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Vegetation of *Alnus sinuata* thicket of the Chugach Mountains, southeastern Alaska—Its classification and ecogeographical interpretations

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Abstract: Vegetation of Sitka alder (*Alnus sinuata*) thickets occurring in the subalpine environment in the Thompson Pass area, the Chugach Mountains, Alaska, was studied. On the southern slopes of the Chugach Mountains facing the Pacific Ocean, the subalpine zone develops in an altitudinal range approximately from 100 m up to 800 m above sea level. There a complex of shrub thickets of *Alnus sinuata* and open dwarf shrub meadows best represented the vegetation. A total of 52 relevés were established to describe the vegetation structure; 32 relevés representing the *Alnus sinuata* thicket and 20 relevés the open dwarf shrub meadow. For each relevé, all the vascular plants were listed and their coverage was assessed. Vegetation synthesis tables were constructed. Vegetation was classified according to phytosociological methods. Two plant associations, Calamagrostido canadensis–Alnetum sinuatae and Empetro nigri–Vaccinietum caespitosi, were identified; the former association represented the *Alnus sinuata* thickets and the latter open dwarf shrub meadow communities. The ecogeographical status of the *Alnus sinuata* thicket is discussed in relation to other subalpine biomes of the northern Amphi-Pacific region. It is concluded that the *Alnus sinuata* thicket represents a mild winter but snowy oceanic subalpine environment of the southern slopes of the Chugach Mountains, Alaska.

key words: *Alnus sinuata* thicket, Chugach Mountains, Alaska, ecogeography, subalpine biome, syntaxonomy

Introduction

The oceanic boreal biome of the northern hemisphere is represented by birch forests and thickets and, on some occasions, by alder thickets or dwarf pine thickets. Some ecological homologies of such vegetations are recognized throughout northwestern Europe, northeastern and northwestern North America, and northeastern Eurasia (Hämet-Ahti and Ahti, 1969; Ahti, 1980).

On the southern coast of Alaska, an extensive development of *Alnus sinuata* (Sitka alder) thickets between the forest line and true alpine zone is a characteristic feature (Griggs, 1936; Daubenmire, 1953; Mitchell, 1968; Talbot *et al*., 2004). Such thickets have been designated as the High Brush Ecosystem (Joint Federal-State Land Use

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Planning Commission for Alaska, 1973) or Closed Tall Alder Shrub (coded as II.B.1.b.) of Viereck *et al.* (1992). Talbot *et al.* (2004) distinguished four community types for the alder thickets in southwestern Alaska covering a geographical range from the western tip of the Alaska Peninsula to the Kenai Peninsula. They are *Alnus viridis–Calamagrostis canadensis* thicket, *Alnus viridis–Rubus spectabilis* thicket, *Alnus viridis–Athyrium filix-femina* thicket, and *Alnus viridis–Oplopanax horridus* thicket.

On the southern slopes of the Chugach Mountains, near the Gulf of Alaska, extensive *Alnus sinuata* thickets cover mountain slopes at altitudes ranging approximately from 100 m to 800 m above sea level (Fig. 1). The thickets are dominated by *Alnus sinuata*, which characteristically exhibits a decumbent growth form 3–5 m tall. The thickets are intermixed with open dwarf shrub meadows to form a mosaic landscape of *Alnus* thickets and open meadow. Such a landscape appears to represent the subalpine zone of the southern slopes of the Chugach Mountains. The *Alnus* thickets may be regarded as one of the representatives of the subalpine biomes of the northern Amphi-Pacific region, which may be defined as approximately the circum-Pacific rim region

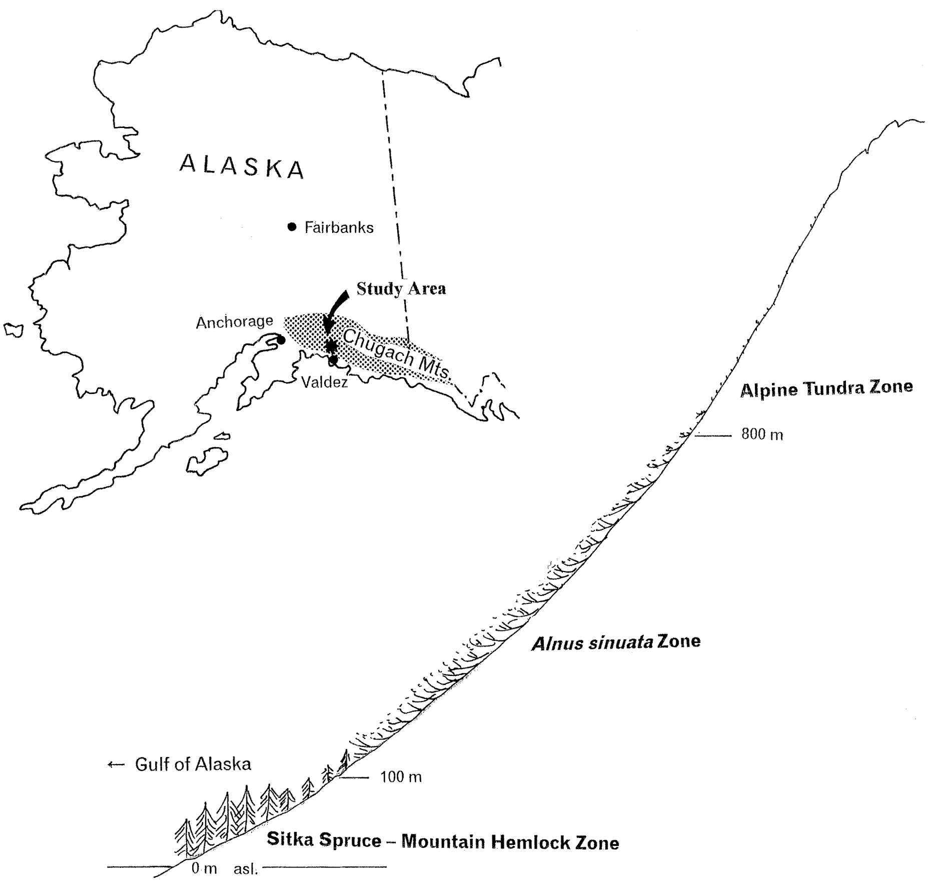

Fig. 1. Location of the study area and a schematic illustration of altitudinal range of the *Alnus sinuata* thickets.

north of 40°N latitude.

This study attempts to describe and classify the *Alnus sinuata* thickets and associated vegetation of the Chugach Mountains following the phytosociological methods and procedures and to present some ecogeographical interpretations in the context of northern Amphi Pacific regions.

Study area

The present study was conducted in southeastern Alaska, on the south slopes of the Chugach Mountains, near Thompson Pass, along the Richardson Highway. This area is located approximately 50 km north of Valdez. Its latitude is approximately 61°10′ and longitude 145°45′W. Elevation ranges from *ca.* 100 m to 800 m above sea level at the summit of Thompson Pass.

There is no information properly representing the climate of the study area. Only the weather records of Valdez (Fig. 2) may approximate the climatic characteristics of the area. Based on the weather record and taking the normal temperature lapse rate into account, the climate of the area, which is 100 m to 800 m higher in elevation than Valdez, appears to be a cool maritime subalpine climate with mean annual temperature *ca.* 0–1°C, mean monthly temperature of the warmest month *ca.* 10–11°C, and that of the coldest month *ca.* −7~−8°C. Annual total precipitation is about 1800 mm, of which 50–60% comes in the form of snow. Usually, September is the wettest month. Snow starts to accumulate in September and stays until July. According to Thornthwaite's (1948) calculation, more than 1200–1300 mm of annual water surplus may take place. Conrad's continentality index (Conrad, 1946) is *ca.* 20 at Valdez, which indicates that the climate is highly oceanic. The climate may be classified as Dfc of Köppen.

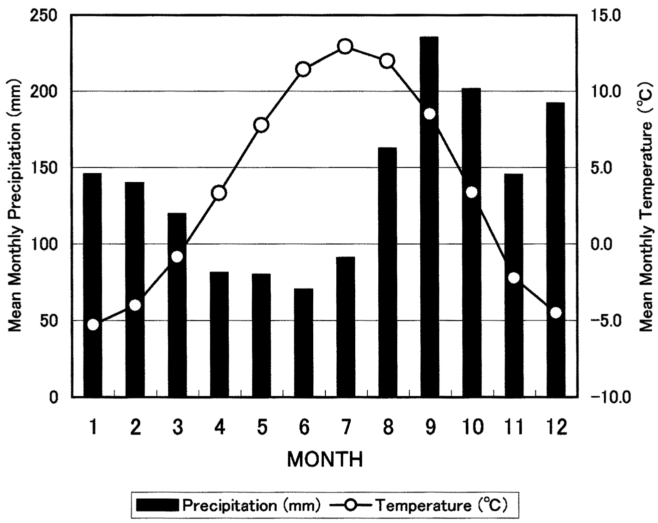

Fig. 2. Climatic characteristic of the area as represented by weather record at Valdez. Data source: Climate of the world, 2003. (http: //www.climate-zone.com/climate/united-states/alaska/valdez)

Fig. 3. *Alnus sinuata* thickets covering an extensive area on the mountain slopes of the Chugach Mountains.

Fig. 4. Trunks of *Alnus sinuata*, showing their typical gnarled growth habit.

Fundamental geology consists of Mesozoic sandstone, shale and conglomerates, which form the foundation of the mountains. However, surficial geology may be represented by extensive occurrence of glacial deposits. The majority of the terrains was once covered by glaciers and became exposed since the end of the last glaciation (Johnson and Hartman, 1969). There are still numerous extant glaciers in the Chugach Mountains, some of which approach close to the sea. Topography is steep and rugged. Soils are generally shallow and not well matured. Rock outcrops smoothened by glacial activity are recognized everywhere.

The vegetation of the area is best represented by dense thickets of *Alnus sinuata.* However, at the base of the mountain slopes near sea level, there are well-developed forests dominated by *Picea sitchensis* occasionally mixed with *Tsuga mertensiana.* Such forests occur from sea level up to 100 m in elevation, where the forests are replaced by the *Alnus sinuata* thickets. The thickets extend upward to approximately 800 m above sea level (Fig. 3). The thickets are frequently intermixed with open dwarf shrub meadows of *Vaccinium caespitosum*, *Empetrum nigrum*, *Artemisia arctica*, and *Carex spectabilis.* The vegetation physiognomy, therefore, consists of mosaics of *Alnus sinuata* thickets and open dwarf shrub meadows. Because such a vegetation complex appears to represent the subalpine zone of the south slopes of the Chugach Mountains, the elevational range of the subalpine zone there may extend from 100 m to 800 m above sea level. Above this elevation, vegetation abruptly changes to the alpine tundra represented and characterized by *Salix arctica*, *Loiseleuria procumbens*, *Vaccinium uliginosum*, *Hierochloe alpina*, *Saxifraga bronchialis*, *Silene acaulis*, and *Leutkea pectinata.*

Methods and procedures

Basically the relevé method was employed to analyze and describe the vegetation structure of the *Alnus sinuata* thickets and open meadows. Relevé is a basic sampling stand, customarily used in phytosociology, in which all the species are listed and their coverage is evaluated. For more details, refer to Mueller-Dombois and Ellenberg (1974). After extensive reconnaissance of the area, relevés of 5 m × 5 m in size were set up. All the vascular plants in the relevés were listed separately for their layer and their coverage was assessed in percentage. Those values were later converted to Domin-Krajina's species significance class (Krajina, 1933). Species recorded were scrupulously checked for their identification. Based on the relevés described in the field, vegetation synthesis tables were constructed separately for the *Alnus sinuata* thickets and open dwarf shrub meadows, and dominance value (DV) was calculated for each species as:

$$DV = ((\sqrt{ASS \times F}) / (\sqrt{10})) \times 100,$$

where DV: dominance value, ASS: average species significance of the species,
F: frequency = number of relevés with the species/total number of relevés.

Characteristic species were then identified. For the *Alnus sinuata* thickets, similarity index among the relevés was calculated according to Sørensen (1948) as modified by Dahl (1956) and a dendrogram showing clustering of the relevés was constructed. Based on the tables and dendrogram, the phytosociological status of the vegetation was determined.

Results and discussion

Vegetation structure and phytosociological classification

The field investigation was conducted in August 2001. A total of 52 relevés were established. Of them, 32 relevés (A1–A32) represented the *Alnus sinuata* thickets and 20 relevés (B1–B20) the open dwarf shrub meadows. Two vegetation synthesis tables were constructed (Appendix I and II). Appendix I shows the vegetation structure of *Alnus* thicket and Appendix II that of open dwarf shrub meadow.

As shown in Appendix I, *Alnus sinuata* thicket is characterized by the presence of such species as: *Alnus sinuata*, *Calamagrostis canadensis*, *Epilobium angustifolium*, *Trientalis europea*, *Vaccinium caespitosum*, and *Spiraea beauverdiana.* These are species showing high dominancy and constancy. Other major constituents include: *Athyrium felix-femina*, and *Veratrum eschcholtzii.* Vegetative cover is high as ground is completely covered by vegetation. The dominant shrub species *Alnus sinuata* characteristically shows a prostrating growth form. Its trunks are crooked and gnarled, and entangled to form dense almost impenetrable thickets (Fig. 4). Crown height is 4 to 6 m tall and stem diameter at the base is approximately 3 to 7 cm. Canopy closure is nearly 100% in most cases. Under the canopy, low shrubs such as *Vaccinium caespitosum*, and *Spiraea beauverdiana*, show a high dominance. The herb layer is well developed, showing luxurious growth of herbaceous species. *Calamagrostis canadensis* and *Epilobium angustifolium* dominate the layer. Species diversity is comparatively high as the average number of species/relevé is 12.5. This kind of the thickets may be regarded as the "cold deciduous shrubland"(coded as IIIB4b(1)) of Mueller-Dombois and Ellenberg (1974).

According to the phytosociological method, for the *Alnus sinuata* thickets of the Chugach Mountains, one plant association with four subassociations was identified. It is Calamagrostido canadensis–Alnetum sinuatae (ass. nov.) with subassociations of Cinnetosum latifoliae, Gymnocarpietosum dryopteridis, Ribetosum tristis, and Rubetosum arcticae. Figure 5 presents the clustering of the 32 relevés described from the *Alnus sinuata* thicket. It clearly shows four groupings of relevés that correspond to the four subassociations. The Calamagrostido canadensis–Alnetum sinuatae is comparable with

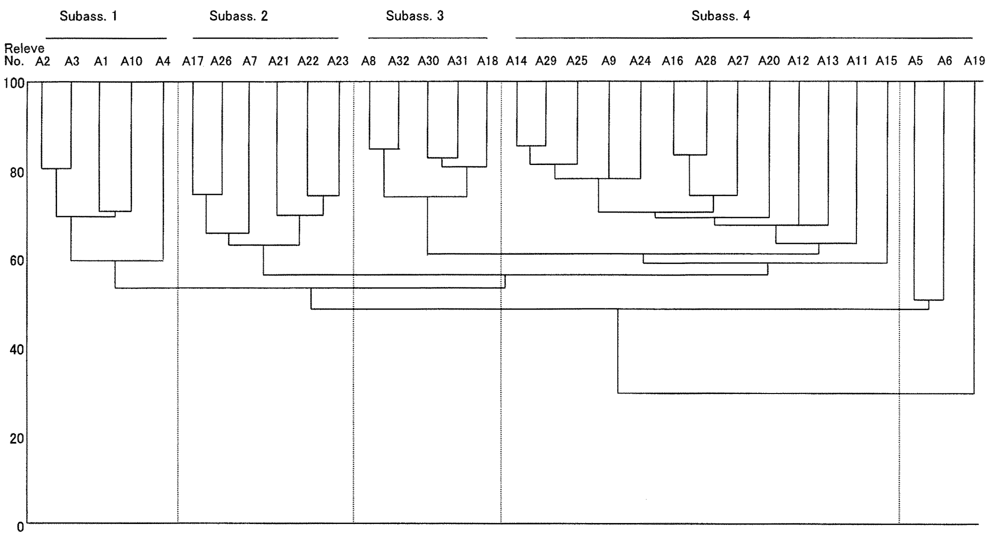

Fig. 5. A dendrogram showing clustering of the relevés representing *Alnus sinuata* thickets. The dendrogram clearly shows the differentiation of the four subassociations. Subass. 1: Cinnetosum latifoliae, Subass. 2: Gymnocarpietosum dryopteridis, Subass. 3: Ribetosum tristis, Subass. 4: Rubetosum arcticae.

the *Alnus viridis–Calamagrostis canadensis* community type of Talbot *et al.* (2004).

The vegetation structure of the open dwarf shrub meadows is shown in Appendix II. Such meadows develop generally forming open patches intermingled with *Alnus thickets.* The meadow vegetation is characterized by the presence of such species as: *Vaccinium caespitosum*, *Empetrum nigrum*, *Artemisia arctica*, *Carex spectabilis*, *Cornus suecica*, *Spiraea beauverdiana*, and *Festuca altaica. Vaccinium caespitosum* is the dominant and contributes greatly to the formation of the vegetative cover. The meadows usually develop in somewhat depressed habitats where snow persists longer, resulting in a short vegetative season. Soils exhibited peaty deposits at the top of the solum. On the other hand, meadows may develop on exposed localities surrounding large rock outcrops where snow does not accumulate. In such habitats soils are regosolic with shallow lithic contacts. The open meadow vegetation may be classified as "cold deciduous dwarf-thicket" (coded IVB4) of Mueller-Dombois and Ellenberg (1974). For the meadow vegetation, one association Empetro–Vaccinietum caespitosi with two variations was recognized. They were: *Arctostaphylos alpina* Variant and *Rubus arctica* Variant.

Table 1 summarizes the phytosociological classification of the *Alnus sinuata* thickets and the open dwarf shrub meadows. As shown in the table, the subalpine vegetation of the south slopes of the Chugach Mountains is physiognomically divided into two formation types, *i.e.*, 1) shrub thicket and 2) open dwarf shrub meadow. The shrub thicket vegetation may be floristically further divided into four subtypes at the level of subassociation. The open meadow type may be further divided into two subtypes at the level of variant. In this manner, the vegetation of the study area is well distinguished physiognomically as well as floristically and each of the units may reflect particular habitat conditions as discussed in the following chapter.

Table 1. Hierarchy of syntaxonomy of *Alnus sinuata* thicket in the Chugach Mountains, Alaska.

1) *Alnus sinuata* thicket	
Calamagrostido canadensis – Alnetum sinuatae (Ass. nov.)	Cinnetosum latifoliae (Subass. nov.)
	Gymnocarpietosum dryopteridis (Subass. nov.)
	Ribetosum tristis (Subass. nov.)
	Rubetosum arcticae (Subass. nov.)
2) Open dwarf shrub meadow vegetation	
Empetro – Vaccinietum caespitosi (Ass. nov.)	*Arctostaphylos alpina* Variation
	Rubus arcticus Variation

Relations of the vegetation units and microhabitat conditions

Table 2 shows the relation of the vegetation units discussed above and microhabitat conditions. *Alnus sinuata* thickets, *i.e.*, Calamagrostido canadensis–Alnetum sinuatae, develop generally in gentle topography of mountain slopes with relatively deep soils. Reflecting subtle differences in habitat conditions, four subassociations are differentiated in such a manner that in comparatively moist habitats with deep soils the subassociation Cinnetosum latifoliae develops, while in more or less mesic habitats the subassociation Gymnocarpietosum dryopteridis, and in comparatively better drained habitats the

Table 2. Vegetation units and microhabitat conditions.

Microhabitat conditions	Physiognomy	Vegetation unit
xeric knolls	open dwarf shrub meadow	*Arctostaphylos alpina* Variant
well drained habitat	*Alnus sinuata* thicket	Ribetosum tristis
moderately drained habitat		Gymnocarpium dryopteridis
moist habitat		Cinnetosum latifoliae
open patches and canopy fringes		Rubetosum arcticae
depressed topography	open dwarf shrub meadow	*Rubus arcticus* Variant

subassociation Ribetosum tristis. The last subassciation, Rubetosum arcticae, occurs at fringes and/or in small openings within the *Alnus sinuata* thickets or in places where canopy coverage becomes low, hence, light conditions are better. The floristic characteristic of this subassociation shows some affinity to open meadows.

Open meadow vegetation, *i.e.*, Empetro–Vaccinietum caespitosi, generally develops in somewhat depressed topography between *Alnus sinuata* thickets. Those habitats collect more snow to provide a shorter growing season similar to the alpine environment at higher elevations. The meadow vegetation includes some alpine elements in the floristic structure. Examples include *Arctostaphylos alpina*, *Anemone narcissiflora*, *Artemisia arctica*, *Leutkea pectinata*, *Loiseleuria procumbens*, and *Salix arctica.* And yet, the presence of such species as *Cornus suecica*, *Linnaea borealis* and *Festuca altaica* suggests that the environment is not yet true alpine but transitional nature from subalpine to alpine.

Of the two variants, the *Arctostaphylos alpina* variant occurs in relatively better-drained habitats with shallow soils such as on top of knolls, ledges, and upper slopes. The habitat conditions may be characterized by the presence of such species as *Arctostaphylos alpina* and *Andromeda polifolia.* The presence of the latter species indicates some degree of peat accumulation on the soil surface, particularly in small depressions. The *Rubus arcticus* variant best represents the open meadow communities. It develops in slightly depressed topography where snow stays long and soils are generally moist with raw humus accumulation at the top of the solum.

Alnus sinuata is known to be a species that often plays an important role in early succession after deglaciation widely in Alaska (Griggs, 1936; Crocker and Major, 1955; Veblen and Alaback, 1996). However, in the present study area, *Alnus* thickets represent a climatic climax vegetation because there is no tree species competing with *Alnus sinuata* in the region and it occurs generally in mesic habitats to form a zonal vegetation.

Ecogeographical status of *Alnus sinuata* thickets

In general, the subalpine zone is defined as the zone developing above the closed forest and below the true alpine zone that lacks trees. In northern high latitudes, however, the distinction between subalpine and subarctic is not clear. Elevations of the subalpine zone descend northward eventually to near sea level to merge with the subarctic zone. In northern high latitudes, vegetation structures of the subarctic and subalpine are also difficult to distinguish.

In order to determine the ecological characteristics of *Alnus sinuata* thickets in the Chugach Mountains, the vegetation structure and environmental characteristics were compared with those elsewhere in the northern Amphi-Pacific region. Eight locations were selected. Table 3 tabulates the eight locations and their biome types as well as elevation ranges. The vegetation structures of the eight locations were compared for occurrences and constancy of major component species (Table 4). Constancy was rated for each location in five classes (V~I) following the phytosociological method (Braun-Blanquet, 1965). In the table, however, when vicariants were present, such species were treated as the same taxa. A vicariant is defined here as a counterpart species occurring in different regions but taxonomically close and having a similar life form and ecologically in an equivalent status. For example, *Cassiope mertensiana* occurring in the Pacific Northwest is considered to be a vicariant to *Cassiope tetragona* growing in the interior and northern North America.

Based on Table 4, the vegetation similarity indices of Sørensen (1948) as modified by Dahl (1956) were calculated for the eight locations. Based on the indices, the eight locations were then projected on an ordination coordinate following the Bray-Curtis method (Bray and Curtis, 1957) (Fig. 6). In the figure, the eight locations appear to be clustered into five groups as: Group I incorporating locations 5 and 6; Group II consisting of locations 1, 2 and 3; and Groups III (locations 4), IV (location 7), and V (location 8). Group I represents the subalpine/subarctic biome of interior Alaska-

Table 3. Comparison of altitudinal ranges of the subalpine/subarctic biomes of northern Amphi-Pacific regions.

No.	Location	Biome	Lower limit (m asl)	Upper limit (m asl)	Altitudinal range (m)	Data source
1.	Toyama, central Japan	*Pinus pumila* zone	2300	3000	700	Kojima, S. (1991)
2.	Hokkaido, northern Japan	*Pinus pumila* zone	1500	2200	700	Kojima, S. (1979)
3.	East Mountains, Kamchatka, Russia	*Pinus pumila* zone	300	900	600	Kojima, S. (1997)
4.	Chugach Mountains (south slopes), Alaska, U.S.A.	*Alnus sinuata* zone	100	800	700	present study
5.	Brooks Range (south slopes), Alaska, U.S.A.	birch-willow zone	700	1300	600	unpublished data
6.	Ogilvie Mountains, Yukon, Canada	spruce-birch-willow zone	900	1600	700	Kojima, S. (1978)
7.	Lake Louise, Rocky Mountains, Alberta, Canada	Engelmann spruce – subalpine fir zone	1600	2200	600	Kojima, S. (1980)
8.	Coast Mountains, British Columbia, Canada	mountain hemlock zone	900	1500	600	Brooke, R.C. *et al.* (1970)

Table 4. Vegetation structure representing eight subalpine/subarctic biomes of the northern Amphi-Pacific regions. Roman numerals indicate constancy class. Only those species exhibiting constancy class more than III in any of the eight biomes are included.

Location*	1	2	3	4	5	6	7	8
Taxa /Data source**	i	ii	iii	iv	v	vi	vii	viii
Pinus pumila	V	V	V	.	.	.	.	.
Rhododendron aureum	III	V	I	.	.	.	.	.
Rubus pedatus	IV	III	.	II	.	.	.	V
Cornus canadensis	III	III	.	.	.	.	.	.
Vaccinium vitis-idaea	V	V	V	.	V	V	.	.
Empetrum nigrum	III	III	V	I	V	V	IV	.
*Vaccinium 1)****	III	I	III	V	V	.	IV	V
Linnaea borealis	I	I	III	I	.	.	II	.
Schizocodon soldanelloides	III	.	.	.	.	.	.	.
Trientalis europaea	II	.	V	.	.	.	.	.
Sasa krurilensis	III	III	.	.	.	.	.	.
*Gaultheria 2)****	III	.	.	.	.	.	.	IV
*Ledum 3)****	.	III	V	.	III	.	IV	.
Spiraea beauverdiana	.	II	II	IV	.	.	.	.
Calamagrostis canadensis	.	I	III	V	I	III	.	.
Larix gmelinii	.	.	III	.	.	.	.	.
*Alnus 4)****	.	.	I	V	.	.	.	.
*Betula 5)****	.	.	I	V	V	II	.	.
Epilobium angustifolium	.	.	.	V	.	.	.	.
Rubus arcticus	.	.	.	III	.	.	.	.
Athyrium filix-femina	.	.	.	III	.	.	.	I
Veratrum escholtzii	.	.	.	III	.	.	.	II
Artemisia arctica	.	.	.	II	.	V	.	.
Erigeron peregrinus	.	.	.	I	.	.	III	V
Phyllodoce empetriformis	.	.	.	I	.	.	.	V
Lycopodium sitchensis	.	.	.	I	.	.	.	II
Salix pulchra	.	.	.	.	V	V	.	.
Carex lugens	.	.	.	.	V	IV	.	.
Petasites frigidus	.	.	.	.	V	V	.	.
Valeriana capitata	.	.	.	.	V	V	.	.
Anemone narcissiflora	.	.	.	.	V	.	.	.
Polemonium acutiflorum	.	.	.	.	IV	.	.	.
Polygonum bistorta	.	.	.	.	III	I	.	.
Pedicularis capitata	.	.	.	.	III	.	.	.
Polyygonum viviparum	.	.	.	.	I	I	V	.
Luzula parviflora	.	.	.	.	.	III	.	.
Abies lasiocarpa	.	.	.	.	.	.	V	.
Picea engelmannii	.	.	.	.	.	.	V	.
Potentilla fruticosa	.	.	.	.	.	.	IV	.
Lonicera involucrata	.	.	.	.	.	.	III	.
Salix barratiana	.	.	.	.	.	.	III	.
Arctostaphylos rubra	.	.	.	.	.	.	III	.
Menziesia ferruginea	.	.	.	.	.	.	III	V
*Cassiope 6)****	.	.	.	.	.	.	III	III
Pedicularis bracteata	.	.	.	.	.	.	V	.
Tsuga mertensiana	.	.	.	.	.	.	.	V
Cladothamnus pyrolaeflorus	.	.	.	.	.	.	.	V
Chamaecyparis nootkatensis	.	.	.	.	.	.	.	V
Leutkea pectinata	.	.	.	.	.	.	.	III
Blechnum spicantha	.	.	.	.	.	.	.	III

* Location

1: central Japan, 2: northern Japan, 3: Kamtchatka, Russia, 4: Chugach Mts., Alaska, 5: Brooks Range, Alaska, 6: Ogilvie Mts, Yukon, 7: Rocky Mts., Canada, 8: Coast Mts, Canada

** Data source

i: Kobayashi (1971), Kojima (2003),
ii: Okitsu & Ito (1984), Okitsu (1987), Kojima *et al.* (1988),
iii: Kojima's field notes,
iv: the present study,
v: Kojima's field notes,
vi: Kojima (1973, 1978),
vii: Corns & Kojima (1977), Kojima (1984), Kojima's field notes,
viii: Brooke *et al.* (1970)

*** Vicariant relations

1) *Vaccinium ovalifolium/membranaceum/caespitosum/uliginosum*
2) *Gaultheria miqueliana/humifusa*
3) *Ledum palustre/groenlandicum*
4) *Alnus maximowicziana/sinuata*
5) *Betula glandulosa/nana*
6) *Cassiope tetragona/mertensiana*

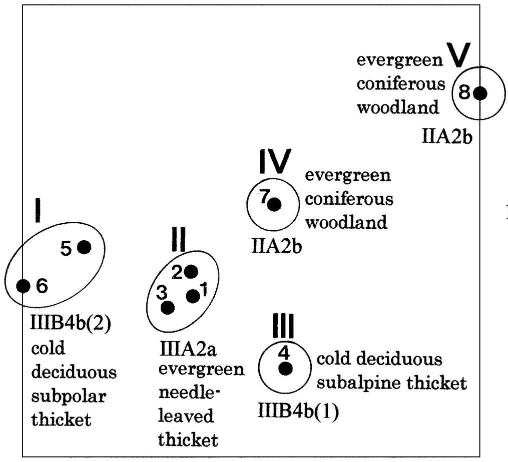

Fig. 6. Relations of eight biomes of the northern Amphi-Pacific region as projected in an ordination coordinate based on vegetation structure. Five groups are well distinguished, each of which represents different biome and physiognomy. Their physiognomic-ecological classification types and codes shown in the diagram follow Mueller-Dombois and Ellenberg (1974).

Yukon, Group II the northeastern Eurasian *Pinus pumila* scrub-forest biome, and Groups III, IV, and V the subalpine biomes of the Chugach Mountains, the Canadian Rocky Mountains, and the west slopes of the Coast Mountains of British Columbia, respectively. From the diagram, obviously locations 5 and 6 show moderate closeness of vegetation, so do locations 1, 2 and 3. On the other hand, the subalpine vegetations of the Chugach Mountains (location 4), the Rocky Mountains, (location 7) and the west coast (location 8) exhibited clear distinctions from each other. Thus, *Alnus* thickets of the Chugach Mountains are not necessarily close to any other vegetation of the northern Amphi-Pacific region from the vegetation structure point of view.

In terms of physiognomy, according to the physiognomic-ecological classification system of Mueller-Dombois and Ellenberg (1974), Group I was classified "cold-deciduous subpolar thicket" coded as IIIB4b(2). This group is characterized by vegetation of caespitose nanophanerophytes forming extensive shrub thickets, hence, lacks tree occurrence. The other four groups, on the other hand, were basically vegetation with tree occurrences of reptant microphanerophytic nature with prostrating and creeping trunks. Of them, Group II was classified "evergreen needle-leaved thicket" coded as IIIA2a; Group III "cold deciduous subalpine thicket" coded as IIIB4b(1); and both Groups IV and V were "evergreen coniferous woodland" coded as IIA2b.

In order to compare environmental characteristics of the biomes, climatic data were obtained and compared for the eight locations (Table 5). The climatic characteristics were numerically graded on a relative scale and their similarities were then calculated by the same method to that used for calculating the vegetation similarity. Based on the similarity indices, eight locations were diagrammatically projected in an ordination coordinate (Fig. 7). In the diagram, the eight locations seemed to be somewhat aligned along a straight line. Then a regression line of the eight locations and its equation were also obtained, $Y = 42.8 - 0.982X$ with $r = 0.98$.

In the figure, the eight locations may be grouped into two clusters (cluster I and II). Cluster I consists of locations 1, 2, 3, 4, 7, and 8. It appears to represent true subalpine biomes of various regions of the northern Amphi-Pacific region. Cluster II consisting of

Table 5. Climatic characteristics of eight locations in the northern Amphi-Pacific region.

Location No.	1	2	3	4	5	6	7	8
Biome:	subalpine	subalpine	subalpine	subalpine	subarctic	subarctic	subalpine	subalpine
Region:	Toyama	Hokkaido	Kamtchatka	Chugach	Brooks	Ogilvie	Rocky	West Coast
Country:	Japan	Japan	Russia	USA	USA	Canada	Canada	Canada
Representing elevation (m asl):	2500	1800	500	600	1000	1200	1900	1200
Data extraporated from the records at:	Toyama	Asahikawa	Petropablovsk-Kamchatsky	Valdez	Arctic Valley	Dempster	Lake Louise	Vancouver
Mean annual temperature (°C)	-0.5	-2.6	-1.4	0.4	-11.2	-7.4	-2.3	3.2
Kira's Warmth Index (month>5°C)	15.1	15.9	10.1	12.8	13.6	10.9	11.9	18.2
Kira's Coldness Index (month <0°C)	45.6	71.3	49.1	33.6	163.5	117.7	63.6	10.7
Conrad's continentality index	42	47	22	20	64	53	39	16
Estimated total snowfall (cm)	1150	460	450	820	100	240	450	660
Snow/total precipitation (%)	50	52	49	50	44	54	63	62
Actual/potential evapotranspiration*	100	100	100	100	60	78	98	84
Annual water surplus (mm/yr)*	1969	320	575	1256	5	164	390	693

* calculated with Thornthwaite

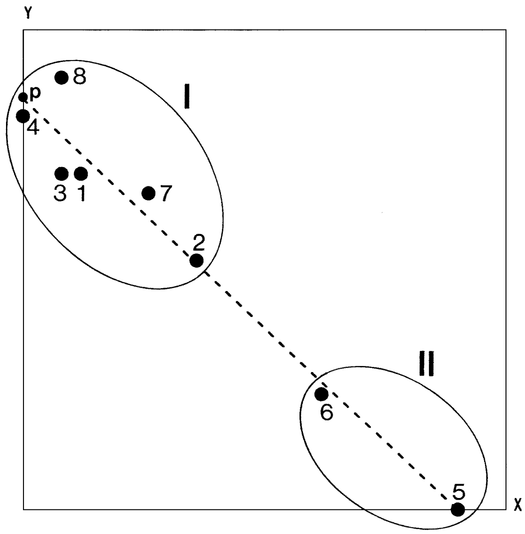

Fig. 7. Relations of eight biomes of the northern Amphi-Pacific region as projected in an ordination coordinate based on climatic characteristics. The dotted line is a regression line derived from the eight points representing the biomes. The eight biomes are grouped into two clusters I and II. Cluster I represents a group of subalpine biomes, and II the subalpine/subarctic biome of the northern Amphi-Pacific region.

locations 5 and 6 represents the subalpine/subarctic biome of interior Alaska-Yukon. Such a differentiation suggests that the subalpine/subarctic biome of interior Alaska-Yukon is considerably different from the true subalpine biomes in terms of climatic characteristics. The next question is what factor accounts for this difference.

In order to identify key factors, which dictate the differentiation and grouping of the eight locations, the abscissas of the eight locations on the regression line were calculated. Then distances from the upper left end point of the regression line (point **p** in Fig. 7) to the abscissas were obtained. Correlation coefficients were then calculated between the distances and the climatic factors shown in Table 6. The highest correlation coefficient was obtained for Kira's coldness index (0.988), followed by mean annual temperature (−0.974) and Conrad's continentality index (0.914). The arrangement and relative positions of the eight locations may be explained by these three factors. Other

Table 6. Correlation coefficients of the eight climatic factors with the regression line.

Mean annual temperature	-0.97
Kira's warmth index	-0.21
Kira's coldness index	0.99
Conrad's continentlity index	0.91
Estimated total snow fall	-0.49
Snow/total precipitation	0.46
Actual /potential evapotransipration	-0.27
Annual water surplus	-0.63

factors did not show any significance at the level of $p < 0.05$.

From the correlation, the differentiation of the two clusters seemed to have been caused principally by mean annual temperature, winter temperature, and continentality of climate. Cluster I represents biomes which developed under a climate of comparatively higher mean annual temperature, particularly a milder winter, and much less continental character. Cluster I, in fact, consists of locations close to sea coast except location 7 which represents the subalpine biome of the Rocky Mountains. Cluster II, on the other hand, included biomes which developed under a climate of substantially lower mean annual temperature, very cold winter, and highly continental nature. Indeed, cluster II (locations 5 and 6) represents the subalpine/subarctic biome of interior Alaska-Yukon. For both clusters, summer temperature appeared not to be a significantly contributing factor.

From the vegetation structure shown in Table 4 and Fig. 6, biomes representing various locations of the northern Amphi-Pacific region are well differentiated from each other. However, from the climatic point of view as discussed above and shown in Fig. 7, the biomes are clearly divided into two types (clusters I and II); one (cluster I) representing oceanic and the other (cluster II) interior continental environment. The *Alnus* thicket representing subalpine biome of the Chugach Mountains is included in the cluster I. Even within the cluster, it is situated in a highly oceanic climate. Indeed, Conrad's continentality index is 20 for the Chugach Mountains, which is the second lowest after the west coast of Canada. It may be concluded that *Alnus* thickets of the Chugach Mountains are actually a manifestation of the highly oceanic subalpine environment of the northern west coast of North America.

Hämet-Ahti (1981) proposed a scheme to subdivide the boreal zone based on latitudinal (thermal) and longitudinal (continentality) gradients. This scheme was further elaborated by Tuhkanen (1984), in which Tuhkanen designated the west coasts of the Eurasian and North American continents as areas of oceanity sectors of O_3 to O_2 of perhumid province. These are the areas, indeed, where climax vegetation is represented by scrubby thickets of *Betula pubescens* in case of Fennoscandia or of *Alnus sinuata* in case of northwestern North America. Far northeastern Eurasia from the southern half of the Kamchatka Peninsula south to eastern Hokkaido, including most of the Kuril Islands is also characterized by a highly oceanic climate, *i.e.*, oceanity sector O_2 of perhumid province (Tuhkanen, 1984). This is the area where scrubby thickets of *Pinus pumila* represent the climax vegetation.

These three regions of northern high latitudes may be considered to represent ecological homology as pointed out by Hämet-Ahti and Ahti (1969). The essential common feature throughout the three regions is establishment of scrubby thicket vegetation in a highly oceanic climate. Watanabe (1979) also stated that in northeastern Asia, subarctic summer green forests, mainly of *Betula ermanii* and occasionally of *Alnus maximowiczii*, are well developed in a cool oceanic climate.

Another important factor is orography. All three regions are characterized by mountainous topography. Great mountain ridges form backbones of the regions. This implies that, in conjunction with the highly oceanic climate, the windward slopes of the mountains will receive considerable snow, as the precipitation tends to concentrate in winter. Such a high amount of snow discourages tree growth. Of tall woody species, only those having a prostrating growth habit may survive under such a condition eventually to form scrubby thickets named "cold deciduous thicket" or "evergreen needle-leaved thicket" by Mueller-Dombois and Ellenberg (1974). The *Alnus sinuata* thickets of the Chugach Mountains may be regarded as a good example of such cases.

In the Kuril Islands and northern Japan, a different but systematically close species, *Alnus maximowiczii*, occurs commonly and forms extensive shrub thickets occasionally (Tatewaki, 1927, 1939, 1958; Watanabe, 1979; Okitsu *et al*., 2001). However, I consider that *Alnus maximowiczii* will not be a final species to constitute climax vegetation because it will not compete successfully with *Pinus pumila* due to its low shade tolerance. It appears only to thrive in a relatively early stage of succession in the volcanic habitats that are quite extensive in the region, and as the soil develops well then *Pinus pumila* becomes established, replacing *Alnus maximowiczii.*

Concluding remarks

The *Alnus sinuata* thickets of the Chugach Mountains develop under a climate of very low continentality with Conrad's index of 20 at Valdez, that is the second lowest after the west coast of British Columbia, Canada. In other words, it occurs under a highly oceanic condition of climate. Annual snowfall is great, estimated at 824 cm. Water surplus is very high (1256 mm/year). As calculated from the weather record of Valdez, the Dfc climate of Köppen's classification extends upwards to *ca.* 600–700 m asl where it is replaced by the ET type climate. Considering the slope aspect effect, the upper limit of the *Alnus* thickets appears approximately to coincide with the boundary between Dfc and ET types of climate. Thus, *Alnus sinuata* thickets represent the subalpine biome of the Chugach Mountains, which develops under a highly oceanic snowy but winter-mild climate of the northern Amphi-Pacific region and consists of vegetation well-adapted to such an environment.

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Appendix I. Vegetation structure and synthesis of Calamagrostido canadensis–Alnetum sinuatae.

Series No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Releve No.	A1	A2	A3	A4	A10	A7	A26	A21	A22	A23	A17	A8	A18	A30	A31
Aspect	S30E	S20W	S30W	N10E	N40W	S20W	due N	S15E	S30W	E	S30E	due S	S45E	knoll	knoll
Slope degree	5	5	8	5	8	10	10	8	5	10	3	8	5	—	—
Calamagrostido canadensis - Alnetum sinuatae															
Alnus sinuata	9	9	9	9	9	9	9	9	10	9	9	10	9	9	9
Calamagrostis canadensis	5	6	5	5	6	7	6	6	5	5	7	4	6	6	6
Epilobium angustifolium	5	4	4	7	6	3	5	5	4	2	4	4	4	5	5
Trientalis europaea	4	+	3	2	2	3	4	+	1	3	4	4	4	4	5
Vaccinium caespitosum	.	.	.	.	.	.	.	2	.	.	1	5	5	3	4
Spiraea beauverdiana	1	5	4	.	.	.	3	2	+	.	+	4	3	.	4
Athyrium filix-femina	1	.	4	.	2	5	5	5	3	.	5	5	2	6	.
Veratrum eschscholtzii	3	1	.	2	2	4	5	6	.	5	3	.	1	.	.
Cinnetosum latifoliae															
Cinna latifolia	4	3	3	4	+	.	1	.	.	.	.	.	.	.	.
Sanguisorba stipulata	4	2	.	4	5	.	.	.	.	1	.	.	.	.	.
Heuchera glabra	.	4	4	2	4	.	.	.	.	.	.	.	.	.	.
Aruncus sylvester	4	4	4	.	4	4	.	.	.	.	.	.	.	.	.
Salix barclayi	6	4	4	.	4	.	.	.	.	.	.	.	.	.	.
Gymnocarpietosum drypteridis															
Gymnocarpium dryopteris	.	.	.	.	.	2	3	5	5	5	.	.	.	.	.
Rubus spectabilis	.	.	.	.	.	2	.	5	3	7	.	Ribetosum tristis			
Rubus pedatus	3	.	.	.	.	2	4	.	3	4	.	4	4	4	4
Ribes triste	.	.	.	.	1	1	.	.	.	.	2	3	3	4	4
Vaccinium ovalifolium	2	4	3	.	.	.	.	.	.	.	.	3	3	2	.
Rubus arcticus	.	1	4	.	.	.	.	+	.	.	3	.	4	.	.
Artemisia arctica	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Castilleja unalaschensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sorbus sitchensis	.	.	.	.	.	5	.	4	.	.	.	5	.	.	.
Oplopanax horridus	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.
Rubus chamaemorus	.	.	.	.	.	.	3	.	.	.	3	.	.	+	+
Lycopodium annotinum	.	.	1	.	.	.	.	.	.	.	+	.	.	.	.
Carex spectabilis	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.
Aconitum delphinifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Streptopus amplexifolius	.	.	+	.	.	4	.	.	.	.	3	.	.	.	.
Sambucus racemosa	.	.	.	1	4	.	.	.	.	.	.	.	.	.	.
Sedum rosea	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
Poa palustris	.	.	+	4	.	.	.	.	.	.	.	.	.	.	.
Achillea millefolium	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Thelypteris phegopteris	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.
Phleum commutatum	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Empetrum nigrum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cornus suecica	.	.	.	.	.	.	+	.	.	.	1	.	.	.	.
Arctostaphylos alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix arctica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Geum calthifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pyrola asarifolia	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.
Epilobium hornemannii	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Viola langsdorffii	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Stellaria longifolia	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.
Geranium erianthum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Epilobium latifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Linnaea borealis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phyllodoce empetriformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzula parviflora	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Campanula lasiocarpa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lycopodium alpinum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Total number of species	13	17	15	15	14	14	12	13	9	9	14	12	12	11	9

Arabic numerals in the table indicate the Species Significance Class of Domin-Krajina (Krajina, 1933).

16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	DV	F
A32	A9	A14	A29	A24	A25	A16	A28	A27	A20	A11	A12	A13	A15	A5	A6	A19		
S30E	S60W	level	S20E	level	due N	knoll	S20E	level	S10E	N30E	N20E	N40W	due S	due N	knoll	level		
3	3	level	8	—	10	—	8	level	5	5	8	5	5	5	—	level		
9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	8	95.0	V
5	5	5	6	6	6	7	7	7	6	6	5	6	6	1	1	.	71.7	V
4	5	5	4	5	5	5	5	5	5	6	5	6	.	6	6	1	66.3	V
+	4	3	4	4	4	4	4	3	3	2	.	4	4	3	.	.	50.6	V
4	5	4	4	5	4	4	+	2	2	3	5	+	4	.	3	6	40.4	IV
.	4	4	3	1	3	2	3	.	4	5	.	+	4	.	.	.	35.2	IV
6	.	.	.	.	.	.	.	.	.	.	2	4	.	.	.	.	27.4	III
.	.	.	.	.	.	3	2	3	.	.	.	.	2	.	.	.	24.0	III
.	3	.	.	.	.	.	.	.	.	4	.	.	.	+	.	.	14.2	II
.	.	4	.	.	5	.	.	4	.	.	.	2	.	2	.	.	18.0	II
.	4	.	.	.	.	.	.	3	+	.	2	4	.	.	3	.	16.2	II
.	.	.	.	.	.	.	.	+	.	.	.	.	+	3	.	.	13.7	II
.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	1	.	11.6	I
+	.	.	.	.	.	+	7	4	.	.	.	.	4	.	.	.	18.8	II
	.	.	.	.	.	5	5	.	2	.	.	.	.	.	.	.	14.1	II
5	.	.	.	2	.	.	.	.	3	.	.	.	.	.	.	.	22.2	II
4	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.	15.4	II
2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11.4	II
			Rubetosum arcticae															
.	4	4	4	2	4	4	4	3	1	.	3	6	4	6	.	.	32.9	III
.	1	+	.	.	+	.	+	+	.	+	+	.	+	.	+	.	7.3	II
.	+	.	.	+	+	+	.	.	+	.	.	.	+	1	1	+	7.0	II
5	.	.	.	.	+	.	.	.	4	.	.	.	.	.	+	.	12.8	II
5	.	.	.	.	.	.	.	.	.	2	.	1	.	.	2	.	8.6	I
+	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	7.8	I
+	.	1	.	1	2	.	.	.	.	.	.	2	.	.	.	.	7.4	II
.	.	.	.	.	.	.	2	.	.	.	.	+	.	4	.	.	6.4	I
.	.	.	.	2	+	.	.	.	+	+	.	.	.	1	1	.	5.7	I
.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	5.6	I
.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	5.1	I
.	.	.	+	.	+	.	.	.	.	.	.	.	.	1	+	.	4.1	I
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	4.0	I
.	.	.	.	.	+	.	.	.	.	.	+	.	.	2	.	.	3.7	I
.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	3.7	I
.	+	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	3.0	I
.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	4	3.0	I
.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	2.4	I
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6	2.4	I
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	2.2	I
.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	2.0	I
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1.4	I
.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1.4	I
.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	1.4	I
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1.4	I
.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1.4	I
.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	1.4	I
.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	1.4	I
.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	1.4	I
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.7	I
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	0.7	I
.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	0.7	I
13	13	10	8	11	17	12	12	13	14	12	13	12	14	15	14	8	Avarage 12.5	

Appendix II. Vegetation structure and synthesis table of Empetro–Vaccinietum caespitosi (Ass. nov.). Arabic numerals indicate Species Significance Class of Domin–Krajina (Krajina, 1933).

Series No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	DV	C
Releve No.	B11	B17	B1	B2	B3	B8	B13	B18	B14	B5	B12	B15	B16	B19	B20	B9	B6	B4	B7	B10		
Ass. Empetro - Vaccinetum caespitosi																						
Vaccinium caespitosum	8	9	8	9	9	8	8	8	8	9	8	8	8	8	8	8	8	8	7	8	90.3	V
Empetrum nigrum	4	5	4	3	2	4	4	5	4	.	5	4	6	5	5	3	5	.	5	5	59.2	V
Artemisia arctica	4	4	3	4	5	4	5	4	.	.	4	5	5	5	4	.	4	3	4	4	54.9	V
Carex spectabilis	4	3	5	3	2	+	4	4	.	4	4	4	4	4	3	3	.	5	.	4	50.7	IV
Cornus suecica	5	5	5	3	3	4	2	1	5	.	4	5	+	4	.	4	6	.	.	.	46	IV
Spiraea beauverdiana	.	4	4	5	3	4	4	4	4	4	3	4	2	4	3	4	.	.	.	.	45.8	IV
Festuca altaica	4	3	4	.	+	2	4	+	3	3	3	3	3	2	.	1	+	+	.	.	38.5	IV
Epilobium angustifolium	.	.	4	4	4	3	.	.	.	.	.	3	+	1	3	4	.	+	.	.	6	III
Anemone narcissiflora	.	.	.	4	4	.	3	3	2	.	.	.	4	4	4	2	2	.	.	3	31	III
Arctostaphylos alpina Variant																						
Arctostaphylos alpina	4	4	5	3	5	5	5	4	4	6	.	.	.	.	.	.	.	.	.	.	33.5	III
Andromeda polifolia	1	.	.	2	2	2	1	.	4	.	.	2	1	.	.	.	4	.	.	.	20.7	III
Loiseleuria procumbens	.	.	.	.	1	.	4	4	.	4	.	.	.	+	.	.	.	4	.	.	16.2	II
Campanula lasiocarpa	.	.	.	.	+	+	.	+	.	+	+	.	.	.	.	.	.	.	.	.	5.6	II
Rubus arcticus Variant																						
Rubus arcticus	.	.	.	+	.	.	+	4	3	.	4	4	4	4	3	.	.	.	.	.	24.6	III
Castilleja unalascensis	.	.	.	.	.	.	.	.	.	.	4	3	2	+	5	.	.	.	.	+	15	II
Geum calthifolium	.	.	.	.	.	.	.	.	.	.	5	3	.	.	5	1	.	.	6	3	18.6	II
Salix arctica	3	.	.	.	.	.	4	.	.	3	.	.	.	.	.	3	.	2	3	4	19.6	II
Calamagrostis canadensis	.	.	.	.	.	.	.	.	2	.	.	.	.	3	4	.	.	.	4	.	11.4	II
Sanguisorba stipulata	.	.	.	.	.	.	.	.	.	.	5	.	.	.	5	.	.	.	4	.	10.2	I
Linnaea borealis	.	.	.	.	.	.	.	1	.	+	3	.	+	.	.	.	.	.	.	.	7.1	I
Lycopodium sitchensis	.	.	.	.	.	.	1	.	.	2	.	.	.	.	.	.	.	.	.	1	5.5	I
Gymnocarpium dryopteris	.	.	3	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	5	I
Leutkea pectinata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	3.5	I
Hierochloe alpina	.	.	.	.	.	.	.	+	.	.	.	.	2	.	.	.	.	.	.	.	3.5	I
Aconitum delphinifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.	.	.	3.5	I
Valeriana sitchensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	3.2	I
Vaccinium vitis-idaea	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2.7	I
Pedicularis verticillata	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	2.2	I
Salix barratiana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	2.2	I
Lycopodium selago	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2.2	I
Rubus chamaemorus	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	2.2	I
Ledum palustre	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1.6	I
Geranium erianthum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1.6	I
Lycopodium clavatum	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1.6	I
Trientalis europaea	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1.6	I
Solidago multiradiata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	1.1	I
Pyrola asariflora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1.1	I
Epilobium latifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1.1	I
Stellaria monantha	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1.1	I
Number of species	9	8	10	10	11	10	13	11	11	8	13	12	11	12	15	11	7	5	8	8	Average 10.2	