages.

The wide ecological range of larch can be explained by several of its eco-biological features, such as its ability to take up water even from relatively cold soil, to transpire and photosynthesize rapidly, and its tolerance of very low winter temperatures. Nevertheless, larch stands react very differently to various climatic and edaphic conditions. All stand parameters, including site index, annual height and diameter increments, cover, and crown and stem shape, vary greatly over the range of soil and climatic conditions (Anonymous 1990).

Table 5.13. Distribution of all roots and those thinner than 2 mm at different soil depths (percentage of total mass) in the *ledosa* community type from different regions, determined from soil samples of 50 × 50 × 100 cm.

Soil depth (cm)	Aldan (Pozdniakov 1975)		Olekma (Pozdniakov 1975)		Kamchatka (Efremov 1964)	
	All roots	<2 mm	All roots	<2 mm	All roots	<2 mm
0–10	95	70	81	36	33	32
10–30	5	29	13	32	33	32
30–50		1	3	20	22	28
50–70			3	12	10	4
70–90					2	2

Table 5.14. Characteristics of larch stands from different edapho-climatic conditions on sites free of permafrost. Names of association groups and description of site characteristics are as in Table 5.15. Ld – *Larix dahurica*, Ps – *Pinus sylvestris*, Bp – *Betula platyphylla*, DBH – diameter at breast height and H – total height of stand.

Association Group	Composition of tree layer	Age of dominant trees	Average for stand		Volume ($m^3.ha^{-1}$)
			H (m)	DBH (cm)	
Lariceta purum licheno-vacciniosa	100Ld	150	13	15	55
Lariceta purum herbosa boreali	100Ld	170	18	19	190
Lariceta purum calamagrostidosa	80Ld 20Bp	170	24	21	278
Lariceta purum ledosa	100Ld	150	12	14	56
Lariceta purum sphagnosa	100Ld	30	5.3	12	35
Pineto sylvestris-Lariceta vaccinio-lichenosa	90Ld10Ps	180	16	16	141
Pineto sylvestris-Lariceta hylocomioso-herbosa taigae	70Ld 30Ps	200	25	32	314
Pineto pumilae-Lariceta fruticulosa boreali	100Ld	120	14	17	97
Pineto pumilae-Lariceta ledosa	100Ld	50	8.6	12	56

Due to its shallow root system and ability to form supplementary roots above the root shoulder, larch is the only tree species in eastern Siberia able to grow on permafrost (Table 5.13). Larch stands stabilize the permafrost regime: removing the trees causes site drying or waterlogging, depending on topography (Dylis 1961). Larch forms the northern treeline in continental (interior) regions of eastern Siberia, with a very high tolerance to climatic and edaphic fluctuations, as shown by tree-ring analyses that reveal long periods of growth suppression (Shcherbakov 1975).

Larch performs best on gentle, moderately to poorly drained slopes or flats with fine-textured clayey podzolic soils under mesic and hygric soil moisture regimes (Sochava 1956). Tall stands were also found, however, on saturated sites with non-stagnant water in floodplains (Shcherbakov 1975). The productivity of larch stands on different sites in different regions is shown in Table 5.14.

7.3 Stand structure and composition

7.3.1 Tree layer

Larch normally forms pure even-aged stands with a one-stratum canopy, varying in cover, without an admixture of any other tree species (Fig. 5.30). Where climate favors the growth of other species (spruces, pines, nemoral broad-leaved trees), larch cannot form mixed stands with them due to its shade intolerance. Pure stands can be stable in these regions only if factors are present that inhibit the development of potential competitors. If spruce saplings commonly occur in larch forests where the ranges of these species overlap, larch is not able to regenerate under any canopy, including its own. Mixtures of larch and spruce or larch and Korean pine observed on the Sikhote-Alin had appeared after wildfire and contained an older generation of larch and younger generation(s) of admixed species.

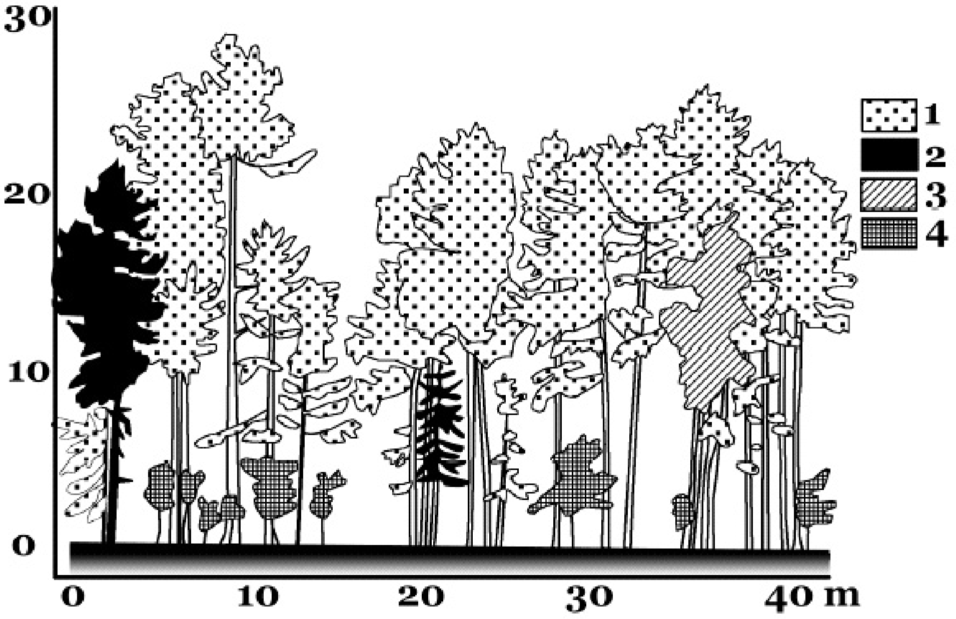

Figure 5.30. Profile of a typical larch stand (5 m deep x 40 m long): 1 = *Larix dahurica*, 2 = *Picea ajanensis*, 3 = *Betula platyphylla*, 4 = *Alnus hirsuta* (after Krylov 1984).

In the western part of the Russian Far East and eastern Siberia larch forms mixed stands with *Pinus sylvestris* (Scots pine) on sandy soils. Both species are shade intolerant and adapted to a wide range of ecological conditions. Saplings of Scots pine appear to be more fire tolerant than larch saplings, and larch is replaced by pine if ground fires are frequent. In the early stages of post-fire succession, however, larch always wins the competition with pine since it can form young stands earlier than pine.

The cover by a larch canopy is usually low, even with many stems in a stand. The canopy remains transparent for light, providing good conditions for understorey development. Under favorable conditions larch may reach 30–35 m in height, but larch stands in the north are never higher than 10–12 m.

Uneven-aged stands are found on sites free from fire over long periods. Such stands may contain several even-aged generations of larch with younger generations appearing in canopy gaps. In some cases all trees in uneven-aged stands may still have the same height and diameter.

7.3.2 Shrub layer

Due to light availability under the larch canopy, a shrub layer is normally well developed, composed of both circumboreal shrubs and shrubs restricted to the eastern part of boreal Asia. On moist flats the shrub layer may contain *Alnus fruticosa*, *Vaccinium uliginosum*, *Betula middendorffii*, *Ledum palustre* and *L. hypoleucum* (south only). In river valleys the shrub layer includes *Rosa acicularis*, *R. amblyotis*, *Sorbaria sorbifolia*, *Spiraea salicifolia*, *Ribes* spp. and *Lonicera* spp. In highlands the main shrubs in the larch stands are *Pinus pumila* (in the north), *Rhododendron dauricum*, *R. parvifolium* and *Ledum palustre*. Some of these species may occur within the herb layer.

7.3.3 Herb layer

The herb layer usually includes many species, and the same sets of species may occur on similar sites across the whole range of larch forests. The species composition of a community depends mostly on substrate conditions. Low shade tolerance characterizes most species of larch forests, and many can also be found in meadow and bog communities without a tree layer.

In wet lowlands *Carex schmidtii*, *C. appendiculata*, *C. globularis*, *Eriophorum vaginatum*, *E. gracile*, *Calamagrostis langsdorffii* can dominate or be main components of the herb layer. Some shrubs and dwarf-shrubs, including *Ledum* spp., *Myrica tomentosa*, *Chamaedaphne calyculata*, etc., may also be present in the herb layer. On well-drained sites in river valleys the mesophilous herbs may be the main component of the herb layer. On uplands the most abundant species are *Vaccinium vitis-idaea*, *Arctostaphylos uva-ursi*, *Solidago spiraeifolia*, *Carex vanheurckii*, and *Pteridium aquilinum*.

The flora of the larch-forest area was formed from different cenoelements at the time of the last Pleistocene glaciation. Meadow and bog complexes, with species including *Carex globularis*, *C. cespitosa*, *Chamaedaphne calyculata*, *Andromeda polifolia* and other ericaceous species, as well as *Larix dahurica*, formed in ancient Beringia from the warmer-climate pre-Pleistocene flora and subsequently adapted to the severe Pleistocene conditions (Vasiliev 1958).

7.3.4 Moss and lichen layer

Mosses and lichens are an important component of larch stands on certain ecotopes. *Sphagnum* spp. mosses occur on wet and very wet sites, *Pleurozium schreberi* and *Hylocomium splendens* form moss layers on mountain slopes, and lichens (*Cladonia* spp., *Cladina* spp. and *Stereocaulon* spp.) are common on slopes in earlier stages of post-fire succession.

7.4 Stand dynamics

7.4.1 Natural dynamics

Because it is shade-intolerant, larch cannot regenerate under any tree overstorey, even of larch. Fire is the most important factor initiating larch regeneration over the whole range of *Larix* in Russia (Sukachov 1924, Sochava 1956, 1957, Dylis 1961, Tikhomirov & Falaleiev 1962, Shcherbakov 1975, Pozdniakov 1975). In the first five years after fire, larch produces many saplings that grow rapidly even at an early age. On productive sites larch reaches heights of 10 m in 30 years, 15 m in 50 years and 20 m in 80–90 years. In Magadan we recorded a maximum of 28 m in even-aged stands 385 years old.

In the case of uninterrupted development, larch stands reach the gap phase after 150–250 years. Larch regeneration takes place only in large gaps, generally formed after windthrows (Pozdniakov 1975). This causes the appearance of a new generation that may reach the canopy in a hundred years and explains why even uneven-aged stands contain two or more even-aged generations. Uninterrupted larch development occurs rarely, though, and cyclic dynamics of larch forests has not been investigated.

7.4.2 Fire-initiated dynamics

The current presence of larch forests over their whole range depends on past or present fire regimes (Fig. 5.31).

Because much flammable material accumulates and droughts occur in spring and summer, fires can envelop very large areas. Intense fires may destroy the forest ecosystems completely, including soil organic com-

Figure 5.31. Fires are an important factor in larch forest dynamics. Wild fire destroyed this larch stand in a while. On the ground are burned branches of *Pinus pumila* (photo by P. Krestov).

ponents and larch saplings in lower stand layers. In the north wildfires may initiate post-fire succession and restore the larch forests, but in the south, at the contact between the larch and dark-conifer areas, fires may favor larch and extend its range into burned areas of dark conifers.

Ground fires usually destroy the herb and moss layers and kill larch saplings. Consequent selection for fire-tolerant species in larch forests makes it more difficult to use indicator species to describe site ecological regimes. In Magadan we observed several sequences of post-fire successions in larch forests. On well-drained mountain slopes the lichen sere is most widespread after fires that mineralize the upper horizons of the soil. Succession starts with colonization by the mosses *Polytrichum commune* and *P. piliferum*. In the next decade, lichens (*Cladina mitis*, *Cladina stellaris, C. rangiferina, Flavocetraria cuculata*) gradually appear and increase until they form a closed cover. At the next stage *Ledum decumbens*, *Vaccinium uliginosum*, *V. vitis-idaea*, *Carex vanheurckii* and some herb species invade the community, finally forming a more or less closed cover. This stage may last about 100 years, until a stable, closed post-fire larch forest with dwarf-shrubs and small boreal herbs is established as the last phase of succession.

The fireweed or *Epilobium* (*Chamerion angustifolium*) sere is most widespread on gentle slopes or flat terrain. This succession is initiated by wildfires on fine-textured soils with no moisture deficit. In the year after fire the mosses *Polytrichum* and *Racomitrium* appear on the burned ground, together with *Chamerion angustifolium*, and larch germinates, either simultaneously or a year or two later. After 5–10 years larch forms a closed cover with an undergrowth mainly of *Epilobium*. The final stable post-fire community is formed in 30–50 years. *Chamerion angustifolium* keeps its high presence, sharing dominance in the herb layer with *Calamagrostis langsdorffii* and *Artemisia latifolia*.

In wetlands a *Sphagnum* sere is most common. Wetland fires usually damage larch trees and herbs in spring or autumn, when the herbs become flammable, but the ground layer with mosses remains undisturbed, due to the saturated conditions. The fire initiates an intensive regeneration of larch. The herb layer recovers in the same or next year, involving the same species, since most of them have well-protected buds: *Carex appendiculata*, *C. globularis*, and *Eriophorum vaginatum*. *Chamerion angustifolium* can invade in the first year after fire and remain for several decades, on the tops of sedge mounds or hummocks.

7.5 Phytocenotic diversity

Despite the long east-west continentality and north-south temperature gradients in Siberia, there are no sharp climatically related changes in the vegetation cover. Larch forests on similar sites remain similar over extensive areas with ultra-continental, continental and, in the north, submaritime climates. The only differences in stand dominance are between the western larch forests with significant amounts of *Pinus sylvestris* on zonal sites, the eastern forests where larch forms pure stands with no other canopy trees, and the northern larch forests with *Pinus pumila* in the understorey (Dylis 1961). This permits a preliminary delineation of three major association classes: *Lariceta dahuricae pinetosium sylvestris* in interior Pacific and eastern Siberia, *Lariceta dahuricae purum* in the eastern coastal area, and *Lariceta dahuricae pinetosium pumilae* north of 60°N (Table 5.15).

7.5.1.1 *Lariceta dahuricae pinetosium sylvestris*

This association class occupies the larch range in the western part of the study area, in the Aldan basin with its ultra-continental climate (Fig. 5.32). The mean temperature of the warmest month is 11–15°C, there are 40–75 days with temperature above 10°C, and average annual precipitation is 150–350 mm.

Table 5.15. Classification of larch forests, with indicator species, ecology, topographical position of association groups. Abbreviations for edatopes as in table 5.7.

Grex associationum	Indicator plants	Edatope	Topography, aspect
Formatio: *Lariceta dahuricae*			
Classus associationum: *Lariceta dahuricae pinetosium sylvestris*			
Pineto sylvestris-Lariceta vaccinio-lichenosa	*Cladina stellaris*, *C. rangiferina*, *Vaccinium vitis-idaea*, *Arctostaphylos uva-ursi*	D–SD, VP–P	Rocky southern slopes
Pineto sylvestris-Lariceta dryacetosa	*Dryas punctata*, *Arctous erythrocarpa*, *Toefieldia coccinea*, *Cotoneaster uniflorum*	SD–F, P–MN	Steep northern slopes at 300–800 m
Pineto sylvestris-Lariceta herbosa boreali	*Lymnas stellerii*, *Equisetum scirpoides*, *Linnaea borealis*	F–M, MN–R	Gentle southern slopes
Pineto sylvestris-Lariceta hylocomioso-vacciniosa	*Hylocomium splendens*, *Pleurozium schreberi*, *Vaccinium vitis-idaea*, *Carex vanheurckii*	SD–F, P	Gentle northern slopes at 300–700 m
Pineto sylvestris-Lariceta ledosa	*Vaccinium uliginosum*, *Carex globularis*, *Ledum palustre*, *Betula middendorffii*, *Aulacomnium turgidum*	M–VM, P–MN	Moist flats and gentle slopes
Pineto sylvestris-Lariceta sphagnosa	*Sphagnum fuscum*, *Rubus chamaemorus*, *Tomenthypnum nitens*, *Aulacomnium palustre*	W, VP–P	Poorly drained valleys with stagnant water
Classus associationum: *Lariceta dahuricae purum*			
Lariceta purum licheno-vacciniosa	*Cladina rangiferina*, *Vaccinium vitis-idaea*, *Empetrum nigrum*, *Ledum decumbens*	SD, P–MN	Northern gentle rocky slopes
Lariceta purum herbosa boreali	*Fragaria orientalis*, *Spiraea media*, *Antennaria dioica*, *Lycopodium clavatum*, *Calamagrostis neglecta*	SD, MN–R	Gentle well-drained slopes
Lariceta purum rhododendrosa	*Rhododendron dauricum*, *Cetraria islandica*, *Diphasiastrum complanatum*	SD, P–MN	Steep southern slopes and ridges
Lariceta purum hylocomioso-herbosa taigae	*Hylocomium splendens*, *Pleurozium schreberii*, *Maianthemum bifolium*	F, P–MN	Gentle (<20°) northern slopes
Lariceta purum ledosa	*Ledum palustre*, *Vaccinium uliginosum*, *Betula middendorffii*, *Pleurozium schreberi*	M, P–MN	Gentle slopes and terraces
Lariceta purum calamagrostidosa	*Calamagrostis langsdorffii*, *Chamerion angustifolium*, *Sanguisorba officinalis*	M–VM, MN–R	Gentle slopes and flats
Lariceta purum caricosa appendiculatae	*Carex appendiculata*, *C. globularis*, *Myrica tomentosa*, *Chamaedaphne calyculata*, *Eriophorum* spp.	VM–W, MN–R	Flats with moving water
Lariceta purum sphagnosa	*Sphagnum* spp., *Aulacomnium palustre*, *Rubus chamaemorus*	W, P	River valleys and flats with stagnant water
Classus associationum: *Lariceta dahuricae pinetosium pumilae*			
Lariceta pinetosium pumilae lichenosa	*Cladina rangiferina*, *C. mitis*, *Flavocetraria cucullata*, *Hierochloë odorata*, *Carex vanheurckii*	D–SD, VP–P	Gentle rocky southern slopes
Lariceta pinetosium pumilae fruticulosa boreali	*Vaccinium vitis-idaea*, *Ledum decumbens*, *Empetrum nigrum*, *Salix reinii*, *S. arctica*	SD–F, P	Gentle northern slopes
Lariceta pinetosium pumilae hylocomiosa	*Hylocomium splendens*, *Pleurozium schreberi*, *Aconogonum tripterocarpum*, *Maianthemum bifolium*	F, P–MN	Gentle concave slopes
Lariceta pinetosium pumilae ledosa	*Ledum palustre*, *Vaccinium vitis-idaea*, *V. uliginosum*	M, P–MN	Gentle slopes and terraces
Lariceta pinetosium pumilae fruticosa boreali	*Betula middendorffii*, *Salix saxatilis*, *S. krylovii*, *S. pulchra*	VM–W, P–MN	Poorly drained river valleys
Lariceta pinetosium pumilae sphagno-caricosa boreali	*Carex globularis*, *C. appendiculata*, *Sphagnum palustre*, *Eriophorum vaginatum*	W, VP–P	Poorly drained valleys with stagnant water from permafrost

Figure 5.32. Typical stand of *Lariceta pinetosium sylvestris* (photo by P. Krestov).

The communities have *Pinus sylvestris* in the tree layer, xeric and xeromesic species are also relatively important, such as *Limnas stelleri*, *Arctostaphylos uva-ursi* and *Rhododendron dauricum*. Most common on mesic sites are the association groups *Pineto sylvestris-Lariceta herbosa boreali* (if richer) and *Pineto sylvestris-Lariceta hylocomioso-vacciniosa* (if poorer). The tree layer in normal communities consists of one stratum originated after fire. *Pinus sylvestris* is the main canopy companion, increasing with more intense ground fires. On sandy soils, mainly on riverbanks, Scots pine occasionally forms pure stands. A complex of boreal-forest and xeric pine-forest species characterizes these association groups as significant components of all community layers: *Vaccinium vitis-idaea*, *Limnas stelleri* (a grass strongly tied to east-Siberian larch forests), *Equisetum scirpoides*, *Carex vanheurckii*, etc.

Intense fires promote the development of lichen communities, united in the association group *Pineto sylvestris-Lariceta vaccinio-lichenosa*. These usually appear after fires that crucially change the soil by burning all organics and permitting the fine soil fraction to be washed out. Lichen communities may remain for a long time on well-drained sites, which have lower productivity. Larch 10–12 m high forms an open canopy, with an admixture of Scots pine. A dense lichen cover (*Cladina mitis*, *C. rangiferina*, *C. stellaris*, *Cetraria islandica*) with scattered patches of ericaceous dwarf-shrubs (*Vaccinium vitis-idaea*, *Arctostaphylos uva-ursi*, *Arctous erythrocarpa*) provides the ground cover. At higher elevations with lower temperatures and higher humidity, a *Dryas* type of community is common, with a layer of *Dryas punctata* and representative tundra plants such as *Arctous erythrocarpa*, *Tofieldia coccinea*, and *Hierochloë alpina*.

7.5.1.2 *Lariceta dahuricae purum*

This association class represents the monodominant larch forests of Russia, southeast of the Dzhugdzhur and Stanovoy mountains and adjacent northeastern China (Fig. 5.33). Since there are very wide plains in this region, most larch stands are represented by a wet sere including the association groups *Lariceta purum ledosa*, *Lariceta purum sphagnosa* and *Lariceta purum caricosa appendiculatae*. The first two are common in the north, in the Zeya-Bureya Plain, and the last in the lower Amur basin. Nearly all stands have an open canopy and low productivity. Communities of *Lariceta purum ledosa* occur mainly on flat, moderately drained uplands. Their undergrowth involves *Ledum palustre* (dominant) mixed with *Vaccinium uliginosum*, *Betula middendorffii* and a moss cover of *Pleurozium schreberi*. A sphagnum type is similar to that in the previous association class. The group *Lariceta purum caricosa appendiculatae* is restricted to lowlands in the southern part of the range. These sites have a high but non-stagnant water table.

The undergrowth contains *Carex appendiculata*, *Myrica tomentosa*, *Chamaedaphne calyculata*, and *Eriophorum* spp. as dominant species. Important companions, usually increasing after fire, are *Calamagrostis langsdorffii* and *Chamerion angustifolium*, which normally occur on the tops of sedge mounds. *Carex globularis*, *Aulacomnium palustre*, and *Sphagnum girgensohnii* occur in the lower areas between the sedge mounds.

7.5.1.3 *Lariceta dahuricae pinetosium pumilae*

This association class is common in the north, north of the Suntar-Hayat mountains but including their southern foothills. Communities of this type form the alpine treeline in mountains throughout the continental areas. This area has the most severe climate in Asia, including the “coldness pole” of Oymiakon, where an absolute minimum temperature of −72°C was recorded in 1964 (Anonymous

Figure 33. Typical stand of *Lariceta purum*, with *Calamagrostis purpurea* dominant in the undergrowth (photo by P. Krestov).

1966–1971). Average annual precipitation ranges from 140 to 170 mm, with 75% falling in summer. At high elevations the precipitation increases to 200–250 mm. Only 40–90 days in a year have a temperature above 10°C. Only 32% of this territory is covered by forests, which occur mainly in depressions and on lower mountain slopes (Shcherbakov 1975).

This entire region was badly disturbed by fires in the past. Only a small fraction of the sites suitable for larch forest has a mesic moisture regime. Due to frequent ground fires and the consequent erosion, the upland sites have well-drained, very light sandy or rocky soils. The lowlands are normally saturated, due to the only shallow thawing of the permafrost layer.

Nearly all larch communities in the area have *Pinus pumila* in the understorey, which may form a closed layer or be present only individually (Fig. 5.34). Species with subarctic or arctic distribution characterize this class: *Salix arctica*, *Arctous erythrocarpa*, *Aconogonum tripterocarpum*, *Salix reticulata*, *S. pulchra*, *S. tschuktschorum*, *Cassiope tetragona*, etc.

The prevalence of dry soil promotes the wide distribution of larch-lichen communities, of the group *Lariceta pinetosium pumilae lichenosa*. These occur on southern slopes and ridges with the most severe droughts appearing in summer. The 8–10 m tall larch forms an open canopy (20–40%). Lichens of the genera *Cladonia* and *Cetraria* cover the ground. *Carex vanheurckii*, *Hierochloë alpina* and *Aconogonum tripterocarpum* occur sporadically. The most productive larch stands, reaching 30 m in height, are found in the moderately drained river valleys and are in the association group *Lariceta pinetosium pumilae calamagrostidoso-grandiherbosa*. These communities have a well-developed shrub layer composed of *Sorbaria sorbifolia*, *Lonicera caerulea*, and *Rosa acicularis*, and a well-developed herb layer composed of *Calamagrostis langsdorffii*, *Cacalia hastata*, *Urtica platyphylla*, etc. Absence of fire over

Figure 5.34. Typical stand of *Lariceta pinetosium pumilae* (photo by P. Krestov)

long periods favors large biomass accumulations and initiates cyclic processes in canopy regeneration. This forest type, however, is restricted to the big river valleys and occurs only very sporadically.

8. BETULETA ERMANII

Forests of *Betula ermanii* (stone birch) characterize the maritime and suboceanic regions of boreal northeast Asia. Over its whole range *Betula ermanii* forms well developed vegetation belts in mountains influenced by oceanic air masses (Fig. 5.35). The *Betula ermanii* belt always lies above the larch belt or dark-conifer belt, represented in this region by *Picea ajanensis*, *Abies nephrolepis* and *A. sachalinensis* (Kabanov 1972). In the southern half of Kamchatka stone birch forms an extensive horizontal zone.

The elevational limit of the *Betula ermanii* belt varies with latitude. In submaritime areas on the mainland this birch belt is well-developed in the south but disappears northward, occurring at 1800–2000 m on the Changbai-shan (Wang 1961), 1400–1800 m in the southern Sikhote-Alin (Kiseliov & Kudryavtseva 1992), 1200–1400 m in the middle Sikhote-Alin (Vasiliev & Kurentsova 1960), and at 700–800 m, only as fragments, in the southern Dzhugdzhur range (Schlothauer 1978). In Magadan *Betula ermanii* forms community fragments on the seacoast.

In maritime and suboceanic climates, stone birch forms forest belts at 1400–1600 m on Hokkaido (Okitsu 1987), at 900–1100 m on Kunashir (Vorobiov 1963), and from sea level to 600 m on Iturup (Vorobiov l.c.). *Betula ermanii* extends north through the Kuril Islands to Urup, where it forms stands from sea level to 400 m; it does not occur in the northern Kurils (Barkalov 2000).

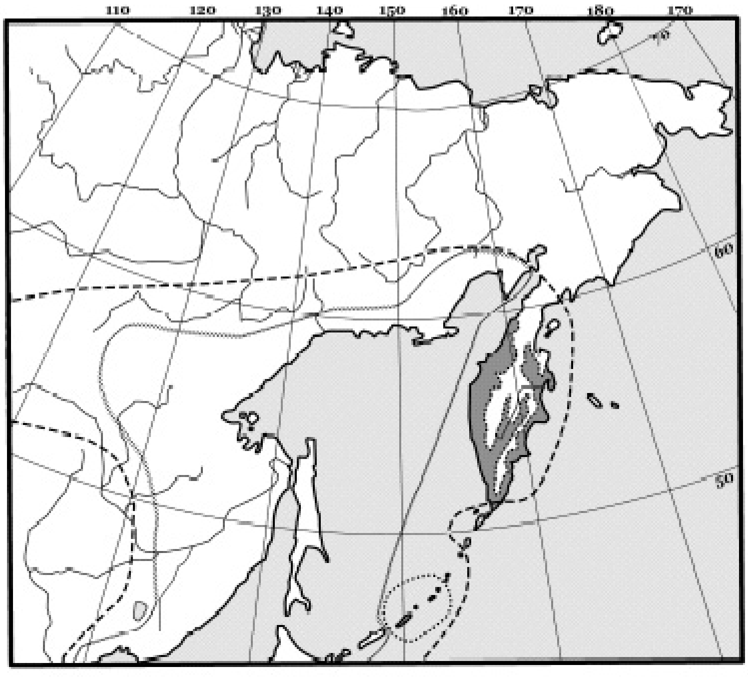

Figure 5.35. Distribution of boreal stone-birch (*Betula ermanii*) forests on zonal sites (shaded area) and in subalpine belts (evenly dashed line), with range of *Betula ermanii* s.l. (unevenly dashed line).

About of 70% of all *Betula ermanii* forest area is in Kamchatka, where it occurs as an extensive horizontal vegetation zone (Shamshin 1999), over a wide range of ecologically different sites. *Betula ermanii* does not occur in wetlands or on permafrost, but its distribution does depend, among other factors, on snow depth and on the timing of snowmelt (length of snow-free period) (Shamshin 1976).

8.1 Physiography

8.1.1 Terrain

Kamchatka lies at the northeast edge of Asia, at 51–60°N and 156–163°E. The peninsula is constituted by two main mountain chains, the Sredinniy (middle) and Vostochniy (eastern). The western slopes of the Sredinniy range gradually fall off to the West Kamchatka Plain, while the eastern slopes of the Vostochniy range fall abruptly to the Pacific coast. The extensive Central Kamchatka Depression lies between these two mountain chains.

The Sredinniy range is the main mountain system of Kamchatka and extends about 1000 km from north to south. The highest mountains reach 1600–1800 m in the south but decrease to 600–800 m in the north. The axial part of the range is a zone of Quaternary volcanism that was glaciated in the Pleistocene. The Vostochniy range unites a system of small ranges dissected by a dense river network. The most seismically and volcanically active part of Kamchatka lies along the eastern slope and near the northern end of the Vostochniy range. Most active volcanoes are in this region: Mutnovskiy (3323 m), Goreliy (1829 m), Avachinskiy (2317 m), Zhupanovskiy (2958 m), Karymskiy (1536 m), Kizimen (2485 m), Kronotskiy (3528 m), Kluchevskoy (4850 m), Tolbachik (3682 m), and Shiveluch (3283 m) (Fedotov *et al*. 1991).

8.1.2 Climate

The climate of Kamchatka is humid and moderately cold (Chukreiev 1970), with a humid snowy winter and short cold summer. The north-south mountains, however, accentuate the climatic gradients across the peninsula. Two climatic provinces are recognized: a submaritime to subcontinental region in the central depression and a maritime to suboceanic province along the coasts.

The maritime-suboceanic coastal climate results from cyclones originating in the northern Pacific Ocean (Anonymous 1966–1971) and has *Betula ermanii* as the zonal vegetation. The cyclones bring damp Pacific air and produce high precipitation in the *Betula ermanii* areas, ranging from 900 mm to 1400 mm per year. The prevalence of cloudy weather in summer causes relatively low mean summer temperatures, ranging from 10°C to 13°C, with maximum in August. Precipitation is distributed nearly equally throughout the year. Maximum snow depth reaches 120–170 cm. Mean annual temperature ranges from −2°C to +2°C, with cold-month mean temperatures from in −8°C to −10°C.

In central Kamchatka the climate abruptly becomes more continental, with mean annual temperatures from −2°C to −3°C, highest monthly mean (July) around 15°C and lowest monthly mean (January) ranging from −18°C to −20°C. This climate is similar to the boreal climate on the mainland. The zonal vegetation here is larch and spruce forest. *Betula ermanii* forms a zonal vegetation belt at 600–800 m in the mountains (Shamshin 1999).

8.2 Eco-biological features of *Betula ermanii*

Betula ermanii belongs to the section Costatae Rogolch. of the genus *Betula*. This is the section that also includes *Betula costata* Trautv., which occurs in southeasternmost Russia and is a component of the mixed forests with broad-leaved nemoral trees and Korean pine. This section also includes *Betula* *raddeana* Trautv., which occurs in the Caucasus mountains (Komarov 1934–1964). The Far Eastern species *Betula ermanii* is a taxonomically broad species including a number of narrower species distinguished by Russian taxonomists. These are *Betula lanata* (Regel) V. Vassil., occurring in continental areas; *B. velutina* V. Vassil. on the Shantar Islands; *B. paraermanii* V. Vassil. on Sakhalin; and *B. ulmifolia* Sieb. et Zucc. in Japan (Vasiliev 1941).

Trees of *Betula ermanii* have very wide, low crowns with side branches developed at the same angle as the axial stem. When the terminal bud of young trees reaches outside the snow cover, the axial shoot is damaged, perhaps killed by snow abrasion, and is replaced by the shoot from the lateral bud. This is the main reason for the crooked stems in many stands. The wide, prostrate crown makes the trees wind-tolerant and causes snow accumulation, which is greater than in the dark-conifer or larch stands under similar conditions (Tarankov & Ponomarenko 1967). The late snowmelt and short snow-free period limits potential conifer competitors. The maximum size of trees is 1.3–1.8 m in diameter and 15–25 m in height. The recorded maximum age is 500 years (Ageienko & Klintsov 1969).

Betula ermanii is shade-intolerant, but its saplings can survive under a birch canopy, unlike other birch species (Alexeyev & Shamshin 1972). The canopy does not affect sapling development. In the opinion of Shamshin (1999), the crown shape results from the adaptation of birch to the cloudy, foggy summer conditions. The distribution of assimilation organs in a horizontal plane permits better use of the diffuse light.

In the area of intense volcanism, *Betula ermanii* shows very high tolerance to burying by tephra (eruption products falling back to the ground, including ash, lapilli and volcanic bombs). The critical depth of basalt tephra for *Betula ermanii* is up to 80 cm in winter, as indicated on the Avacha volcano in southern Kamchatka. During a summer eruption on Tolbachik (central Kamchatka), a 20 cm tephra layer appeared to be fatal for stone birch stands. On Ksudach volcano the critical depth of pumice tephra for most trees was 60 cm (Grishin *et al*. 1996b). After the ashfall *Betula ermanii* may regenerate actively under the protection of surviving trees. Saplings on the tephra deposits usually form a root system on the tephra surface first, since the trees are suffering from a severe nutrient and moisture deficit. After the roots reach the buried soil horizons, the growth of *Betula ermanii* makes a distinct jump and then continues normally. On the currently erupting Karymskiy volcano, a very high tolerance of assimilation organs to the volcanic dust was also recorded (Grishin *et al*. 2000).

8.3 Stand dynamics

Due to the moist summer climate and late snowmelt, fires happen rarely in the *Betula ermanii* forest. Most stands show well-developed gap dynamics with regeneration of birch in gaps formed by the death of one or more canopy trees (Shamshin 1999). Most of the natural birch stands are in a gap phase. One important factor constraining the saplings is the dense tall herb cover. As a result, seedlings may only survive on fallen logs. The number of saplings in this community ranges from 180 to 300 per hectare. Regeneration in small-herb and shrub communities proceeds successfully on the ground, usually with 300 to 800 saplings per hectare. The saplings usually form dense patches in their first decade. Self-thinning starts at 15–25 years. After 60–70 years the young trees reach the main canopy.

After fire in conifer forests *Betula ermanii* may occupy extensive areas close to the *Betula ermanii* zone, including sites of burned *Picea ajanensis* and *Larix dahurica* forests (Man’ko & Voroshilov 1978). In southernmost regions *Betula ermanii* forms secondary stands mixed with *Quercus mongolica*, replacing the burned fir-spruce forests on sea-facing southern slopes (Krestov 2001).

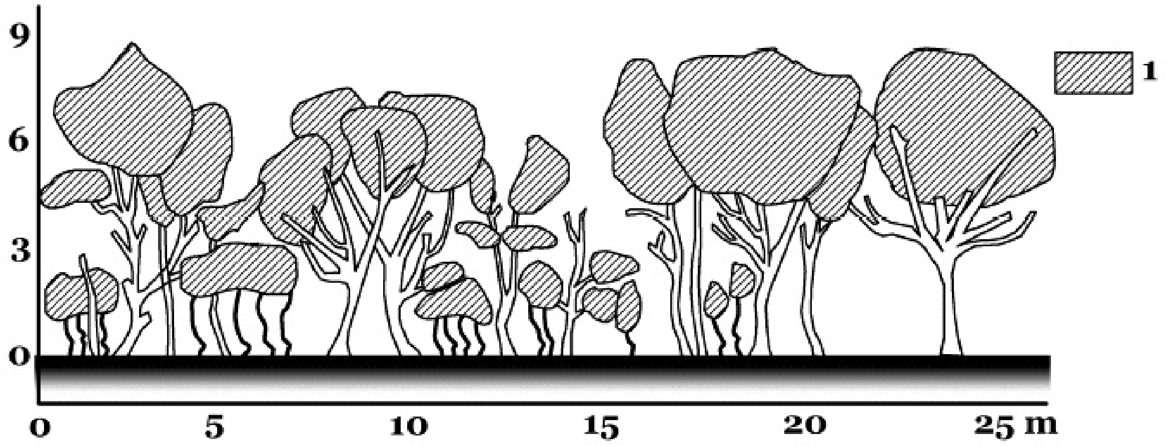

Figure 5.36. Profile of typical *Betula ermanii* stand (5 m deep x 25 m long): 1 = *Betula ermanii* (after Grishin *et al*. 1996b).

Post-fire stands keep their even-aged structure until reaching the gap phase after 150–200 years. If seed sources are available for conifer reforestation within the dark-conifer zone, spruce and fir re-colonize the burned area within a few years after fire and reach the birch canopy after 80–100 years, forming mixed stands. After reaching the gap phase, a new generation of birch appears in the gaps and remains until it is suppressed by more shade-tolerant competitors, namely spruce and fir.

8.4 Phytocenotic structure and composition

Betula ermanii forests are characterized by their monodominant, one-layer uneven-aged structure (Shamshin 1974), their dense canopies but widely spaced stems, and their well-developed herb layers (Fig. 5.36). The species composition of stands varies from site to site, but it always contains a species complex characteristic for suboceanic areas: *Filipendula camtschatica*, *Lonicera chamissoi*, *Aconitum maximum*, etc.

8.4.1 Tree layer

Betula ermanii dominates the stands, forming a well-developed canopy with a cover of 70–80%. *Sorbus sibirica* and *Salix caprea* may occur in the canopy as individuals. Canopy gaps formed by the death of a single tree may reach 20 m in diameter. Birch regeneration occurs in the gaps on decomposing fallen stems. The appearance of birch saplings is inhibited by the dense herb layer (Shamshin 1999). Most old-growth stands have a well-developed, uneven-aged structure with several generations present. Almost half the trees in such stands are younger than 100 years. The usual state of the stone-birch stands is a gap phase, with intensive regeneration of birch in the gaps. In the tall herb communities, saplings can survive only on decomposing fallen logs. In the shrub and small-herb communities, saplings may also be present. The normal number of saplings in the stands varies from 300 to 600 per hectare.

8.4.2 Shrub layer

Alnus fruticosa, *Pinus pumila* and *Sorbus sambucifolia* may form the tall-shrub layer in stone birch stands. In various community types boreal shrubs such as *Lonicera caerulea*, *L. chamissoi*, *Rosa acicularis*, *R. amblyotis*, *Salix bebbiana*, *S. pulchra*, *Juniperus sibirica* and *Spiraea beauverdiana* are common on mesic zonal sites. In stands close to treeline, subalpine shrubs, in particular, *Rhododendron aureum*, *R. camtschaticum* and *Ledum decumbens*, may augment the species composition.

8.4.3 Herb layer

The herb layer varies widely depending on site ecology and includes several strata. Most common in the tallest stratum, reaching 2 m, are *Angelica ursina* (in the south and west), *Heracleum lanatum*, *Senecio cannabifolius*, *Cacalia hastata*, *Cirsium kamtschaticum*, *Veratrum alpestre*, *Aconitum maximum*, *Urtica platyphylla* and *Filipendula camtschatica*. This group is usually called ‘Kamchatkan tall herbs’ (Morozov & Belaya 1988). In the second stratum, 30–80 cm high, the most common species are *Thalictrum minus*, *Pteridium aquilinum*, *Dryopteris expansa*, *Aruncus dioicus*, *Actaea erythrocarpa*, *Trillium camschatcense*, *Artemisia opulenta*, *Saussurea pseudotilesii*, *Trollius riederianus*, etc. A group of small taiga herbs occurs mainly in the lower stratum: *Maianthemum dilatatum*, *Chamaepericlymenum canadense*, *Viola selkirkii*, *Circaea alpina*. These may dominate in communities on fresh sites. At the contact with tundra vegetation near treeline and at contacts between mountain slopes and flats, a complex of alpine and subalpine species may dominate the herb layer: *Rhododendron camtschaticum*, *Loiseleuria procumbens*, *Phyllodoce caerulea*, *Diphasiastrum alpinum*, *Arctous alpina*, etc.

8.4.4 Moss and lichen layer

Because the whole *Betula ermanii* forest area is in a humid climate, and thus has well-developed herb layers, a moss-lichen layer is not typical. Circumboreal green mosses *Hylocomium splendens* and *Pleurozium schreberi* may occur sparsely under the herb layer.

Table 5.16. Classification of Betula ermanii forests, with indicator species, ecology, topographical position of association groups. Abbreviations for edatopes as in table 5.7.

Grex associationum	Indicator plants	Edatope	Topography, aspect
	Formatio: *Betuleta ermanii*		
	Classus associationum: *Betuleta ermanii purum*		
Betuleta ermanii herbosa boreali	*Artemisia opulenta, Saussurea pseudotilesii, Thalictrum minus, Aruncus dioicus*	F–M, MN–R	Flats and gentle slopes with well-drained soils
Betuleta ermanii grandiherbosa	*Filipendula camtschatica, Senecio cannabifolius, Cacalia hastata, Cirsium kamtschaticum, Angelica ursina*	M–VM, MN–R	Flats and gentle slopes on snow- accumulation sites
Betuleta ermanii dryopteridosa	*Dryopteris expansa, Maianthemum dilatatum, Climacium dendroides*	F–M, MN	Medium and steep northern slopes
Betuleta ermanii calamagrostidosa	*Calamagrostic langsdorffii, Veratrum alpestre, Iris setosa, Trisetum sibiricum*	VM, MN	Gentle concave slopes and ephemeral streams
Betuleta ermanii alnosa fruticosae	*Alnus fruticosa, Streptopus amplexifolius, Spiraea beauverdiana*	M–VM, MN–R	Moist flats and gentle slopes near timberline
Betuleta ermanii fruticulosa	*Phyllodoce caerulea, Rhododendron aureum, Empetrum sibiricum, Artemisia arctica*	SD–M, P	Well to imperfectly drained sites near timberline

Figure 5.37. Typical stand of Betuleta purum (photo by P. Krestov).

8.5 Phytocenotic diversity

The rather narrow specialization of *Betula ermanii* to humid snowy climates and the relatively integrated complex of accompanying species makes it difficult to recognize association classes supported by a climatic complex of differential species (Fig. 5.37). The only class, *Betuleta purum,* derives from the comparative analysis of *Betula ermanii* communities (Table 5.16).

Different authors (Kabanov 1972, Balmasova 1994, Shamshin 1999) distinguish up to six association groups, reflecting mainly edaphic differences between the sites. Species richness in the stone-birch communities totals 147 species, with the average number of species per relevé ranging from 20 in tall-herb communities to 50 in communities with herbs of more normal height.

Association groups *Betuleta ermanii herbosa boreali* and *Betuleto ermanii altiherbosa* occupy zonal sites (mesic, drained, gently sloping) and have the widest distribution in the area of stone-birch forests. The differences in understorey vegetation reflect differences in the soil nutrient regime: tall herbs indicate rich soils and medium boreal herbs indicate medium soils. Diagnostic species for the tall-herb communities are *Senecio cannabifolius*, *Filipendula camtschatica* and *Cirsium schantarense*, which can dominate in herb layers that may reach 3 m in height. Important companions in the south are *Angelica ursina* and *Peracarpa circaeoides*. Because of the dense herb layer, a middle stratum is absent. A lower stratum may occur as fragmented synusiae of suppressed small taiga herbs, under the tall-herb stratum: *Maianthemum dilatatum, Trientalis europaea* and *Circaea alpina*. The communities with boreal herbs have a well-developed layer of medium herbs, of which diagnostic species are: *Artemisia opulenta*, *Geranium erianthum*, *Saussurea pseudotilesii*, *Solidago spiraeifolia*, *Thalictrum minus* and *Moehringia lateriflora* (in lower stratum). The lower stratum is well developed, with the prevalence of *Maianthemum dilatatum*, *Lycopodium clavatum*, *Chamaepericlymenum canadense*, *Rubus arcticus*, etc.

9. PINETA PUMILAE

The Siberian dwarf-pine, *Pinus pumila*, is one of the most unusual and interesting woody species in its appearance and adaptations. It occurs widely in northeastern Asia, in Magadan (Kolyma basin, upper Anadyr basin), the Koryakia region, and northern Kamchatka (Tikhomirov 1949, Sochava & Lukitchova 1953, Grosset 1959). As a vertical vegetation belt, dwarf-pine also occurs over all of boreal and north-temperate eastern Asia, including Hokkaido (Kojima 1979, Okitsu & Ito 1984, 1989), eastern Siberia (Molozhnikov 1976, Tiulina 1976), central and southern Kamchatka (Neshataev & Neshataeva 1985, Neshataeva 1994, Khomentovskiy 1995, Grishin 1996) and the southern half of Pacific Russia (Grishin *et al*. 1996a, Krestov 1999). *Pinus pumila* communities form a horizontal vegetation zone across submaritime, maritime and suboceanic sectors of the subarctic zone, named by Kolesnikov (1961, 1963) the Beringian woodlands (Fig. 5.38). *Alnus fruticosa* thickets increase in this zone towards the Pacific Ocean and appear to be the dominant vegetation type on zonal sites in the northern Kurils. Meanwhile, dwarf-pine stands occur on well-drained substrates, such as coastal sand dunes, mountain ridges, old lava flows and tephra deposits (Grishin 2000).

Pinus pumila belongs to the section Cembrae of the genus *Pinus*, together with *P. albicaulis*, *P. sibirica* and *P. koraiensis*. Morphologically *P. pumila* is close to *P. sibirica* except that it never forms straight vertical stems; eco-biologically it appears to be somewhat similar to the western North American species *P. albicaulis* (Khomentovskiy 1995). A closely related species, *P. parviflora* Sieb. et Zucc., occurs in Japan and was described by Regel.

From a total area of 35 million hectares occupied by *Pinus pumila* communities, 25 million hectares represent its horizontal zone, stretching from the Kolyma River to Koryakia and northern Kamchatka (Krylov *et al*. 1983), roughly between latitude 60 and 68°N.

9.1 Physiography

9.1.1 Terrain

The area where *Pinus pumila* forms monodominant communities on zonal sites stretches approximately from 60°N to 67°N, within the intensively dissected mountainous terrain of northeasternmost Asia that includes Magadan, Koryakia and Kamchatka. The basic mountain systems in the continental areas are the Koryakia Uplands, the Anadyr and Aniuy ranges, the Yukagir Uplands, and the Okhotsk-Kolyma Uplands. Mountains in more coastal areas include the foothills of the northern Sredinniy and Vostochniy ranges in Kamchatka, with elevations up to 4850 m (Kluchevskoy volcano). The Koryakia Uplands are separated from the Magadan mountains by the extensive Penzhina lowlands, stretching over several hundred kilometers along the Penzhina River. On Kamchatka *Pinus pumila* occupies the lower montane belt in the north, most of the volcanic mountains along the Pacific coast, and Cape Lopatka at the southern tip. In the rest of its range, *P. pumila* thickets form a well-developed vertical belt above treeline, at elevations from 1600 m in the south (Sikhote-Alin) to 400–500 in the north.

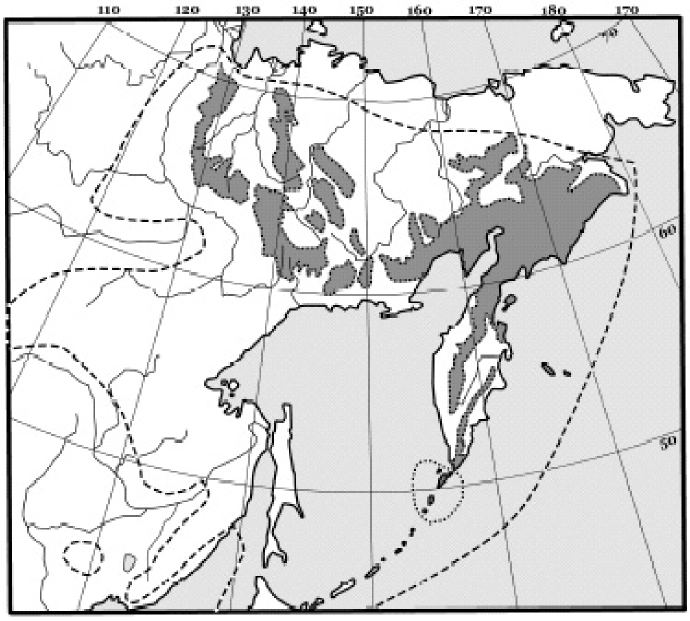

Figure 5.38. Distribution of dwarf-pine (*Pinus pumila*) thickets on zonal sites (shaded area), with the range of *Pinus pumila* (dashed line).

9.1.2 Climate

The climate varies from continental in the interior to suboceanic in eastern and southern Kamchatka and the northern Kuril Islands. By the heat-sum criterion, the area has been included in the subarctic zone (Vitvitskiy 1961), with mean annual temperature below 0°C. Mean January temperature in coastal regions does not fall below −20°C, but in the interior (Magadan) it may fall to −40°C. Snow depth in eastern Kamchatka reaches 1–1.5 m, decreasing toward the interior to 30–40 cm. The proportion of larch in dwarf-pine communities increases along this gradient inland. July mean temperatures vary from 10–15°C in eastern Kamchatka and Koryakia to 15–18°C in interior Magadan. Average annual precipitation ranges from 1100 mm in southeastern Kamchatka to 200 mm in the upper Kolyma basin.

9.2 Eco-biological features of dwarf pine

The ecoform of Siberian dwarf pine seems not to have an analog among other tree or shrub species. Adaptation to severe climatic conditions with deep snow cover results in a very specific crown architecture (Fig. 5.39) and seasonal dynamics. Many authors include the growth form of *Pinus pumila* in the class of dwarf trees (Neshataeva 1983, Sochava 1986, Khomentovskiy 1995). Over most of its range, however, *P. pumila* also occurs as a shrub, with more intensive development of side branches.

Under favorable conditions (well developed soil profile), *Pinus pumila* grows as a dwarf tree with one main stem lying on the ground and well-developed upwardly growing branches, elevated to about 6 m in summer. In northern Sakhalin the largest basal diameters measured were 32 cm, stem length 14 m, and branch height 4 m; on the Shantar Islands the largest recorded basal diameter was 40 cm.

Figure 5.39. A, B. Main crown-architecture types of *Pinus pumila*: A = dwarf tree (photo by P. Krestov), B = cup-shaped dwarf tree (photo by S. Grishin).

These dimensions clearly characterize the typical form of dwarf pine as a dwarf tree. It mostly occurs in valleys or on gentle slopes under the influence of frequent strong winds. Cup-shaped trees occur on slopes and flat surfaces. The branch distribution provides equal access to light. Branches directed downward are better developed than others.

The pine drops its branches onto the ground with the first frosts in autumn, before snow, then lifts them again in spring. Through a series of experiments, monitoring the anatomical properties of the wood, Grosset (1959) showed strong relationships between temperature, humidity, and branch elevation. He also found that the dropping of branches in autumn, even before snow, is caused by the freezing of the water in tracheids of two different types of tissue: pulling tissue that retains its volume after freezing and inclination tissue that contracts after freezing (Fig. 5.40). Having no possibility to show this research in detail, we illustrate its principal results in Tables 5.17–5.19. Different amount of contraction appeared in tissues after the water froze, causing the branches to droop down to the ground.

Although snow depth is widely considered to be the most important factor determining the growth form and seasonal dynamics of dwarf pine, there does not appear to be a direct relationship. In Magadan, with its severe winters, the dwarf-pine thickets are completely covered by snow. Tikhomirov (1949) showed that change in snow regime, caused by removal of a larch layer or change in wind direction, initiates a reconstruction of the dwarf-pine community through death of the tallest individuals and decrease in stand height. In contrast, in some places on Kamchatka with mild winters and very deep snow cover, the dwarf-pine thickets remain above the snow during the whole winter (Khomentovskiy 1995). Snow cover does protect dwarf pine from freezing and from high insolation. The western boundary of the range of dwarf pine closely coincides with the isoline for 40 cm of snow depth (Khomentovskiy 1995).

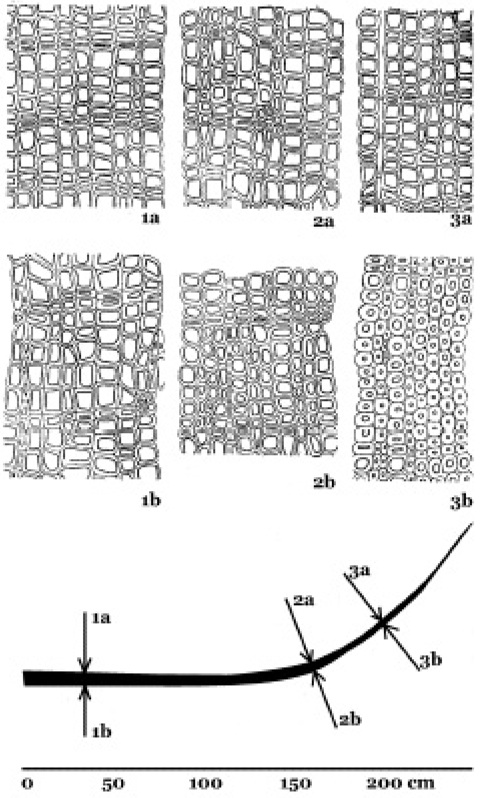

Figure 5.40. Wood structure of two-year-old reptant and upright dwarf-pine stems. In the peripheral parts of reptant stems, the wood is similar on both the dorsal and ventral sides (sections 1a and 1b), and inclination wood is absent. As the stem starts to rise the inclination wood (round cells with thicker walls) is poorly developed on the ventral side (2b). In the erect part of the stem, pulling and inclination wood tissues are clearly differentiated (Grosset 1959).

Although the oldest recorded age of *Pinus pumila* at its base does not exceed 250 years (Grosset 1959), the growth of a *P. pumila* individual continues much longer, due to the constant renewal of the root system (Khomentovskiy 1995). Branch elongation increments, unlike diameter or height increments of erect trees, do not change with age. Rates of branch elongation may also vary from site to site, depending on site quality and regional climate (Okitsu 1988, Sano *et al.* 1977). Khomentovskiy (1995) found that branch elongation by *Pinus pumila* in Kamchatka varies from 30–40 mm per year at low elevation (0–

300 m), through 50–60 mm at 300–900 m, to 10–20 mm from 900 to 1300–1400 m.

Our research on the areas influenced by volcanism showed very low tolerance of *Pinus pumila* to volcanic ash. Even small amounts of tephra destroy the buds on branches, and minor abrasion causes death of the whole branch (Grishin *et al.* 2000). Occurrence of dwarf-pine thickets decreases abruptly in the areas influenced by ashfall, until they disappear completely, as in the northern Kurils. On southern Paramushir, dwarf pine was excluded from the vegetation cover by the activity of the Chikurachki volcano (Grishin 2000).

Table 5.17. Hygroscopic moisture content and contraction of pulling and inclination wood tissue of dwarf pine relative to relative air humidity (after Grosset 1959).

Observation number	Type of wood tissue	Relative air humidity at 20°C											
		98		91		75		50		25		0	
1	Pulling	-	-	26.05	0.23	16.20	0.44	10.75	0.55	6.62	0.66	0.00	0.97
	Inclination	-	-	29.00	3.13	17.62	5.73	12.2	7.14	7.65	8.36	0.00	10.27
2	Pulling	30.00	0.00	23.40	0.02	17.70	0.04	8.84	0.06	6.71	0.06	0.00	0.08
	Inclination	31.2	0.35	26.13	1.06	18.55	2.25	10.06	3.30	7.89	3.58	0.00	4.43

Table 5.18. Contraction (length) of inclination and pulling wood of dwarf pine as temperature decreases from +18°C to −25°C ex situ: length at −25°C as % of length at +18°C (after Grosset 1959).

Observation number	Type of wood tissue	Moisture of wood as % of absolutely dry weight									
		10	20	30	40	50	60	70	80	90	100
1	Pulling	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Inclination	0.00	0.00	0.72	1.18	1.33	1.80	2.00	1.90	1.70	1.50
2	Pulling	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
	Inclination	0.00	0.00	1.25	1.80	2.16	2.12	2.00	1.70	1.50	-
3	Pulling	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
	Inclination	0.00	0.00	0.21	0.57	1.12	1.56	1.85	1.60	1.50	-
4	Pulling	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.28	0.00	0.28
	Inclination	0.00	0.00	0.20	0.56	0.81	1.11	1.30	1.20	1.10	1.00
5	Pulling	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20
	Inclination	0.00	0.00	0.31	0.56	1.11	1.55	1.45	1.40	1.30	-
6	Pulling	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.08	0.08	0.04
	Inclination	0.00	0.00	0.10	0.51	0.81	0.96	1.20	1.10	1.00	0.80

Table 5.19. Change of branch-top vertical position, lengthwise contraction of inclination wood and amount of water freezing in pinewood branches of 130 cm, with 1°C temperature decreases within 5°C intervals (after Grosset 1959).

Parameters	Temperature intervals (°C)					
	50 to 0	0 to −5	−5 to −10	−10 to −15	−15 to −20	−20 to −25
Change of branch top (cm per 1°C)	0.00	5.08	3.35	2.27	2.08	1.72
Lengthwise contraction (%)	0.00	0.15	0.12	0.10	0.05	0.02
Amount of freezing water (% of absolute dry weight of wood)	0.00	7.00	1.20	0.60	0.20	0.20

9.3 Stand structure and dynamics

A main feature of dwarf-pine stands is the lack of any generation structure in the canopy due to the continuous growth. Old-growth stands typically look like completely closed communities, with little or no moss cover and with very few herbs or dwarf-shrubs. A dwarf-pine community may reach this stage after 100–150 years, as roughly estimated by Khomentovskiy (1995). Dwarf pine may regenerate from seeds within occasional gaps appearing after disturbances or forming above dying old basal parts (Tikhomirov 1946). The process of natural regeneration in the old-growth communities has not been studied.

Dwarf pine is an important species in primary succession on new subalpine and subarctic substrates, such as coastal sand dunes, lava flows and ash deposits after volcanic eruptions, and areas affected by wildfires. Seedlings of *Pinus pumila* may appear on the new substrate a year after disturbance, growing from seeds brought by the nutcracker *Nucifraga caryocatactes* ssp. *macrorhynchos* in eastern Siberia or *N. caryocatactes* ssp. *kamtschatkensis* in the northern Far East. In the first 40–60 years dwarf pine grows in length, forming a well-developed crown by the end of the period. New shrubby trees never form a closed cover on new substrates or on space made available after fire, and the whole stand looks like a well-spaced woodland with tundra communities developing between the shrubs. Over all this period, new seedlings appear on the pine-free spaces, gradually forming a closed stand by a stand age of 100–150 years.

Light deficiency under the pine canopy limits the development of herb and moss layers, but these layers can form in old-growth stands with long branches. There is a complex of species closely related to the pine thickets in the subarctic or the subalpine belts: *Rhododendron aureum*, *Carex rigidioides*, *Salix berberifolia*, and *Bistorta elliptica*. Over the whole range of dwarf-pine thickets, the main companions are: *Alnus fruticosa*, *Betula exilis*, *B. middendorffii*, *Calamagrostis lapponica*, *Carex lugens*, *Empetrum nigrum*, *Eriophorum vaginatum*, *Aconogonum tripterocarpum*, *Salix fuscescens*, *Vaccinium uliginosum*, *Petasites frigidus*, *Pinguicula spathulata*, etc. Also *Arctous alpina*, *Cassiope ericoides*, *C. tetragona*, *Diapensia obovata*, *Hierochloë alpina*, *Loiseleuria procumbens*, *Salix glauca* and *Saussurea alpicola* appear at the contacts between dwarf-pine thickets and tundra communities. In dwarf-pine communities within forest zones, on a wide range of ecotopes, *Pinus pumila* may form stands together with *Larix dahurica*, which is present as solitary trees. Such stands may also include *Andromeda polifolia*, *Calamagrostis langsdorffii*, *Carex appendiculata*, *C. globularis*, *Ledum palustre*, *Lycopodium annotinum*, *Linnaea borealis*, *Maianthemum bifolium*, *Pentaphylloides fruticosa*, *Rosa acicularis*, *Salix myrtilloides*, *Spiraea betulifolia*, *Vaccinium myrtillus*, etc.

9.4 Phytocenotic diversity

The wide distribution of *Pinus pumila* causes slight differences in species composition between communities occurring as a horizontal zone, (subarctic Beringian Woodlands) and as subalpine belts (in southeastern and eastern Siberia). Due to the great radiation of subarctic species to the south, through the mountain ranges, the dwarf-pine thickets keep a relatively stable species composition and structure across their whole range. They cannot be classified by differential species indicating climatic variations. All variation within *Pinus pumila* communities is caused mainly by substrate type and proximity to tundra or forest vegetation.

The only association class, *Pineta pumilae purum*, was described over the whole range of *Pinus pumila* (Table 5.20). The main features of this class are: 1) dominance by *Pinus pumila*, which forms a closed canopy (40–95% cover); 2) presence and cenotic activity by a complex of subarctic/subalpine species

Table 5.20. Classification of dwarf pine thickets, with indicator species, ecology, topographical position of association groups. Abbreviations for edatopes as in table 5.7.

Grex associationum	Indicator plants	Edatope	Topography, aspect
	Formatio: *Pineta pumilae*		
	Classus associationum: *Pineta pumilae purum*		
Pineta purum cladinosa	*Cladina stellaris, C. rangiferina, Lerchenfeldia flexuosa, Empetrum sibiricum*	D–SD, VP–P	Well-drained flats and slopes
Pineta purum hylocomiosa	*Hylocomium splendens, Trientalis europaea, Gymnocarpium dryopteris*	SD–F, P–MN	Northern slopes near treeline
Pineta purum fruticosa	*Ledum decumbens, Rhododendron aureum, Spiraea beauverdiana, Vaccinium uliginosum*	F–M, MN–R	Flats with evidence of snow accumulation
Pineta purum sphagnosa	*Sphagnum subtile, S. fuscum, Betula exilis, Rubus chamaemorus*	VM–W, P–MN	Depressions and poorly drained valleys
	Formatio: *Alneta fruticosae*		
	Classus associationum: *Alneta fruticosae purum*		
Alneta purum herbosa taigae	*Maianthemum dilatatum, Trientalis europaea, Lycopodium clavatum*	F, MN–R	Well-drained flats and slopes
Alneta purum dryopteridosa expansae	*Dryopteris expansa, Calamagrostis purpurea*	M, MN–R	Northern slopes
Alneta purum glyceridosa alnastereti	*Glyceria alnasteretum, Cirsium kamtschaticum*	VM, MN	Flats and slopes with snow accumulation
Alneta purum grandiherbosa	*Senecio cannabifolius, Filipendula camtschatica, Urtica platyphylla, Peracarpa circaeoides*	VM, R	Flats with snow accumulation

(*Rhododendron aureum*, *Ledum decumbens*, *Carex rigidioides*, *Sorbus sambucifolia*, *Cassiope ericoides*, *C. tetragona*, *Hierochloë alpina*, etc.); and 3) presence but never canopy formation by other tree species at the contacts with forest vegetation, usually *Larix dahurica*, rarely *Pinus sylvestris*, *Picea ajanensis* or *Betula ermanii*. Phytocenotic diversity is represented by four basic association groups (Table 5.20).

10. ALNETA FRUTICOSAE

This vegetation type occurs on saturated sites throughout the Beringian Woodland area and forms pure stands on zonal sites in easternmost Koryakia, southeastern Kamchatka, and on the northern Kuril Islands (Grishin 2000). Within this area, *Pinus pumila* occupies mainly mountain ridges, very steep slopes and well-drained substrates, such as alluvium deposits, coarse morainal deposits and surfaces of old lava flows. *Alnus fruticosa* occupies a wide range of ecologically different sites from sea level to 600–700(900) m.

Alnus fruticosa shows close relationships with many parameters of the subarctic suboceanic climate, such as the Kira warmth index (Grishin 1995), winter precipitation (snow depth in valleys may reach 5 m), the relatively narrow annual temperature range (only 49°C on the northern Kurils), frequent winter thaws (absolute January maximum of +13°C in the northern Kurils (Anonymous 1966–1971) and very low insolation in summer, due to fog and cloudiness (total hours <1000–1500 per year).

All communities dominated by *Alnus fruticosa* were assigned to formatio *Alneta fruticosae* and to the only association class *Alneta fruticosae purum* (Fig. 5.41). Variation in the community types is caused mainly by edaphic characteristics. The association group *Alneta purum herbosa taigae* is widespread on drier sites with medium soil nutrient regimes. The main zonal communities on the northern Kurils belong to the *Alneta purum dryopteriosa expansae* and *Alneta purum glyceriosa alnastereti*.

Figure 5.41. Typical community of *Alneta purum* (photo by P. Krestov).

11. SUMMARY

This overview of studies on the vegetation cover of the Russian Far East did not include many local, descriptive but not less important works, which describe basic gradients, trends and changes in vegetation. The scientific environment in 20th century Russia was dominated by ideas of discreteness and sharp boundaries in the vegetation cover, with classification based on dominance and poor development of gradient studies. At first this quickly brought valuable results in inventory of the vegetation cover over the huge territory, but it also resulted in a gap in methodological and theoretical understanding of the complex interrelations in the vegetation cover of the region.

Although extensive classification studies in the Russian Far East had generated numerous local classification schemes, no school was strong enough to convince vegetation ecologists to use commonly accepted classification principles. Since the Braun-Blanquet methodology could not be such an integrating basis, for political reasons, researchers used different methodologies for vegetation classification. Forestry chose to simplify existing schemes (as described at the beginning).

Russian reaction to the Braun-Blanquet methodology, after a century of prevalence by Sukachov’s dominance paradigm, was so strong that the main Russian-language vegetation-ecology journals repeatedly rejected phytosociological papers based on Braun-Blanquet until the 1980s. With information exchange between Russian and foreign phytosociologists largely blocked, syntaxonomical schemes developed by Russian authors are hardly commensurate with the well-developed syntaxonomies of adjacent regions (Japan) or regions in the same vegetation zones (boreal and temperate Europe and North America). The many local studies based on limited material collected from too few areas were insufficient to characterize the dominant community types.

All of this outlines a viscous circle of problems, which may be addressed in the near future. These problems are: 1) vegetation classification of eastern Russia, providing the opportunity to assess the biodiversity of the region properly; 2) identification of the position of the Russian Far East in the ecological, biogeographical, social, economic, and cultural values of the world community; and 3) guaranteeing support for these values for future generations.

12. ACKNOWLEDGEMENTS

Some of the studies referenced in this chapter were carried out under support from the Russian Foundation for Basic Research, grants # 01-04-48593, 01-04-63024, 01-04-63096 and 99-05-64556. I thank Drs. Sergei Grishin, Valentine Yakubov, Valentina Verkholat and Prof. Dr. Claus Dierβen for valuable comments on primary versions of manuscript and submitted photographs, Prof. Elgene Box making the English text readable; and editors Drs. Jiří Kolbek and Miroslav Šrůtek for the idea of this book and very valuable supervision at all stages of work.

13. REFERENCES

Ageienko, A.S. & Klintsov, A.P. 1969. Forests of Sakhalin and Kuril Islands. [Lesa Sakhalina i Kurilskih ostrovov.] In: Anonymous. Forests of [Russian] Far East. [Lesa Dalnego Vostoka.] Lesnaya Promyshlennost, Moscow (in Russian).

Alexandrova, V.D. 1973. Russian approaches to classification of vegetation. In: Whittaker, R.H. (ed.), Ordination and classification of communities. Handbook of Vegetation Science, pp. 493–527. W. Junk, The Hague.

Alexeiev, V.A. & Shamshin, V.A. 1972. On ecology and structure of stonebirch forests on Kamchatka. [Ob ecologii i strukture kamennoberezovyh lesov Kamchatki.] Bot. Zhurn. 57: 1055–1068 (in Russian, with English summary).

Aliokhin, V.V. 1930. The map of vegetation of the Asian part of Russia. Scale 1: 16,000,000. [Karta rastitelnosti asiatskoy chasti Rossii. Masshtab 1:16,000,000.] Goskartogeodezia, Leningrad (in Russian).

Aliokhin, V.V. 1950. The map of vegetation of the USSR. Scale 1: 18,000,000. [Karta rastitelnosti SSSR. Masshtab 1:18,000,000.] In: Aliokhin, V.V. (ed.), The plant geography. [Geografiya rasteniy.] Uchpedgiz, Moscow.

Anonymous. 1990. Reference Book for the taxation of forests of [Russian] Far East. [Spravochnik dlya taksatsii lesov Dalnego Vostoka.] Dal'NIILKh, Khabarovsk, 526 pp. (in Russian).

Anonymous. 1966–1971. Reference book on the climate of the USSR [Spravochnik po klimatu SSSR] (Series of volumes). Gidrometeoizdat, Leningrad (in Russian).

Baburin, A.A. 1976. Flora and vegetation of upper-Bikin plateau. [Flora i rastitelnost Verkhne-Bikinskogo plato.] Bulleten GBS 99: 32–33 (in Russian).

Balmasova, M.A. 1994. Birch forests. [Berezoviye lesa.] In: Neshataev, Yu.N., Neshataeva, V.Yu. & Naumenko, A.T. (eds.), Vegetation of Kronotskiy state reserve [Rastitelnost Kronotskogo gosudarstvennogo zapovednika], pp. 41–76. Komarov Botanical Institute, St-Peterburg (in Russian).

Barkalov, V.Yu. 2000. Phytogeography of the Kuril Islands. Nat. Hist. Res. 7: 1–14.

Bobrov, E.G. 1978. Forest forming conifers of the USSR. [Lesoobrazuyushchiye khvoyniye SSSR.] Nauka, Leningrad, 189 pp. (in Russian).

Braun-Blanquet, J. 1951. Pflanzensoziologie. Grundzuge der Vegetationskunde. Springer-Verlag, Wien, 632 pp.

Budishchev, A.O. 1898. Description of forests of southern part of Prymorskaya oblast'. [Opisaniye lesov yuzhnoy chasti Primorskoy oblasti.] 2nd edition. Kancellaria Priamurskogo General-Qubernatorstva, Irkutsk (in Russian).

Cajander, A.K. 1926. The theory of forest types. Acta For. Fenn. 29: 1–108.

Chukreiev, V.K. 1970. The thermic indices for estimation of seasonality and zonality. [Teploviye indeksy dlya otsenki sezonnosti i zonalnosti.] Izvestia Vsesoyuznogo Geographicheskogo Obshchestva 4: 326–333 (in Russian).

Chumin, V.T. 1965. The role of fallen trees in regeneration of spruce forests. [Rol valezha v vozobnovlenii yelovyh lesov.] Publications of Dal'NIILKh 7: 135–149 (in Russian).

Chun, L.J. 1994. The broad-leaved Korean pine forest in China. In: Anonymous. Proceedings of the International Workshop on subalpine stone pines and their environment: the status of our knowledge, pp. 81–84. U.S. Department of Agriculture, Ogden.

Diukarev, V.N., Kozin, E.K. & Rosenberg, V.A. 1971. Age development and phytomass of moss-fern spruce forests of Sikhote-Alin. [Vozrastnoye razvitiye i fitomassa zelenomoshno-paporotnikovyh yelnikov Sikhote-Alinya.] In: Anonymous. Biological productivity of spruce forests [Biologichaskaya produktivnost yelovyh lesov], pp. 77–82. Tartu (in Russian).

Dmitrieva, N.G. 1960. Water cycle and drainage prognosis in Priamurye. [Vodniy tsikl i prognoz stoka v Priamurye.] Nauka, Moscow, 211 pp. (in Russian).

Dobrynin, A.P. 2000. Oak forests of the Russian Far East: biology, geography, origin. [Duboviye lesa rossiyskogo Dalnego Vostoka: biologiya, geografiya, proiskhozhdeniye.] Dal'nauka, Vladivostok, 260 pp. (in Russian).

Dokhman, G.I. 1960. On the system of diagnostic characters of vegetation units. [K sisteme diagnosticheskih ptiznakov edinits rastitelnosti.] Bot. Zhurn. 45: 637–648 (in Russian, with English summary).

Dolukhanov, A.G. 1957. On the key and discussional problems of mountain forests typology. [O nekotoryh uzlovyh i discussionnyh voprosah tipologii gornyh lesov.] Bot. Zhurn. 42: 1158–1171 (in Russian).

Dylis, N.V. & Vypper P.B. 1953. Forests of western slope of middle Sikhote-Alin. [Lesa zapadnogo makrosklona srednego Sikhote-Alinya.] Izdatel'stvo Akademii Nauk SSSR, Moscow, 336 pp. (in Russian).

Dylis, N.V. 1961. The larches of the Eastern Siberia and [Russian] Far East. [Listvennitsy Vostochnoy Sibiri i Dalnego Vostoka.] Izdatel'stvo Akademii Nauk SSSR, Moscow, 210 pp. (in Russian).

Efremov, D.F. 1964. Root systems of larch on Kamchatka. [Korneviye sistemy listvennitsy na Kamchatke.] Izvestia Sibirskogo Otdelenia AN SSSR 8: 12–19 (in Russian).

Ellenberg, H. 1980. Am Ost- und Westlands Eurasiens – ein vegetationsökologischer Vergleich. Phytocoenologia 7: 507–511.

Fedotov, S.A., Masurenkov, Yu.P. & Balesta, S.T. (eds.) 1991. Active volcanoes of Kamchatka. [Aktivniye vulkany Kamchatki.] Vol. 1 and 2. Nauka, Moscow.

Frey, T.E.A. 1973. The Finnish school and forest site types. In: Whittaker, R.H. (ed.), Ordination and Classification of Communities. Handbook of vegetation Science, pp. 403–433. W. Junk, The Hague.

Glagolev, V.A. 1984. The age dynamics of larch forests in Bikin River basin (Middle Sikhote-Alin). [Vosstanovitelno-vozrastnaya dinamika listvennichnikov basseina reki Bikin.] In: Anonymous. Dynamic processes in the forests of the Far East [Dinamicheskiye processy v lesah Dalnego Vostoka], pp. 91–103. Vladivostok (in Russian).

Gorodkov, B.N. 1958a. The vegetation and soils of the Wrangell Island. [Rastitelnost i pochvy ostrova Vrangelya.] In: Tikhomirov, B.A. (ed.), The vegetation of Far North of the USSR and its management [Rastitelnost Dalnego Severa SSSR i yeyo ispolzovaniye], pp. 5–58. Izdatel'stvo Akademii Nauk, Moscow (in Russian).

Gorodkov, B.N. 1958b. Analysis of the vegetation of the arctic desert zone on the basis of the investigations on the Wrangell Island. [Analiz rastitelnosti zony arcticheskih pustyn na osnove issledovaniy na ostrove Vrangelya.] In: Tikhomirov, B.A. (ed.), The vegetation of Far North of the USSR and its management [Rastitelnost Dalnego Severa SSSR i yeyo ispolzovaniye], pp. 59–94. Izdatel'stvo Akademii Nauk, Moscow (in Russian).

Gorovoi, P.G. (ed.) 1973. Flora, vegetation and resources of the Far East. Bibliography (1928–1969 years). [Flora, rastitelnost i rastitelniye resursy Dalnego Vostoka (1928–1969 gg.).] FEB RAS, Vladivostok, 552 pp. (in Russian).

Grichuk, V.P. 1984. Late Pleistocene Vegetation History. In: Anonymous. Late Quaternary environments of Soviet Union, pp. 155–178. Univ. Minnesota Press, Minneapolis.

Grishin, S.Yu. 1995. The boreal forests of northeastern Eurasia. Vegetatio 121: 11–21.

Grishin, S.Yu. 1996. The vegetation of subalpine belt of Kluchevskaya group of volcanoes. [Rastitelnost subalpiyskogo poyasa Klyuchavskoy gruppy vulkanov.] Dal'nauka, Vladivostok, 156 pp (in Russian).

Grishin, S.Yu. 2000. On phytogeography of Kuril Islands. [K fitogeografii Kurilskih ostrovov.] Izvestia Vserossiyskogo Geographicheskogo Obshchestva 132: 65–76 (in Russian).

Grishin, S.Yu., Krestov, P.V. & Okitsu, S. 1996a. The subalpine vegetation of Mt. Vysokaya, central Sikhote-Alin. Vegetatio 127: 155–172.

Grishin, S.Yu., del Moral, R., Krestov, P.V. & Verkholat, V.P. 1996b. The succession after catastrophic eruption of Ksudach volcano (Kamchatka, 1907). Vegetatio 127: 129–153.

Grishin, S.Yu., Krestov, P.V. & Verkholat, V.P. 2000. Influence of 1996 eruptions in the Karymskiy volcano group, Kamchatka, on vegetation. Nat. Hist. Res. 7: 39–48.

Grosset, H.E. 1959. *Pinus pumila* (Pall.) Regel. Materials on its biological study and economical utilization. [*Pinus pumila* (Pall.) Regel. Materialy po yego biologicheskomu issledovaniyu i economicheskomu ispolzovaniyu.] Moskovskoie Obshchestvo Ispytateley Prirody, Moscow, 144 pp. (in Russian, with English summary).

Hämet-Ahti, L., Ahti, T. & Koponen, T.A. 1974. Scheme of vegetation zones for Japan and adjacent regions. Ann. Bot. Fennici 11: 59–88.

Ishikawa, Yu., Krestov, P.V. & Namikawa, K. 1999. Disturbance history and tree establishment in old-growth *Pinus koraiensis* – hardwood forests in the Russian Far East. J. Veget. Sci. 10: 439–448.

Ishizuka K. 1974. Mountain vegetation. In: Numata, M. (ed.), The flora and vegetation of Japan, pp. 173–210. Kodansha, Tokyo.

Ivanov, N.N. 1959. The belts of continentality on the Earth. [Poyasa kontinentalnosti Zemli.] Izvestiya Vsesoyuznogo Geographicheskogo obshchestva 91: 410–423 (in Russian).

Ivashinnikov, Yu.K. 1999. Phisical geography of the Russian Far East. [Fizicheskaya geografia rossiyskogo Dalnego Vostoka.] Far Eastern State University Press, Vladivostok, 324 pp. (in Russian).

Ivashkevich, B.A. 1933. Far Eastern forests and their industrial future. [Dalnevostochniye lesa i ih promyshlennoye budushcheye.] DV OGIZ, Khabarovsk, 169 pp. (in Russian).

Kabanov, N.E. 1972. Stone birch forests in relation to its phytogeography and forestry. [Kamennoberezoviye lesa v otnoshenii ih fitogeografii i lesovodstvennyh svoystv.] Nauka, Moscow, 137 pp. (in Russian).

Kamibayashi, N., Man'ko, Yu.I., Kondho, A. & Gladkova, G.A. 1994. Detection of forest decline in northeast Primorye, Russia. Photogrammetry and Remote Sensing 5: 213–216 (in Japanese).

Kartashov, Yu. G. 1984. Stand structure in spruce forests with *Vaccinium ovalifolium* on Sakhalin. [Struktura nasazhdeniya v chernichnyh yelnikah Sakhalina.] In: Anonymous. Sustainable management of forest resources on the [Russian] Far East [Neistoshchimoye lesopolzovaniye na Dalnem Vostoke], pp. 45–53. Khabarovsk (in Russian).

Kharkevich, S.S. (ed.) 1985–1996. The vascular plants of the Soviet Far East. Vol. 1–8. [Sosudisteye rastenia sovetskogo Dalnego Vostoka.] Nauka, Leningrad.

Kharkevich, S.S., Cherepanov, S.K. (eds.) 1981. Guidebook to the vascular plants of Kamchatka. [Opredelitel sosudistyh rasteniy Kamchatki.] Nauka, Moscow, 410 pp. (in Russian).

Khokhriakov, A.P. 1985. Flora of Magadan Region. [Flora Magadanskoy oblasti.] Nauka, Moscow, 397 pp. (in Russian).

Khomentovskiy, P.A. 1995. Ecology of dwarf pine on Kamchatka. [Ecologiya kedrovogo stlanika na Kamchatke.] Dal'nauka, Vladivostok, 226 pp. (in Russian).

Kim, J.-W. & Manyko, Yu.I. 1994. Syntaxonomical and synchorological characteristics of the cool-temperate mixed forest in the southern Sikhote-Alin, Russian Far East. Korean J. Ecol. 17: 391–413.

Kiseliov, A.N. & Kudryavtseva, E.P. 1992. High mountain vegetation of southern Primorye. [Vysokogornaya rastitelnost yuzhnogo Primorya.] Nauka, Moscow, 117 pp. (in Russian).

Kojima, S. 1979. Biogeoclimatic zones of Hokkaido Island, Japan. J. College of Liberal Arts. Toyama Univ. 12: 97–141.

Kolesnikov, B.P. 1937. Chosenia (*Chosenia macrolepis* (Turch.) Kom.) and its coenoses on the [Russian] Far East. [Chozenia i yeyo tsenozy na Dalnem Vostoke] Trudy DVF AN SSSR. Ser. Bot. 2: 703–800 (in Russian, with English summary).

Kolesnikov, B.P. 1938. Vegetation of eastern slopes of middle Sikhote-Alin. [Rastitelnost vostochnyh sklonov srednego Sikhote-Alinya.] Trudy Sikhote-Alinskogo Gosudarstvennogo Zapovednika 1: 25–208 (in Russian, with English summary).

Kolesnikov, B.P. 1946. To the taxonomy and the historical development of larches (section Pauciseriales Patschke). [K taksonomii i istoricheskomu razvitiyu listvennits (sectsiya Pauciseriales Patschke).] In: Anonymous. Materials on the history of the flora and vegetation of the USSR. [Materialy po istorii flory i rastitelnosti SSSR.] Vol. 2., pp. 321–364. Izdatel'stvo Akademii Nauk SSSR, Moscow (in Russian).

Kolesnikov, B.P. 1955. The outlines of vegetation of [Russian] Far East. [Ocherk rastitelnosti Dalnego Vostoka.] Khabarovskoie Knizhnoe Izdatel'stvo, Khabarovsk, 104 pp. (in Russian).

Kolesnikov, B.P. 1956a. Korean pine forests of the [Russian] Far East. [Kedroviye lesa Dalnego Vostoka.] Trudy DVF AN SSSR, Ser. Bot., Izdatelstvo AN SSSR, Moscow 2: 1–264 pp. (in Russian).

Kolesnikov, B.P. (ed.) 1956b. Geobotanical map of Primorskiy kray. Scale 1: 500,000. [Geobotanicheskaya karta Primorskogo kraya. Masshtab 1: 500,000.] Moscow (in Russian).

Kolesnikov, B.P. 1961. Vegetation. [Rastitelnost.] In: Richter, G.D. (ed.), Far East. Physiogeography [Dalniy Vostok. Ocherki po fizicheskoy geografii], pp. 183–245. Izdatel'stvo Akademii Nauk SSSR, Moscow (in Russian).

Kolesnikov, B.P. 1963. Geobotanical zonation of the [Russian] Far East and distribution of vegetational resources. [Geobotanicheskoye raionirovanie Dalnego Vostoka i zakonomernosti rasprostraneniya rastitelnyh resursov.] Voprosy Geografii Dalnego Vostoka 6: 158–182 (in Russian).

Komarov, V.L. 1917. Vegetation types of southern Ussurian region. [Tipy rastitelnosti yuzhno-ussuriyskogo kraya.] In: Anonymous. Trudy pochvenno-geobotanicheskoy expeditsii po issledovaniyu kolonizatsionnych rayonov Asiatskoy Rossii. Izdatel'stvo Bratyev Sabashnikovykh, St. Petersburg, 296 pp. (in Russian).

Komarov, V.L. (ed.) 1934–1964. Flora of the USSR. [Flora SSSR.] Izdatel'stvo Akademii Nauk SSSR, Moscow (in Russian).

Komarov, V.L. 1927. Flora of Kamchatka Peninsula. [Flora Kamchatki.] Vol. 1. Leningrad, 339 pp. (in Russian).

Komarov, V.L. 1928. Bibliography on flora and vegetation of the [Russian] Far East. [Bibliografiya po flore i rastitelnosti Dalnego Vostoka.] Zapiski Yuzhno-

Ussuriyskogo Otdelenia Russkogo Geographicheskog Obshchestva 2: 1–278.

Komarova, T.A. 1992. Post fire successions in the forests of southern Sikhote-Alin. [Poslepozharniye suktsessii v lesah yuzhnogo Sikhote-Alinya.] Dal'nauka, Vladivostok, 224 pp. (in Russian).

Koropachinskiy, I.Yu. 1989. Pine family – Pinaceae. [Sosnoviye - Pinaceae.] In: Kharkevich, S.S. (ed.), Vascular plants of the Soviet Far East. [Sosudistiye rasteniya sovetskogo Dalnego Vostoka.] Vol. 4., pp. 9–20. Nauka, Leningrad (in Russian).

Kozhevnikov, Yu.P. 1996. Vegetation cover of northern Asia in historical perspective. [Rastitelniy pokrov severnoy Asii v istoricheskoy perspektive.] Mir i Semya, St. Petersburg, 400 pp. (in Russian).

Kozin, E.K. 1981. The scheme of development of virgin fir-spruce forest. [Skhema razvitiya devstvennogo pikhtovo-yelovogo lesa.] Lesnoye Khoziaystvo 10: 50–53 (in Russian).

Kozin, E.K., Grigoriev, V.I. & Rosenberg, V.A. 1975. The materials to the taxation of spruce forests of Sikhote-Alin. [Materialy po taksatsii yelovyh lesov Sikhote-Alinya.] In: Anonymous. The stationary studies in the fir-spruce forests of Sikhote-Alin [Statsionarniye issledovaniya pikhtovo-yelovyh lesov Sikhote-Alinya], pp. 8–29. Vladivostok (in Russian).

Krajina, V.J. 1969. Ecology of forest trees in British Columbia. Ecol. West. N. Amer. 2: 1–147.

Krasheninnikov, S.P. 1949. The description of land Kamchatka. [Opisanie zemli Kamchatka.] Izdatel'stvo Akademii Nauk SSSR, Moscow, 842 pp. (in Russian).

Krestov, P.V. 1997. The main features of phytocenotic diversity of the broad-leaved Korean pine forests of the Russian Far East. [Osobennosti fitotsenoticheskogo raznoobraziya shirokolistvenno-kedrovyh lesov rossiyskogo Dalnego Vostoka.] Komarovskiye Chteniya 46:15–42 (in Russian).

Krestov, P.V. 1999. Floristic aspects of the vertical vegetation zones on the middle Sikhote-Alin Mt. Range. [Floristicheskiye aspekty vysotno-poyasnoy rastitelnosti v srednem Sikhote-Aline] In: Anonymous. Botanical research on the Russian Far East [Botanicheskiye issledovaniya na rossiyskom Dalnem Vostoke], pp. 193–200. Dal'nauka, Vladivostok (in Russian).

Krestov, P.V. 2000. The botanico-geographical relations on the Far East of Russia: an attempt of integrated view. In: Abstracts for the IAVS Symposium in Nagano, July 24 – August 01, p. 48. Nagano.

Krestov, P.V. 2001. Vegetation on Livadiyskiy Mt. Range (southern Sikhote-Alin). [Rastitelnost khrebta Livadiyskiy (yuzhniy Sikhote-Alin).] In: Anonymous. Landscape and vegetation zonality of Livadiyskiy Mt. range, Southern Primorye region [Landshafty i rastitelnaya zonalnost khrebta Livadiyskiy, yuzhnoye Primorye], pp. 7–28. Dal'nauka, Vladivostok (in Russian).

Krestov, P.V. & Ishikawa, Yu. 2000. Natural dynamics in the broad-leaved – Korean pine forests of the Sikhote-Alin Reserve. [Yestestvennaya dinamika v shirokolistvenno-kedrovyh lesah Sikhote-Alinskogo zapovednika.] In: Galanin, A.V. (ed.), Vegetation of the Sikhote-Alin Biosphaeric Reserve: diversity, dynamics and monitoring [Rastitelnost Sikhote-Alinskogo biosfernogo zapovednika: raznoobraziye, dinamika, monitoring], pp. 208–218. Dal'nauka, Vladivostok (in Russian).

Krylov, A.G. 1984. Life form of forest phytocenoses. [Zhiznenniye formy lesnyh fitotsenozov.] Nauka, Moscow, 181 pp. (in Russian).

Krylov, G.V. & Salatova, N.G. 1969. History of botanical and forest researches in the Siberia and [Russian] Far East. [Istoriya botanicheskih i lesnyh issledovaniy v Sibiri i na Dalnem Vostoke.] Nauka, Novosibirsk (in Russian).

Krylov, G.V., Talantsev, N.K. & Kozakova, N.F. 1983. The pine. [Kedr.] Nauka, Moscow, 216 pp. (in Russian).

Kutentsova, G.E. 1960. The forests of *Picea koraiensis* in the Ussuri River basin. [Lesa iz yeli koreiskoy v basseyne reki Ussuri.] Soobshchenia DVF SO AN SSSR 12: 97–101 (in Russian).

Kurentsova, G.E. 1968. Vegetation of Primorskiy region. [Rastitelnost Primorskogo kraya.] Dalnevostochnoye Knizhnoye Izdatelstvo, Vladivostok, 192 pp. (in Russian).

Kurentsova, G.E. 1973. Natural and antropogenic dynamics of vegetation of Primorye and southern Priamurye. [Yestestvenniye i antropogenniye smeny rastitelnosti v Primoriye i yuzhnom Priamuriye.] Nauka, Novosibirsk, 233 pp. (in Russian).

Lavrenko, E.M. 1950. Main features of phytogeographical regionalization of the USSR and bordering countries. [Osnovniye cherty fitogeograficheskogo raionirovaniya SSSR i prigranichnyh stran.] In: Anonymous. The problems of botany. [Problemy Botaniki.] Vol. 1., pp. 530–548. Izdatel'stvo Akademii Nauk SSSR, Moscow (in Russian).

Lavrenko, E.M. (ed.) 1939. The map of vegetation of the USSR. Scale 1: 5,000,000. [Karta rastitelnosti SSSR. Masshtab 1:5,000,000.] Komarov Botanical Institute Press, Leningrad (in Russian).

Lavrenko, E.M. & Sochava, V.B. (eds.) 1954. Geobotanical map of the USSR. Scale 1: 4,000,000. [Geobotanicheskaya karta SSSR. Masshtab 1:4,000,000.] Komarov Botanical Institute Press, Leningrad (in Russian).

Lavrenko, E.M. & Sochava, V.B. (eds.) 1956. The vegetation cover of the USSR. The explanatory notes to the "Geobotanical map of the USSR". [Rastitelniy pokrov SSSR. Poyasnitelniy tekst k Geobotanicheskoy karte SSSR.] Vol. 1 and 2. Izdatel'stvo Akademii Nauk SSSR, Moscow (in Russian).

Man'ko, Yu.I. 1961. Brief sketch of forest vegetation of the upper half of Urmi River. [Ocherk lesnoy rastitelnosti verkhnego techeniya reki Urmi.] Komarovskie Chtenia 9: 42–71 (in Russian).

Man'ko, Yu.I. 1965. The materials on study of decline of the fir-spruce forests in the left side of Amur River basin. [Materialy po izucheniyu usikhaniya pikhtovo-yelovyh lesov levoberezhya Amura.] In: Anonymous. Forestry studies on the Far East [Lesokhoziaystvenniye issledovaniya na Dalnem Vostoke], pp. 21–73. Vladivostok (in Russian).

Man'ko, Yu.I. 1967. Fir-spruce forests of the northern Sikhote-Alin. [Pikhtovo-yeloviye lesa severnogo Sikhote-Alinya.] Nauka, Leningrad, 244 pp. (in Russian).

Man'ko, Yu.I. 1974. Some features of dynamics of forest vegetation of Kamchatka under the influence of dry rivers. [Nekotoriye osobennosti dinamiki lesnoy rastitelnosti Kamchatki pod vozdeystviyem sukhikh rechek.] Bot. Zhurn. 59: 707–716 (in Russian).

Man'ko, Yu.I. 1980. Volcanism and vegetation dynamics. [Vulkanizm i dinamika rastitelnosti.] Bot. Zhurn. 65: 457–469 (in Russian).

Man'ko, Yu.I. 1987. The Ayan Spruce. [Ayanskaya Yel.] Nauka, Leningrad, 280 pp. (in Russian).

Man'ko, Yu.I. & Gladkova, G.A. 1993. On the history of the hypothesis for fir-spruce forests drying in the Far East. [K istorii gipotezy ob usykhanii pikhtovo-yelovyh lesov na Dalnem Vostoke.] Pochvovedenie 9: 94–97 (in Russian).

Man'ko, Yu.I. & Gladkova, G.A. 1995. On factors of fir-spruce forest decline on the [Russian] Far East. [O faktorakh usyhaniya pikhtovo-yelovyh lesov na Dalnem Vostoke.] Lesovedenie 2: 3–12 (in Russian).

Man'ko, Yu.I. & Gladkova, G.A. 2001. Spruce decline in the light of global deterioration of dark-coniferous forests. [Usykhaniye yeli v svete globalnogo uhudsheniya temnokhvoynyh lesov.] Dal'nauka, Vladisvostok, 228 pp. (in Russian).

Man'ko, Yu.I. & Voroshilov, V.P. 1971. On the northern limit of distribution of *Picea ajanensis* in the continental part of Far East. [O severnom predele rasprostraneniya ayanskoy yeli v kontinentalnoy chasti Dalnego Vostoka.] Bot. Zhurn. 56: 1343–1351 (in Russian).

Man'ko, Yu.I. & Voroshilov, V.P. 1973. The spruce forests of Kamchatka and their management. [Yeloviye lesa Kamchatki i ih ispolzovaniye.] In: Anonymous. Soils and vegetation of the permafrost regions of the USSR [Pochvy i rastitelnost merzlotnyh raionov SSSR], pp. 218–224. IBPS, Magadan (in Russian).

Man'ko, Yu.I. & Voroshilov, V.P. 1978. Spruce forests of Kamchatka. [Yeloviye lesa Kamchatki.] Nauka, Moscow, 256 pp. (in Russian).

Man'ko, Yu.I., Gladkova, G.A., Butovets, G.N. & Kamibayashi, N. 1998. An experience of monitoring of fir-spruce forest decline in central Sikhote-Alin. [Opyt monitoringa usykhaniya pikhtovo-yelovyh lesov v Tsentralnom Sikhote-Aline.] Lesovedenie 1: 3–16 (in Russian).

Mayer, H. 1978. Über die Bedeutung der Urwaldforschung für den Gebirgswaldbau. Allgem. Forstzeitschrift 24: 691–693.

Maximowicz, C.J. 1859. Primitiae florae amurensis. Versuch einer Flora des Amurlandes. St. Petersburg, 504 pp.

Miki, S. 1956. Remains of *Pinus koraiensis* S. et Z. and associated remains in Japan. Bot. Mag. Tokyo 69: 447–454.

Mirkin, B.M. & Naumova, L.G. 1998. Vegetation science. (History and modern state of some concept). [Nauka o rastitelnosti (Istoriya i sovremennoye sostoyaniye nekotoryh kontseptsiy).] Gilem, Ufa, 414 pp. (in Russian).

Mishkov, F.F. 1975. Development and species replacement in the hardwood-conifer forests of Khekhtsir Mt. range. [Razvitie i smena vidov v shirokolistvenno-khvoynyh lesah Hehtsira.] In: Anonymous. The use and reproduction of forest resources of the [Russian] Far East [Ispolzovaniye i vosproizvodstvo lesnyh resursov Dalnego Vostoka], pp. 91–108. Dal'NIILKh, Khabarovsk (in Russian).

Miyawaki, A. & Nakamura, Yu. 1988. Übersicht über die japanische Vegetation und Flora in der nemoralen und borealen Zone. Veröff. Geobot. Inst. ETH, Stiftung Rübel 98: 100–128.

Molozhnikov, V.N. 1976. Siberian pine in the montane landscapes of northern Baikal area. [Kedroviy stlanik v gornyh landshaftah severnogo Pribaikalya.] Nauka, Moscow, 203 pp. (in Russian).

Morozov, V.L. & Belaya, G.A. 1988. Ecology of Far Eastern tall-form meadows. [Ecologiya dalnevostochnogo krupnotravya.] Nauka, Moscow, 255 pp. (in Russian).

Moskaliuk, T.A. 1988. The structure and productivity of the northern Okhotian forests. [Struktura i produktivnost severookhotskih lesov.] Dal'nauka, Vladivostok, 144 pp. (in Russian).

Nechaev, A.P. 1975. The role of animals in spruce regeneration on fallen trees. [Rol zhivotnyh v vozobnovlenii yeli na valezhnike.] Flora and Fauna of the [Russian] Far East 3: 14–22 (In Russian).

Nedrigailov, S.N. 1932. Forests and forest resources in northwest Yakutia. [Lesa i lesniye resursy v severo-zapadnoy Yakutii.] In: Anonymous. Forest resources of Yakutia. [Lesniye resursy Yakutii.] Vol. 3., pp. 38–59. Nauka, Moscow (in Russian).

Neshataev, Yu.N. & Neshataeva, V.Yu. 1985. The distribution of *Pinus pumila* communities in Kronotskiy state reserve. [Rasprostraneniye soobshchestv *Pinus* *pumila* v Kronotskom gosudarstvennom zapovednike.] Bot. Zhurn. 70: 382–389 (in Russian).

Neshataeva, V.Yu. 1983. Ecologo-biological analysis of the species composition of the dwarf pine formation in the Kronotskiy Reserve on Kamchatka. [Ecologo-biologicheskiy analiz vidovogo sostava formatsii kedrovogo stlanika v Kronotskom zapovednike na Kamchatke.] Vestnik Leningradskogo Gosudarstvennogo Universiteta 9: 53–63 (in Russian).

Neshataeva, V.Yu. 1994. Dwarf pine communities. [Soobshchestva kedrovogo stlanika.] In: Neshataev, Yu.N., Neshataeva, V.Yu. & Naumenko, A.T. (eds.), Vegetation of Kronotskiy State Reserve [Rastitelnost Kronotskogo gosudarstvennogo zapovednika], pp. 81–105. Komarov Botanical Institute Press, St-Peterburg (in Russian).

Nikolskaya, V.V. 1974. On natural trends of development of physiogeographic provinces of the southern Far East [of Russia.] [O yestestvennyh napravleniyah razvitiya fiziko-geographicheskih provintsiy yuga Dalnego Vostoka.] Nauka, Moscow, 126 pp. (in Russian).

Numata, M. 1972. Ecological interpretation of vegetational zonation of high mountains, particularly in Japan and Taiwan. In: Troll, C. (ed.), Geoecology of the high mountain regions of Eurasia, pp. 288–299. F. Steiner, Wiesbaden.

Okitsu, S. 1987. *Betula ermanii* zone. In: Ito, K. (ed.), Vegetation of Hokkaido, pp. 168–199. Hokudai Tosho Kankoukai, Sapporo.

Okitsu, S. 1988. Geographical variation of annual fluctuations in stem elongation of *Pinus pumila* Regel on high mountains of Japan. Jap. J. Ecol. 38: 177–189.

Okitsu, S. & Ito, K. 1984. Vegetation dynamics of the Siberian dwarf pine (*Pinus pumila* Regel) in the Taisetsu mountain range, Hokkaido, Japan. Vegetatio 58: 103–113.

Okitsu, S. & Ito, K. 1989. Conditions for the development of the *Pinus pumila* zone of Hokkaido, Northern Japan. Vegetatio 84:127–132.

Pickett, S.T.A. & White, P.S. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, 472 pp.

Pogrebnyak P.S. 1955. The fundamentals of the forest typology. [Osnovy lesnoy tipologii.] Naukova Dumka, Kiev, 456 pp. (in Russian).

Pojar, J., Klinka, K. & Meidenger, D.V. 1987. Biogeoclimatic ecosystem classification in British Columbia. For. Ecol. Manage. 22: 119–154.

Pozdniakov, L.K. 1975. Daurian larch. [Daurskaya listvennitsa.] Nauka, Moscow, 402 pp. (in Russian).

Ramenskiy, L.G. 1953. On ecological study and systematization of plant communities. [K izucheniyu ecologii i sistematizatsii rastitelnyh soobshchestv.] Byull. Mosk. Obshch. Ispyt. Prir., Otd. Biol. 58: 35–54 (in Russian).

Ramenskiy, L.G. 1932. Die Projektionsaufnahme und Beschreibung der Pflanzendecke. Handb. Biol. Arb. Meth. 11: 137–190.

Rozenberg, V.A. & Vasiliev, N.G. 1967. On the altitudinal distribution of vegetation on a middle Sikhote-Aline. [K vysotnomu raspredeleniyu rastitelnosti v tsentralnom Sikhote-Aline.] Problemy Botaniki. Rastitel’niy Mir Vysokogoriy SSSR i Voprosy Ego Ispol’zovaniya 9: 143–151 (in Russian).

Rozenberg, V.A. 1959. Dark-conifer forests of the northern end of Sikhote-Alin Mt. range. [Temnokhvoyniye lesa severnoy chasti Sikhote-Alinya.] Soobshchenia DVF SO AN SSSR, Biologia 11: 57–80 (in Russian).

Rozenberg, V.A. 1961. Some aspects of development of fir spruce forests of the southern Sikhote-Alin. [Nekotoriye voprosy razvitiya pikhtovo-yelovyh lesov yuzhnogo Sikhote-Alinya.] In: Anonymous. Agriculture and forestry of the [Russian] Far East [Voprosy selskogo i lesnogo khoziaystva na Dalnem Vostoke], pp. 195–215. Vladivostok (in Russian).

Rozenberg, V.A. 1963. On characteristics of fir-spruce forests of Primorye and lower Priamurye. [K kharakteristike pikhtovo-yelovyh lesov Primorya i nizhnego Priamurya.] In: Anonymous. Materials on the study of forests of the Siberia and Far East [Materialy po issledovaniyu lesov Sibiri i Dalnego Vostoka], pp. 39–49. Krasnoyarsk (in Russian).

Rozenberg, V.A. 1967. The formations of spruce and fir forests of the soviet Far East. [Formatsii yelovyh i pikhtovyh lesov sovetskogo Dalnego Vostoka.] In: Anonymous. The summary of forest studies on the [Russian] Far East [Itogi izucheniya lesov Dalnego Vostoka], pp. 98–101, Vladivostok (in Russian).

Rozenberg, V.A. 1971. The classification of the fir-spruce forests of the Sikhote-Alin. [Klassifikatsiya pikhtovo-yelovyh lesov Sikhote-Alinya.] In: Anonymous. Geographical aspects of mountain forest management [Geograficheskiye aspekty ispolzovaniya gornyh lesov], pp. 22–24. Chita (in Russian).

Sano, Y., Matano, T. & Ujihara, A. 1977. Growth of *Pinus pumila* and climate fluctuation in Japan. Nature 226: 159–161.

Schlothauer, S.D. 1978. Flora and vegetation of western Okhotsk region. [Flora i rastitelnost zapadnoy Okhotii.] Nauka, Moscow, 132 pp. (in Russian).

Schmidt-Vogt, H. 1974. Die systematische Stellung der gemeinen Fichte (*Picea abies* (L.) Karst.) und der sibirischen Fichte (*Picea obovata* Ledeb.) in der Gattung *Picea*. Allgem. Forst- und Jagzeitung 3–4: 45–60.

Schmidt-Vogt, H. 1977. Die Fichte. Bd. 1.: Taxonomie, Verbreitung, Morphologie, Ökologie, Waldgesellschaften. Hamburg, 647 pp.

Seledetz, V.P. 1992. Botanico-geographical base for the protection of vegetation cover of the Russian Far East. [Botaniko-geograficheskaya osnova dlya sokhraneniya rastitelnogo pokrova Rossiyskogo Dalnego Vostoka.] Resume for Dr. Sci. thesis. Dal'nauka, Vladivostok, 45 pp. (in Russian).

Seledetz, V.P. 2000. Method of ecological scales for vegetation studies in the Russian Far East. [Metod ecologicheskih shkal dlya izucheniya rastitelnosti Rossiyskogo Dalnego Vostoka.] FESAEM Press, Vladivostok, 246 pp. (in Russian).

Shafranovskiy, V.A. 1987. *Picea glehnii* (Fr. Schmitd) Mast. on the island Kunashir (Kuril Islands). [*Picea glehnii* (Fr. Schmitd) Mast. na Kunashire (Kurilskiye ostrova).] In: Anonymous. Spruce on the [Russian] Far East, pp. 15–58. FESC, Vladivostok (in Russian).

Shamshin, V.A. 1974. Age structure of stone birch stands of Kamchatka. [Vozrastnaya struktura kamennoberezhnyakov Kamchatki.] In: Anonymous. Materials on forests on the northeast of the USSR. [Materialy po lesam na severo-vostoke SSSR.] IBPS, Magadan (in Russian).

Shamshin, V.A. 1976. Snow cover and soil frozen in the stone birch forests of the southeast Kamchatka. [Snegovoy pokrov i promerzaniye pochv v kamennoberezovyh lesah yugo-vostovnoy Kamchatki.] In: Anonymous. Glaciological research, pp. 97–113. Nauka, Moscow (in Russian).

Shamshin, V.A. 1999. The stone birch forests of Kamchatka: biology, ecology and stand structure. [Kamennoberezoviye lesa Kamchatki: biologia, ecologia i stroyeniye rastitelnih soobshchestv.] GEOS, Moscow, 170 pp. (in Russian).

Shavnin, A.G. 1979. The comparative assessment of productivity in evenaged and unevenaged spruce forests. [Sravnitelnaya otsenka produktivnosti odnovozrastnyh i raznovozrastnyh yelnikov.] Lesnoye Khoziaystvo 5: 54–55 (in Russian).

Shcherbakov, I.P. 1975. Forest cover of northwestern USSR. [Lesnoy pokrov severo-zapada SSSR.] Nauka, Novosibirsk, 344 pp. (in Russian).

Shennikov, A.P. 1935. The principles of botanical classification of meadows. [Printsipi botanicheskoy klassifikatsii lugov.] Sovetskaya Botanika 5: 35–49 (in Russian).

Smagin, V.N. 1965. Forests of Ussuri River basin. [Lesa basseyna Ussuri.] Nauka, Moscow, 270 pp. (in Russian).

Sochava, V.B. 1957. Taiga on the northwest of Mid-Siberian Plains. [Taiga na severo-zapade tsentralno-Sibirskoy ravniny.] Bot. Zhurn. 42: 32–48 (in Russian).

Sochava, V.B. 1956. Larch forests. [Listvennichniye lesa.] In: Anonymous. Vegetation cover of the USSR. Notes to the "Geobotanical map of the USSR" [Rastitelniy pokrov SSSR. Poyasnitelniy tekst k "Geobotanicheskoy karte SSSR"], pp. 249–318. Izdatel'stvo Akademii Nauk SSSR, Moscow (in Russian).

Sochava, V.B. (ed.) 1969a. Vegetation map of Amur River basin. Scale 1: 2,500,000. [Karta rastitelnosti basseyna Amura. Masshtab 1: 2,500,000.] In: Yunatov, A.A. (ed.), Amurskaya taiga. Nauka, Moscow (in Russian).

Sochava, V.B. 1969b. The botaniko-geographical relationships in Amur River basin. [Botaniko-geograficheskiye sootnosheniya v basseyne Amura] In: Yunatov, A.A. (ed.), Amurskaya taiga, pp. 5–15. Nauka, Moscow (in Russian).

Sochava, V.B. 1986. The problems of the physical geography and geobotany: selected papers. [Problemy fizicheskoy geografii i geobotaniki: izbranniye statyi.] Nauka, Novosibirsk, 344 pp. (in Russian).

Sochava, V.B. & Bayborodin, V.N. (eds.) 1977. The correlation ecologo-phytocoenological map [of Asian Russia.] Scale 1:7,500,000. [Korreliatsionnaya ecologo-tsenoticheskaya karta. Masshtab 1:7,500,000.] Institute of Geography of Siberia and Far East Press, Novosibirsk (in Russian).

Sochava, V.B. & Lukitchova, A.N. 1953. Geography of the Siberian dwarf pine. [Geografiya kedrovogo stlanika.] Doklady Akademii Nauk SSSR 90: 1163–1166 (in Russian).

Sokolov, S.Ya., Sviazeva, O.A. & Kubli, V.A. 1977. The ranges of trees and shrubs of the USSR. [Arealy derevyev i kustarnikov SSSR.] Nauka, Leningrad, 164 pp., 91 maps (in Russian).

Solovyov, K.P. 1958. Korean pine - broad-leaved forests of [Russian] Far East and their management. [Kedrovo-shirokolistvenniye lesa Dalnego Vostoka i khoziaystvo v nih.] Khabarovskoye Knizhnoye Izdatel'stvo, Khabarovsk, 368 pp. (in Russian).

Solovyov, K.P. & Sheingauz, A.S. 1981. The groups of forest types for management and systems of magagement acts for the southern part of the [Russian] Far East. [Khozyaystvenniye gruppy tipov lesa i sistemy normativnyh aktov dlya yuzhnoy poloviny Dalnego Vostoka.] Dal'NIILKh, Khabarovsk, 48 pp. (in Russian).

Song J.S. 1988. Phytosociological study of the mixed coniferous and deciduous broad-leaf forests in South Korea. Hikobia 10: 145–156.

Sugawara, S. 1937. Illustrated flora of Saghalien with descriptions and figures of phanerogams and higher cryptogamsindigenous to Saghalien. Vol. 1. Tokyo, 504 pp. (in Japanese).

Sukachev, V.N. & Dylis, N. 1964. Fundamentals of forest biogeocoenology. Oliver and Boyd, Edinburg, 672 pp.

Sukachov, V.N. 1928. Plant communities (Introduction in phytosociology). [Rastitelniye soobshchestva (Vvedeniye v fitosotsiologiyu).] Kniga, Leningrad, 232 pp. (in Russian).

Sukachov, V.N. 1957. General principles and a program for study of forest types. [Osnovniye printsipy i programma k izucheniyu tipov lesa.] In: Sukachov, V.N., Zonn, S.V. & Motovilov, G.P. (eds.), Methods of forest typology. [Metodicheskiye ukazania k izucheniyu tipov lesa.], pp. 9–63. Izdatelstvo Akademii Nauk SSSR, Moscow (in Russian).

Sukachov, V.N. 1924. On a history of genus *Larix*. [K istorii roda *Larix*.] In: Anonymous. Forestry, pp. 25–78. Moscow (in Russian).

Tarankov, V.I. 1974. Microclimate in the forests of southern Primorye. [Mikroklimat v lesah yuzhnogo Primorya.] Nauka, Novosibirsk, 224 pp. (in Russian).

Tarankov, V.I. & Ponomarenko, V.M. 1967. Microclimate on the treeline on the Sikhote–Alin mountains. [Mikroklimat u verkhney granitsy lesa v gorah Sikhote-Alinya.] In: Anonymous. Vegetation cover of highlands of the USSR and its management. [Rastitelniy pokrov vysokogoriy SSSR i yego ispolzovaniye.] Frunze (in Russian).

Tatarinov, V.V., Trus, M.V. & Nechaev, A.A. 1978. The analysis of parcel structure of dark-conifer forests for the age dynamics study. [Analiz partsellarnoy struktury temnokhvoynyh lesov dlya issledovaniya vozrastnoy dinamiki.] Lesovedenie 1:10–20 (in Russian).

Tatewaki, M. 1943. Phytosociological study on the *Picea glehnii* forest. Res. Bull. College Experiment Forest (Hokkaido Imperial Univ.) 50: 371–486.

Tatewaki, M. 1958. Forest Ecology of the islands of the north Pacific Ocean. J. Fac. Agriculture (Hokkaido University) 50: 371–486.

Tikhomirov, B.A. 1946. On the origin of the dwarf pine (*Pinus pumila* Regel) associations. [K proiskhozhdeniyu assotsiatsiy kedrovogo stlannika (*Pinus pumila* Regel).] In: Anonymous. Materials on the history and flora of the USSR [Materialy po flore i rastitelnosti SSSR.] Vol. 2., pp. 491–537. Izdatel'stvo Akademii Nauk SSSR, Moscow (in Russian).

Tikhomirov, B.A. 1949. Siberian dwarf pine, its biology and management. [Kedroviy stlanik, ego biologiya i ispolzovaniye.] Moskovskoie Obshchestvo Ispytateley Prirody, Moscow, 106 pp. (in Russian).

Tikhomirov, B.A. & Falaleiev, E.N. 1962 Characteristics of the larch forests of the USSR. [Kharakteristika listvennichnyh lesov SSSR.] In: Anonymous. The larch. [Listvennitsa.] Vol. 2., Krasnoyarsk (in Russian).

Tiulina, L.N. 1976. Humid Baikalian type of vertical zone vegetation. Izdatel'stvo Nauka, Novosibirsk, 318 pp. (in Russian).

Tolmachov, A.I. 1954. On the origin and development of dark conifer taiga. [Proiskhozhdeniye i razvitiye temnokhvoynoy taigi.] Izdatel'stvo Nauka, Moscow, 156 pp. (in Russian).

Tolmachov, A.I. 1955. The geobotanical regionalization of Sakhalin Island. [Geobotanicheskoye raionirovaniye ostrova Sakhalin.] Nauka, Moscow, 79 pp. (in Russian).

Tolmachov, A.I. 1956. On vertical distribution of vegetation on Sakhalin Island. [Vertikalnoye raspredeleniye rastitelnosti na ostrove Sakhalin.] In: Anonymous. Vegetation cover of Sakhalin [Rastitelniy pokrov Sakhalina], pp. 15–48. Nauka, Moscow (in Russian).

Tolmachov, A.I. 1959. Flora of Sakhalin Island. [Flora ostrova Sakhalin.] Nauka, Moscow, 103 pp. (in Russian).

Trass, H. & Malmer, N. 1973. North European approach to classification. In: Whittaker, R.H. (ed.), Ordination and classification of communities, pp. 529–574. W.Junk, The Hague.

Tsatsenkin, I.A. (ed.) 1978. The procedure instruction on ecological estimating of fodder land of tundra and forest zones of Siberia and Far East [of Russia] on a plant cover. [Metodicheskiye ukazaniya po ecologicheskoy otsenke kormovyh ugodiy tundrovoy i lesnoy zon Sibiri i Dalnego Vostoka po rastitelnomu pokrovu.] Moscow, 302 pp. (in Russian).

Tsveliov, N.N. 1994. On the names of some larches in Russia. [O nazvaniyah nekotoryh listvennits Rossii.] Bot. Zhurn. 79: 90–91 (in Russian).

Vasiliev, N.G. & Kolesnikov, B.P. 1962. The broad-leaved - black-fir [*Abies holophylla*] forests of southern Prymorye. [Shirokolistvenno-chernopikhtoviye lesa yuzhnogo Primorya.] Izdatel'stvo Akademii Nauk SSSR, Moscow, 147 pp. (in Russian).

Vasiliev, N.G. & Kurentsova, G.E. 1960. The altitudinal zonation on Mt. Ko in the middle Sikhote-Alin. [Vysotnaya poyasnost na gore Ko v srednem Sikhote-Aline.] Komarovskie Chteniya 8: 21–40 (in Russian).

Vasiliev, V.N. 1941. Stone birch (*Betula ermanii* Cham. s.l.). [Kamennaya bereza (*Betula ermanii* Cham. s.l.).] Bot. Zhurn. 26: 172–208 (in Russian).

Vasiliev, V.N. 1958. Origin of flora and vegetation of Far East and Eastern Siberia. [Proiskhozhdeniye flory i rastitelnosti Dalnego Vostoka i Vostochnoy Sibiri.] In: Anonymous. Materials on the history and flora of the USSR. [Materialy po istorii flory i rastitelnosti SSSR.] Vol. 3, pp. 361–457. Izdatel'stvo Akademii Nauk SSSR, Moscow (in Russian, with English summary).

Vasiliev, Ya.Ya. 1938. The forest association of Suputinskiy Reserve. [Lesnye assotsiatsii Suputinskogo zapovednika.] Trudy GTS DVF SO AN SSSR 2: 5–136 (in Russian).

Vasiliev, Ya.Ya. 1947. Geobotanical regionalization of southern part of [Russian] Far East. [Geobotanicheskoye raionirovaniye yuzhnoy chasti Dalnego Vostoka.] In: Anonymous. Geobotanical regionalization of the USSR [Geobotanicheskoye raionirovaniye SSSR], pp. 50–60. Izdatel'stvo Akademii Nauk SSSR, Moscow (in Russian).

Verkholat, V.P. & Krylov, A.G. 1982. Analysis of the flora of vascular plants of the oak forests of southern Sikhote-Alin. [Analiz flory sosudistyh rasteniy dubovyh lesov yuzhnogo Sikhote-Alinya.] Komarovskiye Chteniya 29: 3–22 (in Russian).

Vitvitskiy, G.N. 1961. Climate. In: Anonymous. Far East Physiogeography [Fiziogeografiya Dalnego Vostoka], pp. 93–158. Izdatel’stvo Akademii Nauk, Moscow (in Russian).

Vlasov, S.T. 1959. The forests of Sakhalin: Reference Materials. [Lesa Sakhalina: spravochniye materialy.] Yuzhno-Sakhalinsk, 108 pp. (in Russian).

Vorobiov, D.P. 1963. The vegetation of Kuril Islands. [Rastitelnost Kurilskih ostrovov.] Nauka, Moscow, 92 pp. (in Russian).

Vorobiov, D.P. 1982. Guidebook to the vascular plants of Vladivostok and its suburbs. [Opredelitel sosudistyh rasteniy Vladivostoka i ego okrestnostey.] Nauka, Leningrad, 252 pp. (in Russian).

Vorobiov, D.P., Voroshilov, V.P. & Gurzenkov, N.N. 1974. The guidebook to the vascular plants of Sakhalin and Kuril Islands. [Opredelitel sosudistyh rasteniy Sakhalina i Kuril.] Nauka, Leningrad, 372 pp. (in Russian).

Wang, C.-W. 1961. The forests of China, with a survey of grassland and desert vegetation. Maria Moors Cabot Foundation Publ. No. 5, Harvard Univ., Cambridge, Mass, 313 pp.

Yurtsev, B.A., Tolmatchov, A.I. & Rebristaia O.V. 1978. Floristic delineation and subdivision of Arctica. [Floristicheskoye deleniye i raiony Arctiki.] In: Anonymous. Arctic floristic area [Arkticheskaya floristicheskaya oblast], pp. 9–104. Nauka, Leningrad (in Russian).