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Vegetation comparison between the Russian Far East and the Taisetsu Mountains, Central Hokkaido, northern Japan

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ABSTRACT

This study compares the vegetation types of the Russian Far East and those of the Taisetsu range of Hokkaido, in order to clarify the vertical pattern of mountain vegetation belts in relation to the horizontal distribution of vegetation types in the Russian Far East. The Russian Far East consists of two zones, cool-temperate and boreal, and of four sectors, namely continental, maritime, oceanic and extreme-oceanic. Each combination of zone and sector produces a different vegetation type peculiar to that combination. The Taisetsu mountains are located in central Hokkaido (northern Japan) and have vegetation that corresponds, geographically, to that of the southernmost part of the Russian Far East. The vertical distribution on the mountain consists of six vegetation types (from lower upward): *Quercus crispula*–*Acer mono*–*Tilia japonica* forest, *Abies sachalinensis*–deciduous broadleaf mixed forest, *Picea jezoensis*–*Abies sachalinensis* forest, *Betula ermanii* forest, *Pinus pumila* thicket and wind-exposed dwarf scrub. Precise comparison of the species composition and vegetation structure in the two regions reveals that the vegetation types of Taisetsu include all six vegetation types in the Russian Far East, although the geographical location of Taisetsu would not suggest complete correspondence with all the zonal and sectoral types of the Russian Far East. The strong winter wind and heavy snowfall of Taisetsu promote this inconsistency, giving it a vertical zonation that is quite unique in its convergence toward all the possible zonal-sectoral combinations in the Russian Far East.

Keywords: sector, boreal zone, cool-temperate zone, vegetation convergence, vertical zonation

РЕЗЮМЕ

Окицу С. Сравнение растительности российского Дальнего Востока и гор Дайсецу, центральный Хоккайдо, северная Япония. Проведен сравнительный анализ типов растительности российского Дальнего Востока и горного массива Дайсецу на о-ве Хоккайдо с целью установления соотношений между структурой вертикальной поясности горной растительности и горизонтальным распределением растительности на российском Дальнем Востоке. Южная часть Дальнего Востока России включает прохладно-умеренную и бореальную зоны и четыре сектора: континентальный, приморский, океанический и экстремально-океанический. Каждой комбинации зоны и сектора соответствует определенная единица растительности. Горы Дайсецу расположены в центральной части Хоккайдо (северная Япония) и имеют растительность, которая географически соответствует растительности южной части Дальнего Востока России. Горные пояса представлены шестью типами растительности (снизу вверх): широколиственный лес из *Quercus crispula*, *Acer mono* и *Tilia japonica*; смешанный широколиственно-пихтовый лес с *Abies sachalinensis*, пихтово-еловый лес из *Picea jezoensis* и *Abies sachalinensis*, лес из *Betula ermanii*, заросли *Pinus pumila* и ветробойные кустарничковые тундры. Сравнение видового состава и структуры растительности в двух регионах показывает, что типы растительности Дайсецу и российского Дальнего Востока в целом сходны, однако особое географическое положение Дайсецу является причиной существенных отличий растительности горных поясов от аналогичных зональных и секторных единиц растительности Дальнего Востока России. Сильные зимние ветры и снегопады в горах Дайсецу являются главными причинами этой несогласованности, определяя уникальную вертикальную поясность.

Ключевые слова: сектор, бореальная зона, прохладно-умеренная зона, конвергенция растительности, вертикальная зональность

Переведено редколлегией

INTRODUCTION

The study area involves the Russian Far East, including the Kamchatka Peninsula and Sakhalin; and Hokkaido, the northernmost main island of Japan. This area surrounds the Sea of Okhotsk and has two climatic zones (cool-temperate, boreal), plus four east-west sectors (continental, maritime, oceanic and extreme-oceanic) within the two zones. This area has the steepest sectoral (continentality) gradient in the world (Tuhkanen 1984, Krestov et al. 2002), from continental to extremely oceanic, within the relatively short distance of 830 km, from Magadan across the Sea of Okhotsk to the west coast of Kamchatka. This arrangement of zones and sectors produces various types of vegetation.

Clarification of vertical zonation in relation to horizontally diverse vegetation types provides interesting and valuable opportunities for studies in phytogeography and vegetation ecology. Krestov (2003) portrayed vertical vegetation belts in submaritime-maritime and continental sectors of the Russian Far East and concluded that the vertical belts, in most cases, may be considered analogs of the horizontal zones, in terms of physiognomy and species composition.

The Taisetsu Mountains, in central Hokkaido (northern Japan), are situated at the same latitude as the southernmost part of the Russian Far East. The Taisetsu vertical zonation seems to share at least some vegetation types with the Russian Far East, despite its distance of Hokkaido from the Russian mainland. It is thus interesting, both phytogeographically and vegetation-ecologically, to compare the vertical zonation of Taisetsu and the horizontal vegetation distribution of the Russian Far East mainland. Such studies are still few.

Russian researchers clarified the nature and distribution of the vegetation in the Russian Far East through vegetation maps (Lavrenko & Sochava 1954, Sochava 1969). Japanese researchers mapped the vegetation distribution on Hokkaido, including the Taisetsu and other mountains (Tatewaki 1958, 1963a, 1967, Kojima 1979, Itō & Sato 1981, Itō et al. 1982, Miyawaki 1988). These initial studies focus naturally only on the national territories of Russia and Japan, with no comparison between regions. Recently, phytosociological studies have attempted to develop phytosociological systems covering wide areas including the Russian Far East, the Korean Peninsula and northeastern China: for the whole area by Kolbek et al. (2003), Krestov & Nakamura (2007), Krestov et al. (2010) and Nakamura et al. (2007); for coniferous forests by Song (1992), and by Krestov & Nakamura (2002); and for deciduous broadleaved forests by Kim (1992), by Kolbek & Jarolímek (2013), and by Krestov et al. (2006). These studies synthesize species compositions to construct systems of phytosociological classes, orders and alliances. Concrete comparisons of vegetation structure, composition and geography complement such relatively abstract studies.

The present study first arranges the horizontal distribution of the major vegetation types of the Russian Far East, on the basis of its zones and sectors. Then it introduces the vertical distribution of major vegetation types on the Taisetsu mountains. Finally it discusses corresponding vegetation types of the Russian Far East and Taisetsu, with precise comparison of the vegetation character, mainly an species composition. Nomenclature follows Czerepanov (1995) for the Russian territory and Itō et al. (1985, 1987, 1990, 1994) for Hokkaido.

HORIZONTAL DISTRIBUTION OF VEGETATION IN THE RUSSIAN FAR EAST

The four continentality sectors in the Russian Far East are shown in Fig. 1, with their approximate geographic extents. The continental sector occupies eastern Siberia and Magadan; the maritime sector extends over western Okhotsk, the Sikhote-Alin mountains, Sakhalin, and Hokkaido; the oceanic sector covers most of Kamchatka; and the extreme-oceanic sector is on the Kuril Islands.

Climatic conditions in the four sectors of the Russian Far East

Climatic conditions in the four sectors of the Russian Far East are summarized in Table 1 and represent what is probably the steepest sectoral gradient in the world. Values of the Conrad (1946) continentality index range from extremely continental (98) at Yakutsk, in interior northeastern Siberia, to extremely oceanic (27) at Severo-Kurilisk, in the Kuril Islands.

The continental sector is characterized by hot summer and extremely cold winter. The hot summer permits the establishment of forest vegetation, but the extremely cold winter produces deep permafrost. Annual precipitation is low, less than 300 mm, which is usually not enough to support forest vegetation. Slow thawing of the active layer of the permafrost, though, makes sufficient water available to plants gradually over the course of the whole summer.

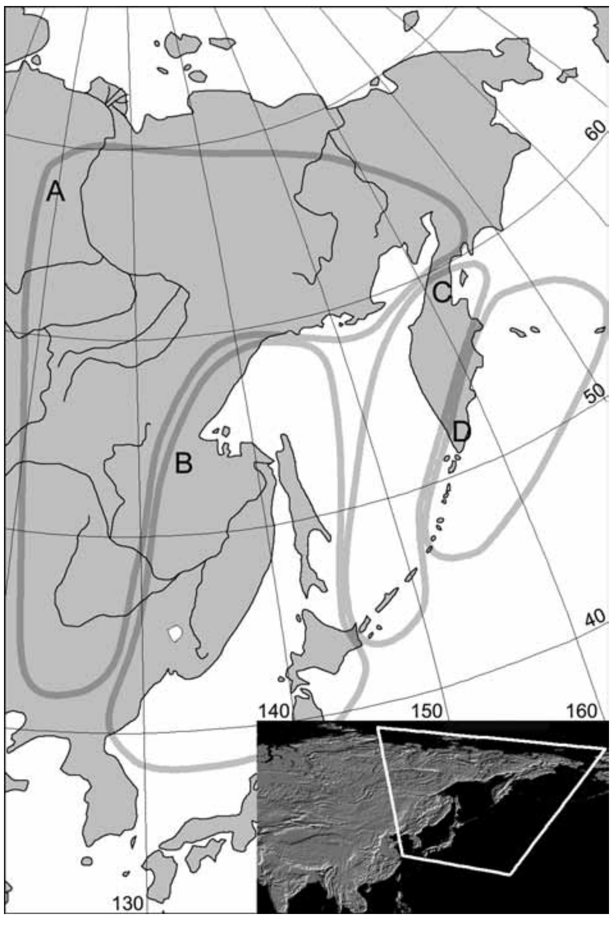


Figure 1 Approximate extents of the four sectors and their major vegetation types in the Russian Far East: A – continental (*Larix cajanderi–Pinus pumila* forests); B – maritime (*Picea jezoensis–Abies nephrolepis* forest, *Pinus koraiensis*–deciduous broad leaved mixed forest and *Picea koraiensis*–deciduous broad leaved mixed forest); C – oceanic (*Betula ermanii* forest); and D – extreme oceanic (treeless scrub and heath)

Table 1. Climatic data from stations representing the four sectors in Northeast Asia, with major vegetation types (compiled from Okitsu 2002a)

Sector	Continental		Maritime				Oceanic	Extreme-Oceanic
Meteorological station	Yakutsk	Seymchan	Poronaysk	Khabarovsk	Vladivostok	Asahikawa	Petropavlovsk-Kamchatskii	Severo-Kurilisk (Paramushir)
Major vegetatiion	*Larix gmelinii–Pinus pumila* forest		*Picea jezoensis–Abies nephrolepis* forest	*Pinus koraiensis*–deciduous broadleaf mixed forest	*Picea koraiensis*–deciduous broadleaf mixed forest	*Pinus koraiensis*–deciduous broadleaf mixed forest	*Betula ermanii* forest	Treeless heath
Yearly mean temperature (°C)	-10,1	-11,3	0,0	1,5	4,3	6,3	1,4	2,7
Mean temperature of warmest month (˚C)	19,5	14,8	15,8	21,3	20,3	20,4	13,0	10,6
Mean temperature of coldest month (˚C)	-42,7	-38,7	-17,8	-22,0	-13,4	-8,5	-8,6	-5,2
Warmth Index (°C)	39,5	27,1	30,4	50,4	56,6	62,1	21,1	17,0
Continentality Index (Conrad 1946)	98	81	52	70	58	47	27	18
Annual precipitatiion (mm)	213	296	760	558	738	1158	912	1461
Total precipitation of six warmest months (mm)	157	158	278	464	613	637	428	778
Total precipitation of six coldest months (mm)	56	138	482	94	125	521	484	683

The maritime sector has a generally mild climate. Summer warmth and sufficient precipitation permit various forest types to occur. This sector has the highest tree diversity in the Russian Far East.

The oceanic sector is characterized by cool summer and relatively mild winter. The high annual precipitation of around 900 mm falls mostly in summer, resulting in many cloudy summer days. Such climatic conditions make growth difficult for conifers, which require higher leaf temperatures in summer than can occur sufficiently on the many cloudy days. Only *Betula ermanii* makes its own forest in this sector.

The extreme-oceanic sector has distinctly low summer temperatures (warm-month mean of 10.6°C) associated with the cloudy or foggy summer days (cf summer precipitation 778 mm at Severo-Kurilsk). Under such climatic conditions trees never form forests. The Warmth Index (WI) amounts to only 17.0, which is a borderline value for forest (Kira 1991). Treeless scrub and heath dominate this sector.

Geographic distribution of the major vegetation types

The major vegetation types of the Russian Far East are also listed in Fig. 1, and their geographic arrangement is summarized in Table 2, within the cool-temperate and boreal bioclimatic zones, and with the four sectors. The boreal zone has all four sectors, but the cool-temperate zone has only a maritime sector in the Russian Far East. More continental cool-temperate climates appear only further west, in Chinese Manchuria; the extreme oceanic sector, though at cool-temperate latitudes, is normally included in the boreal zone due to its very cool summers.

This sequence of vegetation zones is commonly accepted in the Russian school of phytogeography, with the east-west differentiation reflecting the continentality gradient (Grishin 1995, Krestov 2003). The arrangement of zones and sectors, and the distribution of vegetation types in Table 2, follows that of Table 54 in Krestov (2003). Two differences between the two tables do occur: Krestov uses different sectoral names (continental, sub-maritime, maritime and oceanic), and stresses the environmental richness in the maritime sector; Table 2 of this study stresses the extreme-oceanic sector. Krestov covers a wider range, from continental to oceanic, resulting in the occurrence of land in every sector of the cool-temperate zone, unlike Table 2.

Cool-Temperate Zone

Southern Cool-Temperate Zone in the Maritime Sector

The main vegetation type of the cool-temperate zone is mixed forest of *Picea koraiensis* and deciduous broadleaved trees (Table 3; Fig. 2: 1). This area includes the most maritime area of the Daurian broadleaved forests (Krestov 2003), but more xeric species, *Quercus mongolica* and *Betula davurica*, dominate the less maritime mainland area (Ermakov et al. 2000, Kolbek et al. 2003, Krestov et al. 2006) under a somewhat drier climate that is still ascribed to the maritime sector. In this drier area, *Abies holophylla* is the most prominent conifer of the forest and *Picea koraiensis* is the second conifer, occurring especially in well-drained river valleys. The latter sometimes forms pure stands, usually in river valleys or on gentle lower or middle slopes (Kurentsova 1968, Krestov 2003). Qian et al. (2003) report that *Picea koraiensis–Abies nephroloepis* forest occurs at lower elevations in eastern Chinese Manchuria, usually on north-facing slopes, where the habitat is wetter and colder.

Table 2. Major vegetation types of the four sectors in two zones in the Russian Far East, from continental to extreme-oceanic

<table>
<tr><th>Sector</th><th>Continental</th><th>Maritime</th><th>Oceanic</th><th>Extreme-Oceanic</th></tr>
<tr><td>Major region</td><td>Eastern Siberia, Magadan</td><td>Western Okhotsk, Sikhote-Alin, Sakhalin, Hokkaido</td><td>Kamchatka</td><td>Northern Kurils</td></tr>
<tr><td>Environmental significance for vegetation</td><td>Extreme drought in late spring due to permafrost</td><td>Humid and warm</td><td>Humid and cool</td><td>Shortage of sunshine</td></tr>
<tr><td rowspan="2">Boreal Zone</td><td rowspan="2">Larix cajanderi–Pinus pumila forest</td><td>Land absent</td><td rowspan="2">Betula ermanii forest</td><td rowspan="2">Treeless heath</td></tr>
<tr><td>Picea jezoensis–Abies nephrolepis forest (southern)</td></tr>
<tr><td rowspan="2">Cool-temperate Zone</td><td rowspan="2">Land absent</td><td>Pinus koraiensis–deciduous-broadleaf mixed forest (northern)</td><td rowspan="2">Land absent</td><td rowspan="2">Land absent</td></tr>
<tr><td>Picea koraiensis–deciduous-broadleaf mixed forest (southern)</td></tr>
</table>

Table 3. Major woody species of *Picea koraiensis*–deciduous broadleaf mixed forests on the upper course of the river Ussuri, southern Primorye, along a soil moisture gradient (compiled from Okitsu 2014). Figures for woody species indicate relative basal area in the plots (%)

Plot No.	1903	1801	1901	1902	1904	1802	1803
Altitide (m)	622	454	422	411	458	406	406
Topography	slope/upper	slope/middle	slope/lower	slope/lower	flat/lower	flat/flood-plain	flat/flood-plain
Soil moisture	dry/mesic	mesic	mesic	mesic/moist	moist	moist	moist
Common species							
Picea koraiensis	1	1	5	54	30	4	7
Acer mono	1	1	5	10	10	4	2
Pinus koraiensis	11	2	8	3	16	·	·
Xeric species							
Quercus mongolica	70	61	77	·	·	·	·
Betula davurica	13	8	·	·	·	·	·
Xeric/mesic species							
Populus tremula	·	4	1	6	·	·	·
Maackia amurensis	·	1	1	1	·	·	·
Betula costata	·	3	5	3	·	·	·
Picea jezoensis	·	1	1	·	·	·	·
Betula platyphylla	·	8	·	·	·	·	·
Acer pseudosieboldianum	·	·	1	·	·	·	·
Acer tegmentosum	·	·	1	·	·	·	·
Mesic/moisture-demanding species							
Tilia amurensis	5	·	2	13	14	·	·
Abies nephrolepis	·	·	2	9	4	·	·
Tilia mandshurica	·	·	1	4	1	·	·
Acer ukurunduense	·	·	·	·	1	·	·
Moisture-demanding species							
Ulmus laciniata	·	·	·	·	1	1	·
Populus maximowiczii	·	·	·	·	23	43	63
Ulmus japonica	·	·	·	1	·	13	12
Fraxinus mandshurica	·	·	·	·	·	2	15
Chosenia arbutifolia	·	·	·	·	·	37	·
Phellodedron amurense	·	·	·	·	·	·	2

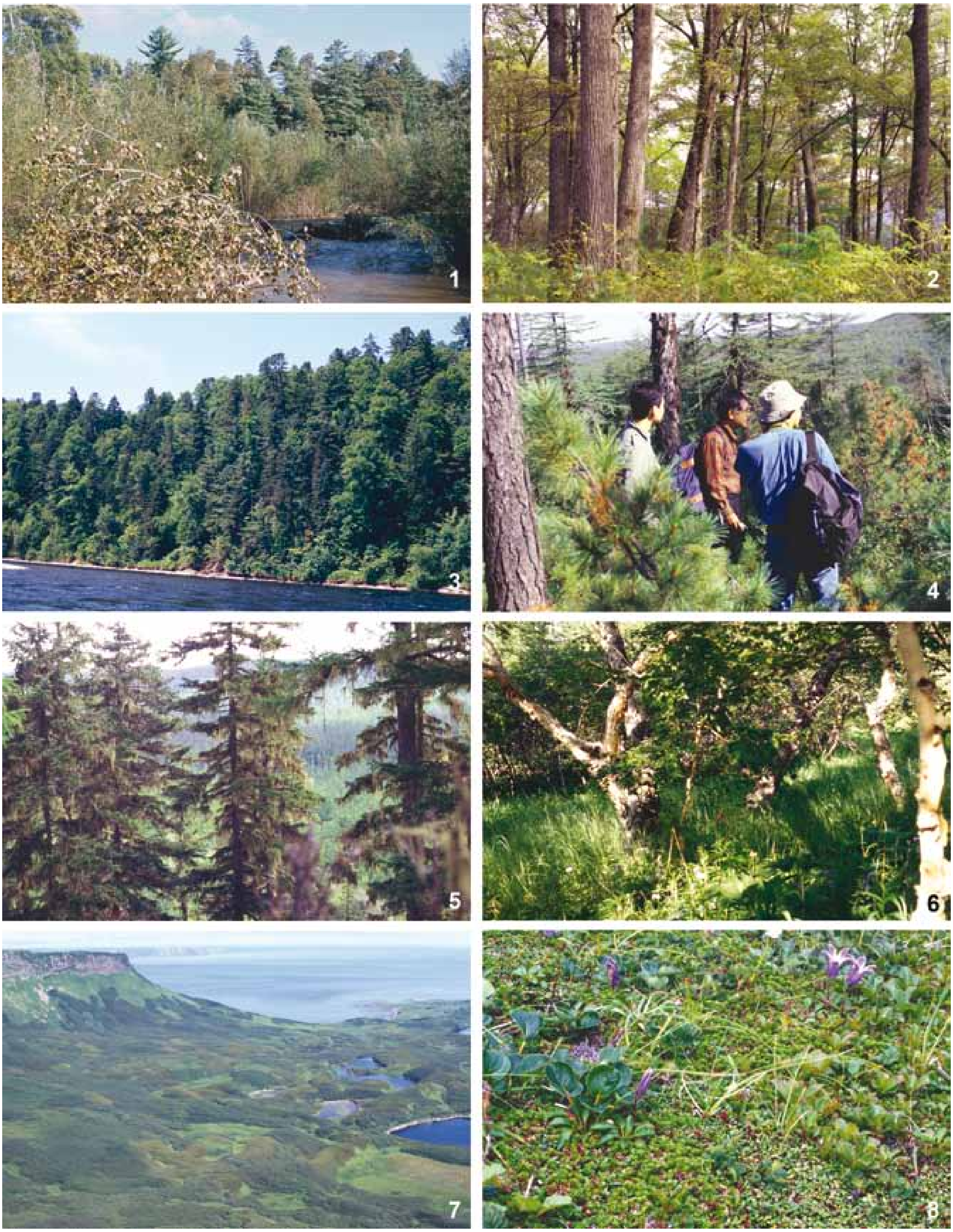
As an example, Table 3 shows major woody species of the *Picea koraiensis*–deciduous broadleaf mixed forests along the upper course of the River Ussuri in southern Primorye, along a soil moisture gradient. *Picea koraiensis* and *Acer mono* appear commonly throughout the gradient. *Pinus koraiensis* occurs frequently on dry-mesic, mesic and moist sites but disappears on the wetter sites in the floodplain. *Quercus mongolica* and *Betula davurica* grow only on the dry-mesic and mesic sites. Major deciduous broadleaved species such as *Tilia amurensis*, *T. mandshurica* and *Acer ukurunduense* represent the mesic and moist sites. *Ulmus japonica*, *Populus maximowiczii* and *Fraxinus mandshurica* develop well on the moist sites in the floodplain, forming mature riparian forests. Fig. 2: 2 shows an example of a well-developed *Ulmus japonica–Fraxinus mandshurica* mixed forest on the river terrace at the confluence of the River Bolshaya Ussurka (Iman) and River Armu, in the middle Sikhote-Alin mountains. Mature trees of the forest attain a diameter of 70 cm at breast height and a tree height of 30 m.

Northern Cool-Temperate Zone in the Maritime Sector

Pinus koraiensis–deciduous broadleaf mixed forest is the representative vegetation type of this region, covering wide areas (Table 4; Fig. 2: 3), and corresponds to Manchurian mixed forests (Krestov 2003). Many phytogeographers (Tatewaki 1958, Kolesnikov 1963, Hämet-Ahti et al. 1974) treat this vegetation as temperate, although the question whether it is temperate or boreal is still raised (Krestov 2003).

Major woody species of P*inus koraiensis*–deciduous broadleaf mixed forest are shown in Table 4, as seen in an old-growth forest in the Ussuri Nature Reserve, Primorskii Region. *Pinus koraiensis* dominates the forest with relative abundance of around 50 %; it is followed, among conifers, by *Abies holophylla*. Common deciduous broadleaved trees of the cool-temperate zone in the Russian Far East also occur frequently,

Figure 2 Major vegetation types of the Russian Far East: 1 – *Picea koraiensis*–deciduous broad-leaf mixed forest along the upper course of the River Usurri, southern Sikhote-Alin. *Pinus koraiensis* also co-occurs. 2 – well-developed *Ulmus japonica–Fraxinus mandshurica* mixed forest on a river terrace at the confluence of the River Bol'shaya Ussurka (Iman) and the River Armu, middle Sikhote-Alin. Mature trees attain a diameter at breast height of 70 cm and the tree height 30 m. 3 – *Pinus koraiensis*–deciduous broadleaf mixed forest along the middle course of the River Anyui, northern Sikhote-Alin. *Pinus koraiensis* dominates the forest; *Picea jezoensis* and *Picea koraiensis* also co-occur in the forest. Major deciduous broad-leaved trees are *Tilia amurensis*, *Betula costata* and *Ulmus japonica*. 4 – a typical stand of *Larix cajanderi–Pinus pumila* forest near Magadan city.



Larix cajanderi attains 30 cm in diameter and *Pinus pumila* reaches to ca. 200 cm in height. 5 – a primeval *Picea jezoensis–Abies nephrolepis* forest along the uppermost course of the river Anyui, northern Sikhote-Alin. Epiphytic *Parmellia* indicates that the forest is old-growth, and large trees indicate a mature stage. 6 – interior view of *Betula ermanii* forest at the forest limit of a high mountain in central Kamchatka. Here tree sizes show a reverse-J distribution, indicating that this forest regenerates constantly, making climax forest. This view contrasts with the generally accepted view that *Betula ermanii* forests are usually secondary and never correspond to a climax. 7 – vegetation landscape of Paramushir Island in the northern Kurils. No tall trees occur, not even *Betula ermanii*, which is the most tolerate of the oceanic climate. Vegetation consists of low shrubs of *Alnus maximowiczii* (dark green) and *Pinus pumila* (yellow green). 8 – close-up view of treeless heath on Paramushir Island, northern Kurils. Major species are *Diapensia obovata*, *Loiseleuria procumbens*, *Arctous alpina* and *Bryanthus gmelinii*. The species composition of the heath is quite similar to that of the wind-exposed dwarf scrub on Taisetsu (Hokkaido)

Table 4. Major woody species of an old-growth *Pinus koraiensis*–deciduous broadleaf mixed forest in the Ussuri Reserve, Primorye (compiled from Ishikawa et al. 1999). Figures for woody species indicate relative abundance by total basal area of the species (%)

Plot No.	1	2	3	4
Maximum DBH (cm)	57	72	64	104
Maximum tree height (m)	25	28	25	33
Pinus koraiensis	46.4	46.6	38.0	59.8
Abies holophylla	12.7	23.4	15.0	1.3
Tilia amurensis	24.4	5.4	9.3	20.4
Acer mono	1.2	2.2	11.1	8.6
Quercus mongolica	4.0	3.6	21.9	·
Acer pseudosieboldianum	2.6	1.3	0.2	·
Carpinus cordata	0.4	1.7	·	0.1
Acer tegmentosum	0.2	0.3	·	0.3
Betula costata	4.0	2.8	·	·
Sorbus alnifolia	0.1	0.1	·	·
Betula platyphylla	3.4	·	4.4	·
Corylus mandshurica	0.1	·	0.2	·
Fraxinus mandshurica	·	4.5	·	3.0
Acer mandshuricum	·	0.4	·	2.8
Populus maximowiczii	·	5.6	·	·
Populus tremula	·	2.1	·	·
Ulmus japonica	·	·	·	3.0
Ulmus laciniata	·	·	·	0.1

such as *Tilia amurensis*, *Acer mono*, *Quercus mongolica* and *Acer pseudosieboldianum*. As shown below, the species composition of the deciduous broadleaved forests is quite similar to that in Hokkaido.

Boreal Zone

Continental Sector

The continental sector corresponds to the eastern Siberian larch area (Krestov 2003), dominated by *Larix gmelinii* / *L. cajanderi*–*Pinus pumila* forest (Fig. 2: 4). Only deciduous conifers, *Larix* species, survive as canopy trees under the extreme cold, dry condition of the area (Sakai & Kinoshita 1974, Gower & Richard 1990, Stephenson 1990). Conditions tend to be milder on the forest floor, and thickets of the evergreen conifer *Pinus pumila* can survive as undergrowth in the *Larix gmelinii* / *L. cajanderi* forest.

Larix gmelinii cover and the forest-floor types of the *Larix cajanderi*–*Pinus pumila* forest in Magadan are compared in Table 5, in order to clarify the zonal position of the fo–rest. The north slopes have low cover by *Larix cajanderi*, plus subarctic elements *Betula exilis* and lichens on the forest floor. These forest-floor components are similar to those in the subarctic tundra (Aleksandrova 1980). North-facing slopes experience harsh conditions underlain by permafrost, and these promote a southern extension of subarctic tundra elements. On the other hand, south-facing slopes have higher crown cover by *Larix cajanderi* and abundant *Pinus pumila* on the forest floor, due to milder conditions and a general absence of permafrost. This milder environment sustains the distribution of the boreal forests. As a result, the south slopes can support the typical *Larix cajanderi*–*Pinus pumila* forest, which belongs mainly to part of the boreal zone (Table 2). A similar type of *Larix cajanderi*–*Pinus pumila* forest occurs near the forest limit on Mt. Dal'nyaya Ploskaya in central Kamchatka (Okitsu 1998). *Pinus pumila* never extends above the forest limit into the alpine tundra belt (Okitsu 1996).

Table 5. Slope aspect, *Larix gmelinii* cover and forest-floor types of the *Larix gmelinii*–*Pinus pumila* forest in Magadan (Okitsu 2002a)

Slope aspect	Number of observation points	Mean *Larix* cover (%)	*Larix* forest floor type			
			Boreal elements		Subarctic elements	
			Pinus pumila	*Betula ovalifolia*	*Betula exilis*	Lichens
North	55	20,9	3	4	15	33
South	62	54,5	28	19	8	7
East	17	41,2	8	8	0	1
West	18	46,9	8	6	2	2
Flat	25	58,8	2	7	14	2
Total	177	–	49	44	39	45

Maritime Sector

The typical vegetation type of this (boreal) maritime sector is *Picea jezoensis*–*Abies nephrolepis* forest (Fig 2: 5), as represented by the dark-conifer forests of the eastern Okhotsk and western Okhotsk areas (Krestov 2003). This forest forms a lower sub-belt within the *Pinus koraiensis*–deciduous broadleaf mixed-forest belt, occupying almost the whole range of ecologically different sites except mires and rock outcrops (Man'ko 1967, Krestov 2003). The forest usually forms simple one- or two-layer stands consisting of *Picea jezoensis*, *Abies nephrolepis* / *A. sachalinensis* and *Betula ermanii*.

Major woody species of the *Picea jezoensis*–*Abies nephrolepis* forests are shown in Table 6, as seen in the subalpine belt of Mt. Vysokaya, in the central Sikhote-Alin (Fig 2: 5). The tree layer has abundant *Picea jezoensis* plus small amounts of *Abies nephrolepis* and *Betula lanata* (*Betula ermanii* s.l.). The other major woody species in the forests are *Acer ukurunduense*, *Sorbus amurensis* and *Weigela middendorffiana*. Woody boreal elements compose these forests exclusively, replacing the cool-temperate elements.

Oceanic Sector

Betula ermanii forest is the dominant vegetation type in the (boreal) oceanic sector, in Kamchatka, corresponding to the northern-Pacific meadow-birchwood area of Krestov (2003). The *Betula ermanii* forest has its forest limit at 960 m on Mt. Dal'nyaya Ploskaya (4050 m), where the maximum tree height reaches only 12 m and maximum tree diameter at the breast height is 25 cm (Fig. 2: 6). The total basal area of this forest attains 15 m^2/ha and the total crown cover is relatively sparse at about 0.8 ha/ha (Okitsu 1999). The diameter of *Betula ermanii* trees shows a clear reverse-J distribution, suggesting continuous regeneration of the species in the sufficient light under the sparse canopy (Okitsu 1999). Once established, the trees remain in the forest for a long time, attaining ages of approximately 500 years. With this stable regeneration, the *Betula ermanii* forest forms a climax plant community, despite the shade-intolerance of *Betula ermanii* (Okitsu 1987a).

Table 6. Major woody species of *Picea jezoensis–Abies nephrolepis* forests of Mt. Vysokaya, central Sikhote-Alin, based on three profiles across forests in the subalpine belt (after Grishin et al. 1996). The figures and the symbol '+' in the table indicate Braun-Blanquet cover levels

Latitude	47°05'
Altitude of profiles (m)	1350–1500
Maximum tree height (m)	15
Maximum DBH (cm)	36
Tree layer	
Picea jezoensis	4-5
Abies nephrolepis	+-3
Betula lanata	+-3
Subtree layer	
Acer ukurunduense	+-2
Sorbus amurensis	+-1
Shrub and herb layer	
Linnaea borealis	+-2
Ledum hypoleucum	+-1
Rhododendron aureum	+-1
Ribes fontaneum	+-1
Ribes triste	+-1
Rubus sachalinensis	+-1
Vaccinium vitis-idaea	+-1
Weigela middendorffiana	+-1
Lonicera edulis	+
Juniperus sibirica	+
Rhododendron mucronulatum	+
Ribes horridum	+
Rosa acicularis	+
Sambucus sibirica	+

Table 7. Species on the forest floor of the *Betula ermanii* forest at its upper limit (1050 m) on Mt. Dal'nyaya Ploskaya, central Kamchatka (Okitsu 2002b). The figures in the table show percent cover of the species

Species	Cover (%)	Species	Cover (%)
**Calamagrostis langsdorffii*	30	**Rumex lapponicus*	+
**Equisetum arvense*	30	**Trisetum sibiricum*	+
**Epilobium angustifolium*	20	**Carex koraginensis*	+
**Geranium erianthum*	10	**Carex pallida*	+
**Aruncus dioicus*	10	**Alium ochotense*	+
**Veratrum oxisepalum*	10	**Pedicularis resupinata*	+
**Poa platyantha*	10	**Sedum rosea*	+
**Equisetum pratense*	5	**Galium boreale*	+
**Thalictrum minus*	5	**Trientalis europaea*	+
**Heracleum lanatum*	+	**Maianthemum dilatatum*	+
**Angelica gmelinii*	+	**Polygonum viviparum*	+
**Moehringia lateriflora*	+	*Bromopsis pumpellianus*	+
**Lathyrus pilosus*	+	*Solidago spiraeifolia*	+
**Pyrola incarnata*	+	*Saussurea pseudotilesii*	+
**Lonicera edulis*	+	*Rosa amblyotis*	+
**Betula ermanii*	+	*Mertensia pubescens*	+
**Pinus pumila*	+	*Delphinium brachycentrum*	+

* = species occurring also in northern Japan.

Typical forest-floor species composition at the forest limit is shown in Table 7, from Mt. Dal'nyaya Ploskaya (Okitsu 2002b). *Calamagrostis langsdorffi* and *Equisetum arvense* dominate the forest floor, with high cover also by *Epilobium angustifolium*, *Aruncus dioicus* and *Geranium erianthum*. Herbaceous species occur abundantly over the whole forest floor. Out of 34 total species, only six do not also occur in northern Japan, including *Bromus pumpellianus*, *Solidago spiraeifolia* and *Saussurea pseudo-tilesii*.

Extreme-Oceanic Sector

This area involves the Kuril Islands and has WI above 15 (see Table 1), which should still permit establishment of some kind of forest vegetation (Kira 1991). This suggests that it is still within the boreal zone. The shortage of sunshine in summer, however, precludes forest and results in treeless heath (Kudo 1922, Tatewaki 1957, Grishin 1995; see Fig. 2: 7 and 8). Even *Betula ermanii* fails to maintain sufficient photosynthetic production under such conditions (Koike 1993, Okitsu 1995, 2002a).

An example of this treeless heath is shown in Table 8, from the eastern slope of Mt. Ebeko on Paramushir Island (northern Kurils). The total number of species of the area surveyed was 58. Thirteen of these 58 species (22 %) occur with frequency of more than 40 % in 43 plots, including *Calamaglostis purpurascens*, *Loiseleuria procumbens*, *Empetrum nigrum*, *Arcterica nana*, *Geum calthifolium*, *Salix arctica*, *Cnidium ajanense*, *Phyllodoce aleutica* and *Cassiope lycopodioides*, *Solidago decurrens*, *Rhododendron aureum* and *Rh. camschaticum*, and *Agrostis flaccida* as common species. On the other hand, 38 of the 58 species (66 %) occurred only sporadically, at frequency of less than 10 %.

The 13 common species of the community include eight dwarf shrubs and five herb species, with the dwarf shrubs dominating all over the plots surveyed. The vegetation type of the study area can be regarded as treeless dwarf-shrub heath, both by species composition and physiognomy. The total number of species decreased upward, from 50 below 400m to 20 above 600 m (Table 8), but the 13 common species showed no clear altitudinal tendency.

This boreal heath is essentially treeless in nature, and Kudo (1922) and Tatewaki (1957, 1958, 1963b) point out that it is the most important vegetation type in the central and northern Kurils. Tuhkanen (1984) also considered the treeless heath in this area to be the representative vegetation of the highly oceanic sector of the northern and middle boreal subzone of eastern Eurasia, including the Kuril Islands. So the treeless heath of Mt. Ebeko corresponds well with the treeless heath of Tatewaki (1958) and Tuhkanen (1984).

Hämet-Ahti and Ahti (1969) state that the occurrence of treeless boreal heath is closely related to the distribution of alder (Alnus) forests, and that the lowlands of Iceland, the Aleutian Islands and the Kuril Islands belong to the boreal heath sections rather than to the Arctic. Hämet-Ahti (1981) stresses also that treeless heaths occur exclusively along the most oceanic coastal areas of the boreal zone. The heath of Mt. Ebeko is a vegetation type corresponding to the highly oceanic climate within the boreal zone.

VERTICAL VEGETATION ZONATION ON THE TAISETSU MOUNTAINS AND CORRESPONDENCE WITH VEGETATION OF THE RUSSIAN FAR EAST

Natural environments of Taisetsu

Taisetsu is used here as a general term for the high Taisetsu mountain range at 43°60'N and 143°10'E in central Hokkaido; its highest peak is Mt. Asahi (2290 m), followed by many peaks exceeding 1900 m, such as Mt. Hakuun (2031 m), Mt. Tomuraushi (2045 m), Mt. Kuro (1984 m) and Mt. Ishikari

Table 8. Verical distribution of major species on the east slope of Mt. Ebeko, Paramushir Island, northern Kurils (amplified from Okitsu et al. 2001). Figures in the table show percent occurrence at the particular altitude. Only species with occurrence frequency of least 10 % at some altitude are listed

Altitude (m)	0-339	400-499	500-599	600-650	Total
Number of plots	21	24	42	20	107
Total numer of species	50	27	26	20	58
Mean number of species per plot	12,4	10,5	9,2	8,4	10,1
Calamagrostis sesquiflora	38	100	76	80	75
Loiseleuria procumbens	57	96	67	75	73
Empetrum nigrum	48	92	71	70	71
Arcterica nana	38	79	62	75	64
Geum calthifolium	48	54	57	85	60
Salix yezoalpina	43	33	79	40	54
Tilingia ajanensis	43	58	57	50	53
Phyllodoce aleutica	62	42	55	35	50
Cassiope lycopodioides	19	38	57	80	50
Solidago virgaurea ssp. *leiocarpha*	71	42	57	15	49
Rhododendron aureum	38	54	50	30	45
Rhododendron camtschaticum	52	50	50	20	45
Agrostis borealis var. *flaccida*	67	29	43	25	41
Carex scita ssp. *riishirensis*	14	33	21	65	31
Oxytropis revoluta	29	71	19	0	29
Vaccinium uliginosum	48	50	7	0	23
Saussurea riederi ssp. *yezoensis*	10	38	21	15	22
Pedicularis verticillata	48	17	0	0	13
Deschampsia flexuosa	0	17	19	0	11
Spiraea betulifolia	24	4	0	25	10
Geranium erianthume	29	17	0	0	9
Harrimanella stelleriana	0	0	21	5	9
Calamagrostis langsdorffii	38	8	0	0	9
Geum pentapetalum	33	4	0	0	8
Anaphalis margaritacea var. *margaritacea*	33	0	0	0	7
Viola biflora	29	0	2	0	7
Penstemon frutescens	5	4	0	20	6
Maianthemum dilatatum	24	4	0	0	6
Cirsium kamtschaticum	19	4	0	0	5
Vaccinium vitis-idaea	19	0	0	0	4
Sibbaldia procumbens	19	0	0	0	4
Rubus arcticus	19	0	0	0	4
Aruncus dioicus var. *tenuifolius*	19	0	0	0	4
Lycopodium alpinum var. *alpinum*	5	13	0	0	4
Rumex acetosella	19	0	0	0	4
Pedicularis verticillata	14	0	0	0	3
Trientalis europaea	10	0	2	0	3
Veronica stelleri var. *longistyla*	14	0	0	0	3
Bryanthus gmelinii	0	0	0	15	3
Cerastium fischerianum	14	0	0	0	3
Sorbus sambucifolia	10	0	0	0	2
Artemisia unalaskensis	10	0	0	0	2
Luzula oligantha	10	0	0	0	2
Senecio cannabifolius	10	0	0	0	2

(1945 m). The Taisetsu mountains consist mainly of plains and gentle slopes, plus the high peaks. The substrates of the mountains are chiefly pre-Pleistocene lava, with two kinds of pyroxene andesite and often well developed platy joints (Konoya et al. 1968). The Taisetsu mountain area presents a most representative vertical distribution for northern Japan, in correspondence with the vegetation of the Russian Far East.

Air temperatures have been recorded only sporadically in the northern parts of the mountains, on Mt. Kuro and Mt. Hakuun (Sakai & Ohtsuka 1970, Itō & Nishikawa 1977, Takahashi 1998). Sakai & Otsuka (1970) report mean air temperatures of +13ºC from mid-June to mid-August, with daily minimum air temperatures from late June to late September fluctuating between about +10º and -10ºC, but mostly within the range +5º to -5º C in 1968 on Mt. Kuro. From August 6 to August 11, 1970, Itō & Nishikawa (1977) recorded highest temperatures between +8º and +18ºC, around noon, at the Hakuun lodge (2000 m).

Snow cover usually appears in mid-October and lasts to mid-June, varying in depth from place to place. Snow depth can be more than 400 cm (Okitsu & Itō 1984), except along windward slopes where snow is sparse even in mid-winter.

Vegetation belts of Taisetsu and corresponding vegetation of the Russian Far East

The Taisetsu mountains show a typical vertical zonation for Hokkaido (Tatewaki 1963a, Kojima 1979; Fig. 3). There are six major vegetation types occurring, from bottom to top, in distinct altitudinal belts: *Quercus crispula–Acer mono–Tilia japonica* forests, *Abies sachalinensis*–deciduous broadleaf mixed forests, *Picea jezoensis–Abies sachalinensis* forests, *Betula ermanii* forests, *Pinus pumila* thickets and dwarf scrub on wind-exposed tops.

Quercus crispula–Acer mono–Tilia japonica forest

Quercus crispula–Acer mono–Tilia japonica forest dominates on the lowest part of the mountain, up to about 500 m. This forest is the representative type not only of lower Taisetsu but over all of lowland Hokkaido. The woody species of forests on Hokkaido are summarized in Table 9. Major tree species are *Quercus crispula*, *Kalopanax septemlobus*, *Acer mono*, *A. japonicum*, *A. palmatum*, *Tilia japonica*, *T. maximowicziana*, *Ulmus laciniata*, and *Fraxinus mandshurica* (cf. Greller 2013). Coniferous *Abies sachalinensis* mixes in these forests to a certain extent.

In addition to this forest, well-developed *Ulmus japonica–Fraxinus mandshurica* mixed forests occurred abundantly on river terraces and floodplains before Hokkaido was opened up for settlement about 130 years ago (Kudo 1925, Tatewaki 1961, Fig. 4: 1; cf. Fig. 2: 2). A remnant *Ulmus japonica* forest patch still remains on the campus of Hokkaido University in Sapporo (Fig. 4: 1). Almost all the forests have now disappeared, due to human activities.

The corresponding forest in the Russian Far East is the *Picea koraiensis*–deciduous broadleaf mixed forest in the maritime sector of the southern cool-temperate zone. Major tree species are *Picea koraiensis*, *Pinus koraiensis*, *Abies nephrolepis*, *Quercus mongolica*, *Tilia amurensis*, *T. mandshurica*, *Maackia amurensis*, *Acer mono* and *A. pseudosieboldianum*. Well-developed *Ulmus japonica–Fraxinus mandshirica* forests, with species such as *Ulmus laciniata* and *Populus maximowiczii*, occupy the floodplains and river terraces (Fig. 2: 2). The composition by deciduous broadleaved trees is quite similar in both forest types, although Hokkaido lacks *Picea koraiensis*. These two forest types correspond well.

Figure 3 Vertical vegetation zones of the Taisetsu mountains of Hokkaido, northern Japan. A – wind exposed dwarf shrub, B – *Pinus pumila* thickets, C – *Betula ermanii* forests, D – *Picea jezoensis–Abies sachalinensis* forests

Major deciduous broadleaved trees of the forest, such as *Quercus crispula*, *Betula platyphylla*, *Tilia japonica*, *Carpinus cordata* and *Acer mono*, came to Hokkaido from the northeast Asian mainland via the Korean Peninsula or Sakhalin (Okitsu 2009). This verifies the correspondence between this *Picea koraiensis*–deciduous broadleaf mixed forest in the cool-temperate Russian Far East and the *Quercus crispula–Acer mono–Tilia japonica* forest of Hokkaido.

Abies sachalinensis–deciduous broadleaf mixed forest

Abies sachalinensis–deciduous broadleaf mixed forest (Fig. 4: 2) appears at altitudes of 300~800 m on mountains of Hokkaido. This forest is characterized by the presence of such tree species as *Abies sachalinensis*, *Quercus crispula*, *Acer mono*, *Tilia japonica*, *Betula ermanii* and *Picea jezoensis* (Table 10). The tree layer develops well and is dominated by the evergreen conifers *Abies sachalinensis* and *Picea jezoensis*, and deciduous broadleaved *Quercus crispula* and *Acer mono*. A mixed occurrence of coniferous trees and deciduous broadleaved trees is a remarkable characteristic of this forest. This forest develops best on mountain slopes of Hokkaido (Tatewaki 1958, Kojima 1979).

This forest corresponds, on the mainland, to the *Pinus koraiensis*–deciduous broadleaf mixed forest in the maritime sector of the northern cool-temperate zone. The forest shares common or taxonomically or ecologically closely related deciduous broadleaved trees such as *Tilia amurensis*, *Acer mono*, *Quercus mongolica*, *Acer pseudosieboldianum*, *Fraxinus mandshurica*, *Kalopanax septemlobus* and *Ulmus japonica*. Kira (1991) supports this correspondence.

The reason for the current absence of *Pinus koraiensis* in Hokkaido remains uncertain. It was already absent from Hokkaido during the Last Glacial period, but it did occur on northernmost Honshu at that time (Morita 2000). *Pinus koraiensis* is replaced in Hokkaido by *Abies sachalinensis*, which has also been characterized as belonging to the cool-temperate to boreal transition (Box & Fujiwara 2012).

Picea jezoensis–Abies sachalinensis forest

The Picea jezoensis–Abies sachalinensis forest covers altitudes 800~1300 m (Fig. 4: 3) in Hokkaido and is characterized by the presence of such tree species as *Picea jezoensis*, *Abies sachalinensis*, *Sorbus commixta*, *Acer ukurunduense* and *Betula ermanii* (Table 11). The tree layer is well developed and is dominated by the two evergreen conifers, *Picea jezoensis* and *Abies sachalinensis*, in proportions that vary with site conditions. *Picea jezoensis* prevails if soils are fertile, while *Abies sachalinensis* occurs over a wide range of habitats. *Betula ermanii* accompanies these conifers frequently, especially at higher altitudes. A unique feature of this forest in the boreal zone is the well-developed *Sasa* understorey.

The corresponding forest type in the Russian Far East is *Picea jezoensis–Abies nephrolepis* forest, which occurs in the maritime sector of the southern boreal zone. The species compositions of the two forests are quite similar as a whole, and these two forest types are almost homologous.

Betula ermanii forest

Betula ermanii forest occurs above the coniferous forest, at altitudes of 1300~1650 m, with a clear upper forest limit, at which treeline *Pinus pumila* thickets replace the *Betula ermanii* forest. In addition to Taisetsu, *Betula ermanii* forests also occur on the Hidaka mountains, in the Pacific coastal region around Kushiro, on the southern Kuril Islands, and on the Kamchatka Peninsula (Kojima 1994). Watanabe (1979) regards these *Betula ermanii* forests as a major component of the subarctic summergreen forest zone. This overview suggests that the *Betula ermanii* forest on the upper Taisetsu mountains corresponds phytogeographically to that in Kamchatka, in the oceanic sector of the boreal zone.

The *Betula ermanii* forest at its upper limit (Fig. 4: 4) has maximum tree height of 15 m and maximum tree diame-

Figure 4 Major vegetation types of Mt. Taisetsu, Hokkaido, northern Japan. 1 – remnant *Ulmus japonica* forest patch inside the campus of Hokkaido University, Sapporo. Before Hokkaido was opened for settlement, ca. 130 years ago, well-developed *Ulmus japonica–Fraxinus mandshurica* mixed forests occurred abundantly on river terraces in the area of *Quercus crispula–Acer-mono–Tilia japonica* forest (cf. Fig. 2:2). Almost all the forests are now gone, due to human activities. 2 – interior view of an *Abies sachlinensis*–deciduous broadleaf mixed forest at Akan, eastern Hokkaido. The big tree in the center is *Quercus crispula*, with a breast-height diameter of 50 cm. The trees with white bark are *Abies sachalinensis*, with breast-height diameters up to about 30 cm (rightmost tree in the photo). 3 – interior view of a *Picea jezoensis–Abies sachalinensis* forest in the headwater area of the River Tokachi, central Hokkaido. The big tree a bit left of center in the photo is *Picea jezoensis*, with a breast-height diameter of about 100 cm. The trees with white bark are *Abies sachalinensis*, with breast-height diameters up to a maximum of about 30 cm. *Picea glehnii* also occurs occasionally (e.g. the big tree at the right, with a breast-height diameter of about 80 cm). 4 – *Betula ermanii* forest at the forest limit on the Taisetsu mountains (1500 m). 5 – well-developed *Pinus pumila* thickets in the central part of the Taisetsu mountains. 6 – dwarf scrub on a wind-exposed top in the Taisetsu mountains. Note that most of the mountain is covered by snow, and the dwarf scrub occurs only on the snow-free area at summits. (Photo taken in late May)

ter of 48 cm at breast height; total basal area of this forest reaches 17 m^2/ha and total crown cover is relatively sparse at 0.8 ha/ha (Okitsu 1987a). The diameters of *Betula ermanii* trees show a clear reverse-J distribution, suggesting continuous regeneration. Forest structure and ecological characteristics of this forest are quite similar to those of the *Betula ermanii* forest at its upper limit on Mt. Dal'nyaya Ploskaya, in central Kamchatka.

The *Betula ermanii* forests of Kamchatka contain many species common to northern Japan, as shown in Table 12. Of 34 species in the *Betula ermanii* forests on Mt. Dal'nyaya Ploskaya, 28 species (82 %) are common to northern Japan; and of 55 species in four *Betula ermanii* stands in central and southern Kamchatka, 48 species (87 %) are common to northern Japan.

In conclusion, the *Betula ermanii* forest of upper Taisetsu corresponds well, phytogeographically, to the *Betula ermanii* forest of the oceanic climate of Kamchatka (cf. Tables 1 and 2). Hämet-Ahti & Ahti (1969) supported this correspondence of these two distant *Betula ermanii* forests, proposing a climatic climax zone of *Betula* forests in areas of boreal oceanic climate, including Fennoscandia (Chernenkova et. al. 2015) and northeasternmost Asia. The *Betula ermanii* forest of the upper Taisetsu mountains would obviously belong to such a *Betula* forest zone developing under the oceanic climate.

Pinus pumila thickets

Thickets of shrubby *Pinus pumila* appear at treeline on the upper Hokkaido mountains, at about 1600~1900 m (Fig. 4: 5). The temperatures at the lower limit of these *Pinus pumila* thickets are not uniform, though, so the *Pinus pumila* belt on Hokkaido can perhaps be described as follows, by Okitsu & Itō (1989). Thermal conditions would allow forest development above the present forest limit, so there may be an area that is theoretically part of the forest belt. In fact, however, forest is missing due to the strong winds and heavy snowfall in winter, or to the rocky substrate. This non-forest area provides an ecological niche for the *Pinus pumila* thickets.

Many Japanese botanists considered the *Pinus pumila* thickets in Japan to belong to the vegetation of the arctic or alpine tundra, due to the shrubby growth form (Okitsu & Itō 1984), but this is incorrect. Dwarf birch (*Betula exilis*) prevails in and is a typical representative plant of the subarctic subzone of northern Eurasia, which corresponds to the southern part of the actual tundra zone (Aleksandrova 1980). *Betula exilis* is completely absent from the Taisetsu mountains as well as the rest of Japan. This shows that the *Pinus pumila* thickets of upper Taisetsu do not belong to the subarctic, arctic or alpine tundra vegetation.

The *Pinus pumila* thickets of Taisetsu are closely related to the vegetation in the boreal zone of the Russian Far East, where *Pinus pumila* thickets constitute a major component of the *Larix cajanderi–Pinus pumila* forests (see Tables 2 and 5; cf. Okitsu 1996). The *Pinus pumila* thickets of Taisetsu correspond phytogeographically to the *Larix cajanderi–Pinus pumila* forests of the continental sector in the boreal zone. The absence of tree forms of *Larix cajanderi* in the upper part of the Taisetsu mountains is due to strong winds and heavy snow in winter, where the prevailing rocky substrate enhances the dominance of *Pinus pumila* thickets (Okitsu 2002a). Abundant macrofossils (Yano 1970, Morita 2000) and pollen (Igarashi 1996) from the Last Glacial period in Hokkaido, associated with a cold, dry continental environment (Ono 1984), support this finding. Okitsu (2002a, b) assumed that the Holocene extinction process of *Larix cajanderi* in Hokkaido involved the following steps: first, after the Last Glacial, the *Larix cajanderi–Pinus pumila* forest ascended the slopes toward a thermal forest limit associated with increasing air temperatures

Table 9. Major woody species of the *Quercus crispula–Acer mono–Tilia japonica* forests in Hokkaido. The figures and the symbol '+' in the table indicate Braun-Blanquet cover levels (Okitsu 2003)

Region*	SH	SH	SH	SH	SH	NH	NH	NH
Running no.	1	2	3	4	5	6	7	8
Quercus crispula	5	4	3	5	4	5	5	5
Kalopanax septemlobus	+	1	2	2	2	2	+	·
Acer mono	2	+	2	·	2	+	1	1
Acer japonicum	+	·	·	+	+	·	+	·
Tilia japonica	+	+	2	·	+	·	·	·
Fraxinus lanuginosa	+	+	2	·	+	·	·	·
Sorbus alnifolia	+	·	·	+	+	·	+	·
Prunus sargentii	·	+	·	·	·	+	+	+
Carpinus cordata	·	·	·	·	+	·	+	·
Magnolia obovata	1	·	·	·	+	·	+	·
Rhus trichocarpa	1	+	·	·	·	·	·	+
Cornus controversa	+	·	·	·	+	·	·	+
Prunus ssiori	+	·	+	·	+	·	+	·
Acer palmatum	+	+	3	·	+	+	·	·
Maackia amurensis	·	·	1	+	·	+	+	·
Abies sachalinensis	·	·	·	1	1	·	·	+
Magnolia kobus	+	+	·	·	+	·	·	·
Fagus crenata	·	·	·	·	·	·	·	·
Viburnum furcatum	·	·	·	·	·	·	·	·
Viburnum wrightii	·	·	·	·	·	·	·	·
Corylus sieboldiana	·	·	·	·	·	·	·	·
Acer rufinerve	·	·	·	·	·	·	·	·
Morus bombycis	+	·	·	·	·	+	·	·
Betula ermanii	·	·	3	·	·	·	·	+
Phellodendron amurense	·	·	2	·	·	·	·	+
Ulmus laciniata	·	·	+	·	+	·	·	·
Cephalotaxus harringtonia	·	·	·	1	2	·	·	·
Tilia maximowiziana	·	·	·	·	·	1	+	·
Ulmus propinqua	·	·	·	·	·	+	1	·
Sorbus commixta	·	·	·	·	·	·	+	+
Sasamorpha borealis	·	·	·	·	·	·	·	·
Sasa paniculata	·	5	5	4	5	4	1	5

* here and after: SH = southern Hokkaido, NH = northern Hokkaido

Table 10. Major woody species of the *Abies sachalinensis*–deciduous broadleaf mixed forests in Hokkaido (Okitsu 2003). The figures and the symbol '+' in the table indicate Braun-Blanquet cover levels

Region	SH	SH	SH	SH	NH	NH	NH	NH	NH	NH
Running no.*	1	2	3	4	5	6	7	8	9	10
Abies sachalinensis	2	4	3	3	3	2	2	4	3	3
Quercus crispula	3	3	3	4	3	5	4	2	4	2
Acer mono	1	+	2	+	2	2	2	2	1	2
Tilia japonica	1	1	+	+	1	1	1	1	2	2
Betula ermanii	3	+	1	·	+	·	+	1	+	+
Picea jezoensis	·	+	4	1	2	·	+	1	+	+
Viburnum furcatum	1	1	3	+	2	+	2	5	·	·
Acer japonicum	5	·	3	5	5	+	2	·	·	·
Sorbus commixta	·	+	2	+	·	+	·	1	1	+
Magnolia obovata	+	1	1	·	·	+	·	·	·	+
Kalopanax septemlobus	·	+	·	·	+	·	1	1	4	3
Sorbus alnifolia	1	+	·	+	·	·	·	·	+	+
Ulmus laciniata	·	1	1	1	·	·	1	·	·	·
Fraxinus lanuginosa	·	+	·	+	·	·	2	+	·	+
Prunus ssiori	·	+	·	·	·	·	·	·	1	·
Carpinus cordata	·	+	·	·	·	·	2	·	·	·
Tilia maximowicziana	+	+	·	·	·	·	·	·	·	1
Euonymus alatus	·	·	·	·	·	·	·	·	+	1
Acer ukurunduense	·	·	+	+	·	·	·	·	+	·
Prunus maximowiczii	·	·	·	1	·	·	·	1	+	·
Acer palmatum	·	·	·	+	·	·	+	·	·	+
Cornus controversa	·	·	·	+	+	·	·	+	+	+
Alnus hirsuta	·	·	·	1	·	·	+	·	+	·
Prunus sargentii	·	·	·	·	·	·	·	·	2	1
Sasa kurilensis	1	2	·	+	·	·	1	·	·	·

* relevés are from: 1 = Esashi; 2, 3 = Sapporo; 4 = Shimukappu; 5, 6 = Horokanai; 7 = Akan; 8 = Sarufutsu; 9, 10 = Kushiro

Table 11. Major woody species of the *Picea jezoensis*–*Abies sachalinensis* forests in Hokkaido (Okitsu 2003). The figures and the symbol '+' in the table indicate Braun-Blanquet cover levels

Region	SH	SH	SH	NH	NH	NH	NH	NH	NH	NH
Running no.*	1	2	3	4	5	6	7	8	9	10
Picea jezoensis	4	4	4	5	5	4	3	4	3	4
Abies sachalinensis	3	1	3	2	3	4	4	3	4	1
Sorbus commixta	3	2	+	+	+	2	1	2	2	·
Acer ukurunduense	1	2	1	+	1	1	2	1	2	·
Betula ermanii	+	2	3	1	2	2	2	2	1	·
Menziesia pentandra	·	+	·	+	+	1	+	·	1	·
Viburnum furcatum	1	·	·	·	·	1	·	·	1	+
Vaccinium smallii	1	·	·	+	+	+	·	·	2	·
Acanthopanax sciadophylloides	+	+	+	·	·	·	·	·	1	·
Acer mono	+	+	1	·	·	·	·	+	·	1
Hydrangea paniculata	+	·	+	·	·	·	·	·	+	+
Ilex rugosa	+	·	·	·	·	·	·	·	·	+
Skimma japonica	+	·	·	·	·	·	·	·	2	+
Prunus ssiori	·	+	·	·	·	·	·	+	·	·
Rubus idaeus	·	+	·	·	+	·	·	·	·	·
Sambucus sieboldiana	·	+	·	·	+	·	·	·	·	·
Euonymus tricarpus	·	+	·	+	+	+	·	·	·	·
Tilia japonica	·	·	1	·	·	·	·	+	·	1
Picea glehnii	·	·	·	·	1	·	·	·	4	·
Daphne miyabeana	·	·	·	·	·	+	+	·	·	·
Kalopanax septemlobus	·	·	·	·	·	·	·	+	·	1
Vaccinium ovalifolium	·	·	·	·	+	·	·	·	2	·
Euonymus macropteris	·	·	·	·	+	·	·	·	+	·
Sasa senanensis	·	·	4	4	4	5	5	5	·	·
Sasa kurilensis	5	4	·	·	·	·	·	·	4	4

* relevés are from the following locations: 1, 2 = Mt. Soranuma, Sapporo (Ito et al. 1979); 3 = Shizunai (Kojima 1982); 4 = R. Ishikari (Tatewaki et al. 1955); 5 = R. Ishikari (Maeda et al. 1977); 6, 7 = R. Tokachi (Kojima 1980); 8 = Mt. Shari (Kojima 1983); 9 = Shirataki (Kojima 1983); 10 = Teshio (Tatewaki & Igarashi 1971)

Table 12. Total numbers of species of *Betula ermanii* forests and the number of species common to northern Japan in two regions of Kamchatka (Okitsu 2002b)

Area	Central and southern Kamchatka	Mt. Dal'nyaya Ploskaya
Total number of species	55	34
Number of species common to northern Japan	48	28
Common species as a percent of the total numbers.	87	82

and disturbance; the ascent of *Larix cajanderi*, however, was stopped by strong wind and heavy snow in the higher mountains, before the thermal limit was reached; only *Pinus pumila* reached a thermal limit. This resulted in the formation of well developed *Pinus pumila* thickets (Fig. 4: 5) between the two different forest limits, i.e. the one set by heavy snow and strong wind, and the other set by temperature.

Wind-exposed dwarf scrub

Dwarf scrub covers the uppermost part of the mountains, on the most wind-exposed sites, at altitudes usually above about 1850 m (Fig. 4: 6); this scrub may also appear topogenically on exposed windy ridges and slopes below 1800 m.

Table 13 shows a floristic comparison of the wind-exposed dwarf scrub on Taisetsu, the treeless heath on Mt. Ebeko, and the alpine tundra on Mt. Dal'nyaya Ploskaya. Taisetsu contains such frequently occurring major species as *Diapensia obovata*, *Arctous alpinus*, *Loiseleuria procumbens*, *Empetrum nigrum*, *Arcterica nana*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea* and *Rhododendron aureum*. Eleven species out of 17 are dwarf shrubs (65 %), and the vegetation on the uppermost parts of these mountains is typical wind-exposed dwarf scrub.

The species composition of the Taisetsu dwarf scrub is more similar to that of the treeless heath on Mt. Ebeko than that of the alpine tundra of Mt. Dal'nyaya Ploskaya. Neither the Taisetsu mountains nor Mt. Ebeko has peculiar high-occurrence species (more than 40 %), but the composition of major species on the two mountains is similar, with *Loiseleuria procumbens*, *Empetrum nigrum*, *Vaccinium uliginosum*, *Rhododendron aureum* and *Arcterica nana*. On the other hand, Mt. Dal'nyaya Ploskaya has 12 species that occur on more than 40 % of sites, out of 25 species listed (48 %). These include *Hedysarum hedysaroides*, *Oxytropis erecta*, *Betula exilis*, *Thalictrum alpinum*, and three Salicaeceae species.

The alpine tundra of Mt. Dal'nyaya Ploskaya is rather different from the vegetation of the Taistsu mountains and Mt. Ebeko. Among other things, Dal'nyaya Ploskaya has *Betula exilis* and *Salix sphenophylla*, which are dominant species in the subarctic tundra subzone (Aleksandrova 1980). Such phytogeographical characteristics of the alpine tundra on Mt. Dal'nyaya Ploskaya suggest that the alpine tundra vegetation is a representative vegetation type in the subarctic tundra subzone and does not correspond to the treeless heath of the highly oceanic sector of the northern boreal subzone.

Okitsu (1996) investigated the geographical distribution of 117 species composing the alpine tundra on Dal'nyaya Ploskaya, in order to confirm its correspondence. Of these 117 species, large numbers are common to the Stanovoye Upland (70), the Chukchi Peninsula (72), and Alaska (81). These three areas all belong to the subarctic tundra subzone (Aleksandrova 1980). Fewer species are common to Mt. Ebeko (45) and the Taisetsu mountains (35), out of the 117 species total.

This comparison suggests that the wind-exposed dwarf scrub on the Taisetsu mountains (and perhaps others of Hokkaido) corresponds to the treeless heath on Mt. Ebeko of the northern Kurils, not only in the physiognomy dominated by dwarf shrubs but also in species composition. This correspondence suggests that the wind-exposed dwarf scrub of Taisetsu is close to the treeless heath developing in the extreme-oceanic sector in the boreal zone.

Table 13. Floristic comparison among the wind-exposed dwarf scrub on the Taisetsu mountains (50 plots: Okitsu 1987b); the treeless heath on Mt. Ebeko, Paramushir, northern Kurils (107 plots: Okitsu et al. 2001); and the alpine tundra of Mt. Dal'nyaya Ploskaya, central Kamchatka (30 plots: Okitsu 1996). The figures in the table show the percent occurrence of the species in plots surveyed in each area. The table shows only major species occurring with at least 40 % frequency in some area (Okitsu 2002b)

Species	Mt. Taisetsu	Mt. Ebeko	Mt. Dal'nyaya Ploskaya
Species common to all three areas			
**Loiseleuria procumbens*	46	83	7
**Empetrum nigrum*	44	89	30
**Vaccinium uliginosum*	42	58	83
**Vaccinium vitis-idaea*	42	7	40
**Rhododendron aureum*	40	35	3
Cnidium ajanense	20	41	3
**Cassiope lycopodioides*	18	61	17
Polygonum viviparum	18	2	77
Hierochloe alpina	16	3	53
Calamagrostis purpurascens	12	80	27
Polygonum bistorta	8	4	47
Species common to Taisetsu and Mt. Ebeko			
**Arcterica nana*	42	81	0
**Rhododendron camtschaticum*	22	41	0
**Agrostis flaccida*	2	43	0
Species common to Taisetsu and Dal'nyaya Ploskaya			
**Arctous alpinus*	48	0	40
**Diapensia obovata*	54	0	17
Pedicularis oederi	12	0	50
Species common to Mt. Ebeko and Dal'nyaya Ploskaya			
Oxytropis revoluta	0	48	0
**Salix arctica*	0	41	17
Carex koraginensis	0	37	70
Species occuring exclusively on Dal'nyaya Ploskaya			
Hedysarum hedysaroides	0	0	100
Oxytropis erecta	0	0	83
Betula exilis	0	0	80
Thalictrum alpinim	0	0	77
Festuca altaica	0	0	67
Anemone sibirica	0	0	60
Saussurea pseudo-tilesii	0	0	60
**Salix sphenophylla*	0	0	57
Sanguisorba officinalis	0	0	57
Poa malacantha	0	0	53
**Salix chamissonis*	0	0	43
**Salix reticulata*	0	0	43

* dwarf shrubs

PHYTOGEOGRAPHICAL RELATIONSHIPS OF THE VEGETATION OF THE UPPER TAISETSU MOUNTAINS: AN OVERVIEW

The phytogeographical correspondence of the vertical zonation on the Taisetsu mountains and the horizontal zonation in the Russian Far East is sunmmarized in Table 14. Four major points emerge from the table:

1. Each of the six vegetation types of Taisetsu corresponds to a particular vegetation type of the cool-temperate or boreal zone in the Russian Far East.

2. The upward sequence of the lower three vegetation types on the Taisetsu mountains, namely *Quercus crispula–Acer mono–Tilia japonica* forest, *Abies sachalinensis*–deciduous broadleaf mixed forest and *Picea jezoensis–Abies sachalinensis* forest, corresponds to the northward sequence of the three vegetation types within the maritime sector of the Russian Far East, namely *Picea koraiensis*–deciduous broadleaf mixed forest, *Pinus koraiensis*–deciduous broadleaf mixed forest and *Picea jezoensis–Abies nephrolepis* forest.

3. The upward sequence of the upper three vegetation types on the Taisetsu mountains, namely *Betula ermanii* forest, *Pinus pumila* thicket and wind-exposed dwarf scrub, does not match the any horizontal sequence in the Russian Far East; in particular it does not match the continental to oceanic to extremely oceanic sectoral gradient within the boreal zone, which is *Larix cajanderi–Pinus pumila* forest, *Betula ermanii* forest and treeless heath.

Strong wind and heavy snowfall in winter in the mountains promote this inconsistency. The *Betula ermanii* forest develops in areas with less strong wind; *Pinus pumila* thickets occupy areas with relatively strong wind and moderate snow; and dwarf scrub appears in the most wind-exposed areas, with strong wind and little snow (Okitsu & Itō 1984).

4. The Taisetsu mountains are located at latitudes even with the southernmost part of the Russian Far East, but the situation of the mountains does not seem easily able to reflect the zonal and sectoral sequences of vegetation types of the Russian Far East. The vertical zonation on the Taisetsu mountains is quite unique, though, in converging

Table 14. Vegetation correspondence between the Taisetsu mountains and the Russian Far East, with bioclimatic zones and sectors

Vertical distribution on the Taisetsu Mtns.		Horizontal distribution of the Russian Far East		
Zone-Sector	Vertical zonation on Taisetsu	Corresponding vegetation of the Russian Far East	Zone	Sector
Vertical zonation within the cool-temperate zone in the martime sector	Wind-exposed dwarf scrub	Treeless heath	Boreal	Extreme-oceanic
	Pinus pumila thickets	*Larix cajanderi–Pinus pumila* forest		Continental
	Betula ermanii forest	*Betula ermanii* forest		Oceanic
	Picea jezoensis–Abies sachalinensis forest	*Picea jezoensis–Abies nephrolepis* forest (southern)		Maritime
	Abies sachalinensis–deciduous broadleaf mixed forest	*Pinus koraiensis*–deciduous broadleaf mixed forest (northern)	Cool-temperate	
	Quercus crispula–Acer mono–Tilia japonica forest	*Picea koraiensis*–deciduous broadleaf mixed forest (southern)		

to include all the possible combinations of two zones and six sectors in the Russian Far East, despite the different ordering.

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