

PHYTOSOCIOLOGICAL STUDY OF THE *PICEA JEZOENSIS* FORESTS OF THE FAR EAST

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Abstract: Forest communities dominated by *Picea jezoensis* (Yezo spruce) are described from across their entire distributional range in eastern Asia, including the territories of the Russian Far East and Japan. A total of 476 relevés are used representing the following dominant types of spruce forests: pure *P. jezoensis*, mixed *P. jezoensis* and *Abies sachalinensis*, mixed *P. jezoensis* and *Abies nephrolepis*, and pure *Picea glehnii* communities. The vegetation is classified into 11 associations, 2 community types, 6 subassociations, 25 variants and 8 subvariants. Nine associations, including the *Asaro heterotropoidis-Abietetum sachalinensis*, *Weigelo middendorffiana-Piceetum jezoensis*, *Lysichito-Piceetum glehnii*, *Swido albae-Piceetum obovatae*, *Oplopanaco elati-Piceetum jezoensis*, *Philadelpho tenuifolii-Piceetum jezoensis*, *Vaccinio-Piceetum jezoensis*, *Rhododendro aurei-Piceetum jezoensis*, and *Moneseto uniflorae-Piceetum jezoensis*, are described for the first time. The ecology and structure of all communities are described and their syntaxonomy discussed. The communities are placed in three alliances, *Piceion jezoensis*, *Abieti nephrolepidis-Piceion jezoensis* and *Pino pumilae-Piceion jezoensis*, all. nov. All of the communities described are considered to belong to the order *Abieti-Piceetalia* of the class *Vaccinio-Piceetea*.

Keywords: Boreal taiga, Hokkaido, Kamchatka, Kuril Islands, Okhotsk region, Phytogeography, Sikhote-Alin, Syntaxonomy, Vegetation survey, Yezo spruce

Nomenclature: ITO & HINOMA (1985), KHARKEVICH (1985–1996)

Electronic appendix (www.ibot.cas.cz/folia): Tables 3 (full version), 5–17

INTRODUCTION

Yezo spruce, *Picea jezoensis*, occurs in the montane subarctic and maritime areas of northeastern Asia between the latitudes 35° N and 56° N (Fig. 1). The range of the Yezo spruce forests includes the northern part of the Sikhote-Alin mountain range, the western coast of the Sea of Okhotsk, Mt. Chanbai, Shantar Islands, Sakhalin Island, the southern Kurils (Iturup and Kunashir Islands) and Hokkaido. In addition, disjunct localities are found in the middle part of Honshu Island (*Picea jezoensis* var. *hondoensis*) (NUMATA et al. 1972), in central Kamchatka (MAN'KO & VOROSHILOV 1978), in Korea (SONG 1991, 1992), and in northeastern China on the mountain range Dunlin (WANG 1961). Within this range, Yezo spruce forests can be considered the zonal vegetation type in the lower part of the Amur River basin (the Sea of Okhotsk coast), on Sakhalin Island, in the southern Kurils (Iturup Island) (KOLEJNIKOV 1961) and on Hokkaido (KOJIMA 1979, 1983). Here, Yezo spruce forms a broad belt at elevations ranging from sea level to the alpine timberline, or, in northern

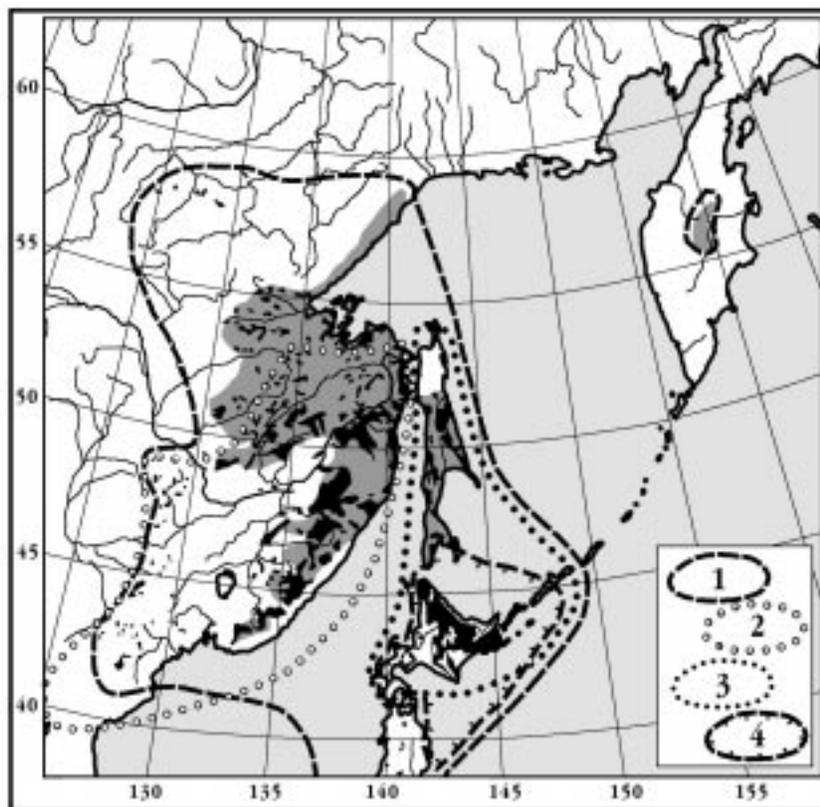


Fig. 1. The distribution range of dark-coniferous *Picea jezoensis* forests. Black shading shows the current range of *Picea jezoensis* dominated forest, dark grey shading shows the potential forest range, i.e., seral larch and birch forests in the sites of former *Picea jezoensis* forests with an evidence of spruce recovery. The ranges of main dominants are as follows: 1 – *Picea jezoensis*, 2 – *Abies nephrolepis*, 3 – *A. sachalinensis*, 4 – *Picea glehnii*.

temperate and boreal zones, up to the altitudinal belt of *Betula ermanii* forests. Spruce forests occupy almost the whole range of habitats in this belt, avoiding only mires, rock outcrops and areas around solfataras, the jets of hot water with sulphur dioxide and hydrogen sulphide in the regions of volcanic activity (ROZENBERG 1959, MAN'KO 1967, NAKAMURA 1988).

Yezo spruce forests occur in different proportions with other forest types across their range. Two species of fir, namely *Abies nephrolepis* in the mainland and *A. sachalinensis* in the island part of the area, are important co-dominants in the main part of the species' range. In the southern part of its range, *Picea jezoensis* grows together with *Abies koreana* and *Thuja koraiensis* in Korea (SONG 1991) and with *Abies veitchii* and *A. mariesii* on Honshu (MIYAWAKI 1985). In the northern portion of its range, however, including Kamchatka, the northernmost parts of the Schmidt peninsula (Sakhalin) and the Maya River basin in the

mainland, Yezo spruce forms pure stands without fir. Elsewhere in its range, other conifers may occur admixed with Yezo spruce stands. In the southern portion of the range of Yezo spruce, *Picea koraiensis* forms pure stands usually in the river valleys or on the low or middle parts of gentle slopes (KURENTOVA 1960, 1968). On these sites it can also occur in a mixture with Yezo spruce. *Picea obovata* and *P. jezoensis* occur together in the Okhotsk part of the range of *Picea jezoensis*, although across all the range *Picea obovata* can occasionally form pure stands, mainly in river valleys. *Picea glehnii* occurs in southern Sakhalin (TATEWAKI 1958, TOLMACHOV 1959), the southern Kurils (VOROB'EV 1963, ISHIZUKA 1974), on Hokkaido (NUMATA et al. 1972) and in northern Honshu on Mt. Hayachine (ISHIZUKA 1961). In contrast to *P. jezoensis*, its optimum lies in waterlogged sites with a water table above or at ground level during the growing season. These species therefore tend to form mixed stands only where their ecological ranges overlap in slope-mire ecotones (MAN'KO 1987).

The ecology and distribution of *Picea jezoensis* in the Russian Far East were thoroughly studied by TOLMACHOV (1954, 1955), ROZENBERG (1959), and MAN'KO (1961, 1965, 1967, 1974, 1980, 1987). It is commonly accepted that fir-spruce forests represent the climax vegetation of the boreal zone in its southern and middle subzones in the subarctic and maritime sectors (KOLESNIKOV 1961, HÄMET-AHTI et al. 1974, GRISHIN 1995). Spruce forests as a zonal vegetation type are characteristic for the western coast of the Sea of Okhotsk, going west into the continent on a distance about 1500 km, and for central Kamchatka, where they form a so-called conifer island. The first area was named by KOLESNIKOV (1961) the Western Okhotsk Area of dark conifer forests and the second area we call the Eastern Okhotsk Area of dark conifer forests.

Phytosociological studies of Yezo spruce forests have been scattered up until now. An extensive phytosociological study of the spruce forests on Hokkaido was undertaken by NAKAMURA (1988). Two associations belonging to the alliance *Piceion jezoensis* SUZUKI-TOKIO ex JINNO et SUZUKI 1973 (*Abieti-Piceetalia* MIYAWAKI et al. 1968, *Vaccinio-Piceetea* BR.-BL. in BR.-BL. et al. 1939) were delineated (NAKAMURA 1988). That phytosociological study covered only the easternmost, island part of the range of Yezo spruce. The subalpine conifer forests of Korea were extensively studied by SONG (1991), who delineated the associations *Taxo-Pinetum pumilae* SONG et NAKANISHI 1985, *Thujo-Abietetum nephrolepidis* SONG 1991 and *Abieti koreanae-Piceetum jezoensis* SONG 1991 within the alliance *Abieti nephrolepidis-Piceion jezoensis* SONG 1991, and the associations *Saso-Abietetum koreanae* SONG et NAKANISHI 1985 and *Betulo saitoanae-Abietetum koreanae* (SONG et NAKANISHI 1985) SONG 1991 within the alliance *Abietion koreanae* SONG 1991. For the spruce forests of northeastern Asia SONG (1992) proposed the new order *Abieti nephrolepidis-Piceetalia jezoensis* SONG 1992 instead of *Abieti veitchii-Piceetalia jezoensis hondoensis* MIYAWAKI et al. 1968, accepted by NAKAMURA (1988) for Hokkaido. The last order, in Song's opinion, "fits only for subalpine coniferous forests because they are not compared with the continental syntaxa" (SONG 1992).

Several phytosociological studies of the *Picea jezoensis* forests have been performed in the major part of their range, on the territory of Russia. However, up until now, no syntaxonomical conclusions have been published in the international literature. A study of Yezo spruce forests on the westernmost edge of their range, in the Tukuringra-Dzhagdy

Mountains, was undertaken by PETELIN (1990), who distinguished five associations on the basis of 46 relevés and proposed the alliance *Betulo lanatae-Piceion ajanensis* for the continental part of the range of *Picea jezoensis*. Data from the remaining majority of the range of *Picea jezoensis* forests have existed in various sources but have never been analyzed using the Braun-Blanquet approach. The present study includes all phytosociological data available from the entire range of *Picea jezoensis* forests and aims at producing a single, unifying phytosociological classification of these forests in the Far East.

STUDY AREA

Picea jezoensis occurs in a topographically complex mountainous territory. Most mountain ranges, especially those situated along the coast of the Sea of Okhotsk and Sea of Japan, extend north to south along the meridians. These include the Sikhote-Alin and the Dzhugdzhur on the continent, the Sredinnii and the Vostochnii on Kamchatka peninsula, the Vostochno-Sakhalinskii and the Zapadno-Sakhalinskii on Sakhalin Island, and the Taisetsu massif and the Hidaka Mts. on Hokkaido. The northern boundary of the area is formed by the mountain ranges of latitudinal orientation, i.e., the Stanovoi, and the Tukuringra-Dzhagdy. The coastal mountain ranges promote abrupt change in climatic continentality between the coastal and inland areas. They intercept most of their precipitation from the damp marine air masses in summer, but they are not barriers for the very cold continental air masses in winter.

The altitudinal limit of *Picea jezoensis* forests in the island part of their range exceeds 1500 m only on the Taisetsu massif in Hokkaido, outside the boreal zone. On Mt. Chanbai, spruce forests occur within an elevation range of 1500–1800 m, although single trees can be found even higher (VAN et al. 1959).

The mountain systems vary in age and orogeny. The most ancient part of the Yezo spruce range, the Aldan shield at the edge of Eastern Siberian Platform, was formed in Precambrian time. The bulk of its range, however, falls within the zone of Mesozoic folded mountains. The eastern edge of the continent was formed in the Tertiary period by folding under the influence of intensive volcanism (NIKOLSKAYA 1974). The youngest Sikhote-Alin and Hidaka Mountain Systems were formed before the late Cretaceous.

The coastline assumed different shapes in different geological epochs. At various times, there were several important land bridges connecting presently isolated islands. During the maximum stage of the last Glacial (ca. 18,000 years BP), northern Sakhalin as well as the Shantar Archipelago were united with the continent (GRICHUK 1984). Hokkaido was united with southern Sakhalin. The separation of Sakhalin from the continent took place at the end of Pleistocene. These land bridges were suitable for species migration. This partly explains the similarity between the species composition of spruce forests of northern Sakhalin and the Amgu River basin, or southern Sakhalin and Hokkaido.

In the regions of modern volcanism on Kamchatka, the Kuril Islands and Hokkaido, different features of volcanic terrain include the cone-shaped mountains, lava fields and tephra fields, reflecting the high dynamics of modern orogenic processes.

The climate within the range of dark-coniferous forest areas is strongly influenced by marine and continental air masses characterized by the monsoon type circulation (Table 1). The increasing continentality with distance from the sea causes a strong heterogeneity in local

Table 1. Climatic data from the geographical range of *Picea jezoensis*.

Area and station	Latitude	Longitude	Mean temperature (°C)			Annual precipitation (mm)
			Annual	Coldest month	Warmest month	
Kamchatka						
Kozyrevsk	56° N	160° E	-1.8	-19.2	15.1	512
Milkovo	55° N	159° E	-2.7	-21.8	15.0	540
Okhotsk region (including Northern Sakhalin)						
Ajan	57° N	138° E	-3.3	-19.7	13.2	791
Enkan Cape	57° N	139° E	-3.4	-20.2	13.3	521
Polini Osipenko	52° N	136° E	-3.3	-29.3	17.8	410
Chumikan	55° N	135° E	-3.9	-23.7	14.5	681
Belogorsk	51° N	128° E	-2.0	-28.8	20.7	480
Bolon'	50° N	136° E	-1.7	-28.3	19.7	650
Nikolaevsk-na-Amure	53° N	141° E	-2.4	-23.9	16.5	513
Okha	54° N	143° E	-2.4	-19.9	14.0	546
Nogliki	52° N	143° E	-2.0	-20.2	14.4	613
Poronaisk	49° N	143° E	0.0	-17.7	15.8	747
Amur basin (including Sikhote-Alin)						
Birobidzhan	49° N	133° E	-0.1	-24.6	20.3	761
Blagoveshchensk	50° N	127° E	0.0	-24.3	21.4	525
Khabarovsk	49° N	135° E	1.4	-22.3	21.1	569
Sovgavan'	49° N	140° E	-0.4	-19.4	16.5	742
Dal'nerechensk	46° N	134° E	1.5	-21.9	20.7	627
Roshchino	46° N	135° E	0.3	-24.4	20.4	789
Ternei	46° N	137° E	2.3	-14.0	17.4	813
Kirovskii	45° N	134° E	1.9	-21.8	21.0	646
Olga	44° N	135° E	3.6	-12.4	18.9	831
Ussuriisk	44° N	132° E	3.2	-19.1	21.2	599
Vladivostok	43° N	132° E	4.8	-13.5	21.0	831
Ryazanovka	43° N	131° E	5.2	-11.4	20.5	961
Islands (including southern Sakhalin, Southern Kurils and Hokkaido)						
Yuzhno-Sakhalinsk	47° N	143° E	2.1	-13.8	17.3	753
Ulegorsk	49° N	142° E	1.6	-14.8	17.0	600
Krilion Cape	46° N	142° E	3.8	-7.6	15.9	960
Kurilsk	45° N	148° E	4.3	-7.2	16.0	1040
Okedo	44° N	144° E	5.7	-9.3	20.2	910
Shirataki	44° N	143° E	5.2	-9.5	19.5	981

climates. As a whole, the climate of these areas is much more severe than that of areas of the same latitude in Europe (ELLENBERG 1980). Mean annual temperature tends to decrease with latitude and elevation, and in most of the range of *Picea jezoensis* it does not exceed zero. Along the sea coast the temperature decreases less rapidly than in the interior. However, in the southern part of the range the mean annual temperature of Yezo spruce sites may reach 2 °C in the southern Sikhote-Alin and 4 °C on Hokkaido.

Mean annual precipitation ranges from 460 mm (lower Amur basin, central Kamchatka) through 1250 mm (southern Kurils) to a maximum of 1800 mm on the mountains of the oceanic side of Hokkaido. In the continental mountain systems the precipitation increases

with elevation up to 1000–1200 mm (TARANKOV 1974). In the Sikhote-Alin Mountains the precipitation on seaward slopes is lower than on the slopes exposed to the interior (DMITRIEVA 1960). Snow cover in the maritime and island regions exceeds 50 cm (TAKAHASHI 1988). The mean annual air humidity within the range of *Picea jezoensis* does not fall below 60%, although it varies considerably from region to region (ANONYMOUS 1966–1971). A specific characteristic of the climate in the area is its relatively high continentality, even on islands such as Shantar Islands, northern Sakhalin and Hokkaido (IVANOV 1959).

In summary, climatic parameters in the territories where *Picea jezoensis* forms pure or mixed fir-spruce stands on mesic well-drained sites are as follows: mean annual temperature ranges from -2 to 3 °C, the period with a temperature higher than 5 °C lasts for 145–155 days, and mean summer precipitation is 370–590 mm. These conditions are much more severe for growth than those in the range of *Picea abies* (SCHMIDT-VOGT et al. 1977, MAN'KO 1987).

MATERIALS AND METHODS

Database

We used a data set of 476 relevés, which partly included our original data collected on Hokkaido (70 rels.), the Sikhote-Alin Mountains (32 rels.), Sakhalin (63 rels.) and Kamchatka (30 rels.). All original relevés were made on an area of 400 m². The rest of the database was formed by relevés extracted from literature and relevés kept in the phytocoenarium of the laboratory of Geobotany of the Institute of Biology and Soil Science in Vladivostok, Russia. The usual area of the relevés from the literature varied from 400 to 2500 m². The relevés were collected between 1932 and 2000 (Table 2).

Vegetation classification and ordination

Classification was made at four hierarchical levels (subvariant, variant, subassociation and association) using the Braun-Blanquet approach (BRAUN-BLANQUET 1964, MUELLER-DOMBOIS & ELLENBERG 1974, WESTHOFF & VAN DER MAAREL 1978). The major software tool for achieving this objective was VTAB – Ecosystem Reporter, Revision 199907a (EMANUEL 1999), which produced various tables required in the analysis and synthesis of vegetation data. It arranges columns (plots or groups of plots) and rows (species) according to user-specified criteria.

Relevés were classified into floristically similar groups by presence-absence criteria using TWINSpan (HILL 1979). Floristically and environmentally aberrant plots were reassigned to the group to which they were most closely related. Groups that could not be ecologically interpreted were merged. A table showing the diagnostic combination of species was made. Subassociations and higher-ranked vegetation units were named in accordance with the rules of phytosociological nomenclature (WEBER et al. 2000).

Detrended correspondence analysis (DCA; HILL & GAUCH 1980) was applied to the constancy table, using the mean cover of species in vegetation units, for ordination of vegetation units to show dissimilarity between all distinguished vegetation units.

Table 2. Sources of relevés.

Author of relevés	Region	Midpoint coordinates		Date	Source
GRISHIN	Shantar Islands	55° N	137° E	1981	MAN'KO (1984)
KABANOV	Southern Sikhote-Alin	43° N	135° E	1934	KABANOV (1937)
KABANOV	Northern Sakhalin	52° N	144° E	1940	KABANOV (1940)
KOLESNIKOV	Southern Sikhote-Alin	43° N	135° E	1934	KABANOV (1937)
KOLESNIKOV	Northern Sakhalin	52° N	144° E	1940	KABANOV (1940)
KORKESHKO	Northern Sakhalin	54° N	144° E	1940	KABANOV (1940)
KRESTOV	Middle Sikhote-Alin	46° N	137° E	1994	Unpubl.
KRESTOV	Sakhalin	50° N	144° E	1999–2000	Unpubl.
KRESTOV	Kamchatka	56° N	160° E	1996–2000	Unpubl.
KURENTOVA	Northern Sikhote-Alin	43° N	135° E	1972	Phytocoenarium (unpubl.)
KURENTOVA	Southern Sikhote-Alin	44° N	135° E	1947–1974	Phytocoenarium (unpubl.)
MAN'KO	Selemdzha	53° N	133° E	1972	MAN'KO & VOROSHILOV (1974)
MAN'KO	Kamchatka	56° N	160° E	1971–1976	MAN'KO & VOROSHILOV (1978)
NAKAMURA	Hokkaido	43° N	143° E	1977–1987	NAKAMURA (1988)
NAKAMURA	Sakhalin	50° N	144° E	1999	Unpubl.
SHAFRANOVSKII	Iturup	45° N	148° E	1985	SHAFRANOVSKII (1987)
SHEMETOVA	Bureya	51° N	131° E	1974	Phytocoenarium (unpubl.)
SHEMETOVA	Southern Sikhote-Alin	44° N	135° E	1962–1983	Phytocoenarium (unpubl.)
VERKHOLAT	Kunashir Island	44° N	146° E	1975	Phytocoenarium (unpubl.)
VERKHOLAT	Southern Sikhote-Alin	43° N	135° E	1971–1973	Phytocoenarium (unpubl.)

Nomenclature and taxonomy

Differences in botanical nomenclature used in Russia, Korea and Japan are considerable. In general, Russian botanists tend to use a narrower species concept than those in other eastern Asian countries. Many taxa considered as subspecies or varieties outside Russia are recognized as species in the Russian literature. For the standardization of nomenclature we used a database (KRESTOV, unpubl.), which includes over 26,000 valid names and synonyms of vascular plants, extracted from the main taxonomic studies from northern Asia. This database united the nomenclature for taxa present both in Russia and Japan, while at the same time largely preserving the main species concepts accepted in Russia and Japan for the species endemic to these regions. In most cases, we used the species concepts accepted in KHARKEVICH (1985–1996) and ITO & HINOMA (1985) for the Russian Far East and Japan, respectively.

In this paper the name *Picea jezoensis* (including *P. ajanensis*) is accepted for both continental and island parts of the range of this species. In the genus *Larix*, we accept a wide concept of species (TSVELEV 1994) and include all the earlier recognized species (e.g. *L. cajanderi*, *L. gmelinii*, *L. kamschatica*, and *L. olgensis*) into *L. dahurica* LAWS. *Betula ermanii* is also accepted as a taxonomically broadly defined species including a number of narrower taxa distinguished at the species level by Russian taxonomists, e.g. *B. lanata*, *B. velutina*, *B. paraermanii*, and *B. ulmifolia* (VASIL'EV 1941).

SYNOPSIS OF THE PICEA JEZOENSIS FORESTS

The hierarchical system of lower syntaxa of zonal *Picea jezoensis* forests includes 2 community types, 11 associations, 9 of which are described for the first time, 6 subassociations, 25 variants and 8 subvariants. All syntaxa were assigned to the higher units

according to the following order. The coding of units is following: A – alliance; 1 – association; 1a – subassociation; 1a1 – variant and 1a1a – subvariant. The alliances described from the peripheral part of the range of *Picea jezoensis* are placed at the bottom of the list. They include the alliance *Abietion koreanae* from the subalpine belt of the warm temperate zone of Korea (SONG 1991) and the alliance *Abietion mariesii* from the subalpine belt of the warm temperate zone of Honshu (MIYAWAKI & NAKAMURA 1988). The asterisk (*) represents associations of the alliance *Abieti nephrolepidis-Piceion jezoensis* described from the subalpine belt of the cool temperate zone of Korea (SONG 1991).

Vaccinio-Piceetea BR.-BL. in BR.-BL. et al. 1939

Abieti-Piceetalia MIYAWAKI et al. 1968

A. *Piceion jezoensis* SUZUKI-TOKIO ex JINNO et SUZUKI 1973

1. *Anaphalis margaritacea-Abies sachalinensis* community
2. *Piceo-Abietetum sachalinensis* OHBA ex NAKAMURA in MIYAWAKI 1988
 - 2a1. *typicum*, 2a2. *Rhododendron albrechtii*, 2a3. *Sasa senanensis* (2a3a. *Tilia japonica*, 2a3b. *Prunus ssiorii*)
3. *Asaro heterotropoidis-Abietetum sachalinensis* KRESTOV & NAKAMURA 2002 ass. nov. hoc loco
4. *Weigelo middendorffiana-Piceetum jezoensis* KRESTOV & NAKAMURA 2002 ass. nov. hoc loco
5. *Piceetum glehnii* SUZUKI-TOKIO ex NAKAMURA in MIYAWAKI 1988
 - 5a. *Piceetum glehnii sasetosum kurilensis* KRESTOV & NAKAMURA 2002 subass. nov. hoc loco
 - 5b. *Piceetum glehnii rhododendretosum brachycarpi* NAKAMURA 1988
 - 5b1. *typicum*, 5b2. *Ilex sugerokii*
6. *Lysichito camtschaticense-Piceetum glehnii* KRESTOV & NAKAMURA 2002 ass. nov. hoc loco
 - 6a1. *typicum*, 6a2. *Carex middendorffii*, 6a3. *Carex pseudololiacea*, 6a4. *Carex schmidtii*

B. *Abieti nephrolepidis-Piceion jezoensis* SONG 1991

7. *Swido albae-Piceetum obovatae* KRESTOV & NAKAMURA 2002 ass. nov. hoc loco
8. *Oplopanaco elati-Piceetum jezoensis* KRESTOV & NAKAMURA 2002 ass. nov. hoc loco
 - 8a1. *typicum*, 8a2. *Huperzia chinensis*, 8a3. *Bergenia pacifica* (8a3a. *typicum*, 8a3b. *Cassiope redowskii*)
9. *Philadelpho tenuifolii-Piceetum jezoensis* KRESTOV & NAKAMURA 2002 ass. nov. hoc loco
 - 9a. *Philadelpho tenuifolii-Piceetum jezoensis typicum* KRESTOV & NAKAMURA 2002 subass. nov. hoc loco
 - 9a1. *Carex sordida*, 9a2. *Anemonoides umbrosa*, 9a3. *Corydalis gigantea*
 - 9b. *Philadelpho tenuifolii-Piceetum jezoensis coryletosum mandshuricae* subass. nov.
 - 9b1. *Acer barbinerve*, 9b2. *Lonicera praeflorens*, 9b3. *typicum*
10. *Lathyrus humilis-Picea jezoensis* community

- 10a1. *Hemerocallis middendorffii*, 10a2. *Abelia coreana*
 **Taxo-Pinetum pumilae* SONG 1991
 **Thujo-Abietetum nephrolepidis* SONG 1991
 **Abieti koreanae-Piceetum jezoensis* SONG 1991
- C. *Pino pumilae-Piceion jezoensis* KRESTOV & NAKAMURA 2002 all. nov. hoc loco
11. *Vaccinio vitis-idaeae-Piceetum jezoensis* KRESTOV & NAKAMURA 2002 ass. nov. hoc loco
- 11a. *Vaccinio vitis-idaeae-Piceetum jezoensis typicum* KRESTOV & NAKAMURA 2002 subass. nov. hoc loco
- 11b. *Vaccinio vitis-idaeae-Piceetum jezoensis coptidetosum trifoliae* subass. nov. hoc loco
- 11b1. *typicum*, 11b2. *Betula middendorffii* (11b2a. *typicum*, 11b2b. *Oxycoccus palustris*)
12. *Rhododendro aurei-Piceetum jezoensis* KRESTOV & NAKAMURA 2002 ass. nov. hoc loco
13. *Moneseto uniflorae-Piceetum jezoensis* KRESTOV & NAKAMURA 2002 ass. nov. hoc loco
- 13a1. *Alnus kamtschatica*, 13a2. *Geranium erianthum* (13a2a. *Salix udensis*, 13a2b. *Carex reventa*), 13a3. *typicum*
- D. *Abietion koreanae* SONG 1991
Saso-Abietetum koreanae SONG 1991
Betulo saitoanae-Abietetum koreanae SONG 1991
- E. *Abietion mariesii* SUZUKI-TOKIO 1954
Abietetum veitchii YAMANAKA 1959
Abietetum veitchii-mariesii MAEDA et SHIMAZAKI 1951
Abietetum mariesii HORIKAWA ex SUZUKI-TOKIO 1954

ASSOCIATION DESCRIPTIONS

1. *Anaphalis margaritacea-Abies sachalinensis* community (Electronic appendix, Table 5)

Distribution and ecology: This community occurs in southern boreal zone in suboceanic sector on southernmost Sakhalin. It is developed on slopes with well-drained, slightly dry soils, in the very moist local climate.

Physiognomy: Open forests of *Abies sachalinensis*, *Picea jezoensis* and occasional mix of *Picea glehnii* and *Betula platyphylla*, possibly in places which were historically logged. The shrub layer includes many heliophilous shrubs, such as *Salix caprea*, *Juniperus sibirica*, and *Salix taraiensis*. The herb layer is well developed. It is characterized by “meadow” species such as *Anaphalis margaritacea*, *Arnica sachalinensis*, and *Lagedium sibiricum*.

Remark: This community was delineated on the basis of only five relevés. This low number is due to the little attention paid by researchers to seral communities. Further study may lead to the delimitation of an association, with the list of diagnostic species possibly extended by *Antennaria dioica*, *Juniperus sibirica*, *Aster glehnii*, and *Ptarmica japonica*.

Table 3. Shortened synoptic table of communities of *Picea jezoensis* forests. Numbers are classes of percentage constancy: 1: 1–20%, 2: 21–40%, 3: 41–60%, 4: 61–80%, 5: 81–100%. Companion species with constancy ≤ 60% in all columns are not shown. A full version of this table with rare species can be found online in electronic appendix.

Column number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36		
Association	1	2	2	2	2	3	4	5	5	5	6	6	6	6	7	8	8	8	8	9	9	9	9	9	10	10	11	11	11	11	12	13	13	13	13			
Subassociation		a	a	a	a		a	b	b	a	a	a	a	a	a	a	a	a	a	a	b	b	b	a	a	b	b	b	a	a	a	a	a	a	a	a		
Variant, subvariant		1	2	3a	3b			1	2	1	2	3	4		1	2	3a	3b	1	2	3	1	2	3	1	2		1	2a	2b		1	2a	2b	3			
Number of relevés	5	21	4	12	8	10	22	23	21	2	12	5	8	7	11	19	15	10	3	7	6	4	9	5	11	4	3	48	33	24	4	10	17	6	25	22		
Number of species per relevé	30	22	37	32	24	21	20	20	28	25	24	23	25	23	36	34	39	25	14	26	41	26	49	49	28	24	28	16	20	31	34	31	38	39	32			
1. <i>Anaphalis margaritacea</i>-<i>Abies sachalinensis</i> community																																						
<i>Solidago decurrens</i>	5	2	2	1	1	1	1	1	1		1	1	1	2		3	1	1		2		3	2	3	1	2		1	2	2	2	2						
<i>Salix caprea</i>	5	1			1	1					1																		1	1	1	3		2		1	1	
<i>Anaphalis margaritacea</i>	4																												1									
<i>Arnica sachalinensis</i>	3																																					
<i>Hieracium umbellatum</i>	3																																					
<i>Platanthera extremorientalis</i>	3																																					
2. <i>Piceo-Abietetum sachalinensis</i>																																						
<i>Hydrangea petiolaris</i>		4	5	5	3		1		2	2		1		2																								
<i>Kalopanax septemlobus</i>		4	4	4	3			1	1		1																											
<i>Toxicodendron orientale</i>		3	5	4	1			1			2		1																									
<i>Galium kamschatcicum</i>		2	3	5	4		1	2	2		1						1	1	1		1	2		1	1	1		1		1		1		1	1	1		
2a2. Variant of <i>Rhododendron albrechtii</i>																																						
<i>Rhododendron albrechtii</i>		5	1				1	1																														
<i>Cirsium kamschatcicum</i>	1	1	4	2			1	1		1		1	2																1					2			1	
<i>Ribes pallidiflorum</i>		1	4				1				1			2					2	2			1	2	2	1				1								
<i>Osmorhiza aristata</i>		1	4	1																			2	1	1													
<i>Lilium debile</i>	1	1	4	1		1	1				1																										2	
<i>Polygonatum odoratum</i>		1	3	1																																		
<i>Arisaema japonicum</i>			3																																			
2a3. Variant of <i>Sasa senanensis</i>																																						
<i>Sasa senanensis</i>		2		5	4			1	2																													
2a3a. Variant of <i>Sasa senanensis</i>; subvariant of <i>Tilia japonica</i>																																						
<i>Acer japonicum</i>			2	4	1			1																														
<i>Acer mayrii</i>			2	4	2																																	
<i>Quercus mongolica</i>		1		4	2	1		1	1			1											1															
<i>Tilia japonica</i>		1		4	1			1																														
<i>Trillium smallii</i>		1		4	1			1																														
2a3b. Variant of <i>Sasa senanensis</i>; subvariant of <i>Prunus ssiiori</i>																																						
<i>Prunus ssiiori</i>		1		1	5			1																														
<i>Rubus pseudojaponicus</i>		1		1	3			1																														
3. <i>Asaro heterotropoidis</i>-<i>Abietetum sachalinensis</i>																																						
<i>Asarum heterotropoides</i>		1		1		4		2																														
<i>Peltigera aphthosa</i>						4	2			1		2		1	1	2		1					2		1	1	2		1	5	4	3	3					
4. <i>Weigela middendorffiana</i>-<i>Piceetum jezoensis</i>																																						
<i>Weigela middendorffiana</i>						5	1	2											1	1	2							1	1	3								
<i>Aconitum umbrosum</i>						3							1						1	2		1	1	2		1	1	1										
<i>Veratrum albiflorum</i>	1		2			3			1		1							1	1									1										
5. <i>Piceetum glehnii</i>																																						
<i>Picea glehnii</i>	2						4	5	5		4	3	3	3															1									
<i>Menziesia pentandra</i>		1	2	1				4	5	5		2	1	3																								
<i>Pogonatum japonica</i>								2	3	3		1		1		1													1			2	2				1	
5a. <i>Piceetum glehnii</i> sasoetosum kurilensis																																						
<i>Sasa kurilensis</i>		3	5	1	2	1		5	2		2	3	4																									
5b. <i>Piceetum glehnii</i> rhododendretosum brachycarpi																																						
<i>Rhododendron brachycarpum</i>								4	5																													
<i>Arachniodes mutica</i>			2	1				2	4	5		1																										
<i>Vaccinium inokumai</i>		1						1	3	5		1																										
5b2. Variant of <i>Ilex sugerokii</i>																																						
<i>Ilex sugerokii</i>																																						
<i>Diphysastrum complanatum</i>	4				1		1	1	5		1																	1		1		1	3	2	3	2		
<i>Scapania</i> sp.					1		1	5																													1	
6. <i>Lysichiton camtschatcense</i>-<i>Piceetum glehnii</i>																																						
<i>Lysichiton camtschatcense</i>																																						
<i>Sphagnum squarrosum</i>																																						
<i>Equisetum palustre</i>																																						
6a2. Variant of <i>Carex middendorffii</i>																																						
<i>Carex middendorffii</i>																																					4	

Column number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36		
<i>Eriophorum vaginatum</i>	3	1
<i>Miscanthus sinensis</i>	3	
<i>Myrica tomentosa</i>	3	
<i>Sphagnum palustre</i>	1	3	.	1	
6a3. Variant of <i>Carex pseudoliacea</i>																																						
<i>Carex pseudoliacea</i>	1	5	
<i>Ephippianthus sachalinensis</i>	.	1	.	1	.	1	1	.	1	2	4	
6a4. Variant of <i>Carex schmidtii</i>																																						
<i>Carex schmidtii</i>	5	1	
<i>Osmundastrum asiaticum</i>	2	1	2	.	2	1	.	.	.	3	1	1	5	.	2	3	.	.	2	.	1	2	1	3		
<i>Trillium camschatcense</i>	1	1	2	1	1	2	.	1	.	1	.	1	3	.	1	
<i>Sphagnum fuscum</i>	1	1	1	3	
7. <i>Swida alba</i>-<i>Piceetum obovatae</i>																																						
<i>Swida alba</i>	.	1	1	.	1	5	
<i>Padus avium</i>	4	
<i>Picea obovata</i>	4	
<i>Aconitum arcuatum</i>	3	.	.	.	1	2	.	1	1	
8. <i>Oplopanaco elati</i>-<i>Piceetum jezoensis</i>																																						
<i>Oplopanax elatus</i>	4	5	3	4	1	
<i>Syringa wolfii</i>	3	3	3	2	2	.	1		
8a2. Variant of <i>Huperzia chinensis</i>																																						
<i>Huperzia chinensis</i>	.	1	.	.	1	.	1	1	5	2	1	
<i>Carex siderosticta</i>	2	5	1	.	.	.	2	3	2	2	
<i>Lonicera maximowiczii</i>	1	2	5	2	.	3	2	.	3	.	2	.	2	1		
<i>Lycopodium obscurum</i>	2	1	2	1	.	1	.	2	2	3	1	.	2	.	1	4	2	.	1	.	2	.	2	.	.	.	1		
8a3. Variant of <i>Bergenia pacifica</i>																																						
<i>Bergenia pacifica</i>	1	.	5	5	1		
<i>Rhododendron mucronulatum</i>	2	1	3	5	1	.	2		
8a3b. Subvariant of <i>Cassiope redowskii</i>																																						
<i>Cassiope redowskii</i>	
<i>Lycopodium clavatum</i>	1	.	.	.	2	1	.	.	.	2	.	1	2	5	1	.	2	.	1	1	.	1	1	.		
<i>Ledum hypoleucum</i>	2	1	3	2	.	.	1	5	1	.	1	.	2	4	1	.	.	.		
9. <i>Philadelpho tenuifolii</i>-<i>Piceetum jezoensis</i>																																						
<i>Philadelphus tenuifolius</i>	1	2	2	1	.	3	3	2	4	5	3	2		
<i>Cacalia auriculata</i>	.	.	.	1	1	1	3	1	1	.	3	5	4	3	3	2	.	.	1	.	1	.	1		
<i>Eleutherococcus senticosus</i>	1	1	1	.	.	2	3	2	5	4	2	
<i>Aconitum fischeri</i>	.	.	.	1	1	2	4	3	3	.	1	2	.	1	1	.	.	1	2	1		
<i>Paris hexaphylla</i>	3	1	1	1	.	2	4	2	3	.	2	1	1		
9a1. Variant of <i>Carex sordida</i>																																						
<i>Carex sordida</i>	4	1	
<i>Cornopteris crenulatoserrulata</i>	3	1	.	1	
9a2. Variant of <i>Anemonoides umbrosa</i>																																						
<i>Anemonoides umbrosa</i>	1	5	2	
9a3. Variant of <i>Corydalis gigantea</i>																																						
<i>Corydalis gigantea</i>	1	5	1	.	1	
9b. <i>Philadelpho tenuifolii</i>-<i>Piceetum jezoensis coryletosum mandshuricae</i>																																						
<i>Corylus mandshurica</i>	1	4	5	1	
<i>Tilia amurensis</i>	2	1	1	.	1	1	.	4	3	3	.	4		
<i>Euonymus pauciflorus</i>	2	1	2	.	2	.	4	4	1	
<i>Phryma asiatica</i>	
<i>Prunus maximowiczii</i>	.	.	1	.	.	1	1	4	3	1	
<i>Schisandra chinensis</i>	.	1	.	1	3	3	2	
9b1. Variant of <i>Acer barbinerve</i>																																						
<i>Acer barbinerve</i>	1	5	2	1	
<i>Carex quadriflora</i>	1	1	4	2	1		
<i>Spiraea ussuriensis</i>	1	.	.	.	1	.	3	.	1		
9b2. Variant of <i>Lonicera praeflorens</i>																																						
<i>Lonicera praeflorens</i>	5	1	
<i>Lunathyrium pycnosorum</i>	.	2	1	1	.	1	.	3	5	1		
<i>Neomolinia mandshurica</i>	2	1	1	.	1	1	2	3	5	2		
<i>Carpinus cordata</i>	
<i>Adiantum pedatum</i>	
<i>Carex ussuriensis</i>	1	1	2	2	.	1	.	2	4	2		
<i>Aralia elata</i>	.	.	1	1	3	1		
10. <i>Lathyrus humilis</i>-<i>Picea jezoensis</i> community																																						
<i>Spiraea betulifolia</i>	1	1	.	.	1	1	.	2	.	1	1	1	.	1	2	.	.	.</																

Column number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36				
<i>Lathyrus humilis</i>	3	4		
<i>Polypodium sibiricum</i>	.	1	.	1	.	1	.	1	1	2	3	2	.	2	.	2	.	1	3	5	1			
<i>Vicia venosa</i>	3	2		
10a1. Variant of <i>Hemerocallis middendorffii</i>																																								
<i>Hemerocallis middendorffii</i>	4		
<i>Convallaria keiskei</i>	1	1	1	1	4	2	1		
10a2. Variant of <i>Abelia coreana</i>																																								
<i>Angelica maximowiczii</i>	2	1	1	3	2	2	.	1	2	.	2	1	2	3	5	2			
<i>Abelia coreana</i>	4	
<i>Carex nanella</i>	1	1	.	.	4	1		
<i>Daphne kamschatcica</i>	4	
11. <i>Vaccinio vitis-idaeae-Piceetum jezoensis</i>																																								
<i>Vaccinium vitis-idaea</i>	3	1	.	.	.	1	1	1	5	3	1	1	5	1	.	.	3	5	1	1	2	.	5	5	5	5	5	2	.	2	3	.	.			
<i>Cladina rangiferina</i>	2	2	2	1	
11b. <i>Vaccinio vitis-idaeae-Piceetum jezoensis coptidetosum trifoliae</i>																																								
<i>Coptis trifolia</i>	3	1	.	.	1	1	.	2	3	3	5	1	4	1	4	4	5	1	1	1	1	2	.	.	.		
11b2. Variant of <i>Betula middendorffii</i>																																								
<i>Dicranum majus</i>	1	1	1	2	.	1	1	5	5	2			
<i>Betula middendorffii</i>	2	4	5	1	1	
<i>Empetrum sibiricum</i>	2	1	1	3	5	.	1	1	.	1		
11b2b. Variant of <i>Betula middendorffii</i>; subvariant of <i>Oxycoccus palustris</i>																																								
<i>Iris setosa</i>	1	1	2	1	1	1	5	.	1	.	1		
<i>Rubus chamaemorus</i>	.	1	1	1	1	1	1	5	
<i>Oxycoccus palustris</i>	4	
<i>Parnassia palustris</i>	4	
<i>Carex globularis</i>	2	.	.	1	.	.	1	1	1	2	4	1		
<i>Vaccinium uliginosum</i>	.	1	1	1	1	4	.	1	.	1	1	
<i>Cornus suecica</i>	.	.	.	1	.	.	.	1	1	3	.	1	.	1	1	
12. <i>Rhododendro aurei-Piceetum jezoensis</i>																																								
<i>Rhododendron aureum</i>	1	4	1	
<i>Streptopus streptopoides</i>	.	.	1	.	1	1	2	.	2	1	.	.	4	1	.	1	1	
<i>Veratrum oxyspalum</i>	1	1	1	1	1	1	2	4	1	
<i>Aegopodium alpestre</i>	.	.	.	1	1	2	1	3	1	.	1	1	1	4	
<i>Carex falcata</i>	.	2	2	.	1	2	1	1	.	1	.	.	.	3	1	1	2	.	3	.	1	1	.	4	1		
<i>Saxifraga punctata</i>	1	1	.	3	
<i>Viola kusnezowiana</i>	3	
<i>Alnus fruticosa</i>	1	.	3	
13. <i>Moneseto uniflorae-Piceetum jezoensis</i>																																								
<i>Orthilia secunda</i>	.	1	.	2	.	.	1	1	5	1	.	.	.	1	1	2	.	1	1	1	1	.	5	5	5	5	.	.		
<i>Chamaenerion angustifolium</i>	3	.	.	1	1	1	.	1	1	1	1	.	5	5	5	4	.	.	.	
<i>Moneses uniflora</i>	1	.	.	.	1	1	1	1	1	1	1	.	5	5	5	4	.	.	.	
<i>Sorbus sibirica</i>	1	.	5	5	4	2	
<i>Ribes triste</i>	.	.	.	1	1	1	1	2	1	.	5	5	3	2	.	.	.	
<i>Solidago spiraeifolia</i>	1	5	5	3	2	
<i>Equisetum pratense</i>	1	.	.	.	3	.	.	1	1	1	1	1	.	3	5	5	4		
<i>Lonicera caerulea</i>	3	2	1	2	2	3	.	2	1	.	1	.	.	1	1	.	.	3	5	4	4		
<i>Pyrola incarnata</i>	4	1	1	.	1	.	3	3	4	3	
<i>Rubus arcticus</i>	1	.	.	.	2	1	1	.	2	3	3	5	5	
13a1. Variant of <i>Alnus kamschatcica</i>																																								
<i>Alnus kamschatcica</i>	1	.	2	.	1	5	1	1	
13a2. Variant of <i>Geranium erianthum</i>																																								
<i>Geranium erianthum</i>	1	1	.	1	1	.	3	5	5	1	.	.	.	
<i>Galium boreale</i>	1	2	1	1	5	4	1		
13a2a. Variant of <i>Geranium erianthum</i>; subvariant of <i>Salix udensis</i>																																								
<i>Salix udensis</i>	1	1	5		
<i>Saussurea oxyodonta</i>	1	1	4	1	1	
<i>Pteridium aquilinum</i>	2	.	.	1	1	.	1	1	.	1	
<i>Corallorhiza trifida</i>	1	1	4	.	1
<i>Lathyrus pilosus</i>
<i>Carex longirostrata</i>	1	.	2	1	3	1	1
<i>Filipendula kamschatcica</i>	.	.	.	1	.	.	.	1	1	1	.	1	.	3	1	1
<i>Pedicularis resupinata</i>	1	1	
13a2b. Variant of <i>Geranium erianthum</i>; subvariant of <i>Carex reventa</i>																																								
<i>Carex reventa</i>	1	2	1	2	2	1	4	1	
<i>Saussurea pseudotilesii</i>	2	1	3	1	
Diagnostic species of <i>Vaccinio-Piceetea</i>																																								
<i>Dryopteris expansa</i>	.	4	5	5	5	3	1	3	3	.	2	.	2	2	1	4	4	3	.	1	5	.	3	2	2	.	.	1	1	1	.	4	2	2	2	1				
<i>Goodyera repens</i>	2	.	3	1	1	2	1	4	3	

Column number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
<i>Gymnocarpium dryopteris</i>	1	1	1	.	1	.	1	4	2	3	2	.	1	.	2	2	2	3	4	1	2	4	2	1	5	4	5	4		
<i>Hylocomium splendens</i>	.	1	2	1	.	3	3	2	3	.	1	3	4	3	5	3	4	4	5	2	3	3	2	.	4	5	5	5	2	2	.	5	4	.	5	4
<i>Linnaea borealis</i>	2	.	.	.	2	3	.	.	.	2	1	3	4	1	2	2	.	.	2	.	1	3	2	3	4	5	5	5	5	5	5	5	5	5	5	
<i>Lycopodium annotinum</i>	.	1	.	1	.	2	2	2	.	2	3	3	.	3	5	3	.	.	2	2	.	2	.	2	.	2	1	4	2	5	5	5	5	5	5	5
<i>Maianthemum bifolium</i>	2	1	.	1	.	2	.	5	3	4	2	.	1	2	2	4	4	2	4	2	2	1	1	.	4	4	4	3
<i>Pleurozium schreberi</i>	.	1	2	.	1	5	4	3	4	3	3	3	5	3	2	2	2	.	1	2	3	1	.	3	3	4	4	3	5	5	5	5	4	5	5	5
<i>Ptilium crista-castrensis</i>	2	2	.	1	.	1	3	3	2	3	1	.	1	4	1	.	2	3	2	3	2	5	2	.	2	3	.
<i>Sphagnum girgensohnii</i>	.	1	.	.	.	2	.	1	.	3	1	4	3	2	1	1	3	1	.	1	2	3	2	4	1	.	1	2	.	.
<i>Trientalis europaea</i>	2	2	.	1	3	2	1	1	3	2	1	2	2	.	1	.	1	1	3	4	1	5	5	4	5	.	.	
Diagnostic species of Abieti-Piceetalia																																				
<i>Picea jezoensis</i>	4	4	5	5	5	5	5	3	4	.	3	1	2	5	5	5	5	5	5	5	5	5	5	4	5	5	5	4	5	5	5	5	5	5	5	
<i>Betula ermanii</i>	4	4	.	4	3	3	4	3	3	.	3	1	1	1	3	1	3	5	3	2	3	1	.	2	2	.	3	3	2	.	5	4	5	2	2	
<i>Cornus canadensis</i>	2	2	.	2	1	3	5	3	4	5	5	5	5	5	1	1	2	2	.	3	2	1	.	3	4	2	4	5	5	4	1	
<i>Maianthemum dilatatum</i>	5	4	5	4	3	4	3	4	3	4	1	2	5	1	2	.	.	.	2	3	.	2	3	.	2	2	5	5	4	.	3	4	4	2	.	
<i>Orthilia obtusata</i>	1	.	1	.	1
Species common in insular sector of Picea jezoensis range and diagnostic species of Piceion jezoensis (framed)																																				
<i>Abies sachalinensis</i>	4	5	5	5	5	4	5	5	5	5	4	5	4	2	3	1
<i>Ilex rugosa</i>	3	3	2	.	3	1	4	3	5	2	1	3	3	1	1
<i>Sorbus commixta</i>	2	4	4	5	3	2	4	5	5	4	1	3	1	1
<i>Vaccinium ovalifolium</i>	2	3	3	3	5	3	1	.	1	1	3	1
<i>Vaccinium praestans</i>	1	1	.	1	2	.	2	3	2	3	3	5	4	3	1	2	2	5
<i>Vaccinium smallii</i>	1	3	2	3	.	1	.	3	4	.	3	5	3	4	1	1	1
<i>Acanthopanax sciadophylloides</i>	.	.	2	3	2	.	.	1	2	3
<i>Acer tschonoskii</i>	.	.	1	2	.	.	1	2
<i>Anemoides sciaphila</i>	.	1	.	2	.	.	1	1	.	1
<i>Cacalia kamschatica</i>	1	2	4	2	2	1	.	1	2	.	1	.	3	2	1	.	.	1	.	1	.	.	
<i>Carex sachalinensis</i>	.	2	2	3	2	.	1	2	.	1
<i>Euonymus planipes</i>	.	1	.	2	2	.	1	1	.	1	.	1
<i>Ilex crenata</i>	.	2	.	1	.	.	1	.	1	2	1
<i>Peracarpa carnosia</i>	.	.	2	2	2	.	1	1
<i>Schizophragma hydrangeoides</i>	.	2	2	3	2	.	1	1
<i>Skimmia repens</i>	.	3	.	2	2	1	.	2	1	.	1	.	1
<i>Tiarella polyphylla</i>	1	1
<i>Tripterispermum japonicum</i>	.	1	2	1	.	.	1	1	.	1	1
<i>Vaccinium japonicum</i>	1	1
<i>Viburnum furcatum</i>	.	1	4	3	2	2	.	2	2	.	1
<i>Viburnum wrightii</i>	.	1	1
Species common in southern portion of continental sector of Picea jezoensis range and diagnostic species of Abieti nephrolepidis-Piceion jezoensis (framed)																																				
<i>Abies nephrolepis</i>	2	5	5	5	5	5	5	5	5	5	5	5	5	4	5	2	.	1		
<i>Acer tegmentosum</i>	1	3	4	2	.	.	4	3	4	3	3	2	
<i>Carex campylophila</i>	1	3	5	2	.	.	3	.	3	4	1	3	
<i>Betula costata</i>	1	3	5	2	.	.	4	3	5	4	3	2	2	1	
<i>Pinus koraiensis</i>	1	4	4	3	.	.	2	3	4	5	5	4	4	1	
<i>Pseudocystopteris spinulosa</i>	1	1	1	3	1	.	.	1	3	.	4	.	3	3	2	1	
<i>Thalictrum tuberiferum</i>	3	4	.	.	.	3	3	2	3	2	2	2	2	1	
<i>Trigonotis radicans</i>	4	2	1	.	.	3	4	.	4	3	2
<i>Sorbus amurensis</i>	2	5	2	4	3	.	.	2	4	.	2	1	3	.	4	2	.	.	4	
<i>Mitella nuda</i>	.	.	1	.	1	5	3	3	2	.	.	3	4	.	4	5	2	3	2	1	
<i>Carex xyphioides</i>	1	2	3	1	1	.	.	1	4	.	2	4	1	3	.	2	1	
<i>Galium davuricum</i>	1	1	1	.	.	3	1	2	2	3	1	3	2	
<i>Pseudostellaria sylvatica</i>	1	1	1	.	.	2	3	2	.	1	3	2	
<i>Galium paradoxum</i>	1	1	.	.	.	1	1	.	2	2	1
<i>Lonicera chrysantha</i>	1	2	1	.	.	1	1	.	1	2	2	1	2	
<i>Paeonia obovata</i>	1	1	1	.	2	1	1
<i>Ribes mandshuricum</i>	1	2	.	.	.	1	1	.	3	1	1
<i>Ribes maximoviczianum</i>	1	1	1	.	.	2	1	3	3	4	1	2	4	
<i>Saussurea subtriangulata</i>	2	1	.	.	.	1	.	2	3	1
<i>Waldsteinia ternata</i>	.	.	.	1	1	.	1	1	1	1	.	.	1	1	.	2	3	2
Species common in northern portion of Picea jezoensis range and diagnostic species of Pino pumilae-Piceion jezoensis (framed)																																				
<i>Pinus pumila</i>	.	.	1	.	1	1	1	.	5	1	2	1	.	1	2	2	5	5	5	4	3	4	4
<i>Lonicera chamosii</i>	2	.	.	.	1	1	1	4	5	1	4	3	4	4
<i>Sorbus sambucifolia</i>	3	1	.	.	1	1	.	.	2	1	.	5	1	2	2	1	4	5	3	.	4	4	1	2	
<i>Equisetum sylvaticum</i>	.	.	.	1	1	.	.	.	2	1	3	2	1	.	.	2	1	1	2	1	5	1	2	2	5	4	
<i>Spiraea beauverdana</i>	2	.	.	.	2	.	.	.	2	.	1	1	2	3	3	3	2	.	1	2	.	
<i>Allium ochotense</i>	1	1	.	3	1	1	2	.	.
<i>Betula platyphylla</i>	4	.	4	.	.	1	1																													

Column number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	
<i>Cacalia hastata</i>	2	1	.	1	.	.	1	.	1	2	1	3	.	3	2	3	3	2	1	.	.	.	1	1	.	1	2	4	3	1		
<i>Calamagrostis purpurea</i>	5	1	.	.	2	4	1	1	.	2	1	1	4	5	3	3	3	2	3	3	4	.	.	3	5	5	4	4	5	5	5	5	5	5	5	5	
<i>Carex pallida</i>	1	1	.	.	.	1	2	1	1	.	2	3	2	2	3	.	1	
<i>Diplazium sibiricum</i>	.	.	.	1	1	.	1	3	3	4	2	.	4	.	3	.	2	2	2	.	.	.	1	1	.	1	.	1	1		
<i>Impatiens noli-tangere</i>	1	1	.	.	1	4	2	2	.	1	.	4	.	1	1	
<i>Larix dahurica</i>	3	1	3	.	1	3	3	.	.	.	3	1	2	.	1	.	2	3	3	4	5	1	3	2	3	4		
<i>Melica nutans</i>	1	2	1	1	1	.	1	1	.	.	1	1	
<i>Milium effusum</i>	.	2	2	1	.	.	2	.	3	.	1	1	.	.	1	.	.	2	1	.	
<i>Moehringia lateriflora</i>	2	1	.	1	1	.	1	.	.	.	1	1	.	2	.	1	.	2	.	1	1	
<i>Rosa acicularis</i>	3	1	.	.	1	.	1	.	1	.	.	3	5	2	2	.	1	2	2	3	1	2	.	2	2	1	2	2	.	2	5	4	2	.	.		
<i>Sorbaria sorbifolia</i>	1	.	1	1	2	2	1	1	.	2	2	.	2	.	2	2	.	1	1	1	.	1	.	1	.	1	.		
Species common in southern (both temperate insular and mainland) portion of <i>Picea jezoensis</i> range																																					
<i>Acer ukurunduense</i>	.	1	2	4	3	2	2	3	4	.	2	.	1	.	2	5	5	4	.	4	5	4	4	5	5	2	.	2	1	1		
<i>Actaea asiatica</i>	.	1	.	3	3	.	1	1	.	.	2	3	.	2	3	1	
<i>Actinidia kolomikta</i>	.	3	4	5	5	1	1	2	2	.	1	.	1	1	4	5	3	.	2	5	2	5	5	4	2	2	1	1	
<i>Cimicifuga simplex</i>	.	1	4	1	1	.	1	1	3	4	1	.	1	3	.	4	1	1	
<i>Circaea alpina</i>	.	2	4	1	1	.	1	.	1	.	1	.	3	4	3	1	.	3	5	3	4	4	2	.	2	.	1	1	1		
<i>Dryopteris crassirhizoma</i>	.	2	5	5	.	1	2	3	1	.	1	2	2	5	5	3	
<i>Euonymus macroptera</i>	1	1	4	2	1	2	1	2	2	3	1	1	2	.	1	2	1	1	.	1	2	2	5	2	2	3	2	1	
<i>Fraxinus mandshurica</i>	.	1	.	1	.	.	1	1	1	1	.	1	1	.	1	2	.	2	2	1	
<i>Huperzia serrata</i>	.	3	3	4	4	.	3	3	.	1	.	.	.	3	5	1	.	.	2	.	2	2	3	
<i>Taxus cuspidata</i>	.	1	4	1	1	2	1	1	.	1	.	1	.	1	1	1	2	3	1	2	.	1	
<i>Viola selkirkii</i>	.	2	5	2	2	.	1	1	.	1	.	.	1	3	5	2	.	1	5	2	4	4	2	3	2	
Species common in northern continental and the whole island part of <i>Picea jezoensis</i> range																																					
<i>Anemonoides debilis</i>	1	1	2	2	1	.	1	1	2	.	2	1	3	2	.	1	.	1	3	.	
<i>Ledum palustre</i>	2	1	1	.	3	3	1	1	3	1	2	3	2	1	1	.	1	2	.
Companions																																					
<i>Oxalis acetosella</i>	1	3	5	2	5	4	3	3	4	3	2	.	4	1	5	5	5	3	.	3	5	4	4	5	4	2	4	2	1	.	4	1	.	1	1		
<i>Dicranum sp.</i>	.	1	.	1	1	3	3	1	4	5	3	2	2	3	.	1	.	2	1	.	1	.	1	.	2	2	.	1	4	5	5	1	5	5	5	4	
<i>Pleuroziopsis ruthenica</i>	.	1	.	1	1	1	2	.	1	1	2	3	1	2	3	2	.	1	.	2	.	2	1	1
<i>Phegopteris connectilis</i>	.	1	3	2	2	2	2	2	.	.	.	1	2	4	5	3	.	2	4	3	3	1	3	2	.	1	1	2	.	2	3	2	2	2	.	.	
<i>Rhyidiadelphus triquetrus</i>	.	1	.	.	3	2	1	.	2	3	3	4	1	.	1	4	2	.	.	2	3	4	2	2	.	.	2	3	1
<i>Alnus hirsuta</i>	1	1	.	1	.	1	.	1	.	1	.	2	1	2	1	.	2	1	1	.	.	1	1	1	3	.	1	3	1	1	1	.	
<i>Clintonia udensis</i>	.	1	3	1	.	1	2	1	.	1	.	.	.	4	3	2	.	4	3	2	1	2	2	4	1	1	
<i>Leptorumohra amurensis</i>	1	1	.	.	3	2	1	.	1	.	1	.	2	5	5	3	.	1	4	2	4	2	4	3	.	1	2	1	2	1		
<i>Rubus sachalinensis</i>	1	1	.	1	.	2	1	.	1	.	1	.	4	1	.	.	1	.	4	1	1	1	.	2	3	.	3	2	.	.	.	
<i>Listera cordata</i>	.	1	.	.	.	1	1	.	1	2	3	.	3	1	1	3	3	1	2	1	1	2	.	.
<i>Hydrangea paniculata</i>	1	2	3	1	2	.	1	.	2
<i>Cardamine leucantha</i>	.	1	3	1	2	.	1	1	1	2	2	.	1	
<i>Acer mono</i>	.	2	3	1	1	.	.	1	.	2	.	1	1	3	4	1	
<i>Ulmus laciniata</i>	.	1	4	2	1	1	1	3	2	
<i>Adoxa moschatellina</i>	.	1	4	1	1	1	1	2	4	.	2	1	1	.	2	1	1	
<i>Monotropa hypopitys</i>	1	1	3	.	.	1
<i>Valeriana fauriei</i>	1	1	.	.	.	3	4	2	2	2	1	.	2	1	

2. *Piceo-Abietetum sachalinensis* (Electronic appendix, Table 3)

Nomenclatural type: NAKAMURA (1988): relevé 50 in Table 84, Hokkaido

Distribution and ecology: This association is distributed in the oroboreal belt in temperate and southern boreal zone in the suboceanic sector on Hokkaido, the southern Kurils and southernmost Sakhalin.

Physiognomy: *Abies sachalinensis* is a constant component of the tree layer, which, in contrast to *Abies nephrolepis*, can form self-regenerating monodominant stands, even without spruce in the southern portion of the range of the association. The tree layer may be differentiated into two strata containing trees of the same species but of different age or performance. Across the range of this association single individuals of *Sorbus commixta* can be present in the canopy, and individuals of *Acer ukurunduense* usually occur in the subcanopy layer. At high elevations *Betula ermanii* can be abundant in the canopy. In the southern part of its range, on southernmost Sakhalin, Kunashir and Hokkaido, single individuals of temperate deciduous trees such as *Kalopanax septemlobus*, *Fraxinus mandshurica*, and *Tilia japonica* are present in the canopy. These forests are characterized by many species which are endemic to Japan and Sakhalin. These include the shrubs *Hydrangea*

paniculata, *Euonymus miniata*, *Viburnum furcatum*, and *Vaccinium smallii*, subshrubs *Ilex rugosa*, *I. sugerokii*, *Skimmia repens*, and *Vaccinium praestans*, and the herbs *Aralia cordata*, *Petasites amplus*, and *Lysichiton camtschatcense*. In the southern half of Sakhalin, in the southern Kurils and on Hokkaido, the small bamboos *Sasa kurilensis* and *S. senanensis* dominate the subshrub-herb layer of the fir-spruce forests. The bryophyte layer is poorly developed.

Lower syntaxa: According to soils and microclimate the association is divided into three variants. The typical variant represents species-poor forests of a very simple structure. The soil moisture regime ranges from fresh to moist and the soil is medium nutrient-rich. The *Rhododendron albrechtii* variant occurs on very moist and moist nutrient-poor sites in the lower part of the dark-coniferous belt within the temperate zone. The *Sasa senanensis* variant occurs on rich and slightly dry soils on gentle slopes. Warmer sites (southerly slopes at lower altitudes) are represented by the *Tilia japonica* subvariant, cooler sites (northerly slopes at higher altitudes) by the *Prunus ssiorii* subvariant.

3. *Asaro heterotropoidis-Abietetum sachalinensis* (Electronic appendix, Table 7)

Nomenclatural type: Append. 1, relevé SK_02

Distribution and ecology: This association occurs in the southern boreal zone in the suboceanic sector of the southern Kurils and southernmost Sakhalin. It is confined to fresh sites with medium soil nutrient regime on moderately steep slopes.

Physiognomy: This association is dominated by *Abies sachalinensis* and *Picea jezoensis* in roughly equal proportions. Subcanopy trees are represented by *Sorbus commixta* and *Acer ukurunduense*. Most species found in this association have wide boreal ranges and occur in different communities. The species characteristic for the Japanese flora include *Euonymus miniata*, *Vaccinium smallii*, the subshrubs *Ilex rugosa*, *Skimmia repens*, and *Vaccinium praestans*, the herbs *Asarum heterotropoides* and *Petasites amplus* and the bamboos *Sasa kurilensis* and *S. senanensis*. The bryophyte layer is moderately to well developed.

4. *Weigelo middendorffianae-Piceetum jezoensis* (Electronic appendix, Table 8)

Nomenclatural type: Append. 1, relevé SK_55

Distribution and ecology: This association occurs in the boreal zone in suboceanic sectors on northern Sakhalin and the oroboreal belt in the maritime sector of the mainland temperate and southern boreal zones. It is found in cold and moist sites in the upper part of the oroboreal belt on Sakhalin and on the highest tops of the Sikhote-Alin mountain system. These localities are characterized by a distinct snow accumulation in winter and late snow melting in summer.

Physiognomy: The canopy is formed by *Picea jezoensis* with admixed *Betula ermanii*. *Abies nephrolepis* is present occasionally in the Sikhote-Alin and *Abies sachalinensis* on Sakhalin. The subcanopy trees are *Acer ukurunduense*, *Sorbus commixta*, and *S. amurensis*. The shrub layer is well developed and represented by *Weigela middendorffiana*, *Rosa acicularis*, *Ribes horridum*, and *R. sachalinense* (only in Sakhalin). The herb layer is well developed and consists of many true boreal species, such as *Cornus canadensis*, *Maianthemum bifolium*, *M. dilatatum*, and *Ephippianthus sachalinensis*. At the same time it

expresses the excessively humid habitat due to high precipitation and late snow melting. The group of hygromesophytes includes *Veratrum albiflorum*, *Aconitum umbrosum*, and *Calamagrostis purpurea*. The bryophyte layer is well developed and formed by *Hylocomium splendens* and *Pleurozium schreberi*.

Remark: This association needs further study. It is possible that in future a group of microthermal species, such as *Rubus pedatus* and *Nephroma arctica*, may be added to the diagnostic species.

5. *Piceetum glehnii* (Electronic appendix, Table 9)

Nomenclatural type: NAKAMURA (1988): relevé 14 in Table 84, Hokkaido

Distribution and ecology: This association is distributed in lowlands and on newly formed substrates (tephra, alluvial or diluvial deposits, lava flows, lahars) in the suboceanic sector of the oroboreal belt and southern boreal zone. It occurs on the islands of Hokkaido, Iturup and Kunashir, where it forms monodominant communities in different habitats such as mires, sand dunes, volcanic rocks, ultrabasic rocks, around solfataras and near the timberline.

Physiognomy: This association includes communities dominated by *Picea glehnii* (cover 40–60%), *Picea jezoensis* (up to 10%), and *Abies sachalinensis* (10–40%) with a well developed shrub layer of *Vaccinium ovalifolium*, *V. smallii*, and *Sasa kurilensis*, a poorly developed herb layer with *Vaccinium praestans*, *Lycopodium obscurum*, *Cornus canadensis*, and *Oxalis acetosella*, and a poorly developed bryophyte layer with prevalence of *Pleurozium schreberi*. Lowland habitats are characterized by species of the temperate zone such as *Fraxinus lanuginosum*, *Carex blepharicarpa*, *Hydrangea paniculata*, *Magnolia kobus* var. *borealis*, *Sasa chartacea*, *Sorbus alnifolia*, *Ilex sugerokii*, *Lonicera alpigena*, and *Viola hultenii*. Moreover, species of the *Vaccinio-Piceetea* dark-coniferous forests (*Cornus canadensis*, *Oxalis acetosella*, *Pleurozium schreberi*, *Hylocomium splendens*) are also very constant and abundant, as well as a number of species with suboceanic distribution (*Vaccinium praestans*, *V. smallii*, *Ilex rugosa*, and *Menziesia pentandra*).

Lower syntaxa: Two subassociations were distinguished. The *Piceetum glehnii sasetosum kurilensis* subass. nov. hoc loco (nomenclature type: Append. 1, relevé IT_05) occurs in the northern part of the association range on Iturup, Kunashir, and in southernmost Sakhalin, mostly on mesic sites of well-drained gentle slopes. The *Piceetum glehnii rhododendretosum brachycarpi* (nomenclature type: identical with the type of the association) is distributed exclusively on Hokkaido, mainly above 1000 m a.s.l. on convex gentle slopes of inclination 3–20°. The soils are shallow and much drier than in *Piceetum glehnii sasetosum kurilensis*. The tree layer is dominated by *Picea glehnii* with an occasional admixture of *Abies sachalinensis*, often in the understory. The shrub layer is poorly or well developed, and includes *Rhododendron brachycarpum*, *Vaccinium inokumai*, *V. ovalifolium*, and *Acanthopanax sciadophylloides*. The herb layer is poorly developed, and includes indicators of drier sites, such as *Orthilia secunda* and *Vaccinium vitis-idaea*. Common species are *Arachniodes mutica*, *Streptopus streptopoides*, *Maianthemum dilatatum*, and *Coptis trifolia*. The moss layer is well developed and composed of *Pogonatum japonicum*, *Dicranum scoparium*, *Rhytidiadelphus triquetrus*, *Hylocomium splendens*, and *Pleurozium*

schreberi. The driest communities were considered as the variant of *Ilex sugerokii*, which is also characterized by *Diphasiastrum complanatum* and *Scapania* sp.

6. *Lysichito camtschaticense-Piceetum glehnii* (Electronic appendix, Table 10)

Nomenclatural type: Append. 1, relevé SK_38

Distribution and ecology: The association occurs in lowlands in the suboceanic sector of the southern boreal zone on Hokkaido, Iturup and southern Sakhalin, in cold and very wet sites.

Physiognomy: The tree layer is dominated by *Picea glehnii* with an occasional admixture of *Abies sachalinensis*, often in the understory. The shrub layer is moderately well developed and includes *Vaccinium smallii*, *Ledum palustre*, *L. hypoleucum*, and *Chamaedaphne calyculata*. The herb layer is well developed with a prevalence of *Lysichiton camtschaticense*, frequent *Cornus canadensis*, *Lycopodium annotinum*, and *Oxalis acetosella*, and occurrence of the bog subshrubs *Andromeda polifolia* and *Oxycoccus palustris*. The cover of bryophytes is uneven and depends on the pattern of wetter and drier microsites. *Pleurozium schreberi*, *Hylocomium splendens*, and *Ptilium crista-castrensis* are common in drier microsites, and *Sphagnum augustinowiczii*, *S. squarrosum*, *S. fuscum*, *S. compactum*, and *Aulacomnium palustre* in wetter microsites.

Lower units: Four variants reflect different edaphic conditions. The typical variant occurs on poor to medium-rich, wet soils. The *Carex pseudololiacea* variant represents warmer, oligotrophic, moist to extremely moist sites. The *Carex middendorffii* variant represents colder, oligotrophic, very moist and wet forest sites on organic soils, and the *Carex schmidtii* variant represents oligotrophic and cold sites on gleysols with a lower water table. The last two variants are transitional to treeless mires.

7. *Swida albae-Piceetum obovatae* (Electronic appendix, Table 11)

Nomenclatural type: Append. 1, relevé SE_22

Distribution and ecology: This is an azonal association of low elevations in continental and maritime sectors of the southern boreal zone, occurring on alluvial deposits in broad river valleys, with a local climate which is slightly warmer than the zonal climate in the northern part of the Sikhote-Alin as well as in the mountain systems of the Badzhal and the Tukuringra-Dzhagdy.

Physiognomy: The communities are dominated by *Picea obovata* and *P. jezoensis*. *Abies nephrolepis* is present in the subcanopy layer. The important feature of the association is the well developed layer of *Padus avium*. The shrub layer includes *Swida alba*, *Spiraea salicifolia*, and *Sorbaria sorbifolia*. The herb and bryophyte layers include many true boreal species. Hygro-mesic features are expressed by the presence and high performance of *Aconitum arcuatum*, *Athyrium filix-femina*, and *Smilacina davurica*.

8. *Oplopanaco elati-Piceetum jezoensis* (Electronic appendix, Table 12)

Nomenclatural type: Append. 1, relevé SA_121

Distribution and ecology: The association occurs in the oroboreal and subalpine belts in the maritime sectors of the northern and middle temperate zone. It is found at altitudes

exceeding 800–900 m on the southern spurs of the Sikhote-Alin Mts., on the extreme southern limit of fir-spruce forests.

Physiognomy: The forest stands normally consist of at least two tree species, *Abies nephrolepis* and *Picea jezoensis*, which form a dense tree layer. The canopy may also contain single trees or groups of *Pinus koraiensis*, *Sorbus amurensis*, and *Betula ermanii*. *Oplopanax elatus* in the shrub layer is a characteristic feature of the association. *Syringa wolfii* may be occasionally present in the shrub layer. This association is much richer in species than any other *Picea jezoensis* association. Besides boreal species mentioned above, the association is characterized by species endemic to the Far Eastern sector of boreal zone, so-called Okhotian and Manchurian species. They include small herbs *Huperzia serrata* and *H. chinensis*, ferns *Leptorumohra amurensis* and *Pseudocystopteris spinulosa*, sedges *Carex callitrichos* and *C. xyphium*, forbs *Smilacina davurica*, *Saussurea subtriangulata*, and *Actaea erythrocarpa*, shrubs *Euonymus macroptera*, *Lonicera chrysantha*, and *Oplopanax elatus*, a subshrub *Chimaphila japonica*, and the low tree *Acer ukurunduense*. The bryophyte layer is well developed and formed by *Pleurozium schreberi*, *Hylocomium splendens*, *Pleuroziopsis ruthenica*, *Climacium dendroides*, and *Rhytidiadelphus triquetrus*.

Lower syntaxa: The association includes three variants. Variant *typicum* represents communities in the mesic, warmer sites on the moderately steep and gentle slopes. The variant of *Huperzia chinensis* represents communities in mesic colder sites. The variant of *Bergenia pacifica*, subvariant *typicum* represents communities on rocky slopes with uneven regime of moisture, while subvariant *Cassiope redowskii* occurs at timberline on rocky sites.

9. *Philadelpho tenuifolii-Piceetum jezoensis* (Electronic appendix, Table 13)

Nomenclatural type: Append. 1, relevé SA_79

Distribution and ecology: The association is confined to the oroboreal belt in the maritime sector of the northern temperate zone and southern boreal zone, with subarctic cold boreal climate typical of the boreo-nemoral ecotone of mainland northeastern Asia. It occurs on slopes and well-drained flat sites in the central and northern Sikhote-Alin and on the southern spurs of the Badzhal and the Tukuringra-Dzhagdy mountain systems.

Physiognomy: The communities are dominated by *Picea jezoensis* and *Abies nephrolepis*. In addition to conifers, a number of broadleaved species, such as *Acer mono*, *Betula costata*, *Fraxinus mandshurica*, *Pinus koraiensis*, and *Tilia amurensis*, are characteristic for this association. Normally the tree layer is not or only poorly differentiated in strata, but if differentiated, the second stratum contains the same species as the canopy, with a greater proportion of *Abies nephrolepis*. The shrub layer is poorly to moderately developed, but it may contain a number of shrubs of temperate origin. It includes sparse individuals of *Rosa acicularis*, *Actinidia kolomikta*, *Lonicera maximowiczii*, *Ribes pallidiflorum*, *Philadelphus tenuifolius*, and *Eleutherococcus senticosus*. The herb layer includes small taiga herbs, such as *Maianthemum bifolium* and *Oxalis acetosella*, and species common to the valley-bottom forests (e.g. *Aconitum fischeri*, *Athyrium sinense*, and *Cacalia hastata*). The moss layer is well developed, including *Hylocomium splendens* and *Pleurozium schreberi*. Both the herb and moss layers vary greatly in structure and composition from place to place.

Lower syntaxa: We distinguished two subassociations. The *Philadelpho tenuifolii-Piceetum jezoensis typicum* subass. nov. hoc loco (nomenclature type: identical with the type of the association) represents wetter and richer sites on gentle slopes and in river valleys. It includes three variants: the variant of *Anemonoides udensis* occurs on gentle slopes, the variant of *Carex sordida* in moist and nutrient-rich sites on poorly drained river terraces and gentle slopes, and the variant of *Corydalis gigantea* in cold, narrow valleys of small streams. The *Philadelpho tenuifolii-Piceetum jezoensis coryletosum mandshuricae* subass. nov. hoc loco (nomenclature type: Append. 1, relevé SA_106) occurs in the southern part of the range of the association. It is characterized by temperate species, such as *Corylus mandshurica*, *Euonymus pauciflora*, *Phryma asiatica*, *Prunus maximowiczii*, and *Schisandra chinensis*. All these species are constantly present but are not important components of community structure, which is otherwise more typical of boreal forests. We delimited three variants in this subassociation: the typical variant is characteristic of gentle slopes and well-drained river valleys, the variant of *Acer barbinerve* represents warm, moderately nutrient-rich, mesic sites at the southern limit of the association range, and the variant of *Lonicera praeflorens* is found in colder sites with fresh and rich soils.

Remark: The current position of this association in *Vaccinio-Piceetea* is preliminary because of the temperate diagnostic species. The final syntaxonomical decision may be accepted only after a comprehensive phytosociological analysis of the class *Quercetea mongolicae* SONG 1988 in the Russian Far East.

10. *Lathyrus humilis-Picea jezoensis* community (Electronic appendix, Table 14)

Distribution and ecology: This community is found in the oroboreal belt in the maritime sector of the northern temperate zone and southern boreal zone. It occurs on gentle to steep (20–40°) southerly slopes and ridges in the central and northern Sikhote-Alin in the edaphic conditions marginal for spruce forests because of the dry period in summer.

Physiognomy: The tree layer is dominated by *Picea jezoensis* and *Abies nephrolepis* with the occasional admixture of *Pinus koraiensis*. The sparse shrub layer is formed by *Spiraea betulifolia*, *Ribes maximoviczianum*, and *Euonymus macroptera*. The herb layer is represented by *Polypodium sibiricum*, *Lathyrus humilis*, and *Vicia venosa*. The bryophytes are present with a high constancy but never have high cover.

Lower syntaxa: The community includes two variants, representing warmer (*Hemerocallis middendorffii*) and colder (*Abelia coreana*) habitats.

Remark: The syntaxonomical status of this community may be clarified after a comprehensive phytosociological study of temperate forests with broadleaved trees and *Pinus koraiensis* of the *Quercetea mongolicae*. Due to a high proportion of temperate species, this community could possibly be related to that temperate class.

11. *Vaccinio vitis-idaeae-Piceetum jezoensis* (Electronic appendix, Table 15)

Nomenclatural type: Append. 1, relevé SA_04

Distribution and ecology: This association, confined to the middle subzone of boreal zone, represents the central, most typical type of the *Picea jezoensis* forests in the Far East. The distribution range covers an area with subarctic true boreal climate in the coastal area

of the Sea of Okhotsk, the inland Far East, and Okhotian Island area: Shantar Archipelago and northern half of Sakhalin Island north of Schmidt's line.

Physiognomy: Canopy and subordinated layers have a simple structure and low species richness, being often represented by a one-layer canopy, dominated by *Picea jezoensis*. The shrub and herb layers may vary widely in structure but boreal species predominate, e.g. *Vaccinium vitis-idaea*, *Spiraea betulifolia*, *Rosa acicularis*, *Calamagrostis purpurea*, *Cornus canadensis*, and *Linnaea borealis*. The bryophyte layer is well developed in wet to mesic habitats, with a prevalence of *Hylocomium splendens*, *Pleurozium schreberi*, *Rhytidiadelphus triquetrus*, *Ptilium crista-castrensis*, and *Sphagnum girgensohnii*.

Lower syntaxa: Two subassociations were delimited. The *Vaccinio vitis-idaeae-Piceetum jezoensis typicum* subass. nov. hoc loco (nomenclature type: identical with the type of association) represents mesothermal vegetation occurring in the interior regions of the Far East, stretching from the northern to the southern limits of the range of the association, mostly on fresh to moist, nutrient-poor to medium-rich soils on well-drained mountain slopes and terraces. Characteristic features of these communities are the well developed tree layer of *Picea jezoensis* with *Abies* species only occasionally present or lacking altogether, the poorly developed shrub layer and the herb and bryophyte layers including species common to the Far East sector of the boreal zone, e.g. *Linnaea borealis*, *Maianthemum bifolium*, *Cornus canadensis*, *Calamagrostis purpurea*, *Pleurozium schreberi*, *Hylocomium splendens*, and *Ptilium crista-castrensis*.

The *Vaccinio-Piceetum jezoensis coptidetosum trifoliae* subass. nov. hoc loco (nomenclature type: Append. 1, relevé SK_09) represents microthermal moist and mesic vegetation at higher elevations of the inland Far East and at low to medium elevations of the coastal regions. The tree layer is composed of pure *Picea jezoensis* or mixed *Picea jezoensis* and *Abies sachalinensis* and/or *A. nephrolepis*. The shrub layer is poorly to moderately developed from *Rosa acicularis*, *R. amblyotis*, and *Spiraea beauverdiana*. The herb and bryophyte layers are well developed and vary in structure and species composition with edaphic conditions. We propose two variants in this subassociation. Variant *typicum* represents the central part of the subassociation's edaphic range, occurring in microthermal, moist and mesic, nutrient-poor sites, mainly on Sakhalin and Shantar islands. The variant of *Betula middendorffii* represents moderately to poorly drained, moist to very moist, very cold, and nutrient-poor sites. Subvariant *typicum* occurs in moderately drained sites with the water table never reaching the ground surface. Waterlogged sites are represented by the subvariant of *Oxycoccus palustris*, which is characterized by oligotrophic mire species such as *Carex middendorffii*, *Oxycoccus palustris*, *Parnassia palustris*, *Rubus chamaemorus*, and *Vaccinium uliginosum*.

12. *Rhododendro aurei-Piceetum jezoensis* (Electronic appendix, Table 16)

Nomenclatural type: Append. 1, relevé SE_05

Distribution and ecology: This association occurs in the subalpine belt in middle and southern subzones of boreal zone, being found in moist sites near the timberline or near the contact of *Picea jezoensis* and *Betula ermanii* forests, throughout nearly the entire range of *Picea jezoensis* forests.

Physiognomy: The mixed tree layer includes *Picea jezoensis* and *Betula ermanii* in different proportions. The shrub layer is well developed and formed by subalpine species, such as *Rhododendron aureum*, *Pinus pumila*, and *Alnus fruticosa*. The herb and dwarf shrub layers are also well developed, and always contain subalpine species. Characteristic species include *Phyllodoce caerulea*, *Diphasiastrum alpinum*, *Rhododendron aureum*, *Aegopodium alpestre*, *Polytrichum alpinum*, *Streptopus streptopoides*, and *Veratrum oxysepalum*.

13. *Moneseto uniflorae-Piceetum jezoensis* (Electronic appendix, Table 17)

Nomenclatural type: Append. 1, relevé KA_32

Distribution and ecology: This association occurs in the northern and middle subzones of boreal zone, in the extreme northeastern portion of the range of the Yezo spruce forests, in cold and very cold boreal maritime climate on Kamchatka peninsula with minor extension to the Sea of Okhotsk regions on northern Sakhalin.

Physiognomy: 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 sibirica* 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 taiga species, such as small herbs *Maianthemum bifolium*, *Cornus suecica*, *Oxalis acetosella*, *Linnaea borealis*, and *Goodyera repens*, ferns *Diplazium sibiricum*, *Dryopteris expansa*, *Gymnocarpium dryopteris*, and *Phegopteris connectilis*, forbs *Streptopus streptopoides*, *Solidago spiraeifolia*, and *Veratrum oxysepalum*, and 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 kamtschatica*. A characteristic feature is a high performance of meadow species, e.g. *Calamagrostis purpurea* and *Chamaenerion angustifolium*.

Lower units: Three variants were delimited. The typical variant represents vegetation of nutrient-poor fresh soils in the interior part of *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 spruce-dominated tree layer. 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 kamtschatica* occurs near the higher limits of the spruce forest zone, around the

late-melting snow beds. The dwarf tree *Alnus kamtschatica* 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*, have a higher performance than in the above described variants.

ORDINATION

Ordination of associations along the first two DCA axes (Fig. 2) showed a strong gradient of the first axis from the maritime-suboceanic oroboreal and true boreal (left) to continental oroboreal (right) spruce forests. The second axis was highly correlated with temperature showing the gradient from microthermal spruce forests of Kamchatka and Okhotsk area (top) to the mixed warm communities of Hokkaido (bottom). The ordination showed clear differences between the insular and mainland communities in the southern part of *Picea jezoensis* range.

DISCUSSION

Previous classification schemes of the *Picea jezoensis* forests (MIYAWAKI et al. 1968, SONG 1992) were developed in the peripheral southern part of their range. Before the current study it was unclear whether these schemes would also be applicable to the whole range and whether new higher units are needed.

Picea jezoensis forests in northeastern Asia vary along climatic gradients. In the 20th century their classification was approached from different viewpoints, mainly by phytogeographers and forest ecologists of Russia and Japan. Coarse vegetation units of these forests were delineated in the vegetation maps of the Soviet Union (LAVRENKO 1947, ALEKHIN 1951, LAVRENKO & SOCHAVA 1954) and the Russian Far East (SOCHAVA 1969). KOLESNIKOV (1961) suggested a scheme for Far Eastern vegetation regionalization using criteria of climatic climax potential vegetation. According to this scheme, the spruce forests of the Russian Far East were related to the southern Okhotsk dark-coniferous taiga area, based on the dominance of *Picea jezoensis* in zonal habitats. The climatic differences within the range of spruce forests led to the division of this area into the Amur-Sikhote-Alin province with continental to subarctic climate and the Sakhalin province including islands and mainland regions with maritime climate. The *Picea jezoensis* forests of Kamchatka were considered as a part of Northern Pacific broadleaved forest-meadow area, with a climate close to that of the subarctic mainland, despite their location in a zone of cold suboceanic climate. The major division criterion in this scheme was climatic continentality.

Until now the most comprehensive study of Far Eastern spruce forests was done by MAN'KO (1967, 1987), who used an approach based on dominance and differentiated these forests into four subformations: pure spruce, spruce with fir, fir with spruce and pure fir. Within each subformation a number of climatic variants (geographical facies according to MAN'KO 1987) were distinguished. The main criteria were the physiognomic and floristic features related to climate. In classifying forests into subformations, MAN'KO (1987) emphasized latitudinal subzones, while the climatic variants reflected the continentality sectors.

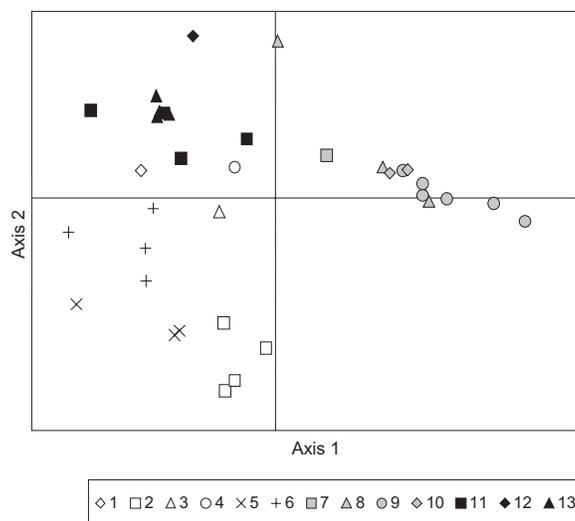


Fig. 2. DCA ordination of vegetation units of *Picea jezoensis* forests based on average values of species cover in the constancy table. Numeration of associations and communities corresponds with that used in the text. Open symbols and crosses correspond to the *Piceion jezoensis*, grey symbols to the *Abieti nephrolepidis-Piceion jezoensis*, and black symbols to the *Pino pumilae-Piceion jezoensis*.

In the insular part of the range of *Picea jezoensis* the boundary line between boreal and temperate zones corresponds to Schmidt's Line that crosses central Sakhalin as a floristic boundary line between the Euro-Siberian and Sino-Japanese floristic regions (TATEWAKI 1958). The low-elevation forests of Hokkaido are composed of *Abies sachalinensis*, *Picea jezoensis*, and *Quercus crispula*. As the species composition of those forests is rich in temperate floristic elements and the canopy maintains a mixed structure under the current climate, TATEWAKI (1958) found an analogy with mixed forests (*Pinus koraiensis* and broadleaved species) of the

Asian mainland in the Russian Far East (Primor'e), northeastern China and northern Korea. He proposed the delineation of a mixed forest zone as a climatic analogue of the mixed forests in the Appalachians and Central Europe.

With rising elevation, the mixed broadleaved-conifer forests on Hokkaido shift into the spruce-fir forests, which are physiognomically similar to the zonal fir-spruce forests in the Okhotsk region. However, the application of different criteria to the phytogeographical regionalization of Hokkaido resulted in at least two different major concepts. Using a phytosociological approach, MIYAWAKI et al. (1978) expanded the *Piceion jezoensis* region to include zonal *Abies sachalinensis-Picea jezoensis* and *Picea glehnii-Pinus parviflora* var. *laevis* communities. In most of Hokkaido the region can be considered as oroboreal, however in the northern and western parts of the island this vegetation type also occurs at lower elevations. KOJIMA (1979, 1991), using the concept of biogeoclimatic zones developed in northwestern North America (KRAJINA 1965, POJAR et al. 1987), delineated the biogeoclimatic zone of *Abies sachalinensis*, which includes pure conifer forests at mid-elevations of Hokkaido, covering an altitudinal range approximately from 500 to 1500 m and never approaching the sea coast. The major argument for the narrower oroboreal zone in Hokkaido was the climatic similarity to the Sikhote-Alin and Okhotsk area (mean annual temperature -1 °C to +4 °C, mean annual precipitation 900 to 1500 mm). KOJIMA (1979) assigned the vegetation of this zone to the *Abietetalia sachalinensis*.

A comprehensive study of subalpine spruce-fir (*Abies nephrolepis* and *A. koreana*) forests in southern Korea was made by SONG (1991). On the basis of comparison of Japanese and Korean forests, SONG (1992) proposed two orders, restricting the *Abieti veitchii-Piceetalia jezoensis hondoensis* MIYAWAKI et al. 1968 to the Honshu and Shikoku Islands and introducing the new *Abieti nephrolepidis-Piceetalia jezoensis* for the mainland regions as well as for the Hokkaido and other northerly islands of Asia. At that time, however, SONG (1992) did not have access to the data from the major part of the range of *Picea jezoensis* in Russia.

In summary of this brief review of earlier phytogeographical concepts, we may state that the most important phytogeographical boundary within the range of *Picea jezoensis* is the boundary between boreal and temperate vegetation. It divides vegetation complexes at the class level: boreal *Vaccinio-Piceetea* vs. temperate *Fagetea crenatae* (insular regions) or *Quercetea mongolicae* (mainland regions). The influence of the temperate flora on the boreal vegetation in the insular and mainland regions gives the second important boundary within boreal zone. In the mainland the spruce forests contain species distributed mainly in mainland Asia, such as *Pinus koraiensis*, *Acer tegmentosum*, *Carex campylorhina*, *Betula costata*, *Pseudocystopteris spinulosa*, and *Thalictrum tuberiferum*. In the insular part, including Sakhalin, the southern Kurils, and Japan, the boreal coniferous forests are by contrast enriched by the Japanese temperate flora, e.g. *Hydrangea petiolaris*, *Ilex rugosa*, *Magnolia obovata*, *Sasa kurilensis*, *Vaccinium ovalifolium*, *V. praestans*, and *V. smallii*. The third important boundary divides the northern spruce forests, characterized by species with circumboreal distribution, from the rest of the spruce forests, characterized by temperate or southern boreal species. The boundary coincides with the northern limits of *Abies nephrolepis*, *A. sachalinensis*, *Leptorumohra amurensis*, *Acer ukurunduense*, *Rhytidiadelphus triquetrus*, *Huperzia serrata*, *Equisetum hyemale*, and many other species. The distribution of higher syntaxonomical units should correspond to these lines (Table 4).

Class and order level

All *Picea jezoensis* communities delineated in this study belong to the class *Vaccinio-Piceetea*, characterized by the species *Vaccinium vitis-idaea*, *Linnaea borealis*, *Orthilia secunda*, *Listera cordata*, *Goodyera repens*, *Phegopteris connectilis*, *Sphagnum girgensohnii*, *Hylocomium splendens*, *Pleurozium schreberi*, *Dicranum majus*, and *Rhytidiadelphus triquetrus*. This class represents zonal boreal vegetation in eastern Asia. To the south, it borders the *Quercetea mongolicae* on the mainland and *Fagetea crenatae* in the insular regions, and in the north, it is replaced by the *Betulo-Ranunculetea* in Kamchatka and the *Pinetea pumilae* (AKHTYAMOV 1999, preliminarily proposed) in the inland regions.

At the order level Yezo spruce forests are related to the *Abieti-Piceetalia* MIYAWAKI et al. 1968. As mentioned by SONG (1992), there have been some disagreements among Japanese authors (MIYAWAKI et al. 1968, OHBA 1983, NAKAMURA 1988) in the selection of diagnostic species for this order. However, the most recent list of diagnostic species by NAKAMURA (1988) describes well the coniferous forests on both the islands and the mainland. The most important diagnostic species for the order are *Betula ermanii*, *Cornus canadensis*, *Maianthemum dilatatum*, and *Picea jezoensis*. However, at a local level this

Table 4. Boreal and temperate vegetation zones and their continentality sectors in northeastern Asia. Upper rows within each zone show the dominant type, and lower rows show the corresponding syntaxa for each zone-sector combination. Shaded blocks are zonal *Picea jezoensis* forests and framed non-shaded blocks are *Picea jezoensis* forests in oroboreal and subalpine belts.

Continental	Continentality sectors		
	Submaritime	Maritime	Oceanic
Dwarf-shrubs zone			
	<i>Pinus pumila</i> <i>Pinetea pumilae</i>	<i>Alnus fruticosa</i> <i>Pinetea pumilae</i>	<i>Alnus fruticosa</i> <i>Pinetea pumilae</i>
Northern boreal zone			
<i>Larix dahurica</i> <i>Pinus pumila</i> <i>Piceetalia excelsae</i> / <i>Abieti-Piceetalia</i> (?)	<i>Larix dahurica</i> <i>Pinus pumila</i>	<i>Picea jezoensis</i> <i>Pino pumilae-</i> <i>-Piceion jezoensis</i>	<i>Betula ermanii</i> <i>Betulo-Ranunculetea</i>
Southern boreal zone			
<i>Larix dahurica</i> <i>Piceetalia excelsae</i> / <i>Abieti-Piceetalia</i> (?)	<i>Larix dahurica</i>	<i>Picea jezoensis</i> <i>Abies nephrolepis</i> <i>Abieti nephrolepidis-</i> <i>-Piceion jezoensis</i>	<i>Picea jezoensis</i> <i>Abies sachalinensis</i> <i>Piceion jezoensis</i>
Northern temperate zone			
<i>Quercus mongolica</i> <i>Betula davurica</i> <i>Quercu mongolicae-</i> <i>Betuletea davuricae</i>	<i>Quercus mongolica</i> , <i>Pinus koraiensis</i> , <i>Fraxinus</i> spp., <i>Tilia</i> spp., <i>Betula costata</i> <i>Quercetea mongolicae</i> with <i>Abieti-Piceion</i> in oroboreal belt		<i>Abies sachalinensis</i> <i>Quercus crispula</i> (s.str.) <i>Fagetea crenatae</i> with <i>Piceion jezoensis</i> in oroboreal belt
Southern temperate zone			
Desert / steppe ?	Evergreen broadleaved ?	Evergreen broadleaved with <i>Abietion</i> <i>koreanae</i> in subalpine belt	Evergreen broadleaved <i>Camellieta japonicae</i> with <i>Abietion mariesii</i> in subalpine belt

order can be also characterized by *Acer ukurunduense*, *Actinidia kolomikta*, *Euonymus macroptera*, *Taxus cuspidata*, and *Viola selkirkii*. Therefore we do not accept SONG's (1992) proposal of the new order *Abieti nephrolepidis-Piceetalia jezoensis* for the mainland Asia and northern islands (Sakhalin, Kurils and Hokkaido) as opposed to the *Abieti-Piceetalia* MIYAWAKI et al. 1968 in the subalpine belt of Honshu.

Another classification scheme for the Far Eastern *Picea jezoensis* forests was proposed by PETELIN (1990), who assigned these forests to the order *Vaccinio-Piceetalia* BR.-BL. in BR.-BL. et al. 1939 (= *Piceetalia excelsae* PAWŁOWSKI et al. 1928). However, numerous studies in Japan (NAKAMURA 1988, KOJIMA 1991), Korea (SONG 1992) and Russia (KOROTKOV et al. 1991) have demonstrated a clear difference between Euro-Siberian and Far Eastern coniferous forests.

The order *Abieti-Piceetalia* occurs in submaritime, maritime and oceanic sectors of the eastern Asian boreal zone. In the west, it comes into contact with the *Piceetalia excelsae* in zonal habitats. However, it is difficult to recognize the exact western boundary of the order

due to the poorly developed syntaxonomy of *Larix dahurica* forests, which occupy extensive areas in subcontinental and continental sectors of boreal Asia.

Alliance level

Abieti-Piceetalia includes five alliances. Two of them, *Abietion mariesii* and *Abietion koreanae*, represent subalpine vegetation in the southern part of the range of *Picea jezoensis* on Honshu/Shikoku and in South Korea, respectively. Occurring in relatively narrow vertical belts and being isolated from the main coniferous forest area, they have a high proportion of warm temperate and cool temperate species, e.g. *Tsuga diversifolia*, *Chiogenes japonica*, and *Coptis quinquefolia* in Japan and *Angelica polymorpha*, *Pternopetalum tanakae*, and *Stephanandra incisa* in Korea. These two alliances are not treated in this paper.

Two other alliances, *Piceion jezoensis* and *Abieti nephrolepidis-Piceion jezoensis*, represent zonal vegetation in the southern boreal and oroboreal zones in insular and mainland parts of northeastern Asia, respectively. The differences between these alliances are in the influences of the Manchurian and Japanese temperate floras. The species composition of both alliances includes many boreal species characteristic of the class and order; however, there are also many temperate species, such as *Sasa kurilensis* and *Ilex rugosa* on the islands and *Pinus koraiensis*, *Acer tegmentosum*, and *Thalictrum tuberiferum* in mainland regions. The geographical differentiation of these alliances has been supported by many phytogeographical studies, which have revealed a strong contrast between island and mainland vegetation (TATEWAKI 1958, KOLESNIKOV 1961, MAN'KO 1987).

Although our knowledge of northern continental *Picea jezoensis* forests in the Russian Far East has been until recently insufficient for the development of higher-unit syntaxonomy, several proposals were made in a manuscript by PETELIN (1990). He suggested including all the continental Yezo spruce forests into the alliance *Betulo lanatae-Piceion ajanensis* PETELIN 1990 ms., characterized by *Picea jezoensis*, *Pinus pumila*, *Sorbus sibirica*, and *Betula ermanii*. The area of that study, however, was located at high elevations (800–1350 m) in the westernmost part of the range of *Picea jezoensis*, where the communities are affected by a subalpine flora, the two representatives of which, i.e., *Betula ermanii* and *Pinus pumila* were considered as diagnostic species.

Our data show that in the northern part of their range, the structure of spruce forests is much simpler, and species composition is much poorer than in the forests within the southern boreal subzone. Most communities are characterized by species commonly distributed in the circumboreal or Eurasian boreal zone, e.g., *Pleurozium schreberi*, *Hylocomium splendens*, *Ptilium crista-castrensis*, *Vaccinium vitis-idaea*, and *Maianthemum bifolium*. A distinct feature of the northern communities is the presence of species related to subarctic/subalpine vegetation, e.g. *Pinus pumila*, *Lonicera chamissoi*, *Sorbus sambucifolia*, *Equisetum sylvaticum*, and *Spiraea beauverdiana*. As these vegetation characteristics correlate with a very severe climate (Table 1), which has also been noted by phytogeographers (KOLESNIKOV 1961, MAN'KO 1987), we consider it appropriate to recognize a new alliance *Pino pumilae-Piceion jezoensis* (Appendix 2) representing the pure spruce forests occurring in the northern continental zone and also in central Kamchatka, northern Sakhalin and the Shantar Islands.

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APPENDIX

Appendix 1. Nomenclatural holotypes of newly described associations and subassociations

3. Asaro heterotropoidis-Abietetum sachalinensis ass. nov. (relevé SK_02)

Author: P. KRESTOV; 15 August 1999; plot size: 400 m²; Central Sakhalin, near the town Pobedino, 49.761° N, 142.704° E, altitude 120 m; flat land; cover tree layer 60%, shrub layer 15%, herb layer 24%, moss layer: +.

Tree layer I: 5: *Abies sachalinensis*; 2: *Betula ermanii*, +: *Picea jezoensis*; **tree layer II:** 1: *Abies sachalinensis*; **tree layer III:** 2: *Taxus cuspidata*; 1: *Abies sachalinensis*.

Shrub layer I: 1: *Euonymus macroptera*; **shrub layer II:** +: *Euonymus macroptera*, *Vaccinium smallii*, *Viburnum furcatum*.

Herb layer: 3: *Dryopteris expansa*; 2: *Carex falcata*; 1: *Asarum heterotropoides*, *Cornus canadensis*, *Maianthemum dilatatum*, *Ilex rugosa*, *Oxalis acetosella*, *Leptorumohra amurensis*, *Cacalia auriculata*; +: *Calamagrostis purpurea*, *Lycopodium clavatum*, *Trillium camschatcense*, *Anemonoides umbrosa*, *Luzula rufescens*, *Solidago decurrens*.

Moss layer: 2: *Dicranum* sp., 1: *Pleurozium schreberi*.

4. Weigelo middendorffianae-Piceetum jezoensis ass. nov. (relevé SK_55)

Author: P. KRESTOV; 17 August 1999; plot size: 400 m²; Central Sakhalin, Mt. Lopatina, 50.843° N, 143.103° E, alt. 1470 m; slope 25° NE; cover tree layer 80%, shrub layer 3%, herb layer 20%, moss layer 30%.

Tree layer I: 3: *Picea jezoensis*, *Abies sachalinensis*; 1: *Betula ermanii*; **tree layer II:** +: *Sorbus commixta*, *Abies sachalinensis*; **tree layer III:** +: *Acer ukurunduense*.

Shrub layer I: +: *Weigela middendorffiana*; **shrub layer II:** 2: *Vaccinium ovalifolium*; 1: *Spiraea beauverdiana*.

Herb layer: 1: *Cornus canadensis*; +: *Gymnocarpium dryopteris*, *Linnaea borealis*, *Lycopodium annotinum*, *Trientalis europaea*, *Maianthemum dilatatum*, *Ilex rugosa*, *Vaccinium praestans*, *Calamagrostis purpurea*, *Oxalis acetosella*, *Lycopodium clavatum*, *Anemonoides debilis*.

Moss layer: 2: *Hylocomium splendens*, *Pleurozium schreberi*; +: *Ptilium crista-castrensis*, *Sphagnum girgensohnii*, *Dicranum* sp., *Peltigera aphthosa*, *Rhytidiadelphus triquetrus*.

5a. Piceetum glehnii sasetosum kurilensis subass. nov. (relevé IT_05)

Author: V.A. SHAFRANOVSKI; 12 July 1985; plot size: 900 m²; Kunashir Isl., Mt. Mendeleeva, 43.970° N, 145.748° E, alt. 280 m; slope 30° NW; cover tree layer 90%, shrub layer 30%, herb layer 40%, moss layer 20%.

Tree layer I: 5: *Picea glehnii*; +: *Abies sachalinensis*; **tree layer II:** +: *Sorbus commixta*, *Picea glehnii*, *Abies sachalinensis*.

Shrub layer I: 2: *Vaccinium ovalifolium*; +: *Sorbus commixta*; **shrub layer II:** 4: *Menziesia pentandra*; 2: *Vaccinium smallii*; 1: *Sasa kurilensis*; +: *Picea glehnii*, *Abies sachalinensis*.

Herb layer: 3: *Cornus canadensis*, *Vaccinium vitis-idaea*; 2: *Vaccinium praestans*; 1: *Ilex rugosa*; +: *Maianthemum bifolium*, *Oxalis acetosella*, *Lycopodium obscurum*, *Calamagrostis sachalinensis*.

Moss layer: 2: *Pogonatum japonicum*, *Pleurozium schreberi*.

6. Lysichito camtschatcense-Piceetum glehnii (relevé SK_38)

Author: P. Krestov; 12 July 2000; plot size: 400 m²; Southern Sakhalin, Aniva Bay, 46.640° N, 142.904° E, alt. 30 m; flat land; cover tree layer 40%, shrub layer 10%, herb layer cover 40%, moss layer 50%.

Tree layer I: 2: *Picea glehnii*, *Larix dahurica*; 1: *Abies sachalinensis*; **tree layer II:** 1: *Abies sachalinensis*.

Shrub layer I: +: *Vaccinium ovalifolium*; **shrub layer II:** 4: *Ledum palustre*.

Herb layer: 1: *Osmundastrum asiaticum*, *Vaccinium vitis-idaea*; +: *Lysichiton camtschatcense*, *Cornus canadensis*, *Maianthemum dilatatum*, *Coptis trifolia*.

Moss layer: 2: *Sphagnum palustre*; 1: *Pleurozium schreberi*; +: *Ptilium crista-castrensis*, *Dicranum* sp., *Aulacomnium palustre*, *Sphagnum* sp.

7. Swida albae-Piceetum obovatae ass. nov. (relevé SE_22)

Author: YU. I. MAN'KO; 18 July 1972; plot size: 400 m²; Selemdzha basin, upper part, 52.958° N, 132.795° E; alt. 190 m; flat land; cover tree layer 95%, shrub layer +, herb layer 3%, moss layer 85%.

Tree layer I: 3: *Picea jezoensis*, *Abies nephrolepis*, *Larix dahurica*; 2: *Picea obovata*; **tree layer II:** +: *Sorbus amurensis*, *Abies nephrolepis*; **tree layer III:** 1: *Padus avium*, +: *Acer ukurunduense*, *Alnus hirsuta*.

Shrub layer I: 1: *Swida alba*, +: *Abies nephrolepis*, *Picea jezoensis*; **shrub layer II:** 1: *Rosa acicularis*, *Lonicera caerulea*; +: *Abies nephrolepis*, *Picea jezoensis*.

Herb layer: 3: *Oxalis acetosella*; 2: *Linnaea borealis*, *Maianthemum bifolium*, *Mitella nuda*, *Smilacina davurica*; 1: *Gymnocarpium dryopteris*, *Trigonotis radicans*, *Calamagrostis purpurea*, *Atragene ochotensis*, *Pyrola incarnata*, *Circaea alpina*, *Equisetum pratense*, *Listera cordata*, *Aruncus dioicus*, *Carex falcata*, *Paris hexaphylla*, *Galium boreale*, *Ribes pallidiflorum*, *Saussurea triangulata*, *Aegopodium alpestre*; +: *Aconitum arcuatum*, *Trientalis europaea*, *Athyrium filix-femina*, *Diplazium sibiricum*, *Rubus arcticus*, *Schizachne callosa*, *Cacalia hastata*, *Rhizomatopteris sudetica*, *Filipendula palmata*, *Vaccinium vitis-idaea*.

Moss layer: 3: *Hylocomium splendens*; 2: *Rhytidiadelphus triquetrus*; +: *Ptilium crista-castrensis*.

8. Oplopanax elati-Piceetum jezoensis ass. nov. (relevé SA_121)

Author: V.P. VERKHOLAT; 3 August 1972; plot size: 400 m²; Southern Sikhote-Alin, Livadiiskii Mt., 43.121° N, 132.799° E, alt. 850 m; slope 20° N; cover tree layer 75%, shrub layer 1%, herb layer 50%, moss layer 90%.

Tree layer I: 3: *Picea jezoensis*; 2: *Betula ermanii*; 1: *Abies nephrolepis*, *Pinus koraiensis*; **tree layer II:** +: *Sorbus amurensis*, *Abies nephrolepis*, *Pinus koraiensis*; **tree layer III:** 1: *Acer ukurunduense*, *Abies nephrolepis*.

Shrub layer I: +: *Syringa wolfii*, *Picea jezoensis*, *Abies nephrolepis*, *Pinus koraiensis*; **shrub layer II:** 1: *Oplopanax elatus*; +: *Lonicera caerulea*, *Rosa acicularis*.

Herb layer: 2: *Linnaea borealis*, *Lycopodium annotinum*, *Cornus canadensis*, *Carex campylorhina*; 1: *Calamagrostis purpurea*, *Picea jezoensis*; +: *Leptorumohra amurensis*, *Carex xyphium*, *Solidago decurrens*, *Polypodium vulgare*, *Orthilia secunda*, *Pyrola renifolia*, *Lycopodium clavatum*, *Dryopteris expansa*, *Oxalis acetosella*.

Moss layer: 3: *Hylocomium splendens*, *Pleurozium schreberi*; 2: *Pleuroziopsis ruthenica*; +: *Polytrichum commune*, *Sphagnum girgensohnii*.

9. Philadelpho tenuifolii-Piceetum jezoensis ass. nov. (relevé SA_79)

Author: P. KRESTOV; 24 July 1994; plot size: 400 m²; Central Sikhote-Alin, near Dersu town, 45.783° N, 135.458° E, alt. 450 m; slope 15° SW; cover tree layer 80%, shrub layer 30%, herb layer 70%, moss layer 0%.

Tree layer I: 3: *Picea jezoensis*; 2: *Abies nephrolepis*; 1: *Betula costata*, *Fraxinus mandshurica*; **tree layer II:** 2: *Acer tegmentosum*; **tree layer III:** +: *Acer tegmentosum*.

Shrub layer I: 2: *Actinidia kolomikta*; +: *Sambucus racemosa*, *Picea jezoensis*, *Abies nephrolepis*; **shrub layer II:** 2: *Eleutherococcus senticosus*; 1: *Lonicera chrysantha*; +: *Philadelphus tenuifolius*, *Picea jezoensis*, *Abies nephrolepis*.

Herb layer: 2: *Carex campylorhina*, *Dryopteris expansa*; 1: *Athyrium sinense*, *Abies nephrolepis*, *Cacalia auriculata*, *Lunathyrium pycnosorum*, *Neomolinia mandshurica*, *Thalictrum tuberiferum*, *Viola selkirkii*; +: *Aconitum fischeri*, *Chrysosplenium pilosum*, *Cimicifuga simplex*, *Circaea alpina*, *Diplazium sibiricum*, *Filipendula palmata*, *Galium paradoxum*, *Huperzia serrata*, *Impatiens noli-tangere*, *Milium effusum*, *Mitella nuda*, *Oxalis acetosella*, *Phegopteris connectilis*, *Polypodium sibiricum*, *Rubia cordifolia*, *Saussurea subtriangulata*, *Stellaria bungeana*, *Tilingia ajanensis*, *Trigonotis radicans*, *Urtica angustifolia*.

9b. Philadelpho tenuifolii-Piceetum jezoensis coryletosum mandshuricae subass. nov. (relevé SA_106)

Author: V.P. VERKHOLAT; 3 August 1972; plot size: 400 m²; Southern Sikhote-Alin, Livadiiskii Mt., 43.138° N, 132.799° E, alt. 850 m; slope 5° E; cover tree layer 80%, shrub layer 40%, herb layer 80%, moss layer 2%.

Tree layer I: 4: *Picea jezoensis*; 3: *Abies nephrolepis*; 2: *Betula costata*; 1: *Pinus koraiensis*; +: *Tilia amurensis*, *Fraxinus mandshurica*; **tree layer II:** 1: *Prunus maximowiczii*, *Acer tegmentosum*, *Abies nephrolepis*; **tree layer III:** 2: *Acer ukurunduense*.

Shrub layer I: 2: *Actinidia kolomikta*; 1: *Acer barbinerve*, *Acer tegmentosum*; +: *Corylus mandshurica*, *Syringa wolfii*, *Pinus koraiensis*; **shrub layer II:** 1: *Philadelphus tenuifolius*, *Eleutherococcus senticosus*, *Euonymus macroptera*, *Lonicera chrysantha*; +: *Spiraea ussuriensis*, *Sorbaria sorbifolia*, *Fraxinus mandshurica*, *Ribes mandshuricum*, *Abies nephrolepis*.

Herb layer: 2: *Thalictrum tuberiferum*, *Leptorumohra amurensis*, *Diplazium sibiricum*; 1: *Cacalia auriculata*, *Lunathyrium pycnosorum*, *Maianthemum bifolium*, *Acer tegmentosum*, *Carex campylorhina*, *Trigonotis radicans*, *Mitella nuda*, *Circaea alpina*, *Dryopteris crassirhizoma*, *Athyrium sinense*, *Aconitum fischerii*, *Euonymus macroptera*, *Cacalia hastata*, *Cimicifuga simplex*, *Milium effusum*, *Aegopodium alpestre*, *Rubia cordifolia*, *Scutellaria ussuriensis*; +: *Paris hexaphylla*, *Phryma asiatica*, *Carex quadriflora*, *Lycopodium annotinum*, *Cornus canadensis*, *Pseudocystopteris spinulosa*, *Carex xyphium*, *Oxalis acetosella*, *Viola selkirkii*, *Waldsteinia ternata*, *Valeriana fauriei*, *Adoxa moschatellina*, *Galium paradoxum*, *Lycopodium obscurum*, *Impatiens noli-tangere*, *Lilium distichum*, *Filipendula glaberrima*, *Saussurea umbrosa*, *Rhizomatopteris sudetica*, *Galium kamschaticum*, *Hylomecon vernalis*, *Urtica angustifolia*, *Asarum sieboldii*, *Cinna latifolia*, *Lamium barbatum*, *Osmorhiza aristata*, *Abies nephrolepis*, *Betula costata*, *Acer tegmentosum*.

11. *Vaccinio vitis-idaeae-Piceetum jezoensis* ass. nov. (relevé SA_04)

Author: P. KRESTOV; 12 August 1994; plot size: 400 m²; Central Sikhote-Alin, Mt. Vysokaya, 45.981° N, 136.538° E, alt. 1490 m; slope 20° W; cover tree layer 90%, shrub layer 0.1%, herb layer 5%, moss layer 90%.

Tree layer I: 5: *Picea jezoensis*; 2: *Abies nephrolepis*, 1: *Betula ermanii*; **tree layer II:** +: *Sorbus amurensis*.

Shrub layer I: +: *Picea jezoensis*, *Abies nephrolepis*; **shrub layer II:** +: *Picea jezoensis*, *Abies nephrolepis*.

Herb layer: 3: *Vaccinium vitis-idaea*; 2: *Lycopodium annotinum*, *Cornus canadensis*, *Leptorumohra amurensis*, *Smilacina hirta*; 1: *Gymnocarpium dryopteris*; +: *Oxalis acetosella*, *Picea jezoensis*, *Abies nephrolepis*.

Moss layer: 3: *Pleurozium schreberi*; 2: *Hylacomium splendens*; +: *Cladina rangiferina*, *Ptilium crista-castrensis*.

11b. *Vaccinio vitis-idaeae-Piceetum jezoensis coptidetosum trifoliae* subass. nov. (relevé SK_09)

Author: P. KRESTOV; 8 August 1999; plot size: 400 m²; Northern Sakhalin, Schmidt peninsula, 54.138° N, 142.611° E, alt. 150 m; slope 5° S; cover tree layer 80%, shrub layer 5%, herb layer 20%, moss layer 5%.

Tree layer I: 3: *Larix dahurica*; 2: *Picea jezoensis*; **tree layer II:** 1: *Picea jezoensis*.

Shrub layer I: 1: *Betula middendorffii*, *Pinus pumila*; **shrub layer II:** 1: *Spiraea beauverdiana*, *Picea jezoensis*.

Herb layer: 2: *Vaccinium vitis-idaea*, *Coptis trifolia*, *Linnaea borealis*, *Cornus canadensis*, *Carex* sp.; 1: *Gymnocarpium dryopteris*, *Vaccinium praestans*, *Ledum palustre*; +: *Rubus chamaemorus*, *Calamagrostis purpurea*, *Anemonoides debilis*, *Picea jezoensis*.

Moss layer: 2: *Sphagnum girgensohnii*; 1: *Pleurozium schreberi*, *Dicranum* sp.

12. *Rhododendro aurei-Piceetum jezoensis* ass. nov. (relevé SE_05)

Author: Yu.I. MAN'KO; 5 July 1972; plot size: 400 m²; Selemdzha basin, upper part, 53.126° N, 133.273° E, alt. 300 m; slope 4° SW; cover tree layer 90%, shrub layer 1%, herb layer 30%, moss layer 40%.

Tree layer I: 5: *Picea jezoensis*; 2: *Betula ermanii*; **tree layer II:** +: *Sorbus amurensis*, *Picea jezoensis*.

Shrub layer I: 1: *Pinus pumila*; **shrub layer II:** 2: *Rhododendron aureum*, *Vaccinium myrtillus*; 1: *Spiraea beauverdiana*, *Picea jezoensis*; +: *Sorbus amurensis*.

Herb layer: 2: *Calamagrostis purpurea*, *Phyllodoce caerulea*, *Carex pallida*, *Trollius riederianus*; 1: *Streptopus streptopoides*, *Veratrum oxysepalum*, *Saxifraga punctata*, *Dryopteris expansa*, *Linnaea borealis*, *Lycopodium annotinum*, *Maianthemum bifolium*, *Cornus canadensis*, *Vaccinium vitis-idaea*, *Oxalis acetosella*, *Smilacina davurica*, *Saussurea neoserrata*, *Solidago decurrens*, *Aruncus dioicus*, *Gentiana nipponica*, *Coptis trifolia*; +: *Aegopodium alpestre*, *Viola kusnezowiana*, *Rubus arcticus*, *Cacalia hastata*, *Diphasiastrum alpinum*, *Picea jezoensis*.

Moss layer: 2: *Pleurozium schreberi*; 1: *Hylocomium splendens*, *Ptilium crista-castrensis*, *Sphagnum girgensohnii*; +: *Polytrichum alpinum*.

13. Moneseto uniflorae-Piceetum jezoensis ass. nov. (relevé KA_32)

Author: P. KRESTOV; 17 July 1996; plot size: 400 m²; Central Kamchatka, volcano Shiveluch, 56.620° N, 160.870° E, alt. 110 m; slope 10° W; cover tree layer 95%, shrub layer 10%, herb layer 40%, moss layer 85%.

Tree layer I: 3: *Larix dahurica*; 1: *Betula ermanii*, *Picea jezoensis*; **tree layer II:** 4: *Picea jezoensis*.

Shrub layer I: +: *Pinus pumila*, *Picea jezoensis*; **shrub layer II:** 1: *Lonicera caerulea*, *Lonicera chamissoi*, *Spiraea beauverdiana*; +: *Rubus sachalinensis*, +: *Juniperus sibirica*, *Vaccinium uliginosum*, *Picea jezoensis*.

Herb layer: 2: *Linnaea borealis*; 1: *Chamaenerion angustifolium*, *Maianthemum bifolium*, *Trientalis europaea*, *Rubus arcticus*; +: *Orthilia secunda*, *Moneses uniflora*, *Solidago spiraeifolia*, *Equisetum pratense*, *Pyrola incarnata*, *Geranium erianthum*, *Saussurea pseudotilesii*, *Dryopteris expansa*, *Goodyera repens*, *Gymnocarpium dryopteris*, *Lycopodium annotinum*, *Equisetum sylvaticum*, *Calamagrostis purpurea*, *Atragene ochotensis*, *Diphasiastrum complanatum*, *Carex pallida*, *Galium kamschaticum*.

Moss layer: 5: *Pleurozium schreberi*; 1: *Polytrichum commune*; +: *Ptilium crista-castrensis*, *Hylocomium splendens*, *Dicranum* sp., *Peltigera aphthosa*.

Appendix 2. Description of a new alliance

***Pino pumilae-Piceion jezoensis* KRESTOV & NAKAMURA 2002 all. nov. hoc loco**

Nomenclatural type: *Vaccinio vitis-idaeae-Piceetum jezoensis* KRESTOV et NAKAMURA 2002 (described in this paper)

Diagnostic species: *Betula platyphylla*, *Equisetum sylvaticum*, *Pinus pumila*, *Pyrola incarnata*, and *Sorbus sibirica*.

Synonyms: *Betulo lanatae-Piceion ajanensis* PETELIN 1990 ms.

The alliance includes species-poor communities dominated by *Picea jezoensis* in the northern part of its distribution range. The climate has continental features in the upper part of the Bureya and the Selemdzha River, along the sea of Okhotsk coast, on northern Sakhalin, Shantar Islands and in central Kamchatka. These forests occupy the lower vegetation belt in the mountains, well drained river valleys and intermontane depressions. The climate in this region is much more severe than in the ranges of the other alliances of *Picea jezoensis* forests: mean annual temperature falls to -4 to -2 °C and mean annual precipitation drops to 400–600 mm. However, the actual moisture is compensated by low temperatures which decrease the evapotranspiration rates.

