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Vegetation and natural habitats of Kamchatka

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Abstract

Since 2002 we started a series of projects that aimed at the classification of the eastern part of Russia by Braun-Blanquet methods. Phytosociological data obtained in series of projects started in 1996 served as a basis for Kamchatka's vegetation classification presented for the first time in this paper. Most peculiar for Kamchatka the stone birch (*Betula ermanii*) forests were placed in a new order, Betuletalia ermanii that belongs to the class Betulo-Ranunculetea described from Japan. These forests occur in a severe sub-oceanic climate with cold summers, mild winters, and a nearly equal distribution of precipitation throughout the year. Other important zonal vegetation types associated with the stone birch forests, the *Alnus fruticosa* thickets and tall herb meadows, were assigned to new alliances belonging to the order Streptopo-Alnetalia maximowiczii. All representatives of the Betulo-Ranunculetea in Kamchatka are developed in areas of snow accumulation and characterize the cold, wet, sub-oceanic climate within the northern boreal zone. Relatively stronger continental climatic conditions in the central Kamchatkan depression support isolated populations of *Larix cajanderi* and *Picea jezoensis* related to the class Vaccinio-Piceetea. These forest types form a belt at lower elevations. Another important vegetation type are *Pinus pumila* thickets that occupy lower elevations in the north of Kamchatka (Koryakia), form a distinctive vegetation belt above the tree line and occur at azonal sites along the sea coasts on sandy deposits. The Alpine vegetation belt is characterized by a complex of dwarf-shrub, graminoid and herb tundra communities (classes Carici-Kobresietea, Loiseleurio-Vaccinietea, Phyllodoco-Harrimanelletea, Dicentro-Stellarietea, Montio-Cardaminetea and Salicetea arcticae) that occur under conditions of a heat deficit and a very short growing season. Azonal habitats, such as wide valleys, sites affected by cold air drainage, coastal mires, snow patches, volcanic deposits and others, occupy large areas on Kamchatka. Several vegetation types, mainly coastal tundras, mesic and hygric meadows, *Betula platyphylla*, *Populus suaveolens* and *Alnus hirsuta* forests, may be widely distributed on azonal sites. River valleys are occupied by forests of *Populus suaveolens*, *Salix udensis*, *S. rorida* and *Chosenia arbutifolia*.

Key words: bioclimate, phytosociology, biogeography, boreal zone, oceanicity, alpine tundra, *Betula ermanii*, *Pinus pumila*, *Alnus fruticosa*

1. Introduction

Before the 17th century no information on the nature of northeastern Eurasia was known in Europe. Russians reached the eastern edge of the Asian continent in the 17th century. In 1648 the party of Semen DEZHNEV went down the Kolyma River and circled the Chukotka Peninsula and established the first Russian settlement on the Anadyr River. In 1651 Mikhail STADUKHIN reached the basis of the large peninsula from the Anadyr settlement. Further exploration of the peninsula by the expedition led to the discovery of a big river that was named after one of the expedition members, Ivan KAMCHATOI. Since 1690s Kamchatka became the name for the whole peninsula.

The first detailed description of Kamchatka was made by Vladimir ATLASOV, who crossed Kamchatka in 1697 from north to south. Stepan KRASHENINNIKOV, a student of GMELIN, 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. In 1740 George STELLER arrived on Kamchatka and became supervisor of KRASHENINNIKOV in his study of Kamchatka's nature. Cooperation between the two scientists produced two significant books with the same name. KRASCHENINNIKOV'S "Description of the Land Kamchatka" (KRASHENINNIKOV 1755) was published after the death of his teacher, whose manuscript was abundantly cited. STELLER'S manuscript named "Beschreibung von dem Lande Kamtschatka" was delivered in Saint-Petersburg in 1747 (POLEVOY 1999), where it obtained the status of a secret document and remained unpublished until 1774, when the first edition of the book was published in Frankfurt and Leipzig (STELLER 1774). During an entire century these books remained the main sources on Kamchatka's nature.

The history of the botanical exploration of Kamchatka was continued by many non-professional botanists, whose collections reached the major scientific centers in Saint-Petersburg and Moscow. In the first floristic compendium of the Russian Empire by LEDEBOUR (1843-1853), 474 species of vascular plants were mentioned for Kamchatka. Most important botanical expeditions to Kamchatka were undertaken by Vladimir KOMAROV in 1908-1909 and Eric HULTÉN in 1920-1922. Their studies (KOMAROV 1927-1930, HULTÉN 1927-1930) mentioned 825 and 782 vascular species, respectively, in the flora of Kamchatka. The next step in floristic studies was a series of botanical expeditions organized by Sigizmund KHARKEVICH in 1972-1976 in hardly accessible regions of Kamchatka. As result, nowadays 1168 species are known for the flora of the peninsula (KHARKEVICH & CZEREPANOV 1981). Most recent studies by YAKUBOV & CHERNYAGINA (2004) have confirmed this number.

Most of vegetation studies in Kamchatka were performed in the 20th century. Vegetation analyses appeared in many local descriptive studies and focused mainly on important forest, meadow and tundra types (KABANOV 1972, MANKO & VOROSHILOV 1978, NESHATAEV et al. 1994, SHAMSHIN 1999, NESHATAEVA 2004). Some general large-scale vegetation surveys included information on selected vegetation types of Kamchatka (LAVRENKO & SOCHAVA 1956, KABANOV 1969, KRESTOV 2003). The vegetation of Kamchatka was never mapped, but an impression of the distribution of vegetation types can be obtained from the small scale maps of larger areas (ALEKHIN 1950, LAVRENKO & SOCHAVA 1954).

The principles of vegetation classification developed by SUKACHEV (SUKACHEV & DYLIS 1964) were traditionally used for distinguishing and ordering community types. For a long time the BRAUN-BLANQUET approach could not be used as an integrating basis for vegetation survey because of the strong resistance of domestic approaches towards that classification (MIRKIN & NAUMOVA 1998). 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. A first attempt of vegetation classification using the BRAUN-BLANQUET method was undertaken by NESHATAEVA (1990), who classified Kamchatka's communities of *Pinus pumila*, but did not complete the formalisation of the vegetation units according to the Code (WEBER et al. 2000).

Since 2002 we started a series of projects that aimed at a classification of the eastern part of Russia using the BRAUN-BLANQUET method. Results of these projects became the basis for Kamchatka's vegetation survey for this paper.

2. Material and methods

2.1 Study area

Kamchatka lies at the northeast edge of Asia, at 51–60°N and 156–163°E (Fig. 1). The peninsula consists of two main mountain chains, the Sredinnii (middle) and Vostochnii (eastern) ranges. The Sredinnii range is the main mountain system of Kamchatka and extends about 1000 km from north to south. The axial part of the range is a zone of Quaternary volcanism that was glaciated in the Pleistocene. The Vostochnii 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 Vostochnii range. The lowland between the two ranges with Kamchatka River valley inside is called the central Kamchatka depression.

Kamchatka is surrounded by the Sea of Okhotsk in the west, the Pacific Ocean in the southeast and the Bering Sea in the east. The location of the main body of the peninsula, far from the mainland, and the cool currents that drift along both sides of Kamchatka, suggest that well expressed gradients in climatic parameters are lacking. The climate of Kamchatka is humid and moderately cold (CHUKREEV 1970), with a humid, snowy winter and a short, cold summer. The north-south mountains, however, accentuate the climatic gradients across the peninsula. Two climatic provinces are recognized in Kamchatka: a submaritime to subcontinental region in the central depression and a maritime to suboceanic province along the coasts.

2.2 Phytosociological data

The phytosociological database was formed as a result of numerous field studies in Kamchatka and includes over 1000 releves of *Pinus pumila* and *Alnus fruticosa* krummholz, *Betula ermanii*, *Larix cajanderi* and *Picea jezoensis* forests, alpine tundra and many other formations. Releves were made in accordance with standard phytosociological techniques described by MUELLER-DOMBOIS & ELLENBERG (1974) and include full species lists, a number of environmental data and exact geographical positions. The classification systems were produced according the BRAUN-BLANQUET (1964) method and published in part(KRESTOV & NAKAMURA 2002, NAKAMURA & KRESTOV 2007, KRESTOV et al. 2008).

2.3 Climatic data and bioclimatic maps

The climatic database for northern Asia that currently includes records from over 2200 climatic stations in Russia, Korea, Japan and China (KRESTOV & NAKAMURA 2007) was used in identifying bioclimates in Kamchatka. Bioclimates were described using the following climatic parameters: annual temperature (T, °C), average temperature of the coldest (Tmin, °C) and warmest (Tmax, °C) months, annual precipitation (P, mm) and continentality Index (Ic = Tmax – Tmin). For the assessment of critical amounts of heat for plants we employed KIRA'S warmth index (WK), that was calculated as WK = Σmax {0, (Ti – 5)}, and coldness index, calculated as CK = -Σmin {0, (5 – Ti)}, where Ti is the mean temperature in ºC of the i-th month (KIRA, 1977). To evaluate the importance of snow cover, especially in continental regions with a water deficit and in oceanic regions, the precipitation in months with average temperatures below 0ºC (Tn) was also calculated. The distribution pattern of these indices in Northeast Asia was modelled (KRESTOV & NAKAMURA 2007) and mapped on a topographical basis provided by the USGS (1996).

2.4 Data analysis

The analysis of species combinations of higher units delineated in this study and in published phytosociological surveys is based on a floral database compiled from modern sources

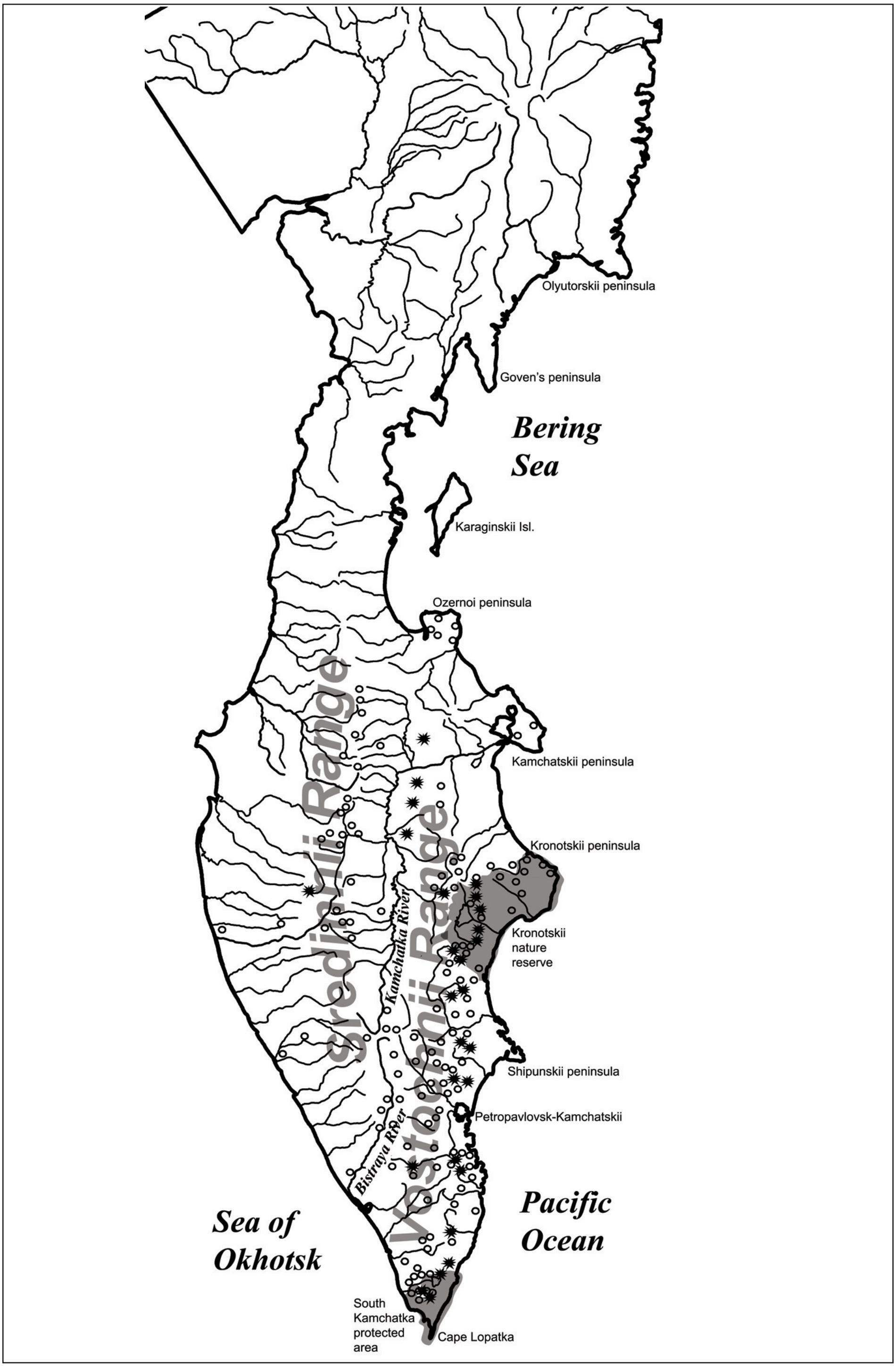

Figure 1. Kamchatka peninsula with major geographical names. Empty circles show dormant and stars – active volcanoes.

of floristic data (ANONYMOUS 1959-1998, LEE 1996, RI & HOANG 1984, ITO 1985-1994, KHARKEVICH 1985-1996, KRASNOBOROV et al. 1988-1997, OHWI & KITAGAWA 1992, WU & RAVEN 1994-2005) for the 95 geographical districts of northern Asia, including Russia east of the Ural Mts., Mongolia, northeast China, Korea and Japan (KRESTOV 2005, QIAN et al. 2003, see also http://www.geopacifica.org/FLORA/regions.html). Floristic relationships between the species composition of higher vegetation units and full species lists for each of the geographic districts of northern Asia were assessed by means of the SIMPSON'S (1960) similarity index (originally – faunal resemblance index), $I_{Sim} = a/(a+b)$ in which a is the number of taxa common to a vegetation unit and a floristic district, and, b is the number of taxa restricted to that vegetation unit. When I_{Sim} is multiplied by 100, the resulting value represents the percent of taxa in the species composition of a vegetation unit shared with a particular floristic district. The areas whose flora contributes 31-50, 51-70 and more than 70 % of the species composition of higher vegetation units were mapped by classifying a particular floristic district to either one of the three similarity classes based on its I_{Sim} value.

3. Phytogeography

3.1 Bioclimates

The maritime-suboceanic coastal climate results from cyclones originating in the northern Pacific Ocean (ANONYMOUS 1968) and has *Betula ermanii* as the zonal vegetation. Mean annual temperature ranges from -2°C to +2°C, with cold-month mean temperatures from in -8°C to -10°C. 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 a maximum in August. Precipitation is distributed nearly equally throughout the year. Maximum snow depth reaches 250 cm (ANONYMOUS 1968), however, secondary redistribution of snow leads to the formation of extensive snow fields with a depth up to 15 m.

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).

Bioclimatic indices calculated for Northeast Asia (Fig. 2) show that Kamchatka belongs to the maritime and suboceanic sectors of the boreal zone (KRESTOV 2006, KRESTOV & NAKAMURA 2007). However, the combination of vegetation indices that are important represents a unique climatic situation. High humidity, relatively low temperatures, a shorter growing season, and extremely heavy snowfall create here unique ecological conditions supporting dwarf alder (*Alnus fruticosa*), dwarf-pine (*Pinus pumila*) and Ermann's birch (*Betula ermanii*) forests that could be called snow forests.

The absence of a water deficit, being favorable for plants, also softens the seasonal climate. Cooler summers and milder winters of the humid oceanic climate together with a deficit of heat provide favorable conditions for frost intolerant plants, which have their northernmost distribution in the rainforests. A smaller difference between summer and winter temperatures is characteristic for the oceanic regions, where climatic conditions support the development of rainforests. Mild winters prevented the formation of permafrost in the Pleistocene along the Pacific Coast in the high latitudes. Even in northern areas, where the growing season is too short for trees, and only dwarf alder and stone birch are able to form stands, we see vigorous populations of heat-dependent orchids, lilies and ferns. High humidity creates con-

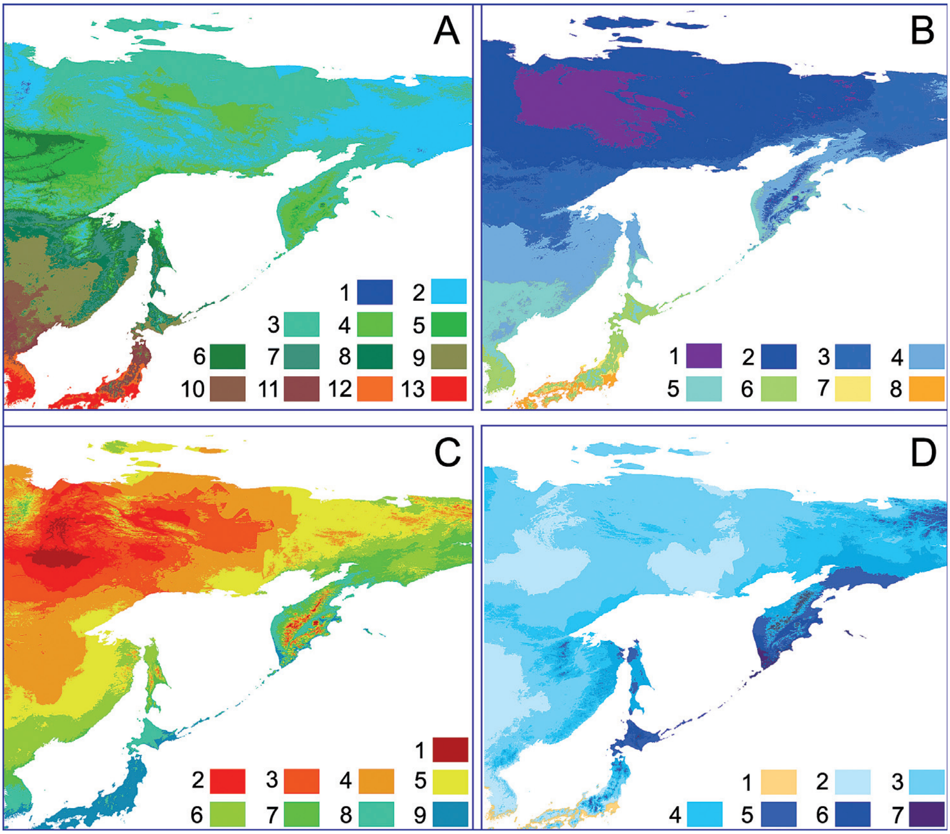

Figure 2. Distribution of selected bioclimatic indices in Kamchatka and Northeast Asia. A – Kira's warmth index (KIRA 1977): 1: 0-10; 2: 10-15; 3: 15-20; 4: 20-25; 5: 25-30; 6: 30-35; 7: 35-40; 8: 40-45; 9: 45-55; 10: 55-65; 11: 65-85; 12: 85-100; 13: >100. B – Kira's coldness index (KIRA 1977): 1: >-10; 2: -10 – -20; 3: -20 – -50; 4: -50 – -100; 5: -100 – -150; 6: -150 – -200; 7: -200 – -250; 8: <-250. C – Continentality index (RIVAS-MARTÍNEZ et al. 1999): 1: >60; 2: 55-60; 3: 50-55; 4: 45-50; 5: 40-45; 6: 35-40; 7: 30-35; 8: 25-30; 9: <25. D – Precipitation in months with mean temperature below 0ºC: 1: <20; 2: 20-70; 3: 70-120; 4: 120-170; 5: 170-300; 6: 300-400; 7: >400.

servative environments for many species in times of climatic change. Local forest of Sakhalin fir on Kamchatka peninsula as well as the isolated Yezo spruce forests in central Kamchatka occurring 2000 km away from their main ranges are good examples of Pleistocene refugia of humidity-dependent species. Late snow melting and abundance of water in early summer, as well as foggy and rainy weather during the growing season, decrease the probability of, or even prevent wildfires in the area.

3.2 Vegetation pattern

The vegetation distribution in Kamchatka shows a regularity (Fig. 3) that is controlled by the regional climatic pattern. Most peculiar for Kamchatka are the stone birch (*Betula ermanii*) forests that occupy zonal sites across the peninsula with their highest concentration in its southern half. They are formed in a severe sub-oceanic climate with cold summers, mild winters, and a nearly equal distribution of precipitation throughout the year. Other important zonal vegetation types associated with the stone birch forests, the *Alnus* fruticosa thickets and

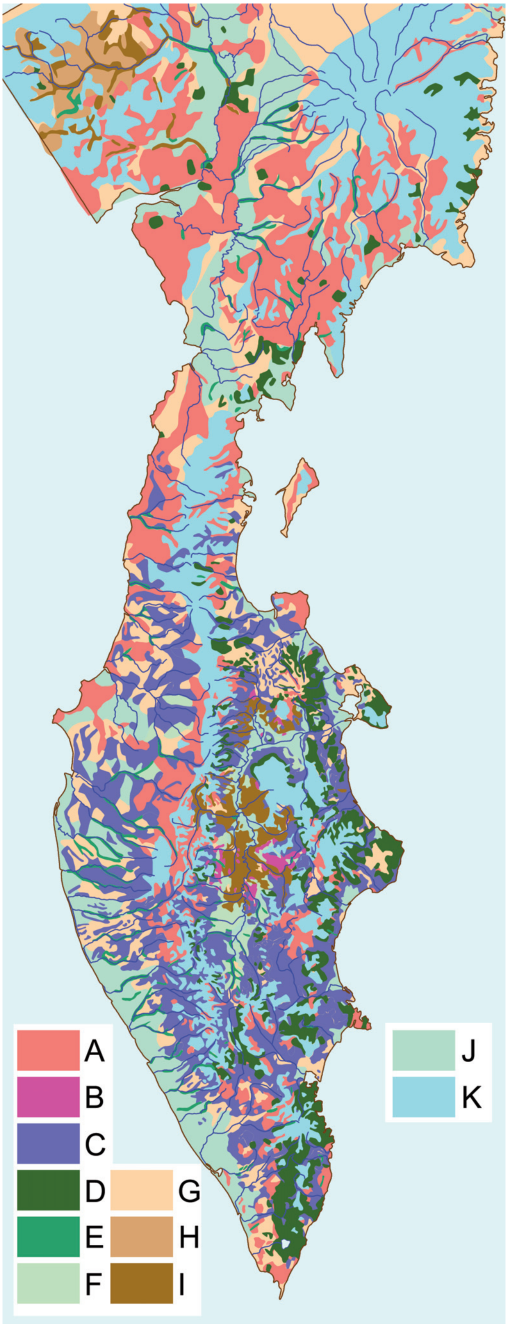

Figure 3. Distribution of major vegetation types in Kamchatka (compiled from KRUCHININ et al. 1973). A: *Pinus pumila* thickets; B: *Picea jezoensis* forests; C: *Betula ermanii* forests; D: *Alnus fruticosa* thickets; E: *Salix udensis*, *Populus suaveolens* and *Chosenia arbutifolia* valley forests; F: *Betula platyphylla* forests; G: complex of tundra and *Pinus pumila* patches; H: complex of tundra and *Pinus pumila* patches with scattered *Larix cajanderi*; I: *Larix cajanderi* forests; J: meadows and wetlands; K: alpine tundra.

the tall-herb meadows, are developed in areas of snow accumulation. Both vegetation types characterize the cold, wet, sub-oceanic climate within the northern boreal zone.

The continental climatic conditions in the central Kamchatkan depression support isolated populations of *Larix cajanderi* and *Picea jezoensis* that form forests at lower elevations. Another important vegetation type is *Pinus pumila* thicket that occupies lower elevations in the north of Kamchatka (Koryakia), form the distinctive vegetation belt above the tree line, and occur on azonal sites along the sea coasts on the sandy deposits.

Azonal habitats, such as wide valleys, sites affected by cold air drainage, coastal mires, snow patches, volcanic deposits and others, occupy large areas on Kamchatka. Several vegetation types, mainly coastal tundras, mesic and hygric meadows, *Betula platyphylla*, *Populus suaveolens* and *Alnus hirsuta* forests, may be widely distributed on azonal sites. River valleys are occupied by forests of *Populus suaveolens*, *Salix udensis*, *S. rorida* and *Chosenia arbutifolia*.

3.3 Vegetation change along the elevation gradient

Kamchatka is a montane area. The change of climate along the elevation gradient causes a change in vegetation. The areas described are characterized by a definite sequence of vertical belts and by the altitude at which each zone occurs. The latter varies depending on a number of geomorphologic factors, among which the general exposure has the clearest effect on the altitude of a belt, positioning it higher on southern and lower on northern slopes. The general sequence of vertical zones in Kamchatka and the adjacent islands repeats the sequence seen from south to north in the maritime and suboceanic regions of Asia, starting with dark-conifer evergreen forests, *Betula ermanii* forests, *Pinus pumila* thickets and alpine tundra (Fig. 4). One of the characteristic features of zonality in the conditions of the oceanic climate in Kamchatka is the lack of a spruce belt in the areas south of central Kamchatka, where the vegetation cover includes a complete set of vertical zones.

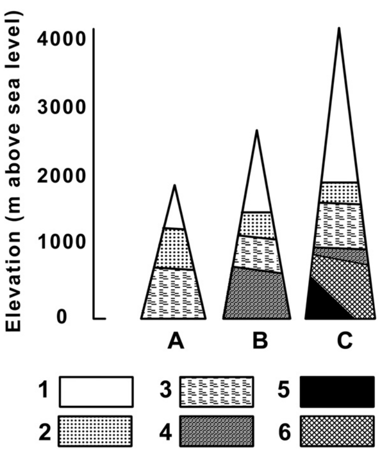

Figure 4. Major vertical vegetation zones in Paramushir Island (Northern Kurils) (A), southern (B) and central (C) Kamchatka (after KRESTOV 2003). 1 – plantless belt, 2 – alpine tundra, 3 – *Pinus pumila*, 4 – *Betula ermanii*, 5 – *Picea jezoensis*, 6 – *Larix cajanderi*.

4. Zonal vegetation

4.1 Higher units of vegetation classification

A preliminary prodromus of Kamchatka's zonal vegetation at this stage of phytosociological study comprises 28 syntaxa of the association, 12 of the alliance, 9 of the order and 6 of the class ranks. This prodromus does not cover a great diversity of azonal vegetation types represented in wet habitats and volcanic substrates with a wide spectrum of ecological conditions.

Class
    Order
        Alliance

Betulo ermanii-Ranunculetea acris japonici OHBA 1968
    Betuletalia ermanii prov.
        Pino pumilae-Betulion ermanii prov.
        Artemisio opulentae-Betulion ermanii prov.
    Streptopo-Alnetalia maximowiczii OHBA 1973
        Dryopterido expansae-Alnion fruticosae prov.
        Filipendulion camtschaticae prov.
Vaccinio-Piceetea BR.-BL. in BR.-BL. et al. 1939
    Ledo palustris-Laricetalia cajanderi ERMAKOV 2004
        Ledo palustris-Laricion cajanderi ERMAKOV 2004
        Rhododendro aurei-Laricion cajanderi KRESTOV 2008
    Abieti-Piceetalia jezoensis MIYAWAKI, OHBA & OKUDA 1968
        Pino pumilae-Piceion jezoensis KRESTOV & NAKAMURA 2002
    Vaccinio-Pinetalia pumilae SUZUKI-TOKIO 1964
        Vaccinio-Pinion pumilae SUZUKI-TOKIO 1964
Salicetea chamissonis prov.
    Salicetalia reticulato-arcticae prov.
        Salicion reticulato-arcticae prov.
Loiseleurio-Vaccinetea EGGLER 1952
    Arctericetalia SUZUKI-TOKIO et UMEZU 1964
        Bryantho gmelinii-Vaccinion vulcanori prov.
Carici-Kobresietea bellardii OHBA 1974
    Oxytropidietalia pumilio prov.
        Oxytropidion pumilio prov.
Phyllodoco-Harrimanelletea KNAPP 1954
    Harrimanelletalia KNAPP 1954
        Salicion polaris prov.

4.2 Betulo ermanii-Ranunculetea acris

This class is represented in Kamchatka by an ecologically distinct complex of forests of Ermann's stone birch, dwarf alder thickets and tall herb meadows and characterizes the suboceanic areas of the peninsula. A characteristic feature of this class is the well developed adaptation of basic floristic groups that constitute the vegetation to the specific conditions of the oceanic climate, such as cool, humid and foggy summers, mild and snowy winters. Great snow accumulation and its late melting cause considerable shortening of the growing season that can be an important limiting factor for regeneration of the coniferous species.

***Betula ermanii* forests – Betulion ermanii**

Bioclimatic diagnosis: WK = 20±6, CK = –103±7, CI = 28±6, Pn = 403±22.

Forests of *Betula ermanii* occur in 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. The *Betula ermanii* belt always lies above the larch belt or *Picea-Abies* belt. In the southern half of Kamchatka stone birch forms an extensive horizontal zone. About 70% of all *Betula ermanii* forest area is in Kamchatka, where it occurs as an extensive horizontal vegetation zone, 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 snow melt (length of snow-free period).

Betula ermanii has very wide and low crowns and usually a crooked stem. 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. *Betula ermanii* dominates the stands, forming a well-developed canopy with a cover of 70-80%. *Alnus fruticosa*, *Pinus pumila* and *Sorbus sambucifolia* may form the tall-shrub layer in stone birch stands. The herb layer varies widely depending on local site ecology and includes several strata. Most common in the tallest stratum, reaching 2 m, is *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’. The communities of mesic habitats have a well-developed layer of medium tall herbs, of which *Artemisia opulenta*, *Geranium erianthum*, *Saussurea pseudotilesii*, *Solidago spiraeifolia*, *Thalictrum minus* and *Moehringia lateriflora* (in lower stratum) are diagnostic. The lower stratum is well developed, with the prevalence of *Maianthemum dilatatum*, *Lycopodium clavatum*, *Cornus canadensis*, *Rubus arcticus*, etc. Because the whole *Betula ermanii* forest area is in a humid climate, and thus has well-developed herb layers, a moss-lichen layer on the ground is not abundant. However, the mosses and lichens are very diverse on the birch stems (HULTÉN 1974).

The order Betuletalia ermine includes 2 alliances that are characterized by complexes of diagnostic species with a chiefly amphi-Pacific distribution (Fig 5D). The alliance Pino pumilae-*Betulion ermanii* includes 3 associations representing colder and dryer communities: Salici arcticae-*Betuletum ermanii*, Equiseto hyemali-*Betuletum ermanii*, Geranio erianthi-*Betuletum ermanii*. The associations occur in the northern part of *Betula ermanii'*s distribution area, at higher elevation and on the well drained volcanic deposits. The alliance Artemisio opulentae-*Betulion ermanii* unites the core part of the Betuletalia ermine and includes the associations Artemisio opulentae-*Betuletum ermanii* and Lilio debili-*Betuletum ermani* that develop in mesic, mesothermic conditions on the lower and middle parts of mountain slopes mainly in the southern and central parts of Kamchatka.

***Alnus fruticosa* thickets – Dryopterido-Alnion + Calamagrostido-Alnion**

Bioclimatic diagnosis: WK = 19±4, CK = –101±6, CI = 28±6, Pn = 430±18.

Dwarf alder (*Alnus fruticosa*) thickets usually indicate the saturated azonal sites with unstable soils or paths of snow avalanches. However their proportion increases with proximity to the Pacific Ocean and they appear to be the dominant vegetation type on zonal sites in easternmost Koryakia, southeastern Kamchatka, and on the northern Kuril Islands in conditions of a subarctic and boreal suboceanic climate characterized by a very low amount of heat and high (over 1500 mm) precipitation, most of which falls in winter.

Table 1. Synoptic table of *Betula ermanii* forests, *Alnus fruticosa* thickets and tall herb meadows

Group No.	1	2	3	4	5	6	7	8	9
No. of releves	9	13	15	25	27	31	21	26	24
Betuletalia ermanii and Betulo ermanii-Ranunculetea acris									
Betula ermanii	**V**	**V**	**V**	**V**	**V**	.	.	.	.
Geranium erianthum	**V**	**V**	**IV**	**V**	**V**	.	.	I	I
Saussurea pseudotilesii	**V**	**V**	I	**IV**	**III**	.	.	I	.
Solidago spiraeifolia	**III**	**V**	**V**	I	**III**	.	I	II	I
Rosa amblyotis	**III**	**IV**	II	II	**III**	.	.	.	.
Epilobium angustifolium	II	**V**	**IV**	**IV**	**IV**	.	.	I	.
Carex pallida	I	**IV**	**III**	II	**III**	.	.	.	.
Lonicera caerulea	**III**	**IV**	**IV**	II	**III**	.	I	.	.
Trisetum sibiricum	II	**IV**	**IV**	**III**	**IV**	.	.	.	I
Sorbus sambucifolia	II	II	**IV**	**IV**	**III**	.	II	I	.
Galium boreale	**III**	**III**	II	I	**III**	.	.	.	.
Rubus arcticus	**III**	**III**	**III**	I	**III**	.	I	I	.
Moehringia lateriflora	I	**IV**	II	I	**III**	.	.	I	I
Spiraea beauverdiana	**IV**	II	**V**	I	II	.	I	I	.
Pedicularis resupinata	II	II	**III**	II	**III**	.	.	.	.
Lonicera chamissoi	.	II	**III**	II	**III**	.	.	.	.
Pleurozium schreberi	**V**	**IV**	**III**	.	**III**	I	I	.	.
Brachythecium reflexum	I	II	**IV**	**IV**	**III**	.	.	.	.
Pino pumilae-Betulion ermanii									
Pinus pumila	**III**	**IV**	**IV**	.	I	.	.	I	I
Avenella flexuosa	**IV**	I	**V**	.	I	I	I	.	.
Juniperus sibirica	**III**	**III**	I	.	I	.	.	.	.
Polytrichum commune	**IV**	II	**IV**	.	I	.	I	.	.
Cornus suecica	**III**	I	**V**	I	I	.	.	.	.
Artemisia arctica	**III**	**IV**	**III**	.	I	.	.	I	.
Dicranum scoparium	**IV**	**V**	**IV**	I	I	.	.	.	.
Lycopodium complanatum	**III**	**IV**	II	.	.	.	.	.	.
Poa platyantha	**III**	**IV**	**III**	I	II	.	.	I	.
Carex riishirensis	**III**	**III**	**III**	.	II	I	.	I	.
Salici arcticae-Betuletum ermanii									
Vaccinium uliginosum	**V**	I	I	.	.	.	.	.	.
Empetrum nigrum	**V**	.	I	.	.	.	.	.	.
Festuca altaica	**IV**	I	I	.	I	.	.	.	.
Salix arctica	**IV**	I	.	.	I	.	.	.	.
Cladonia arbuscula	**III**	.	.	.	.	.	.	.	.
Cladonia rangiferina	**III**	.	.	.	.	.	.	.	.
Vaccinium minus	**III**	.	.	.	.	.	.	.	.
Equiseti hyemali-Betuletum ermanii									
Equisetum hyemale	II	**V**	.	II	II	.	.	.	I
Carex longirostrata	I	**IV**	I	I	II	.	.	.	.
Hedysarum hedysaroides	I	**III**	.	.	.	.	.	.	.
Cypripedium yatabeanum	.	**III**	.	I	I	.	.	.	.

contd Table 1

Geranio erianthi-Betuletum ermanii									
Linnaea borealis	.	I	**IV**	.	I	.	.	I	.
Lycopodium annotinum	I		**III**	.	I	.	I	I	.
Gymnocarpium dryopteris	.		**III**	I	I	.	I	.	.
Artemisio opulentae-Betulion ermanii									
Thalictrum minus	II	II	I	**V**	**V**	.	I	.	II
Aruncus dioicus	.	.	I	**V**	**IV**	.	I	I	II
Artemisia opulenta	I	II	.	**IV**	**IV**	.	I	I	II
Allium ochotense	.	I	.	**V**	**IV**	I	I	I	I
Brachythecium salebrosum	.	.	.	**III**	**III**	.	.	.	.
Lilio debili-Betuletum ermanii									
Lilium debile	.	.	.	**IV**	II	I	I	I	II
Athyrium filix-femina	II	.	II	**IV**	II	I	I	.	I
Hypnum pallescens	.	.	I	**III**	I	.	.	.	.
Brachythecium starkei	.	.	.	**III**	I	.	.	.	.
Trillium camschatcense	.	I	.	**III**	I	I	II	.	I
Hypnum plicatulum	.	.	.	**III**	I	.	.	.	.
Equisetum arvense	.	.	I	**III**	I	.	.	I	I
Ptilidium pulcherrimum	.	.	.	**III**	I	.	.	.	.
Artemisio-Betuletum ermanii									
Streptopo-Alnetalia maximowiczii									
Alnus fruticosa	II	.	I	I	I	**V**	**V**	**V**	**III**
Viola selkirkii	.	I	I	.	II	**III**	**IV**	**III**	**IV**
Dryopterido-Alnion fruticosae									
Dryopteris expansa	.	.	I	II	II	**V**	**V**	I	II
Glycerio-Alnetum fruticosae									
Glyceria alnasteretum	.	.	.	.	.	**V**	.	I	I
Streptopus amplexifolius	.	.	I	I	.	**III**	I	I	II
Fritillaria camschatica	.	.	.	.	.	**III**	I	I	.
Dryopterido-Alnetum fruticosae									
Calamagrostido-Alnion & C.-A. fruticosae									
Filipendulion camtschaticae & Peracarpo-Filipenduletum									
Filipendula camtschatica	.	.	I	**V**	II	II	II	I	**V**
Senecio cannabifolius	.	I	.	**V**	I	II	II	II	**V**
Peracarpa circaeoides	.	.	.	.	.	.	I	.	**IV**
Aconitum maximum	.	.	.	.	I	.	I	.	**IV**
Heracleum lanatum	.	.	I	II	I	I	I	.	**III**

All communities dominated by *Alnus fruticosa* were assigned to the order Streptopo-Alnetalia maximowiczii originally described in subalpine belts in Japan. The floristic composition of *Alnus fruticosa* communities is to some extent similar to that of *Betula ermanii* forests. Diagnostic species of the order in Japan include *Dryopteris expansa*, *Alnus maximowiczii*, *Streptopus streptopoides* var. *japonicus*, *Tiarella polyphylla*, *Vaccinium smallii*, *Viburnum furcatum* and *Viola selkirkii*. In Kamchatka this diagnostic block, with exclusions of *Tiarella polyphylla*, *Vaccinium smallii* and *Viburnum furcatum*, is present in *Alnus fruticosa* communities and in communities of tall herbs dominated by *Filipendula camtschatica*, *Senecio cannabifolius* and *Cacalia hastata*. Communities of *Alnus fruticosa* are assigned to the alliances Dryopterido-Alnion and Calamagrostido langsdorffii-Alnion. The Dryopterido-Alnion includes 2 associations: Glycerio-Alnetum fruticosae (floristically rich communities widely distributed on zonal sites in the Northern Kuril islands and in the south of the Kamchatka peninsula) and the Dryopterido-Alnetum fruticosae (widely distributed across the whole Kamchatka peninsula at zonal and azonal sites on lower and medium elevations). The Calamagrostido langsdorffii-Alnion includes one species-poor association of the same name that occurs on zonal and azonal sites in the subalpine belt across the whole peninsula, extending the ecological range of such habitats towards the north.

Tall herb meadows – Filipendulion camtschaticae

Bioclimatic diagnosis: WK = 20±5, CK = –114±10, CI = 26±7, Pn = 455±14.

This community type is one of most peculiar features of Kamchatka that was first described by STELLER and KRASHENINNIKOV. The description of tall herbs and photos made by HULTÉN (1974) are world-wide known. This kind of meadow is formed under conditions of a humid climate with cool summers and mild snowy winters in the island arcs of the Asian Pacific, in Kamchatka as well as in the subalpine zone of great mountain massifs, such as the Caucasus and the Alps. In Kamchatka this community type is constituted by *Filipendula camtschatica*, *Senecio cannabifolius*, *Reynoutria sachalinensis*, *Cacalia hastata*, *Angelica ursina,* reaching a height of 4-4.5 m. One of the most important ecological conditions supporting the development of this vegetation type is a very deep snow cover that, in a cool spring and summer, melts only in July, considerably shortening the growing season and making it too short for the development of forest or shrub communities.

At the current stage of our phytosociological knowledge, we delineated only one association, Filipenduletum camtschaticae, on Kamchatka, that was assigned to the alliance Filipendulion camtshaticae in the order Streptopo-Alnetalia maximowiczii (Table 1). In addition to the dominants listed above, in the lower stratum communities include some important species, such as *Peracarpa circaeoides*, *Aconitum maximum*, *Streptopus amplexifolius*, *Trientalis europaea*, *Maianthemum dilatatum*, *Galium kamtschaticum*, characteristic for the different levels of the Betulo-Ranunculetea hierarchy.

4.3 Vaccinio-Piceetea

This class is represented in Kamchatka by 3 ecologically and bioclimatically different orders. The Abieti-Piceetalia jezoensis represents Asian coniferous forests that occur in Kamchatka at their northern limit. The Ledo-Laricetalia cajanderi is widely distributed in very extensive areas of Siberia under continental climatic conditions (ERMAKOV et al. 2002) and occurs in Kamchatka at its easternmost limit. The larch and spruce forests belonging to these two orders are concentrated in the central Kamchatkan depression and called a ’conifer island’. The order Vaccinio-Pinetalia pumilae represents subalpine and subarctic vegetation in the pre-oceanic areas of northeast Asia and has in Kamchatka the most important part of its range.

***Larix cajanderi* forests – Ledo-Laricetalia + Pino-Piceion jezoensis**

Bioclimatic diagnosis: WK = 30±4, CK = –148±11, CI = 44±6, Pn = 163±8.

Larch forests in Kamchatka are restricted to the central depression (middle part of the Kamchatka River basin) and form pure even-aged stands with a one-stratum canopy, varying in cover, without an admixture of any other tree species. The cover by a larch canopy is usually low, even with many stems in a stand. The canopy remains open, providing good light conditions for understorey development. Under favorable conditions larch may reach 30–35 m in height. Due to the high 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

Table 2. Synoptic table of *Larix cajanderi* and *Picea jezoensis* forests

Group No.	11	12	14	16	19	20	21	22
No of releves	19	10	26	70	11	12	9	9
species per releve	20	32	26	37	31	21	28	16
Abieti-Piceetalia yezoensis & Vaccinio-Piceetea								
Dryopteris expansa	·	·	II	II	·	·	·	·
Vaccinium vitis-idaea	II	**V**	**V**	II	**V**	**V**	**V**	**III**
Gymnocarpium dryopteris	·	·	I	**V**	I	·	II	·
Hylocomium splendens	I	I	**III**	**III**	·	I	**IV**	·
Linnaea borealis	I	**III**	**IV**	**V**	**III**	**V**	**III**	II
Lycopodium annotinum	I	·	**III**	**V**	II	I	II	·
Maianthemum bifolium	I	·	II	**IV**	**V**	II	II	·
Pleurozium schreberi	II	I	**III**	**V**	·	I	**IV**	I
Ptilium crista-castrensis	·	·	**III**	II	·	·	·	·
Sphagnum girgensohnii	II	I	**III**	I	·	·	·	·
Trientalis europaea	I	·	I	**V**	**IV**	I	·	·
Ledo-Laricion & Ledo palustris-Laricetalia cajanderi								
Phyllodoce coerulea	I	**III**	**III**	·	·	·	·	·
Rhododendron aureum	**IV**	**IV**	**IV**	I	·	·	·	·
Betula divaricata	**V**	**III**	**III**	I	·	·	·	·
Empetrum sibiricum	I	II	**III**	I	·	·	II	·
Rubus chamaemorus	**IV**	**III**	II	·	·	·	·	·
Ledum palustre	**V**	**V**	**III**	I	II	**V**	·	·
Chamaedaphno calyculatae-Laricetum cajanderi								
Chamaedaphne calyculata	**V**	·	I	·	·	·	·	·
Sphagnum angustifolium	**V**	·	·	·	·	·	·	·
Aulacomnium palustre	**III**	·	·	·	·	·	·	·
Oxycoccus microcarpus	**III**	·	I	·	·	·	·	·
Ledo palustris-Laricetum cajanderi								
Calamagrostis lapponica	·	**V**	II	·	·	I	II	·
Arctagrostis latifolia	·	**IV**	·	·	·	·	·	·
Arctous erithrocarpa	·	**III**	·	·	·	·	·	·
Salix myrtilloides	I	**III**	·	·	·	·	·	·
Equisetum scirpoides	·	**III**	·	·	I	II	I	·
Rhododendro aurei-Piceetum jezoensis								
Saxifraga punctata	·	·	**IV**	·	·	·	·	·
Cassiope ericoides	·	·	**III**	·	·	·	·	·
Viola kusnezowiana	·	·	**III**	·	·	·	·	·
Alnus fruticosa	·	·	**III**	·	·	·	·	·
Pino pumilae-Piceion jezoensis & Abieti-Piceetalia								
Betula ermanii	·	·	I	**III**	II	I	**III**	·
Cornus canadensis	I	·	·	II	**III**	I	**III**	II
Maianthemum dilatatum		·	·	**III**	**III**	·	II	·
Orthilia obtusata	·	II	I	II	**III**	II	II	I
Picea jezoensis	·	·	I	**V**	**IV**	I	II	I
Orthilia secunda	·	·	I	**V**	**V**	**V**	II	**III**
Chamaenerion angustifolium	I	·	I	**V**	**V**	**IV**	**IV**	**III**

contd Table 2

Equisetum pratense	I	II	I	**IV**	**V**	II	**IV**	**III**
Lonicera caerulea	I	·	·	**IV**	**V**	**V**	**V**	II
Pyrola incarnata	I	I	I	**III**	**III**	**V**	**V**	**IV**
Juniperus sibirica	I	·	·	I	**V**	**V**	**IV**	**V**
Rubus arcticus	I	II	I	**IV**	**V**	**III**	**III**	·
Moneseto uniflorae-Piceetum jezoensis								
Moneses uniflora	·	I	I	**V**	·	·	·	·
Sorbus sibirica	·	·	I	**IV**	I	·	I	**III**
Ribes triste	·	·	I	**IV**	·	I	**III**	·
Solidago spiraeifolia	·	·	·	**IV**	I	I	**III**	·
Salix udensis	·	·	·	**III**	·	·	·	·
Saussurea oxyodonta	·	·	I	**III**	·	·	·	·
Corallorhiza trifida	·	·	I	**III**	·	·	·	·
Carex longirostrata	·	·	·	**III**	·	·	·	·
Filipendula camtschatica	·	·	·	**III**	·	·	·	·
Geranio erianthi-Laricetum cajanderi								
Geranium erianthum	·	·	·	**III**	**V**	·	II	·
Galium boreale	·	·	·	**III**	**V**	I	I	I
Saussurea pseudotilesii	·	·	·	II	**V**	I	·	·
Rosa amblyotis	·	·	·	·	**V**	**III**	·	II
Spiraea media	·	·	·	·	**V**	**III**	I	·
Anthriscus sylvestri	·	·	·	·	**III**	·	·	·
Junipero sibiricae-Laricetum cajanderi								
Goodyero repentis-Laricetum cajanderi								
Goodyera repens	·	·	I	**III**	·	·	**IV**	·
Festuca altaica	·	·	·	·	·	I	**IV**	·
Ledum decumbens	I	·	·	·	I	I	**III**	·
Poa platyantha	·	·	·	·	·	·	**III**	·
Populi suaveolentis-Laricetum cajanderi								
Populus suaveolens	·	·	·	·	I	·	·	**V**
Stereocaulon sp.	·	·	I	·	·	·	·	**V**
Cladina rangiferina	II	·	I	·	I	I	I	**IV**

boreal Asia. On moist flats the shrub layer may contain *Alnus fruticosa*, *Vaccinium uliginosum*, *Betula divaricata* and *Ledum palustre*. In river valleys the shrub layer includes *Rosa amblyotis*, *Sorbaria sorbifolia*, *Spiraea salicifolia*, *Ribes* spp. and *Lonicera* spp. In highlands the main shrubs in the larch stands are *Pinus pumila*, *Rhododendron aureum* and *Ledum palustre*. 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 the larch forests was formed from different floristic sets (Fig 5B) that survived at the time of the last Pleistocene glaciations in the coastal refugia. The species composition of a community depends mostly on substrate conditions.

All larch communities in Kamchatka are assigned to the alliance Pino pumilae-Piceion jezoensis that unites the coniferous forests of the northern subzone of boreal zone. They have *Pinus pumila* in the understorey, which may form a closed layer or be present in single individualls. This alliance includes species poor communities dominated by *Picea jezoensis* at well drained, zonal sites in the northern part of its distribution range (KRESTOV & NAKAMURA 2002) and by *Larix cajanderi* on the sites with a cold soil or with near surface permafrost. The floristic composition of the alliance is characterized by humidity-dependent, oceanic species distributed on both the Asian and American sides of the Pacific basin. Larch communities belonging to this alliance are considerably enriched with species from the diagnostic block of the Ledo-Laricetalia cajanderi, but strongly differ from the latter by the presence of mesic species that are widely distributed in oceanic regions.

The slopes with well developed fresh to moist, well drained soils with a fair nutrient content on volcanic or morainal deposits in the central Kamchatkan depression are occupied by the Geranio erianthi-Laricetum cajanderi (KRESTOV et al. 2008). *Larix cajanderi* forms a relatively dense canopy (70-80 %). The shrub layer is formed by *Juniperus sibirica*, *Spiraea media* and *Pinus pumila*. The herb layer includes many suboceanic, boreal forest species: *Artemisia opulenta*, *Geranium erianthum* and *Saussurea pseudotilesii*. The moss layer is poorly developed.

The other three associations represent successional larch forests on well drained volcanic deposits or alluvial sands. The Junipero sibiricae-Laricetum cajanderi is found on azonal sites in the subcontinental sector of the northern subzone of the boreal zone in central Kamchatka. It occupies both sloping and plain sites with thick layers of volcanic ash or sand in the soils, thus making the drainage very rapid and creating edaphically induced drought during the growing season. The Goodyero repentis-Laricetum cajanderi is found on azonal sites in the northern subzone of the boreal zone of the northern portion of central Kamchatka, in cooler and wetter climatic conditions. It occupies a similar range of sites as the previous association but represents the later successional stage on the tephra deposits. Soils of the association's habitats have a well developed humic horizon capable of holding water. The Populi suaveolentis-Laricetum cajanderi is found on azonal sites in the subcontinental sector of the northern subzone of the boreal zone in central Kamchatka, on the Tolbachik, Kluchevskoy and Shiveluch volcanoes. It represents the initial stage of succession on sites where forests were destroyed by tephra deposits (less then 40 cm) resting on well developed, buried soils. These edaphic conditions favor trees since their roots reach the buried, humic horizons, that accelerate growth (GRISHIN et al. 1996a). However, the understorey vegetation is stunted, given the friable and unstable volcanic material.

***Picea jezoensis* forests – Pino-Piceion jezoensis**

Bioclimatic diagnosis: WK = 42±8, CK = –93±13, CI = 33±5, Pn = 250±21.

Yezo spruce, *Picea jezoensis*, occurs in the central Kamchatkan depression as a mix in the larch forests. It forms also more or less continuous forests in the north of Kamchatka's 'conifer island' (MAN'KO & VOROSHILOV 1978). These forests are represented by a single association Moneseto-Piceetum jezoensis that belongs to the alliance Pino pumilae-Piceion jezoensis. The association occurs in the extreme northeastern portion of the range of the Yezo spruce forests in a cold and very cold, boreal, maritime climate on the Kamchatkan peninsula with minor extensions across the Sea of Okhotsk on northern Sakhalin, and represents species-poor communities of the Pino-Piceion jezoensis with few species from the East Asian flora that constitute the alliance and order (Fig 5C). The origin and modern isolation of spruce forests in Kamchatka was subject of discussions. Recently, the relict nature of *Picea* in Kamchatka was confirmed by allozyme analysis (POTENKO 2007) that showed considerable, species-level genetic differences between Kamchatka and the closest mainland populations and supported KOMAROV'S (1934) treatment of Kamchatka spruce populations as a distinct species *Picea kamtschatkensis*.

These forests have a simple structure. The tree layer contains only *Picea jezoensis* with an admixture of *Betula ermanii* at higher elevations. Solitary broadleaved trees of *Sorbus sibiri-*

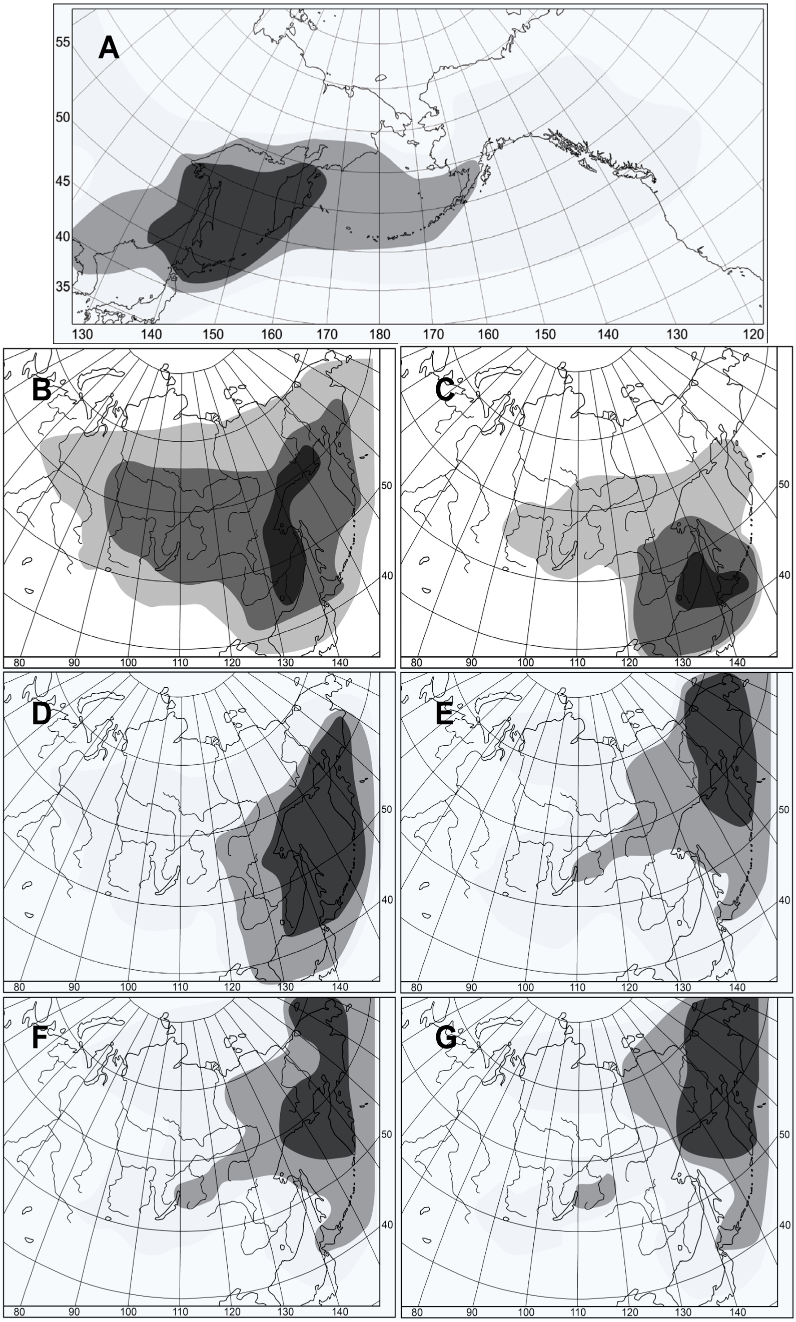

Figure 5. Occurrence of representatives of floristic complexes of larch forests of the orders Vaccinio-Pinetalia pumilae (A), Ledo palustris-Laricetalia cajanderi (B), Abieti veitchii-Piceetalia jezoensis (C), Betuletalia ermanii (D), Carici-Kobresietea bellardii (E), Loiseleurio-Vaccinietea (F), and Salicetea chamissonis (G) in the floristic districts of northern Asia. Dark gray – floristic district includes over 70 % of total species composition of vegetation unit, medium gray – 50-70 %, weak gray – 30-50%.

ca occur under the main canopy. After severe fires these forests recover through a *Larix dahurica* stage; therefore occasionally a mixture of spruce, forming the young canopy, and larch can be found. The stands are species-poor, composed mainly of common vascular plants of circumboreal distribution. The most important species are the small herbs of the taiga: *Maianthemum bifolium*, *Cornus suecica*, *Oxalis acetosella*, *Linnaea borealis*, and *Goodyera repens*; the taiga ferns *Diplazium sibiricum*, *Dryopteris expansa*, *Gymnocarpium dryopteris*, and *Phegopteris connectilis*; the taiga forbs *Streptopus streptopoides*, *Solidago spiraeifolia*, and *Veratrum oxysepalum*, and the taiga shrubs *Rosa acicularis*, *Juniperus sibirica*, *Spiraea beauverdiana*, and *Ribes triste*. The association is characterized by species whose distributions are restricted to Kamchatka or the oceanic sector of northern Asia, e.g. *Saussurea oxyodonta*, *S. pseudotilesii*, *Lonicera chamissoi*, *Filipendula camtschatica* and *Alnus fruticosa*. A characteristic feature is the high performance of meadow species, e.g. *Calamagrostis purpurea* and *Chamaenerion angustifolium*.

Ecological variation within this association is reflected by three variants. The typical variant represents vegetation of nutrient-poor, fresh soils in the interior part of the *Picea jezoensis* range in central Kamchatka and on the coast of the Sea of Okhotsk. The variant of *Geranium erianthum* represents forests in the majority of the range of the association with a true maritime climate, i.e. relatively mild, wet winters and cold, wet summers. In contrast to other variants, *Betula ermanii* is a common component of the tree layer dominated by spruce. The shrub layer is less well developed; however, the herb layer is more developed in comparison with the typical variant. The constant species include *Geranium erianthum* and *Galium boreale*. Due to a wetter climate and deep and late-melting snow cover, herbs are much more significant than in the typical variant. Herb species composition varies along the edaphic gradients and allows the consideration of two subvariants. The subvariant of *Salix udensis* represents vegetation of moist to very moist, mesotrophic to nutrient-rich soils. It is characterized by *Corallorhiza trifida*, *Filipendula camtschatica*, *Lathyrus pilosus*, *Pedicularis resupinata*, *Salix udensis*, and *Saussurea oxyodonta*. The subvariant of *Carex reventa* represents drier sites. The variant of *Alnus fruticosa* occurs near the higher limits of the spruce forest zone, around the late-melting snow beds. The dwarf tree *Alnus fruticosa* and the shrub *Sorbus sambucifolia* are frequent in the shrub layer. Moist and wet soil indicators, such as *Carex pallida*, *Ribes triste* and *Aruncus dioicus*, are more vigorous than in the above described variants.

Abies sachalinensis forests

The distribution of *Abies sachalinensis* on Kamchatka is restricted to the very small area of 20 hectares in the southeast of the peninsula (NESHATAEVA & FET 1994). This species was treated by KOMAROV (1927-1930) as *Abies gracilis*, a relict species, and an endemic of Kamchatka. Recent genetic studies (SEMERIKOVA & SEMERIKOV 2007) showed the closeness of the Kamchatkan population to *Abies sachalinensis* that is widely distributed in Sakhalin, Hokkaido and the southern Kuril Islands (NAKAMURA & KRESTOV 2005). Phytosociologically the fir forest on Kamchatka has not been studied. NESHATAEVA & FET 1994 delineated two associations, the Abietetum gracili dryopterioso-maianthemosum and the Abietetum gracili altiherbosum in accordance with Sukachev's approach to vegetation classification. The *Abies sachalinensis* forest in Kamchatka is very important for understanding the Pleistocene development of the vegetation.

Pinus pumila thickets – Vaccinio-Pinetalia pumilae

Bioclimatic diagnosis: WK = 23±4, CK = –160±13, CI = 38±4, Pn = 276±27.

The Siberian dwarf-pine, *Pinus pumila*, is one of the most unusual and interesting woody species in its appearance and adaptations. As a vertical vegetation belt, dwarf-pine occurs over all of boreal and north-temperate eastern Asia, including Hokkaido (OKITSU & ITO 1984, 1989), eastern Siberia (MOLOZHNIKOV 1976, TIULINA 1976), central and southern Kamchatka (NESHATAEV & NESHATAEVA 1985, NESHATAEVA 1994, KHOMENTOVSKIY 1995) and the southern half of Pacific Russia (GRISHIN et al. 1996b). *Pinus pumila* communities form a horizontal vegetation zone across submaritime, maritime and suboceanic sectors of the subarctic and boreal zone, including northern Kamchatka, in conditions of a humid climate with heavy snow covering the ground almost 8 months per year.

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 and seasonal dynamics. Many authors include the growth form of *Pinus pumila* in the class of dwarf trees. Under favorable conditions (a 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 the summer. In Kamchatka the largest basal diameters measured were 36 cm, stem length 16 m, and branch height 4 m; the largest basal diameter recorded on the Shantar Islands was 40 cm.

The high density of 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*, *Ledum decumbens*, *Empetrum nigrum*, *Sorbus sambucifolia*, that allow to place Kamchatkan *Pinus pumila* communities in the alliance Vaccinio-Pinion pumilae of the order Vaccinio-Pinetalia pumilae described from Japan. The main features of this order are: 1) dominance of *Pinus pumila*, which forms a closed canopy (40–95% cover); 2) presence and coenotic activity by a complex of subarctic/subalpine species with amphi-Pacific ranges (Fig. 5A); and 3) presence but never canopy formation by other tree species at the contact zones with forest vegetation, usually *Larix cajanderi*, rarely *Picea jezoensis* or *Betula ermanii*.

Two associations, the wetter and warmer Vaccinio-Pinetum pumilae SUZUKI-TOKIO 1964 and the drier and cooler Ledo decumbentis-Pinetum pumilae SUZUKI-TOKIO 1964, are widely distributed in Kamchatka in the subalpine belt. In the northern part of Kamchatka the proportion of the Ledo decumbentis-Pinetum pumilae increases.

4.4 Alpine tundra

The alpine vegetation in oceanic regions of Northeast Asia in Russia is poorly studied. A number of publications from Kamchatka (NESHATAEV et al. 1994), the Sikhote-Alin mountains (GRISHIN et al. 1996b) and the Commander Islands (KRESTOV 2004) are known at present, and this number does not provide a general view on the alpine vegetation of the region. Recently the Kamchatkan alpine vegetation was characterized and classified as a first approximation by NAKAMURA & KRESTOV (2007).

The phytosociological diversity of the alpine vegetation in the oceanic sector of Northeast Asia is much higher in comparison with continental sectors. The majority of Kamchatkan alpine tundra fits into five classes (see prodromus), of which only three represent tundra communities in zonal habitats. The floristic composition of the Kamchatkan alpine tundra is characterized by species with a circumboreal and circumpolar distribution with great influence of the Beringian floristic center (Fig. 5E, F, G). Most species with amphipacific ranges are concentrated on the azonal sites, such as snow patches, cryoturbation fields or steps of solifluction teraces.

4.5 Post-volcanic vegetation

The 30 active volcanoes of Kamchatka in historical time produced a great variety of new substrates and damaged or totally destroyed ecosystems over an area of more that 50.000 km^2 (FEDOTOV & MASURENKOV 1991). On the damaged areas different successional sequences started at different times. All of them still wait for appropriate study, but the first steps for understanding the successional patterns under variable conditions on the main volcanic substrates have been done. A series of studies (MAN'KO & SIDELNIKOV 1998, GRISHIN et al. 1996a, 2000 a, b, DIRKSEN & DIRKSEN 2007 and others) on volcanoes that experienced great eruptions, such as Ksudach (thick pumice tephra deposits in 1907), Kluchevskoi (thick basaltic tephra deposits in 1932 and 1938), Avachinsky (basaltic tephra deposits in 1945), Bezymianny (explosion and scoria deposits in 1956), Shiveluch (explosion and scoria deposits in 1964) and Tolbachik (thick basaltic tephra deposits and extensive lava flow in1975, extensive lava flow in 1976) have confirmed the general pattern that increasing deposit depth impacts successively larger plants and that different substrates start different successional sequences of vegetation communities.

In comparison with post-volcanic successions in other regions of the world the Kamchatkan successional patterns are very diverse, the succession lasts as long as 2000 years or longer and the number of vascular plants species involved in primary succession (nearly 200) exceeds that of successions in southern regions.

5. Distribution of vegetation types along basic climatic gradients and the Holocene history of Kamchatkan vegetation

Bioclimates were described using 22 climatic indices, of which Kira's warmth and coldness indices (KIRA 1977), the continentality index, the ombro-evapotranspirational index (RIVAS-MARTÍNEZ et al. 1999) and winter precipitation mostly contributed to or determined the geographical pattern of Kamchatkan vegetation. An analysis of indices, calculated with the aid of developed models, showed significant differences of vegetation units at the order rank along bioclimatic axes. Kira's warmth index decreases from values of 38 in the central Kamchatkan middle temperate zone (Abieti-Piceetalia, Piceion) to 5 in the alpine belt (Loiseleurio-Vaccinietea). Among boreal vegetation units the orders of the Betulo-Ranunculetea have the lowest warmth index, as explained by cool summers in an oceanic climate. Kira's coldness index varies between values of -80 and -230 within boreal and alpine vegetation zones. The orders Betuletalia ermine and Streptopo-Alnetalia, representing boreal deciduous broadleaved forests, are characterized by relatively high values of the coldness index that, in this case, is comparable to that of temperate orders in the southern Russian Far East. The ranges of orders along the continentality gradient are reflected by changes in vegetation types within a zone with proximity to the ocean. In Kamchatka, the lowest values of the continentality index are characteristic for the class Betulo-Ranunculetea, and the deciduous coniferous order Ledo-Laricetalia is developed under conditions of severest continentality for the whole of Kamchatka. Communities of *Betula ermanii*, *Alnus fruticosa* and tall-forb meadows are characteristic to the regions with slower melting of heavy snow deposits.

The distribution of major bioclimatic indices in Kamchatka suggests that high oceanicity results in relatively warm winters and cold summers. The winters are warm enough for the survival of many species whose main range is in the southern part of the boreal and the northern part of the temperate zones. However, the summers appear to be too cold for many boreal and temperate potential dominants due to the short growing season. The late snow melting, far beyond the point when the day temperatures exceed the values of +10ºC, shortens the growing season, causing physiological stress for many tree species, especially conifers.

An analysis of the floristic groups in different topo- and chronosequences enforced with available fossil data allowed to reconstruct the possible ways of formation of the modern vegetation cover of Kamchatka. The aridization and fluctuating continentality-oceanicity were the most striking factors changing vegetation in the Holocene. At the time of the late Pleistocene aridization of the climate favoured the intense migration of xeric floristic elements, which take a significant part in the modern vegetation of the alpine zone and of the fields of volcanic deposits across the whole of Kamchatka. In the Holocene increasing temperatures and humidity caused the rapid expansion of *Betula ermanii* forests over areas with an oceanic climate. Presently, the most extensive areas occupied by this vegetation type occur in the southern half of Kamchatka. They are characterized by a complex of widely distributed, boreal species with a great proportion of amphi-Pacific floral elements and enriched with temperate species. Poor paleobotanic data from Kamchatka were recently analyzed, radiocarbon-dated and correlated with modern tephrochronological data by DIRKSEN & DIRKSEN (2008). According to this reconstruction, Kamchatka, in the Pleistocene, was affected by aridization to a much lesser degree than the Asian mainland. The expansion of *Betula ermanii* forests over the whole peninsula was indicated as from 8000 years BP, and they reached their maximal range between 5000 and 4500 years BP. Further climatic fluctuations caused the increase of continentality in a period between 6000 and 4500 years BP. After that time a period of higher oceanicity took place. From approximately 3500 years BP to the present the continentality of the climate increased. In this period *Larix cajanderi* (from 3000-2500 years BP) and *Picea jezoensis* (from 2000-1000 years BP) expanded in central Kamchatka. The coniferous species reached their maximal ranges approximately 900 years BP. In the last 300 years a significant advance of *Picea jezoensis* forests has taken place that, according to DIRKSEN & DIRKSEN (2008). This corresponds to the cooling event of the Little Ice Age.

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