Vegetatio **127**: 155–172, 1996.

The subalpine vegetation of Mt. Vysokaya, central Sikhote-Alin

Sergei Yu. Grishin[1], Pavel Krestov[1] & Susumu Okitsu[2]
[1]*Institute of Biology and Pedology, Russian Academy of Sciences, Vladivostok, 690022, Russia;* [2]*Chiba University, 648 Matsudo, Matsudo City, 271 Japan*

Received 10 November 1994; accepted in revised form 26 July 1996

Key words: Ecotone, Floristic composition, Sikhote-Alin, Upper timberline, Vegetation change, Vegetation structure

Abstract

The subalpine vegetation structure of Mt. Vysokaya, the Central Sikhote-Alin, is described. This vegetation consists mainly of subalpine spruce-fir forest, a complex of subalpine meadows, shrubs, groves of *Betula lanata* (*B. ermanii* s.l.), krummholz of *Pinus pumila* and alpine tundras. Significant disturbances in the vegetation structure were noted, especially in the forest-tundra ecotone accompanying a sharp reduction of the belts of *Betula lanata* and *Pinus pumila*. The altitudinal level of the upper timberline reaches 1600 m a.s.l. which is 250 m less than the expected altitude calculated by Kira's warmth index. An undergrowth of scattered trees of *Picea* and *Betula* are growing up to the mountain top. Based on these data and a review of the literature, we concluded that a catastrophic lowering of the timberline and devastation of the subalpine vegetation belt occurred several centuries ago, probably as result of fires.

Nomenclature: follows Cherepanov (1981), Vyshin (1990).

Introduction

The high-mountain vegetation of the Sikhote-Alin has not yet been studied sufficiently. This study was carried out on Mt. Vysokaya (1746 m), a relatively large mount of the central part of the chain (Figure 1). It is situated on the main watershed of the chain, about 70 km west of the coast of the Sea of Japan, 45°58′N, 136°37′E. The vegetation of Mt. Vysokaya was only studied in 1937 by Kolesnikov (1969), who published five geobotanical releves of the high-mountain vegetation.

This paper aims to characterize the subalpine vegetation, especially in the forest-tundra ecotone, including the composition of the vegetation, floristic pattern, size, age and growth increments of timberline tree and shrub species. It also discusses the spatial structure of the vegetation and altitudinal position of the upper timberline.

Study area

Natural history

The Sikhote-Alin is related to modern geosynclinal systems. The active processes of folding ceased in the Late Mesozoic. In the Neogene-Quarternary some extrusions of basalt lava appeared. On Mt. Vysokaya this lava is represented by andesite and andesite-dacite (Geological Map of Primorsky Kray 1986).

The Quarternary glaciation probably affected the uppermost peaks of the Central Sikhote-Alin including Mt. Vysokaya (Kolesnikov 1969). The nivation takes place in high-mountain belt since the Quarternary and leads to the development of block streams composed of igneous rocks on the slopes situated above the upper timberline and flat stone fields on the mountain tops (The History of the Terrain Development of Siberia and Far East 1972).

Table 1. The mean monthly air temperature and precipitation at the meteorological station 'Mt. 1647 m', situated on the altitude of 1570 m. close to Mt. Vysokaya (Reference Book on a Climate of the USSR. 1968l).

	Month												Year
	1	2	3	4	5	6	7	8	9	10	11	12	
Air temperaturer (°C)	–24.0	–20.7	–14.6	–5.1	2.3	8.6	13.1	12.9	6.1	–1.9	–13.8	–21.4	–4.9
Precipitation (mm)	12	16	35	60	74	141	166	141	136	58	35	26	900

Climate

Only one set of climate data is available for this high-mountain area. Data were obtained between 1950s and 1960s at the station 'Mt. 1647 m', situated in the subalpine belt of the Sikhote-Alin, at 1570 m a.s.l., near Mt. Vysokaya (Reference book on climate of the USSR 1968). The mean monthly air temperature and precipitation are shown in Table 1. The periods of the main daily temperature exceeding 5 °C average 112 days and those more than 10 °C average 71 days per year, respectively. The sums of these mean daily temperatures are 1217 and 919, respectively. Even in the warmest months (July and August) there may be freezing temperatures. The calculated altitude of Kira's 15 °C warmth index (Kira 1977) is ca. 1850 m using an average lapse rate of 0.49 °C /100 m.

The mean depth of the snow cover in late winter is about 50 cm. The snow covers the ground from October to May. The severe northwestern wind in winter is very important for the dynamics and structure of vegetation situated above timberline. During the growing season period the mean wind speed is 4–5 m s^{-1}, then, in November–February, it reaches 15 m s^{-1} and may gust to 40 m s^{-1} (hurricane force).

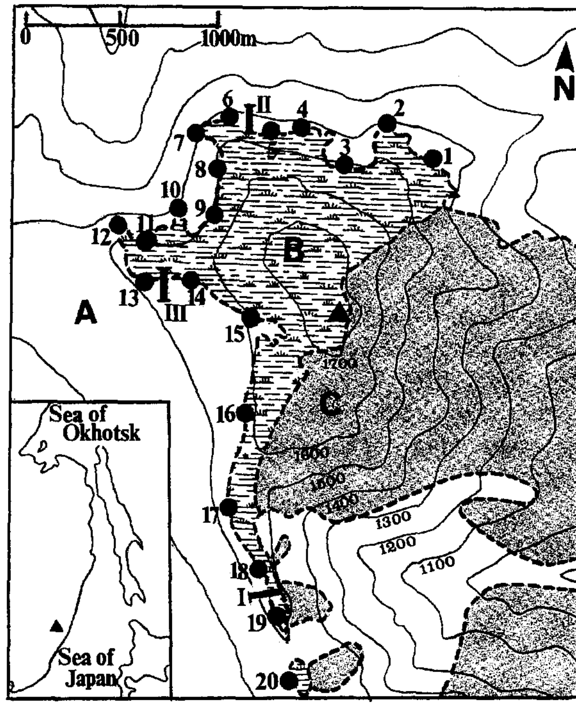

Figure 1. Study area: A: closed forest, B: alpine tundra, C: post fire vegetation, I–III: position and number of geobotanical profiles.

Vegetation and soils

The vegetation of the Central Sikhote-Alin is in the subboreal subzone, which is transitional between boreal and temperature zones. In the lower mountain belt, up to 500–600 m a.s.l., Korean pine (*Pinus koraiensis*) – broadleaved species (*Quercus mongolica, Tilia amurensis, T. mandshurica, Juglans mandshurica, Ulmus japonica* etc.) mixed forests occur. The dark-coniferous forests, dominated by *Picea ajanensis* (*P. jezoensis*) and *Abies nephrolepis*, are distributed from 600 to 1500 m. The subalpine forests of *Betula lanata*, as well as *Pinus pumila* thickets, make broad belts on some mountains. The high-mountain tundra vegetation, usually in a complex matrix with low thickets of *Pinus pumila*, occurs on peaks above 1500 m (Kolesnikov 1955, 1969). The altitudinal position of the vegetational belts on the western macroslope of the Sikhote-Alin is somewhat higher than on the eastern one.

The vast territories of the Central Sikhote-Alin repeatedly suffered from fires during this century. For example, the high-mountain forests of the eastern and southern slopes of Mt. Vysokaya suffered several burns within last 20–30 years.

The soils of the subalpine fir-spruce forests are classified as brown taiga soils (Ivanov 1976). Under the leaf litter they have a monotonous, almost unlayered brown profile that is 20–50 cm depth. On the lichen heaths the soil depth may be reduced to a few centimeters. In the subalpine belt these soils often 'hang' on large rocks and blocks.

Material and methods

The structure of the vegetation was studied using 3 profiles across the subalpine belt, each 120 m long and 5 or 10 m wide (Figure 1). The vegetation profiles were mapped at the scale of 1:100. Profile No. 1 was extended into the forest belt between 1400–1500 m a.s.l., which seems to show a representative structure of a closed forest below the subalpine belt on Mt. Vysokaya. On the profiles the diameter at breast height and height of trees and dwarf shrubs were measured. The altitudinal position of the timberline was traced using aerial photographs and large-scale topographic maps (Beaman 1962).

About 100 releves were made both within and outside the profiles. Altogether we recorded over 200 species of vascular plants, mosses and lichens in the subalpine belt communities.

The cenotical and ecobiomorphological analysis of their floras were made to reveal floristic relations between the different vegetational belts. Ten cenoelements were distinguished. The cenoelement is a group of species peculiar to certain vegetation type or syntaxa regardless of their life form and ecology. For example, *Maianthemum bifolium*, *Linnaea borealis* and *Picea ajanensis*, differing the life form each other, all occur mainly in dark coniferous forests, therefore they all belong to the type of cenoelement taiga's species. Nine ecobiomorphes were distinguished. The ecobimorphes are groups of species of a similar ecology and life form regardless of cenoelements. For further details of cenoelements and ecobiomorphes see the legend of Figure 6.

To clarify the soil properties of the vegetation we examined soil humidity and nutrition. The edaphic grid (terminology from Krajina 1969) was constructed from two axises of soil humidity and soil nutrition. The axis of soil humidity in the study area includes 5 steps: xeric, meso-xeric, mesic, meso-hygric and hygric(hydrophytic). The axis of soil nutrition includes 4 steps: oligotrophic, oligo-mesotrophic, mesotrophic and megatrophic. Thus the edaphic grid gives 20 combinations of categories of soil humidity and nutrition, similar to those of some western authors (e.g. Cajander 1926; Heimburger 1934; Curtis 1959; Arnborg 1960; Masing 1969 and others). The ecological optimal position of the species in the grid was determined by the ecological analysis of the flora according to the techniques of Pogrebnyak (1954), Vorob'ev (1959) and Krylov (1984).

Results

The structure of subalpine vegetation

The subalpine vegetation of Mt. Vysokaya is mostly a forest-tundra ecotone between the upper limit of the closed forest and the alpine tundra, although post fire vegetation prevails on the eastern slope of the mountain (Figure 1). It consists of a mosaic of subalpine shrubs, meadows, groups of *Betula lanata* and a narrow but clear band of the subalpine dwarf pine *Pinus pumila*. This belt stretches for only within 100–200 m horizontally and 50–70 m vertically.

Figure 2 illustrates the three vegetation profiles studied, and Figure 3 presents the vegetation map and crown projection map of profile I. The subalpine vegetation comprises mainly four bands: (1) Subalpine spruce forests; (2) A complex composed of subalpine shrubs, meadows, and groups of *Betula lanata*; (3) Dwarf pine forests; and (4) Lichen-herb-subshrub communities of alpine tundra.

Subalpine spruce forests

Dark-coniferous trees form the timberline that is the upper limit of the closed forests (Figures 2, 3). The altitudinal range of the timberline varies between 1350 m and 1600 m (Figures 1, 2). It is dominated by *Picea ajanensis* with *Abies nephrolepis* and *Betula lanata* in the overstory (Figure 2). The total basal area of the trees between the altitude of 1400 and 1500 m is fairly constant, ca. 35 m^2 ha^{-1}, although that of *Picea ajanensis* slightly is reduced toward the timberline while that of *Betula lanata* increases to almost 30% of the total basal area of the three species. The share of *Abies nephrolepis* is insignificant.

Figure 4 shows the height and diameter distribution of *Picea ajanensis* trees at the timberline in profile I. The tree height of the spruce in the overstory is 12–15 m and the diameter at breast height reaches 36 cm. The size distribution of the spruce suggests unevenaged stands and, therefore, the stability of the forest. Kolesnikov (1969) also noted this phenomenon for the subalpine forest of the Middle Sikhote-Alin. Numerous viable seedlings occur in the stands of subalpine forests.

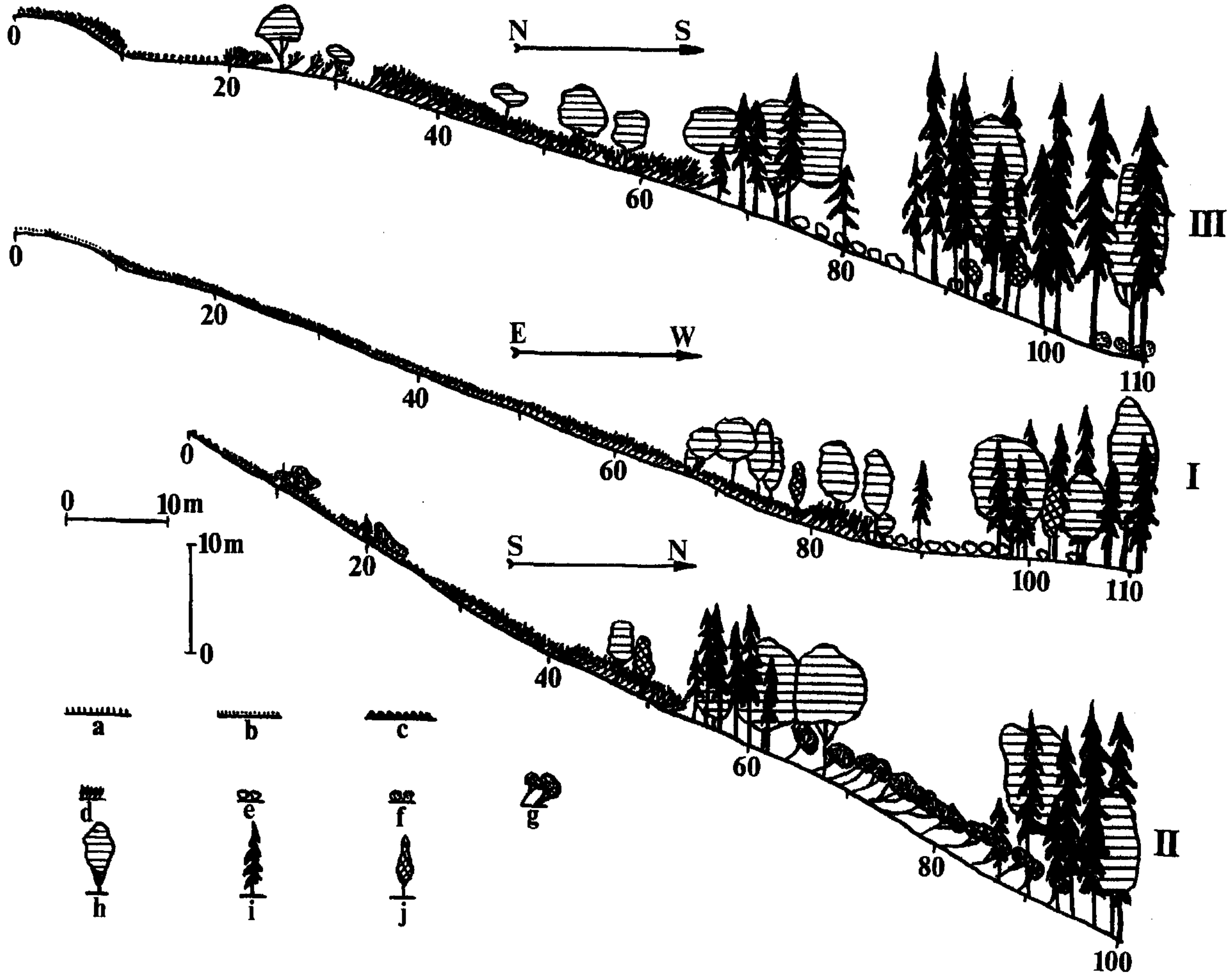

Figure 2. Vegetation diagrams of three profiles studied (I–III). Figures in the profile show the distance (m). (a) subalpine meadows, (b) lichen tundras, (c) thaluses, (d) dwarf-pine thickets, (e) *Weigela middendorffiana* thickets, (f) *Ribes triste* thickets, (g) *Alnus fruticosa* thickets, (h) *Betula lanata* trees, (i) *Picea ajanensis* trees, (j) *Sorbus amurensis* trees.

Figure 5 illustrates the relationships of tree age to three height (A), and to diameter at breast height (B) of the spruce. Tree age correlates both with tree height and diameter at breast height ($r = 0.728$ and $r = 0.799$, respectively, both of them $p < 0.001$). The spruce continuously grows and finally reaches to the canopy. Together with Figure 2, it is clear that spruce population maintains itself even at the upper limit of the closed forest.

The size of *Betula lanata* and *Abies nephrolepis* is similar to those of *Picea ajanensis*. The small trees of *Sorbus amurensis* and *Acer ukurunduense* scatters in the second layer of stands. The understory consists of *Weigela middendorffiana*, *Rosa acicularis*, and *Ribes horridum*; of *Rhododendron aureum* near the timberline; and of *Ribes triste* and *R. fontaneum* near streams.

A total of 103 species of vascular plants, mostly taiga and boreal forest elements, occur in the subalpine spruce forests. Figure 6.1 shows the relationships between different cenotical elements of the subalpine spruce forest flora. The structural elements (synusia) of the forest phytocenoses consists of taiga needle-leaved trees, taiga ferns and small herbs, and taiga and boreal forest tall herbs. For the most forest phytocenoses a well-developed cover of green moss is typical.

On the basis of ecological analysis of the phytocenosis structural elements, 7 main groups of spruce forests are distinguished (Figure 7). As a

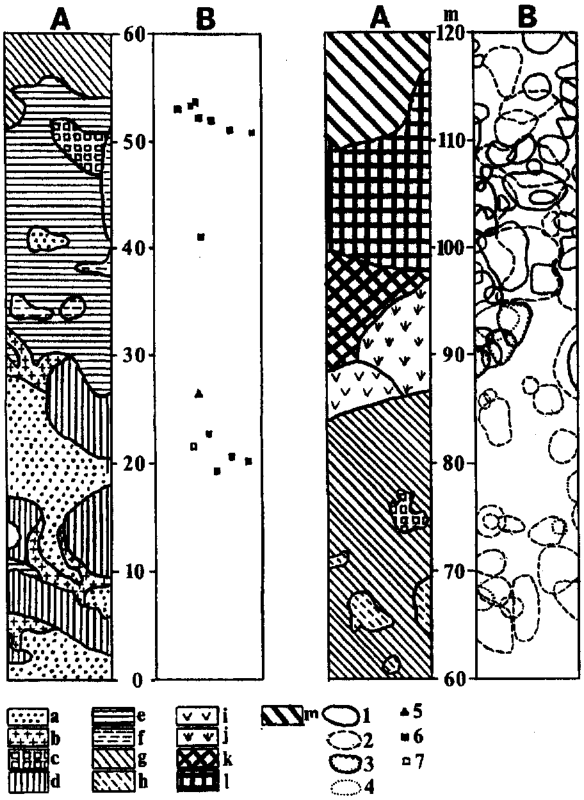

Figure 3. Vegetation map (A) and crown projection map (B) of profile I. Figures in the profile show the distance from the zero point (m). For vegetation map: (a) lichen tundra, (b) *Ledum decumbens* thickets, (c) *Rhododendron aureum* thickets, (d) *Pinus pumila-Ledum hypoleucum-Vaccinium uliginosum*, (e) *Pinus pumila-Rhododendron aureum-Ledum hypoleucum*, (f) open *Pinus pumila-Rhododendron aureum-Ledum hypoleucum*, (g) open *Betula lanata-Pinus pumila-Hylocomium splendens-Pleurozium schreberi*, (h) open *Pinus pumila-Ledum hypoleucum-Hylocomium splendens*, (i) open *Weigela middendorffiana-Calamagrostis purpurea-Cacalia hastata*, (j) *Weigela middendorffiana*, (k) *Abies nephrolepis-Picea ajanensis-Betula lanata-Dryopteris amurensis-Pleurozium schreberi*, (l) *Picea ajanensis-Betula lanata-Carex xyphium*, (m) open *Picea ajanensis-Calamagrostis purpurea*. For crown projection map: (1) *Picea ajanensis*, (2) *Betula lanata*, (3) *Abies nephrolepis*, (4) *Sorbus amurensis*, (5) young growth of *Picea ajanensis*, (6) young growth of *Betula lanata*, (7) young growth of *Sorbus amurensis*.

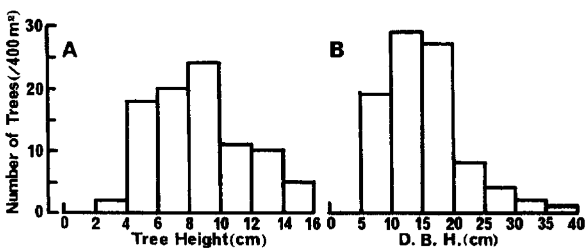

Figure 4. The tree height (A) and diameter at breast height (D.B.H.) (B) distribution of *Picea ajanensis* trees (>2 m in height and >5 cm in D.B.H.) at the uppermost part of the closed forest in profile I.

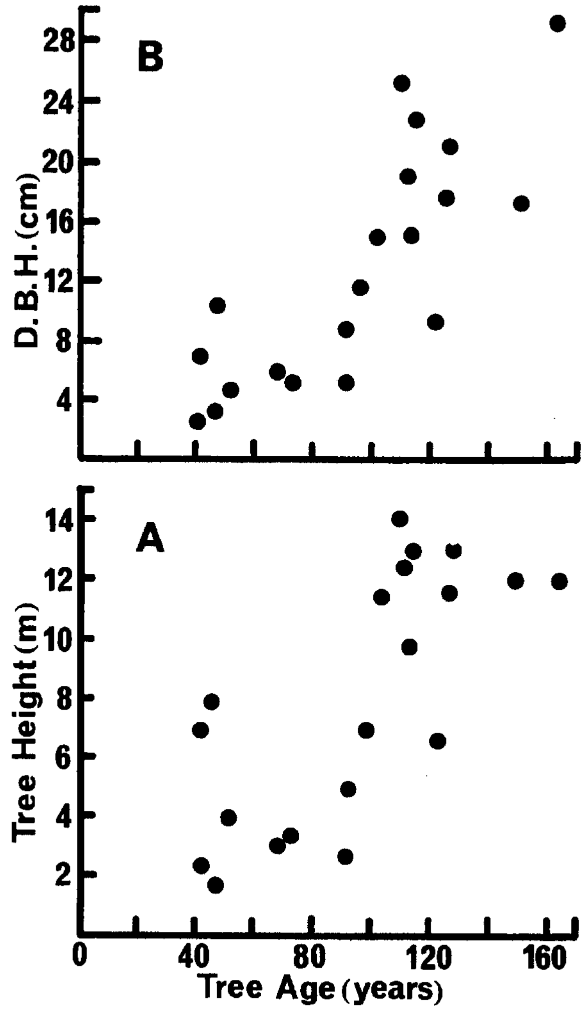

Figure 5. The relationships of tree age to tree height (A) and to diameter at breast height (D.B.H.) (B) of *Picea ajanensis* at the uppermost part of the closed forest in profile I.

whole, their ecological range comprises locations with mesooligotroptic-mesomegatrophic soils, and with a moisture ranged from xeromesic to hygromesic (Figure 7).

Picea-Abies-Betula forests with green mosses and small taiga herbs (Figure 7.1) occur in the subalpine forest strip on the slightly convex slopes of medium steepness. They include phytocenoses with the herb layers dominated by species of taiga small herbs: *Chamaepericlymenum canadense, Oxalis acetosella, Coptis trifolia, Maianthemum bifolium.*

Picea-Abies forests with taiga graminoids (*Carex xyphium*) (Figure 7.2) and *Picea* forests with *Weigela middendorffiana* (Figure 7.3) occur on gently sloping sites with more rich soils.

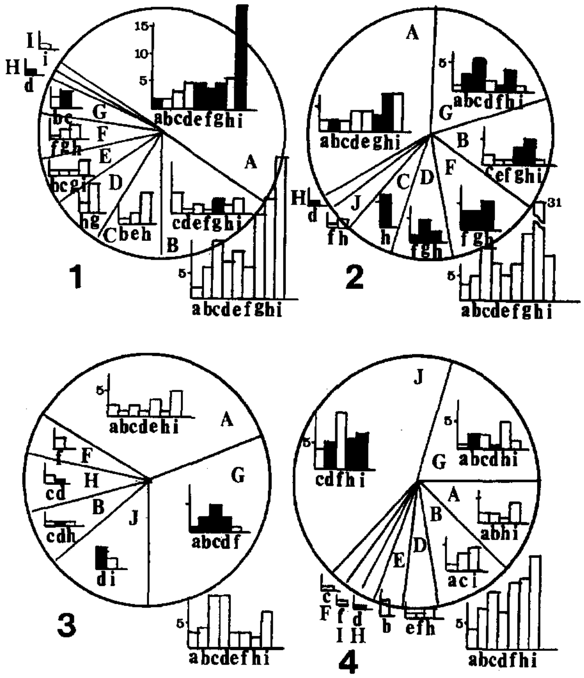

Figure 6. Cenotical (sectors) and biomorphological (histograms) spectra of the species composition of: (1) subalpine spruce forests (103 sp.), (2) complex of subalpine shrubs, meadows and birch forests (87 sp.), (3) dwarf-pine krummholz (42 sp.), and (4) alpine tundra (75 sp.). The species forming synusia and layers in phytocenoses are shaded in. The types of cenoelements: (A) taiga's species, (B) boreal deciduous forest's species, (C) nemoral forest's species, (D) alpine meadow's species, (E) meadow's species, (F) riverian deciduous forest's species, (G) subalpine dwarf-pine forest's species, (H) xeric coniferous forest's species, (I) moss bog's species, (J) alpine tundra's species. The biomorphes: (a) needle-leaved trees, (b) hardwood trees, (c) shrubs, (d) undershrubs, (e) ferns, (f) graminoids, (g) tall herbs and forbs, (h) small herbs.

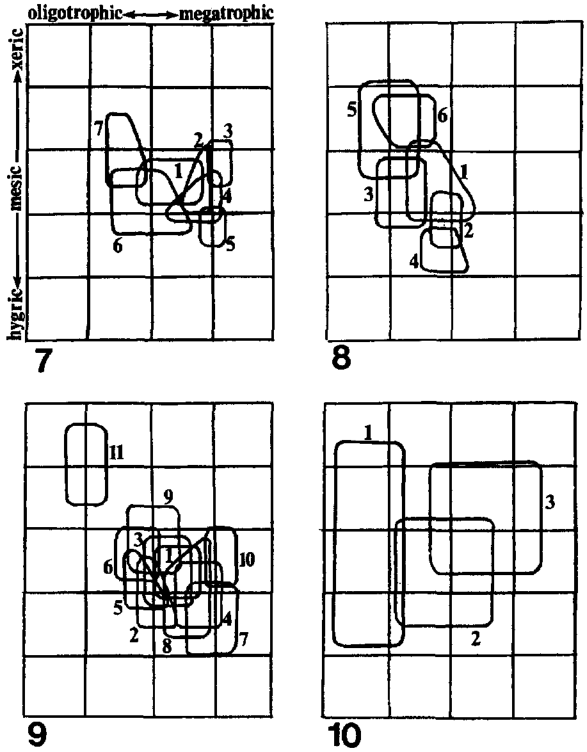

Figure 7–10. Ecological ranges of subalpine vegetation in Mt. Vysokaya. Figure 7. Subalpine spruce forests. Figure 8. Dwarf-pine krummholz. Figure 9. Complex of subalpine shrubs, meadows and birch forests. Figure 10. Alpine tundra. Soil characteristics are shown in coordinate system with trophication (abcissa) and moisture (ordinata). For further explanation see the text.

Picea-Abies forests with taiga ferns, in which *Dryopteris amurensis*, *D. austriaca*, and *Phegopteris connectilis* dominated the herb layer, occur on the slightly concave gently sloping sites with the moister soils (Figure 7.4).

Open *Picea-Abies* forests, with taiga and boreal forest tall herbs, occur on gently sloping sites associated with spring streams (Figure 7.5). Their herb layer is dominated by *Aconitum fischeri*, *Ligularia fischeri*, *Filipendula purpurea*, and *Cacalia hastata*. Characteristic of this group is the absence of moss cover.

Picea-Abies-Betula forests with green mosses and lacking significant taiga herbs occur on the steep (around 30°) slopes. A well-developed moss cover is formed by green moses: *Rhytidiadelphus triquetrus*, *Rh. squarrosus*, *Hylocomium splendens*, and *Pleurozium schreberi* (Figure 7.6).

Picea-Abies-Betula forests with green mosses, *Bergenia pacifica* and *Vaccinium vitis-idaea* occur on well drained rocky parts of steep slopes. Patches of *Bergenia pacifica* are developed in the gaps of stands, while those of *Vaccinium vitis-idaea* are situated under the dense canopy (Figure 7.7).

Most of the subalpine spruce forests consist of green moss and of taiga small herb groups. Their ecological range is characterized as oligomeso- and mesotrophic mesic one. They are widely distributed on steep slopes.

Complex of subalpine shrubs, meadows, and birch forests

The small parcels of the opened crook-stem *Betula lanata* forest, thickets of *Alnus fruticosa*, and subalpine-like meadows stretch in a narrow strip between the timberline and dwarf pine krummholz (Figures 2, 3). The strip is very heterogeneous and interrupted. The communities that form it are often only fragments. The degree of development of this strip and the relationships of the communities and their fragments that constitute it depend upon the variations in ecological regimes on the boundary between the two clearly distinguished vegetational types that reflect different types of environment. The unique floristic (Figure 6.2) and ecological (Figure 9) pattern of the communities of this strip allow us to refer them to the common vegetation complex. A total of 87 vascular species were noted there.

The communities of *Betula lanata* stretches in a narrow (10–30 m) interrupted strip of opened stands (Figure 3). Trees are much reduced in size here compared to birch trees growing in the overstory of the subalpine spruce forests (Figure 2). The height of the trees does not exceed 5–6 m and their D.B.H. is not more than 10–18 cm. In the highest stands of *Betula lanata* (1520 m a.s.l., Figure 2, profile I; Figure 3), the trees are up to 3–4 m high and D.B.H. is around 10 cm.

The forests of *Betula lanata* usually have a well developed shrub layer consisting of *Pinus pumila*, *Alnus fruticosa* or *Rhododendron aureum*, and sometimes have a closed grass layer of *Calamagrostis langsdorffii*. The stands of *Betula lanata* with *Pinus pumila* occur very closely to dwarf pine strip and sometimes within it. Due to this, the flora of birch communities is enriched with species of subalpine cenoelement (Figure 6.2).

The ecological range of this group comprises the mesic locations with oligomesotrophic soils (Figure 9.1). The similar but moister locations are characterized by *Betula lanata* forests with *Ledum hypoleucum* and *Rhododendron aureum* (Figure 9.2).

The *Betula-Picea-Abies* forests with *Alnus fruticosa* and meadow graminoids co-occur at timberline. The grass layer of the forests is dominated by *Calamagrostis langsdorffii*. Well-developed synusia of taiga species occur sometimes under the grass layer. The ecological range of the forests is characterized as mesotrophic mesic one (Figure 9.3).

The thickets of *Alnus fruticosa* arises on the north slopes near the timberline. In one case, *A. fruticosa* forms a 30 m wide strip of sparse but large bushes (5 m high and 10–15 cm in basal diameter) (Figure 2, profile II). In another case, *A. fruticosa* forms a sparse understory in opened forest of *Betula lanata* on a steep slope (Figure 2, profile III). The stands of *Alnus fruticosa*, as a whole, are characterized by a high density of overstory. There is a developed understory of *Rhododendron aureum* and *Ledum hypoleucum*, sometimes a developed herb or grass layer, and rarely a developed moss cover.

The group of *Alnus* stands with tall herbs and grass (Figure 9.4) is most common. Phytocenoses of this group are characterized by the presence of a sparse shrub layer of *Weigela middendorffiana* and *Rhododendron aureum*, and by a developed grass layer with scattered specimens of the boreal forest tall herbs *Cacalia hastata* and *Angelica cincta* dominated by *Calamagrostis langsdorffii.*

Alnus stands with an understory of *Rhododendron aureum* and *Ledum hypoleucum* (Figure 9.5) are not common. The understory of these phytocenoses is of a high density, but no herb or grass layer is developed. Phytocenoses of this group develop under a mesic conditions on mesotrophic soils (Figure 9.5).

Alnus stands with green mosses, sparse herb layer of the taiga species *Maianthemum bifolium* and *Trientalis europaea* and small patches of the meadow graminoid *Calamagrostis langsdorffii* occur with the alpine tundra belt on leeward locations and in terrain cavities. The ecological range of this group comprises locations with mesic mesotrophic soils (Figure 9.6).

Tall herb meadows (Figure 9.7) occur on the gently sloping locations of the south exposition near the timberline as small sparse patches or a narrow strip. The meadows are dominated by the species of taiga and boreal forests and the subalpine meadow cenoelements (*Aconitum fischeri*, *Veratrum alpestre*, *Cacalia hastata*, *Sanguisorba sitchensis*, *Angelica saxatilis*, *Saussurea triangulata*, *Ligularia fischeri*, *Heracleum dissectum*, and *Filipendula purpurea*). They develop on the hygric and mesohygric locations with mesomegatrophic soils. The herb layer is closed and is about 1 m high.

The dry meadows occur at the elevations of terrain on the mesic locations with well drained mesotrophic soils (Figure 9.8). In addition to species already listed for the first group, in this group the species of subalpine forbs (*Hieracium coreanum*, *Saussurea porcellanea*, and *Solidago spiraefolium*) and taiga small herbs (*Trientalis europaea* and *Pyrola minor*) play an important role in the herb layer structure.

The subalpine shrub brakes are distributed near the timberline and are very similar floristically to subalpine spruce forests. The brakes of *Rhododendron aureum* occur on north steep slopes on the mesic locations with oligomesotrophic soils (Figure 9.9). *R. aureum* forms a closed layer. Under this layer the taiga species *Lycopodium annotinum* and *Linnaea borealis* occur individually. On the taluses *R. aureum* forms a complex with *Bergenia pacifica*.

The brakes of *Weigela middendorffiana* are distributed on the gently sloping locations near the timberline. They form the closed layer 2 m high. A layer of small taiga herbs is usually sparse. *Calamagrostis langsdorffii* and sole specimens of the boreal forest tall herbs (*Cacalia hastata*, *Veratrum oxycepalum*) dominate in the gaps of thickets. The ecological range includes the hygromesic locations with megamesotrophic soils (Figure 9.10).

The shrubs of *Juniperus sibirica* occur in the upper part of the considering strip, on the south slopes. *Juniperus sibirica* forms a slightly closed layer of 0.4–0.6 m high. The herb layer consists of species of small herbs and subalpine forbs (*Antenaria dioica* and *Scorsonera radiata*). It rather scatters with a coverage of 20–30%. In the gaps of the herb layer a lichen cover of *Cladonia amaurocraea* and *C. bellidiflora* is developed. The ecological range of this group comprises mesoxeric habitats with oligotrophic soils (Figure 9.11).

Dwarf pine krummholz

The dwarf pine krummholz is an obligatory component of the subalpine vegetation of the Russian Far East. On Mt. Vysokaya it forms narrow but clear strip of some tens of meters wide (Figures 2, 3). The lower edge of the strip forms a sharp contact with dark-coniferous forests or rarely with the *Betula lanata* forests and often with *Weigela middendorffiana* brakes or parcels of subalpine meadows. The upper edge of this strip is uneven and sinuous. It is composed of separated patches of undershrubs, lichen patches and low dense brakes of *Rhododendron aureum*. The height of *Pinus pumila* varies from 0.5 m in the upper part of the strip to 3–4 m in the lower part (Figure 2). The length of the trunks correlates with the height of brakes and may be as large as 6 m. The basal diameter varies from 2–3 cm to 8–10 cm but some individuals have a diameter of 15–20 cm.

The structure of the dwarf pine phytocenoses varies greatly depending upon the position on the slope and the terrain form. The most characteristic are the high density of branches, the presence of a shrub layer of *Rhododendron aureum*, *Rh. sichotense*, and *Ledum hypoleucum* in some instances and an undershrub layers of *Cassiope redowskii*, *Vaccinium uliginosum*, and *Arctous alpina*. In the lower parts a cover of green or bog mosses and fruticose lichens is revealed. Single trees of *Picea ajanensis*, *Abies nephrolepis*, and *Betula lanata* with low crowns were noted over the whole strip.

The flora of these dwarf pine forests is poor, with only 42 species of vascular plants. The taiga and subalpine cenotic groups of these species constitute most of them (Figure 6.3). The phytocenoses are composed of the subalpine dwarf pine *Pinus pumila*, subalpine shrubs, and alpine tundra undershrubs. The taiga species do not play a significant role in the structure of the communities, despite their number is large.

On the basis of ecological analysis, 6 groups of communities are distinguished. As a whole, they cover the habitats with the soil richness ranged from oligo- to oligomesotrophic and the moisture spectrum from mesoxeric to hygric (Figure 8).

Dwarf pine communities with *Rhododendron aureum* (Figure 8.1) are widely distributed. They constitute the most of the lower part of the dwarf pine strip. They are characterized by a developed dwarf pine layer of high density, by the presence of a layer of the subalpine shrub *Rhododendron aureum*, and by a developed green moss cover consisted mainly of *Hylocomium splendens*.

On gently sloping locations with moister conditions, the dwarf pine communities with *Rhododendron aureum* and *Ledum hypoleucum* occur (Figure 8.2). The shrub layer in the communities is closed and the herb layer is absent. The moister the habitat, the more significant is the role of *Ledum hypoleucum* in the community structure.

On stony locations of the lower part of the dwarf pine strip on the south slopes, the communities with green mosses occur (Figure 8.3). The branches of *Pinus pumila* are completely closed up and are of the greatest size here. The shrub layer is absent. There is a closed moss cover that consists mostly of the green mosses *Pleurozium schreberi* and *Hylocomium splendens*, and that also involves the fruticose lichens *Cladonia alpestre* and *Cetraria islandica*.

The group of dwarf pine communities with subalpine undershrubs (Figure 8.4) occurs on the north slopes in the upper part of the strip. The dwarf pine layer is not too closed and is not high (0.3–0.7 m).

There is also a layer of the subalpine undershrubs *Ledum decumbens*, *Vaccinium uliginosum*, and *Cassiope redowskii*.

The group of dwarf pine communities with lichens (Figure 8.5) is common on the south steep slopes. The dwarf pine layer is opened and the fruticose lichen layer of *Cladonia alpestre* and *Cetraria islandica* is well developed.

The dwarf pine communities with *Rhododendron sichotense* are similar to those of the above mentioned group and also occur on the south slopes (Figure 8.6).

The vegetation cover of the dwarf pine strip is a mosaic (Figure 3). Three groups that are the most spread in the strip are the dwarf pine communities with *Rhododendron aureum* and green mosses, these with *Rhododendron aureum* and *Ledum hypoleucum*, and these with fruticose lichens. In the upper part of the strip the patches of dwarf pine form complexes with the patches comprised of *Vaccinium-Cladonia* or *Cassiope* tundra. The edges of the patches of *Pinus pumila* are fringed with narrow strips of *Ledum decumbens*. A heterogeneity of the dwarf pine is defined mostly by moisture schedule, insulation, and distribution of snow cover.

Alpine tundra

The complex of the alpine tundra communities is distributed from the upper limit of the dwarf pine strip to the top of the mountain (Figure 2). The structure and flora of the communities of this complex vary widely. However, their common feature is the absences of tree and shrub layers.

This vegetation may be arbitrarily called 'the high mountain vegetation'. It was adequately described by Kolesnikov (1969), who distinguished the alpine lawns, the alpine tundra, and the lichen communities on the taluses.

The mountain tundras, dominated by fruticose lichens (*Cladonia alpestre*, *C. amaurocraea*, *C. pleurota*, *Cetraria islandica*, *Thamnolia verticularis*), are widespread. The 75 species of vascular plants are noted there. Most are species of alpine tundra and subalpine cenoelements. The alpine tundra undershrubs, alpine and subalpine forbs, and small herbs represent the structural elements of the tundra communities (Figure 6.4).

On the basis of ecological analysis, three main groups of the alpine tundra communities are distinguished. The lichen tundra, dominated by different species of the genus *Cladonia*, covers the habitats with poor tundra gley soils on the stony parts of the leeward slopes and often form complexes with dwarf pine patches (Figure 10).

The herbs and undershrub cover scatters, and consists of single individuals of *Vaccinium uliginosum*, *Arctous alpina*, *Luzula sibirica*, *Carex tenuiformis*, *C. tenuiflora*, and *Trientalis europaea*. The ecological range of the group comprises the locations with oligo- and mesooligotrophic soils and with the widest spectrum of moisture (Figure 10.1).

The bog mosses and heath tundras, dominated by the alpine tundra undershrubs *Cassiope redowskii*, *C. ericoides*, and *Diappensia obovata* and mosses of the genus *Sphagnum* (mainly *Sphagnum girgensohnii*), are developed on the north slopes (Figure 10.2). Their ecological range differs from this in above mentioned group, as it includes the locations on oligo- and mesotrophic soils with stable mesic and hygric moisture.

Tundras dominated by alpine tundra forbs, small herbs, and undershrubs *Dryas ajanensis*, *Oxytropis charkewiczii*, *Hedysarum branthii*, *Pentaphylloides fruticosa*, *Artemisia lagocephala*, *Anemonastrum brevipedunculatum*, etc. occur on the south slopes (Figure 10.3). The ecological range of this group comprises xeromesic locations with meso- and megatrophic soils.

The high mountain vegetation complex is significantly enriched with subalpine and even taiga cenoelements (Figure 6.4). *Picea ajanensis*, *Betula lanata*, *Pinus pumila*, and *Alnus fruticosa* 1.0–1.5 m high occur from the upper limit of krummholz to the mountain top. These trees have the twisted and shrub-like forms. In the unfavorable conditions of the windward slopes, among the closed moss and undershrub vegetations, small suppressed individuals of spruce up to 15 cm high were noted.

Alnus fruticosa on the slopes within the alpine tundra belt forms patches 1–2 m high and 2–5 m wide. *Pinus pumila* forms the small patches about 1 m high (Figures 2, 3).

The top of Mt. Vysokaya is a plain about 200 × 500 m in size, covered by open (the coverage is about 50%) vegetation (Figure 1). The stones scattered over the surface are partially (30%) covered by crustaceous and foliose lichens. There is also an opened herb layer of small (0.5–1.0 m in diameter) dense parcels of *Dryas ajanensis*, *Salix berberifolia*, *Cassiope ericoides*, *Bergenia pacifica*, *Ledum decumbens*, *Vaccinium uliginosum*, *Arctous alpina*, *Rhododendron redowskianum*, *Rh. parviflorum*, and *Rh. aureum*.

Under the canopy of low dense parcels of *Pinus pumila* 0.3–0.5 m high and about 3 m wide, *Bergenia pacifica*, *Vaccinium vitis-idaea*, and *Ledum decumbens* form an opened layer. These are also some shrubs (*Betula divaricata*, *Alnus fruticosa*, *Pentaphylloides fruticosa*, and *Sorbaria rhoifolia*), herbs (*Saussurea porcellanea*, *Anemonastrum brevipedunculatum*, *Bupleurum euforbioides*, *Silene stenophylla*, *Bistorta major*, *Artemisia lagocephala*, *Hedysarum branthii*, *Popoviocodonia stenocarpa*, *Sanguisorba* *officinalis*, and *Rhodiola rosea*), and graminoids (*Carex rigidioides*, *Ptilagrostis alpina*, etc.) on the mountain top.

Discussion

The subalpine vegetation of Mt. Vysokaya comprises four bands: (1) subalpine spruce forests; (2) a complex composed by subalpine shrubs, meadows, and groups of *Betula lanata*; (3) dwarf pine forests; and (4) lichen-herb-undershrub communities of alpine tundra.

The structure of the subalpine vegetation described here agrees generally with that of other high-mountain areas of the Central Sikhote-Alin (Kolesnikov 1938, 1969; Pryaluhina 1958; Vasilyev & Kurentzova 1960; Vasilyev 1965; Rosenberg & Vasilyev 1967; Vasilyev & Kolesnikov 1974). However, there are some interesting differences.

We focus discussion on following problems: (1) structure of the subalpine belt comparing with those of the other regions, (2) the altitudinal position of the timberline.

A structure of the subalpine belt: comparisons with other regions

A subalpine belt in Eurasia and north America is situated between forest and alpine belts. Löve (1970) stated that the subalpine belt is the forest-tundra ecotone with dwarfed tree growth and subalpine meadows, in some areas supporting good mountain pastures and heaths. Along the subalpine belt, generally tree size and density gradually decrease from closed forest limit to open tundra (Tranquillini 1979).

In the mountains from the Pacific coast to lake Baikal of eastern Eurasia, the subalpine belt shows generally a similar structure of such changes. Three main types of the composition in the subalpine belt appear there (Grishin 1995): (1) *Betula ermanii-Alnus* spp. with subalpine meadows in oceanic sector, (2) *Picea ajanensis* and *Betula ermanii-Pinus pumila* in marine sector (coastal parts of the Sea of Okhotsk and Sea of Japan), (3) *Larix dahurica-Pinus pumila* with shrub-lichen communities in continental sector.

Mt. Vysokaya is situated in the marine sector, and is typical. Such vertical zonation arises also on the Middle and Southern Sikhote-Alin (see above cited publications), on Sakhalin (Tolmachev 1956), Hokkaido (Okitsu & Ito 1984, 1989), northeastern China (Xu & Lin 1981; Okitsu 1993), i.e. in a southern half of boreal zone in Far Eastern Asia. The subalpine belt usually occupies 200–400 vertical meters in the Far East, including Sikhote-Alin. On Mt. <?>Dal'naya Ploskaya, Kamchatka, the belt width reaches 1.5–2 km, and on extremely gentle (3°) base of volcano Kluchevskoy – up to 5–6 km (Grishin 1988a,b).

However, the subalpine belt of Mt. Vysokaya does not exceed the altitudinal interval of 50–75 m. Nevertheless, Kolesnikov (1969) marked its presence in 1937, and evaluated its sizes up to vertically 150–200 m. Thus, the modern position and width of this belt is not climatically caused and is as appear connected to strong infringements of vegetation.

The *Pinus pumila* belt is in similar situation. In Sikhote-Alin it normally occupies 100–200 vertical meters. On Mt. Vysokaya this belt does not exceed 50 m and is interrupted by stone blocks, and on the northern slope partly by continuous lichens.

Thus, serious distortions of a spatial structure, composition and parameters of subalpine *Betula ermanii* forest and *Pinus pumila* belt are obvious on Mt. Vysokaya. One might speculate from the spatial structure of the subalpine zone that the present altitudinal position of the timberline does not correspond to the present climatic condition. The following section discusses this point.

Altitudinal position of the timberline

The altitudinal position of the timberline on Mt. Vysokaya, situated around 1450–1550 m a.s.l. (Figure 1) is similar to that of Mt. Ko (2004 m) and Mt. Budisheva (1822 m), both situated about 100 km northward of Mt. Vysokaya (Vasilyev & Kurentzova 1960; Vasilyev 1965).

Does the position of the upper timberline on Mt. Vysokaya depend mainly on the climate conditions? We are sure that it does not. The following evidence proves these conclusions: (1) warmth indices (the temperature of the warmest month, Kira's WI and others) for the level of 1570 m considerably exceed these for climatic timberline; the altitude of WI 15 °C month of Mt. Vysokaya is ca. 1850 m a.s.l., (2) a high abundance of undergrowth and bush-shaped trees of spruce and larch, as well as the parcels and shrubs of alder and pine krummholz, growing up to the mount top, (3) the relatively large structural features of tree stands (the heights and diameters of tree stems and the radial increments) on the upper limit of closed forest, (4) the floristic composition of herb and shrub layers of the forest communities at their upper limit is characterized by almost total absence of alpine species, which are common at the timberline, and (5) disturbed, not climax, vegetation structure in the subalpine belt.

What are the reasons for the lowered position of the timberline and the disturbance in the vegetation structure? Climatic events of the last few centuries apparently could not influence the dynamics of the timberline. For example, the Far Eastern analogue of the 'little ice age' started in Japan about 700 years ago (Sakaguchi 1983), and if the same situation existed in the Sikhote-Alin, there were no climatically conditioned lowering of the tree line in recent centuries.

The cause of the sharp lowering of the timberline was, probably, connected to a catastrophic fire (or several fires). This fire happened rather long ago, since there are no any visible traces of it now. After burning of the forest and krummholz vegetation, accompanied by soil erosion on steep slopes, its restoration seems to be unfavorable due to a complex of factors. The most essential factor is a very severe wind regime (Sochava 1944). It is easy to imagine, that steep (30°) slopes are not covered with snow during the most part of winter, including the most cold and windy period (December–February). Okitsu & Ito (1984) pointed out that the performance of *Pinus pumila* thickets closely correlate with the snow depth of the stands; *P. pumila* occurs vigorously on the sites with sufficient snow depth. The most severe winds are recorded on the windward northern and northwestern slopes.

Additionally, the survivalship of seedlings and understory at the slopes of southern expositions is also a serious problem, due to a strong insulation over the most part of winter and spring. An essential factor is also the accumulation of a deep snow layer on the timberline that suppresses the growth of trees.

Thus, after the catastrophic lowering of the timberline and the subalpine belt as a whole, the peculiar combination of unfavorable ecological conditions do not allow the restoration of the vegetation to its initial state, although theoretically (by heat input) the timberline height may exceed by 200–250 m its current uppermost position. This situation seems to be characteristic of the whole southern half of the Sikhote-Alin: there are no mountains where the timberline reaches its estimated climatic limit. The fires, including very old ones, affect the structure of subalpine vegetation over a very long time. The restoration of the vegetation may only be the result of a unique combination of several series of climatically favorable years, without any events that might be critical for the vegetation situated here at the extreme limit of its existence.

Acknowledgement

We thank Dr A. Goncharov for field assistance.

References

Arnborg, T. 1960. Can we find a common platform for the different schools of forest type classification? Silva Fenn. 105: 13–15.

Beaman, J. H. 1962. The timberlines of Lstaccihuatl and Popocatepetl, Mexico. Ecology 43: 377–385.

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

Cherepanov, S. K. 1981. Vascular Plants of the USSR. Nauka, Moscow, Leningrad (in Russian).

Curtis J. T. 1959. The vegetation of Wisconsin: An Ordination of Plant Communities. Univ. Wisconsin, Madison.

Geological Map of Primorsky Kray. 1986. Scale 1:1000000. Leningrad (in Russian).

Grishin, S. Yu. 1988a. The upper timberline at Kluchevskoy volcano group (Kamchatka). Pp. 193–201. In: Kharkevich, S. S. (ed.), Plant cover of high mountain ecosystems of the USSR. Far East Branch of the USSR Academy of Sciences, Vladivostok (in Russian).

Grishin, S. Yu. 1988b. The structure of timberline ecotone vegetation on Dalnaya Ploskaya volcano (Kamchatka). Komarovskie Chtenia 35: 159–175 (in Russian).

Grishin, S. Yu. 1995. The boreal forests of the north-eastern Eurasia. Vegetatio 121: 11–21.

Heimburger, C. C. 1934. Forest-type studies in the Adirondack region. Mem. Cornell Univ. (N.Y.) Agric. Exp. Stn. 165: 1–122.

Ivanov, G. I. 1976. The Soil Formation on the South Far East of Russia. Nauka, Moscow (in Russian).

Kira, T. 1977. A climatological interpretation of Japanese vegetation zones. Pp. 21–30. In: Miyawaki, A. & Tuexen, R. (eds.), Vegetation science and environmental protection. Pp. 21– 30. Maruzen Co. Ltd., Tokyo.

Kolesnikov, B. P. 1938. The vegetation of the eastern slopes of the Middle Sikhote-Alin. Transactions of Sikhote-Alin State Reserve 1: 25–208 (in Russian).

Kolesnikov, B. P. 1955. A sketch of vegetation of the Russian Far East. Khabarovsk (in Russian).

Kolesnikov, B. P. 1969. High Mounting Vegetation of Middle Sikhote-Alin. Vladivostok (in Russian).

Krajina, V. J. 1969. Ecology of forest trees in British Columbia. Ecol. West. N. Am. 2: 1–146.

Krylov, A. G. 1984. Life Form of Forest Phytocenoses. Nauka, Moscow (in Russian).

Löve, D. 1970. Subarctic and subalpine: where and what? Arct. Alp. Res. 1: 63–73.

Masing, V. 1969. Structural analysis of plant cover and classification problems. Pp. 49–59. In: Plant Taxonomy, Geography and Ecology in the Estonian S.S.R. Tallin.

Okitsu, S. 1993. The establishment and phytogeographical comparison of the needle-leaved and deciduous-broadleaved mixed forest of Hokkaido, northern Japan, inferred from the *Pinus koraiensis*-deciduous-broadleaved mixed forest of the Sikhote-Alin' Range, Primorie, Geographidal Review of Japan 66A: 555–573 (in Japanese).

Okitsu, S. & Ito, K. 1984. Vegetation dynamics of the Siberian dwarf pine (*Pinus pumila* Regel) in the Taisetsu mountain range, Hokkaido, Japan. Vegetatio 58: 105–113.

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

Pogrebnyak, P. S. 1954. The Fundamentals of the Forest Typology. Kiev (in Russian).

Pryaluhina, A. F. 1958. On alpine and subalpine vegetation of Bikin-Iman watershed. Botanichesky Zhurnal 43: 92–96 (in Russian).

Reference Book on a Climate of the USSR. Parts 2; 4. 1968. Gidrometeoizdat. Leningrad (in Russian).

Rosenberg, V. A. & Vasilyev, N. G. 1967. The problems of vegetation pattern of Middle Sikhote-Alin. Pp. 143–151. In: The Problems of Botany. Vol. 9. The Vegetation of High Mountains of the USSR and the Problems of Their Use. Frunze (in Russian).

Sakaguchi, Y. 1983. Warm and cold stages in the past 7600 years in Japan and their global correlation. Bull. Dep. Georgr. Univ. Tokyo 15: 1–31.

Sochava, V. B. 1944. The causes of forestless of the golets of the Eastern Siberia and Priamurye. Priroda 2: 63–65 (in Russian).

The History of the Terrain Development of Siberia and Far East. The South of Far East of Russia. 1972. Nauka, Moscow (in Russian).

Tolmachov, A. I. 1956. Vertical distribution of vegetation on Sakhalin, Pp. 15–48. In: Plant cover of Sakhalin. USSR Academy of Sciences Publ., Moscow, Leningrad (in Russian).

Tranquillini, W. 1979. Physiological ecology of the alpine timberline. Tree existence at high altitudes with special reference to the European Alps. Springer-Verlag, Berlin.

Vasilyev, N. G. 1965. The Mount Budishcheva. Pp. 18–31. In: A. F. Budishchev as the First Investigator of the Forests of the Far East of Russia. Vladivostok (in Russian).

Vasilyev, N. G. & Kolesnikov, B. P. 1974. Features of high mountain vegetation pattern or Arsenyev Mountains (The Middle Sikhote-Alin). Pp. 111–117. In: The Problems of Botany. Vol. 12. Plant World of Highlands and Its Mastering. Nauka, Leningrad.

Vasilyev, N. G. & Kurentzova, G. E. 1960. Altitudinal zonation of vegetation cover on the Mt. Ko in the Middle Sikhote-Alin. Komarovskie chtenia 8: 21–40 (in Russian).

Vorob'ev, D. V. 1959. The technique of forest typological investigations. Kharkov (in Russian).

Vyshin, I. B. 1990. Vascular Plants of the High Mountains of Sikhote-Alin. Vladivostok (in Russian).

Xu, W.-D. & Lin, C.-Q. 1981. Preliminary study of relations between vertical distribution of vegetation and thermal climate in Changbai Mountain. Research of forest ecosystems. Changbai Mountain Res. Station, Academia Sinica. 2: 88–95 (in Chinese with English summary).

Appendix

Table A1. Distribution of species in main vegetational formations

Species name	Main vegetational formations							
	Paj	Shr	Mea	Aln	Ber	Pin	Jun	Tun
Vascular plants								
Abies nephrolepis (Trautv.) Maxim.	+ – 3	+			+	+		+
Acer ukurunduense Trautv. et Mey.	+ – 2			+	+			
Aconitum fischeri Rchb.	+	+	+	+	+			
Actinidia kolomikta (Maxim.) Maxim.	+			+	+			
Adoxa moschatellina L.	+		+	+	+			
Aegopodium alpestre Ledeb.	+		+	+	+			+
Anaphalis margaritaceae (L.) A. Gray							+	+
Anemonastrum brevipedunculatum (Juz.) Holub								+
Anemonastrum sibiricum (L.) Holub								+
Angelica cincta Boissieu	+		+ – 1	+	+			
Angelica maximowiczii (Fr. Schmidt) Benth. ex Maxim.	+		+	+	+			
Angelica saxatilis Turcz. ex Ledeb.			+					
Antennaria dioica (L.) Gaertn.							+	
Aquilegia amurensis Kom.			+					+
Arctous alpina (L.) Niedenzu						+		+ – 3
Artemisia lagocephala (Bess.) DC.								+ – 2
Aruncus dioicus (Walt.) Fern.	+			+	+	+		
Athyrium filix-femine (L.) Roth	+		+ – 1					
Atragene ochotensis Pall.	+		+	+	+	+		
Bergenia pacifica Kom.	+ – 2			+ – 2	+ – 2	+ – 2		+
Betula divaricata Ledeb.								+ – 1
Betula lanata (Regel) V. Vassil.	+ – 3	+		+ – 1	+ – 5	+		+
Bistorta elliptica (Willd. ex Spreng.) Kom.						+		+
Bistorta major S.F. Gray			+			+		+
Bistorta vivipara (L.) S.F. Gray								+
Boschniakia rossica (Cham. et Schlecht.) B. Fedtsch.				+	+			
Bupleurum euphorbioides Nakai							+	+
Cacalia auriculata DC.	+		+					
Cacalia hastata L.	+	+	+	+	+			
Calamagrostis korotkyi Litv.								+
Calamagrostis purpurea (Trin.) Trin.	+ – 2	+ – 4	+ – 5	+ – 4	+ – 4	+ – 1		
Caltha palustris L.	+		+					
Carex pallida C.A. Mey.	+		+	+	+	+	+	+
Carex rigidioides Gorodk.								+
Carex tenuiflora Wahlenb.								+
Carex tenuiformis Levl. et Vaniot							+	+
Carex xyphium Kom.	+		+					
Cassiope ericoides (Pall.) D. Don								+ – 4
Cassiope redowskii (Cham. et Schlecht.) G. Don fil.								+ – 4
Chamaepericlymenum canadense (L.) Aschers.	+ – 4		+ – 1	+ – 2	+ – 2			

Table A1. continued

	Main vegetational formations							
	Paj	Shr	Mea	Aln	Ber	Pin	Jun	Tun
Chamerion angustifolium (L.) Holub	+ – 1	+	+ – 2	+	+	+		
Chrysosplenium ramosum Maxim.	+		+	+				
Cimicifuga simplex (Wormsk. ex DC.) Turcz.	+		+					
Cinna latifolia (Trev.) Griseb.	+		+					
Circaea alpina L.	+ – 1			+	+	+		
Cirsium schantarense Trautv. et Mey	+		+	+	+			
Clintonia udensis Trautv. et Mey	+			+	+	+		
Coptis trifolia (L.) Salisb.	+ – 1			+	+			+
Corydalis gigantea Trautv. et Mey.	+ – 1							
Crepis burejensis Fr. Schmidt							+	+
Diapensia obovata (Fr. Schmidt) Nakai								+ – 1
Diphasiastrum alpinum (L.) Holub							+	
Diphasiastrum complanatum (L.) Holub		+				+		
Diplazium sibiricum (Turcz. ex G. Kunze)	+ – 2		+	+	+			
Dryas ajanencis Juz.								+
Dryopteris amurensis Christ	+ – 4		+	+	+			
Dryopteris austriaca (Jacq.) Woynar ex Schinz et Thell.	+ – 2		+	+	+			
Dryopteris fragrans (L.) Schott					+	+		
Ephippianthus sachalinensis Reichenb. fil.	+							
Equisetum pratense L.	+							
Equisetum sylvaticum L.	+		+	+	+			
Festuca blepharogyna (Ohwi) Ohwi								+
Festuca extremiorientalis Ohwi	+	+	+	+	+			
Festuca ovina L.							+ – 1	+
Filipendula glaberrima Nakai	+ – 1	+	+ – 4	+	+			
Galium boreale L.			+	+	+	+		
Galium davuricum Turcz. ex Ledeb.	+		+					
Galium kamtschaticum Stell. ex Schult. et Schult. fil.	+ – 1		+					
Gentiana triflora Pall.						+		+
Gentianella auriculata (Pall.) Gillett								+
Geranium erianthum DC.	+	+ – 1	+	+	+			
Goodyera repens (L.) R. Br.	+							
Gymnocarpium dryopteris (L.) Newm.	+		+	+	+			
Halenia corniculata (L.) Cornez								+
Hedysarum branthii Trautv. et Mey.								+
Heracleum dissectum Ledeb.	+	+	+					
Hieracium coreanum Nakai						+	+	
Hieracium virosum Pall.	+	+	+	+	+	+		+
Hieracium umbellatum L.	+		+					
Hierochloe alpina (S.) Roem. et Schult.								+ – 1
Huperzia selago (L.) Bernh. ex Schrank et Mart.				+	+	+		

Table A1. continued

	Main vegetational formations							
	Paj	Shr	Mea	Aln	Ber	Pin	Jun	Tun
Huperzia serrata (Thunb.) Rothm.	+							
Juniperus sibirica Burgsd.	+						3–4	
Kitagawia eryngifolia (Kom.) M. Pimen.								+
Larix gmelinii (Rupr.) Rupr.						+		
Ledum decumbens (Ait.) Lodd. ex Steud.						+ – 1		+ – 3
Ledum hypoleucum Kom.	+ – 1		+	+ – 4	+ – 3	+ – 5		
Ligularia fischeri (Ledeb.) Turcz.	+ – 1		+					
Linnaea borealis L.	+ – 2			+	+	+		
Listera nipponica Makino	+							
Lonicera edulis Turcz. ex Freyn	+		+	+	+	+		+
Luzula sibirica V. Krecz.	+		+					+
Lycopodium annotinum L.	+ – 1			+ – 1	+	+		
Lycopodium clavatum L.	+							
Lycopodium juniperoideum Sw.	+							
Lycopodium obscurum L.	+							
Maianthemum bifolium (L.) F. W. Schmidt	+ – 3	+	+	+ – 2	+ – 2	+		+
Malaxis monophyllos (L.) Sw.	+							
Matteuccia struthiopteris (L.) Todaro	+		+ – 1					
Mitella nuda L.	+							
Moehringia lateriflora (L.) Fenzl	+			+	+			
Ophelia tetrapetalla (Pall.) Grossh.								+
Orostachis malacophylla (Pall.) Fisch.				+	+	+	+	+
Orthilia secunda (L.) House	+			+	+			
Oxalis acetosella L.	+		+	+	+	+		
Oxytropis charkeviczii Vyschin								+
Paeonia obovata Maxim	+							
Paris hexaphylla Cham.	+		+					
Parnassia pallustris L.			+					+
Patrinia sibirica (L.) Juss.							+	+
Pedicularis resupinata L.	+		+	+	+	+		
Pedicularis verticillata L.		+	+	+	+			
Pentaphylloides fruticosa (L.) O. Schwarz								+
Phegopteris connectilis (Michx.) Watt.	+ – 1		+ – 2	+	+			
Phylodoce caerulea (L.) Bad.								+
Picea ajanensis (Lindl. et Gord.) Fisch.	4–5	+			+ – 1	+		+
Pleurospermum uralense Hoffm.	+	+	+ - 1					
Poa skvortzovii Probatova	+							
Polemonium racemosum (Regel) Kitam.	+			+	+			
Polypodium sibiricum Sipl.	+			+	+	+		
Popoviocodonia stenocarpa (Trautv. et Mey.) Fed.								+
Populus suaveolens Fisch.				+	+			
Pseudostellaria sylvatica (Maxim.) Pax	+							

Table A1. continued

	Main vegetational formations							
	Paj	Shr	Mea	Aln	Ber	Pin	Jun	Tun
Pteridium aquilinum (L.) Kuhn.			+				+	
Ptilagrostis alpina (Fr. Schmidt) Sipl.								+ – 1
Pyrola japonica Klenze ex Alef.							+	
Pyrola minor L.	+			+	+		+	
Pyrola renifolia Maxim.							+	
Rhodiola rosea L.								+ – 1
Rhododendron aureum Georgi	+ – 1			+4	+ – 3	+ – 4		+
Rhododendron dauricum L.						+	+	
Rhododendron mucronulatum Turcz.	+					+	+	
Rhododendron parvifolium Adam								+
Rhododendron redowskianum Maxim.								+
Ribes fontaneum Boczkarnikova	+ – 1							
Ribes horridum Rupr.	+							
Ribes triste Pall.	+ – 1							
Rosa acicularis Lindl.	+			+	+			
Rubus komarovii Nakai								+
Rubus sachalinensis Levl.	+ – 1							
Salix berberifolia Pall.								1
Salix caprea L.					+			+
Salix rorida Laksch.					+			+
Salix saxatilis Turcz. ex Ledeb.								+
Salix taraikensis Kimura								+
Salix udensis Trautv. et Mey.								+
Sambucus sibirica Nakai	+							
Sanguisorba officinalis L.			+			+		
Sanguisorba sitchensis C. A. Mey			+ – 3					
Sanguisorba tenuifolia Fisch. ex Link			+					
Saussurea porcellanea Lipsch.							+	+ – 1
Saussurea triangulata Trautv. et Mey.	+	+	+	+	+	+		
Saxifraga aestivalis Fisch. et Mey.								+
Saxifraga manchuriensis (Engl.) Kom.	+							
Scorzonera radiata Fisch. ex Ledeb.							+ – 1	
Selaginella borealis (Kaulf.) Rupr.	+			+	+	+		
Selaginella rupestris (L.) Spring								+
Selaginella shakotanensis (Franch. ex Takeda) Miyabe et Kudo						+		
Sibbaldia procumbens L.								+
Silene stenophylla Ledeb.							+	+
Smilacina hirta Maxim.	+		+					
Solidago spiraeifolia Fisch. ex Herd.	+	+	+	+	+	+		+
Sorbaria rhoifolia Kom.								
Sorbaria sorbifolia (L.) A. Br.	+			+	+			
Sorbus amurensis Koehne	+ – 1				+	+		

Table A1. continued

	Main vegetational formations							
	Paj	Shr	Mea	Aln	Ber	Pin	Jun	Tun
Sorbus sambucifolia (Cham. et Schlecht.) M. Roem.				+	+	+ − 1		+
Sorbus sibirica Hedl.	+				+			
Spiraea beauverdiana Schneid.	+		+	+ − 1	+ − 1	+		+
Stellaria bungeana Fenzl	+							
Stellaria fenzlii Regel	+ − 1			+	+			
Streptopus streptopoides (Ledeb.) Frye et Rigg	+		+	+	+			
Thalictrum contortum L.	+	+	+	+	+			
Thalictrum minus L.	+		+	+	+			
Thalictrum tuberiferum Maxim.	+							
Tilingia ajanensis Regel et Til.			+	+	+	+		+
Tofieldia coccinea Richards								+
Trientalis europaea L.	+	+	+	+	+	+	+	+
Urtica angustifolia Fisch. ex Hornem.	+		+	+				
Vaccinium uliginosum L.								+ − 4
Vaccinium vitis-idaea (L.) Avror	+ − 1			+	+ − 1	+ − 2	+ − 3	+
Valeriana fouriei Briq.	+		+					
Veratrum oxycepalum Turcz.	+	+	+ − 1					
Viola biflora L.								+
Weigela middendorffiana (Carr.) C. Koch	+ − 1	4 − −5		+ − 1	+			
Mosses								
Aulacomnium turgidum (Wahlenb.) Schwaegn.					+	+		+
Dicranum flagelifolium L.	+			+	+			
Dicranum majus Turn.	+			+				
Dicranum scorparium Hedw.	+							
Hylocomium splendens (Hedw.) B.S.G.	+ − 5			+ − 3	+ − 3	+ − 5		
Leucodon pendulus Lindb.	+		+	+				
Mnium spinulosum B.S.G.	+			+	+	+		
Oxystegus cylindricus (Brid.) Hilp.	+			+	+			
Pleurozium schreberi (Brid.) Mitt.	+ − 5			+ − 4	+ − 4	+ − 5		
Pogonatum dentatum (Brid.) Brid.	+			+	+	+		
Pogonatum japonicum Sull. et Lesq.	+			+	+			
Polytrichum commune Hedw.	+			+	+	+	+	
Polytrichum juniperinum Hedw.						+	+ − 1	+
Ptilium crista castrensis (Hedw.) De Not.	+ − 1			+	+	+		
Racomitrium fasciculare (Hedw.) Brid.	+			+			+	+
Rhabdowesia kusenevae Broth.						+	+	
Sphagnum girgensohnii Russ.	+ − 2			+	+	+		
Tetraphis pellucida Hedw.	+			+	+			
Lichens								
Cetraria cuculata (Bell.) Ach.						+	+	+
Cetraria islandica (L.) Ach.						+	+ − 2	+ − 1

Table A1. continued

	Main vegetational formations							
	Paj	Shr	Mea	Aln	Ber	Pin	Jun	Tun
Cladina rangiferina (L.) Nyl.						+ – 2	2–4	3–5
Cladina stellaris (Opiz.) Brodo						+ – 2	1–3	3–5
Cladonia amaurocraea (Flk.) Schaer.						+ – 2	+ – 2	+ – 2
Cladonia balfourii Cromb.								+
Cladonia cornuta (L.) Hoffm.							+	+
Cladonia ecmocyna Leight.						+	+	+
Cladonia gracilis (L.) Willd.	+			+	+	+	+	+ – 1
Cladonia pleurota (Flk.) Schaer.						+	+	+
Gemadophylla ericetorum (L.) Zahlbr.	+			+	+	+		
Lobaria linita (Ach.) Rabenh.	+			+	+			
Ochrolechia parella (L.) Massal.	+							
Peltigera membranacea (Ach.) Nyl.	+			+				
Peltigera polydactyla (Neck.) Hoffm.					+	+		
Thamnolia vermicularis (Sw.) Schaer.								+

Remark: Average species abundant is shown in Braun-Blanquet scale. Main formations: Paj – fir-spruce forests; Shr – shrubs; Mea – meadows; Aln – alder thickets; Ber – stone birch forests; Pin – dwarf pine thickets; Jun – juniper thickets; Tun – alpine tundra.