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Climatic preferences and frequent co-occurrence of boreal and temperate plants in Hokkaido Island, northern Japan

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Abstract

Effects of climatic factors on the forest plant distribution were examined in Hokkaido Island, northern Japan, where boreal and temperate plants frequently co-occur, and the relationship of floral make-up with phytogeography and life form was analysed. From the climatic preference of tree species consisting of mixed forest, the co-occurrence of boreal and temperate plants was found over a wider thermal range in regions of little rainfall. However, co-occurrence in a certain forest site was more notable in the understory than in the crown. A particular case of this involves southern evergreen shrubs and herbs in a boreal coniferous forest. Another is the presence of northern summergreen herbs in a temperate hardwood forest. It is speculated that the co-occurrence dates back at least to the late Quaternary, when a decrease in temperature associated with the glacial period forced understory plants to adapt their life form or leaf habit to snowcover and the light conditions of interior forests. Recent geographical evidence suggests that the island has been isolated from the southern island for at least 70000 years. Thus, the postglacial re-expansion of southern species does not appear to be due to immigration but rather due to their expansion from refuges on the island such as Oshima Peninsula for snow-tolerant species and Hidaka District for snow-intolerant species.

Nomenclature: Nakaike, T. 1982; New flora of Japan, Pteridophyta. Shibundo, Tokyo, and Ohwi, J. & Kitagawa, M. 1984. New flora of Japan. Shibundo, Tokyo.

Introduction

In the upper-middle latitudes of Europe, eastern Asia and eastern North America, the boreal coniferous forest formation meets the temperate hardwood forest formation. These areas are called 'pan-mixed forest zone' (Tatewaki 1958), 'hemiboreal forest zone' (Hämet-Ahti *et al.*; 1974) or 'boreonemoral zonoecotone' (Walter 1979). The general properties of the forest zone are: 1) mosaic arrangements of pure stands of boreal forest and temperate forest, where boreal conifers and temperate hardwoods are complementarily distributed, and their interactions are tensional both in space and in time (Walter 1979); and 2) scattered establishment of mixed forests, in which boreal trees and temperate trees concurrently grow, where their interactions are competitive

(Woods & Whittaker 1981) or are in dynamic equilibrium due to the frequent occurrence of catastrophic disturbance (Ishikawa & Ito 1989).

As in northeastern Europe and eastern North America, mixed forests are occasionally found in Hokkaido, the northernmost island of Japan, which belongs to the Asian boreo-nemoral ecotone. However, the extent of the floral mixture has scarcely been studied, especially for the forest understory where temperate dwarf bamboos are exclusively dominant. The boreal plants of Hokkaido have undoubtedly come from the northeastern Eurasian Continent, migrating mostly through Sakhalin Island and/or the Kurile Islands, while the temperate plants including Japanese endemics have come from Honshu Island through the Oshima Peninsula, the southernmost area of Hokkaido (Kawano 1971; Maekawa 1974). During the postglacial periods, many temperate hardwood species immigrated from Honshu and rapidly took the place of the boreal coniferous forests, which had almost monopolized the island in glacial periods (Tsukada 1983).

Since the distribution of forest plants is primarily limited by temperature, their distribution is expected to be controlled by outlined the thermal conditions on the margins of their ranges. However, precipitation often distorts the effects of temperature (Austin *et al.* 1984). Especially in Japan, the distribution of many forest plants is usually controlled by snowfall and/or rainfall, e.g. the thermal tolerance ranges of many plants appear to vary among regions of different snowfall or rainfall conditions (Uemura 1989). In particular, snowcover is considered to influence the distribution of many plants. For instance, in deep-snow regions where plants were well protected from the frost damage by deposited snow, some evergreen broad-leaved shrubs are occasionally found in deciduous forest (Sakai 1968). In order to examine the process of floral mixture in the boreo-nemoral forest ecotone, therefore, the inter- and intra-specific variation of distribution should be analysed among the dominant species of forest plants.

In addition to the climate, geographical isolation has been considered to influence the distribution of plant species, especially in an island, e.g. the distribution of alder in Britain is explicable not only by immigration from the continent in the postglacial age but also by expansion from a certain refugia in the island (Bush & Hall 1987). The flora in the Japanese Archipelago also has a unique background of geohistory, because this island has been frequently isolated from the Eurasian Continent or neighboring islands (Ohshirna 1982). In particular, the Hidaka District of Hokkaido is isolatedly colonized by some temperate plant species which are common on the southern island Honshu (Uemura & Takeda 1987).

In the present study, I attempt to analyse the effects of proximal climate such as temperature, snowfall and rainfall on the distribution of forest plant species in Hokkaido, which has a variety of climate and a history of frequent geographical isolation, and then I elucidate the co-occurrence of northern and southern plants with reference to the influence of those climatic variables and the postglacial migration.

Area studied

Hokkaido Island (79000 km^2) is one of the latitudinally lowest boreo-nemoral forest ecotones in the northern hemisphere, being situated within the range of 41° 24′–45° 31′ N and 139° 45′–145° 50′ E (Fig. 1). The climate of Hokkaido is primarily controlled by: 1) the front of polar air masses which often cross the northern part of the island in winter, 2) the cold Kurile current flowing down to the eastern parts of the Pacific side of Hokkaido, 3) the warm Sea of Japan current reaching up to the southwestern part of the island, and 4) a very cold Siberian monsoon providing heavy snowfall to the Sea of Japan side in winter. Based on the climatic diagrams, Hokkaido was divided into the following climatic divisions (Kojima 1979): the southwestern region, facing the Sea of Japan, which is warm and snowy; the southern central region, facing the Pacific Ocean, which is warm with little snowfall; the northern region facing the Sea of Japan and being cool and

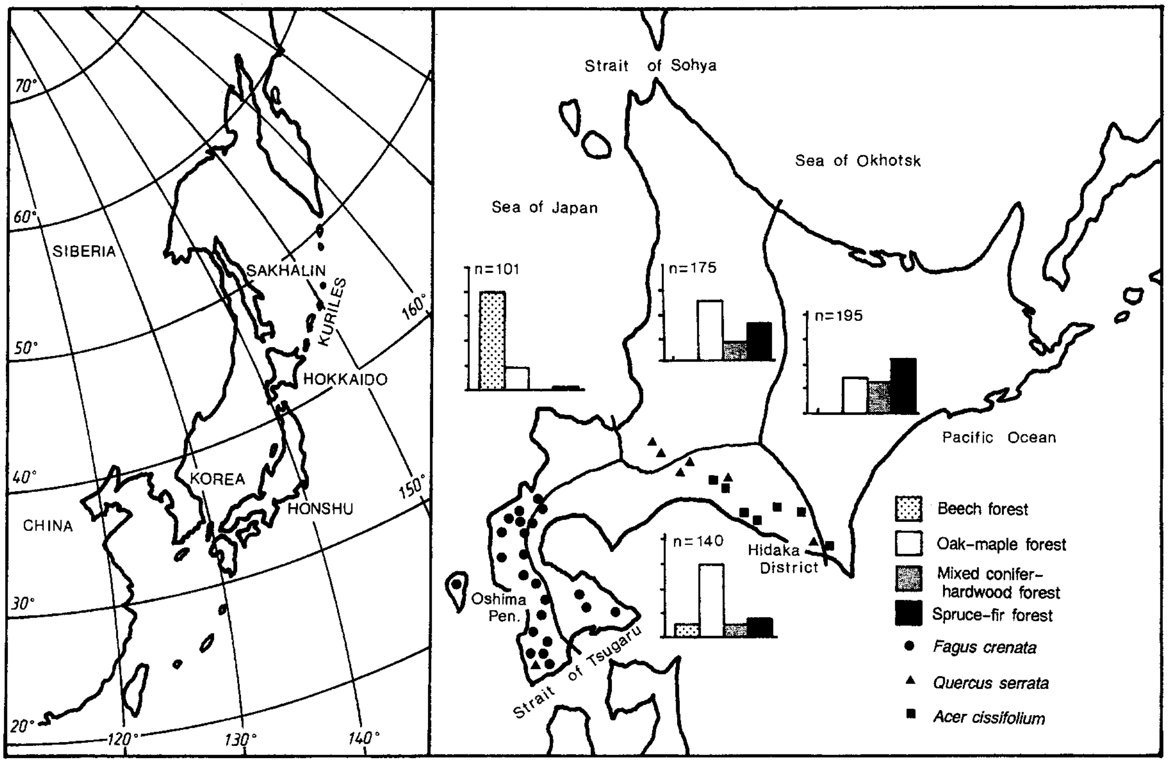

Fig. 1. Forest distribution in the four climatic divisions. Histograms show frequency of each forest type. Distribution of three tree species which are absent in mixed conifer-hardwood forest is also shown.

snowy; and the eastern region facing the Pacific Ocean and the Sea of Okhotsk and being cool with minimal snowfall and rainfall.

In its forest flora Hokkaido is similar to the other boreo-nemoral ecotones of Europe and North America, being dominated by *Picea*, *Abies*, *Fagus*, *Quercus*, *Tilia*, *Acer*, *Carpinus*, *Ostrya*, *Fraxinus*, etc. However there are some particular features in Hokkaido, for instance, higher species richness, well-developed vertical structure, and distribution of many vine species such as *Vitis coignetiae*, *Actinidia arguta*, *A. polygama*, *Hydrangea petiolaris* and *Schizophragma hydrangeoides* (Tatewaki 1958). Another feature is a forest floor broadly predominated by many dwarf bamboos such as *Sasa kurilensis*, *S. senanensis* and *S. nipponica*.

The outline of natural forest vegetation is as follows. Boreal spruce-fir forest composed of *Abies sachalinensis*, *Picea jezoensis* and *P. glehnii* is dominant in the eastern region. Temperate hardwood forests are classified into two types, i.e. beech forest and oak-maple forest. Beech forest largely dominated by *Fagus crenata* is restricted to the southwestern region, particularly to the Oshima Peninsula. Oak-maple forest is dominant in the southern central and eastern regions, consisting of *Quercus mongolica* var. *crispula* and *Acer mono* in association with *Tilia japonica*, *Tilia maximowicziana*, *Kalopanax pictus*, *Betula maximowicziana*, *Magnolia obovata*, *Ostrya japonica*, *Cercidiphyllum japonicum*, etc. Another conspicuous type of forest is mixed conifer-hardwood forest composed of boreal conifers and many temperate hardwoods, except *Fagus crenata*.

Methods

The vegetation was surveyed at 506 stands in 120 areas chosen over the entire island of Hokkaido. The quadrats were set on closed and undisturbed sites in primary forests, with sizes ranging from 15 × 15 m to 20 × 20 m. Coverage, life form and leaf habit for all vascular plant species were recorded both in the crown and in the understory of each stand. This was complemented by additional vegetation records from 105 stands in 31 areas reported in the literature. Of the combined total of 611 stands, 170 were grouped into spruce-fir forest, 100 into beech forest, 249 into oak-maple forest, and 92 into mixed conifer-hardwood forest, defined by the 20–80% of the proportion of temperate hardwoods in the canopy. Of these, 101 stands were from the southwestern region, 140 from the southern central region, 175 from the northern region, and 195 from the eastern region (Fig. 1).

To evaluate their correlation to proximal climatic factors, a direct gradient analysis as proposed by Whittaker (1967) was performed on these plant species, in order to determine the habitats they would normally be found in. The following variables were calculated for the analysis.

The climate in each stand was estimated from the climatic records at 79 weather stations in Hokkaido. Empirically, the mean monthly temperature was given by $Tw - 0.6 \times 10^{-2} (As - Aw)$, where Tw is the mean monthly temperature at the nearest weather station, and As and Aw are the altitudes (m) of the stand concerned and the nearest weather station, respectively. The mean monthly precipitation was treated as identical to that of the nearest weather station, because there is still no agreement upon the way to estimate the stand value. From these values, the following indices were calculated for each site: warmth index $WI = \Sigma (T_1 - 5)$, where T_1 is the mean monthly temperature exceeding 5 °C (Kira 1977); coldness index $CI = \Sigma (T_2 - 5)$, where T_2 is the mean monthly temperature less than 5 °C (Kira 1977); annual rainfall Ra (mm), represented by the amount of mean monthly precipitation from April to November; and winter precipitation Pw (mm), the amount from December to March. As an index of snow conditions, days of snow 50 cm or more deep per year $D50$ (days) is used. In the present study, $D50$ at each stand was estimated from the following regression formula derived from the 1891-1963 meteorological records: $D50 = 84.0 \ln |CI\, Pw\, 10^{-3}| - 148.1$ $(r = 0.884, P < 0.001)$. The correlations in each pair of WI, $D50$ and Ra are not statistically significant ($P > 0.1$ in the Mann-Whitney U-test): $r = -0.097$ in WI–$D50$, 0.084 in WI–Ra, and 0.141 in $D50$-Ra, indicating that these factors are independent of each other. As an index of floral mixture, the evenness J' proposed by Pielou (1975) was used: $J' = -\Sigma (p_n \ln p_n + p_s \ln p_s) (p_n + p_s) / \ln 2$, where p_n and p_s are relative richness of northern species and southern species, respectively. A total of 537 vascular plant species were identified, and 164 species found in more than 24 stands were used for analyses.

Terminology

To indicate the climatic conditions, the following criteria were adopted: 'cold (C)' means $WI < 35$ °C; 'cool (c)', $35\ °C \leq WI < 65\ °C$; 'warm (W)', $65\ °C \leq WI$; 'deep-snow (S)', $90\ \text{days} \leq D50$; 'shallow-snow (s)', $D50 < 30$ days; 'much rainfall (R)', $900\ \text{mm} \leq Ra$; 'little rainfall (r)', $Ra < 700$ mm.

Vascular plant forms, including species, subspecies and varieties, were divided into phytogeographical groups based on their normal home ranges (cf. Kawano 1971; Hultén 1972; Nakaike 1975; Ohwi & Kitagawa 1984). Those plants were divided into the following four groups: northern plants (N), mainly distributed in northeastern Eurasia, including circumpolar plants; southern plants (S), mainly distributed south of Hokkaido; plants endemic to Hokkaido and its vicinity (H); and widespread plants (O).

Finally, these forms were divided into eight life form categories based on the morphology and leaf phenology: evergreen trees (Te), summergreen trees (Ts), evergreen woody vine (Ve), summergreen woody vine (Vs), evergreen shrubs (Se), summergreen shrubs (Ss), evergreen herbs (He), and summergreen herbs (Hs). In these divisions, plant species with overwintering leaves are clustered into evergreen categories.

Results

Commodal groups

According to the similarity of the stand distribution along *WI*, *D50* and *Ra*, the 164 species were divided into 18 commodal groups, named by designations of their *WI*, *D50* and *Ra*, respectively (see Appendix). Fig. 2 represents the stand distribution of typical species in each group. The distribution of 135 of the 164 species (82.3%) appeared to be controlled by temperature, show-

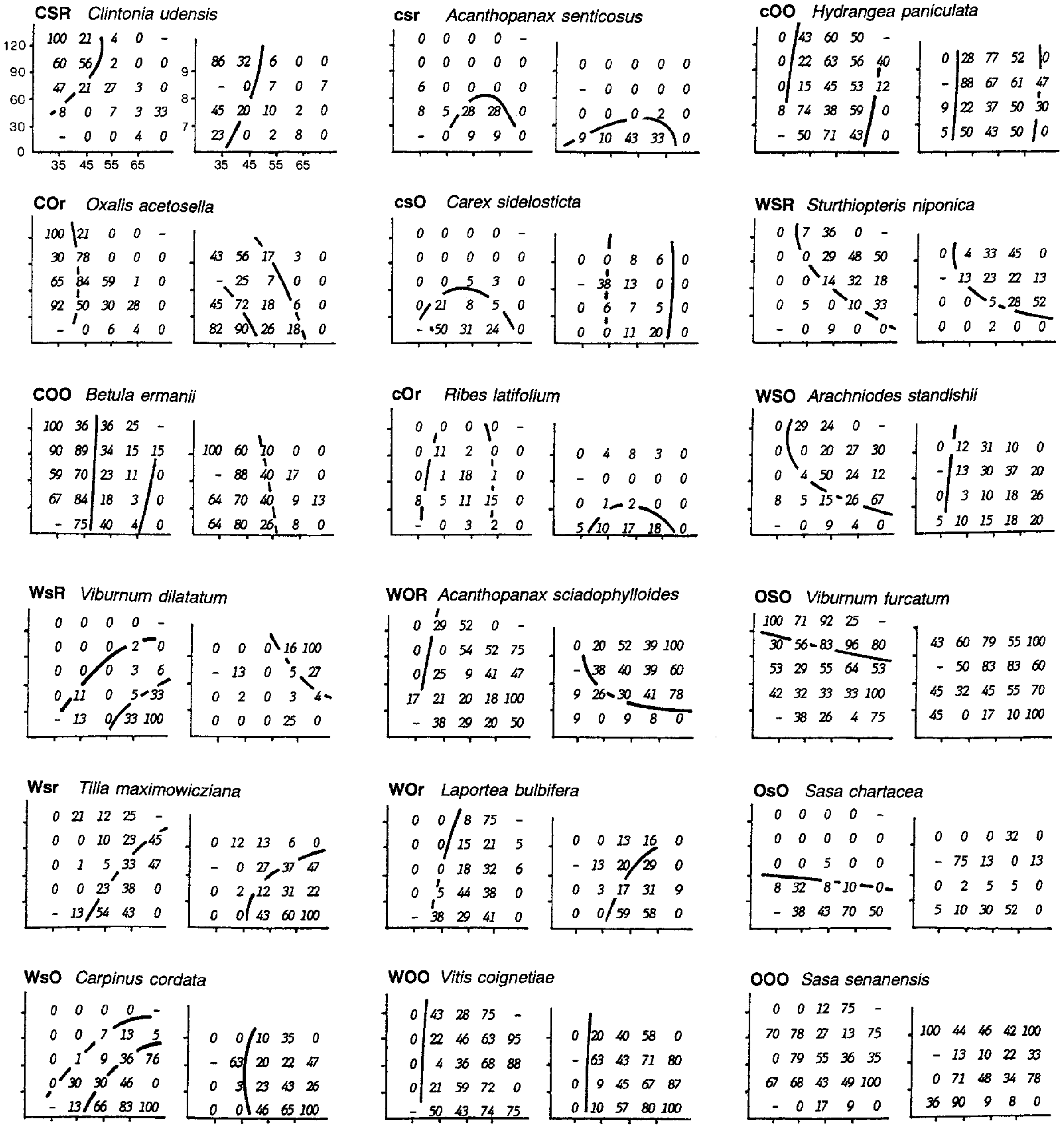

Fig. 2. Distribution of representative species of 18 commodal groups along *WI* (*x*-axis: °C) and *D50* (*y*-axis: days) in the left graph and *WI* and *Ra* (*y*-axis: 100 mm) in the right graph. Values given are $100 \times Fs/Ft$, where *Fs* and *Ft* are the numbers of stands inhabited by a given species and total stands in the whole data set, respectively. Isolines are also shown by solid lines.

ing specific patterns along *WI*. Though the distribution of the forest plant species are primarily controlled by temperature, snowcover and rainfall are additional factors affecting their behavior because 77 and 59 species of them also showed specific modes along *D50* and *Ra*, respectively.

Occurrence of commodal groups in four forest types

According to the occurrence in 20% or more stands of each forest type, the 164 plant species were divided into the following three groups (Table 1): I, species mainly associated with spruce- fir forest. They were subdivided into two types: Ia, found exclusively in spruce-fir forest and Ib, found also in mixed conifer-hardwood forest; II, species mainly distributed in summergreen forests, with five subgroups, i.e. IIa, species found only in beech forest; IIb, only in oak-maple forest, IIc, common to beech and oak-maple forests; IId common to oak-maple and mixed forests; and IIe, unexclusively associated with spruce-fir forest; III, species which were widely distributed, with three subgroups, i.e. IIIa, common to spruce-fir and beech forests and IIIc, to all forests, but IIIb was not found in beech forest. No species group was exclusively associated with mixed forest.

Many species of group I preferred cold climate and little rainfall: all of them were C, and about a half were r. The difference between Ia and Ib is merely dependent on the thermal range. Species of II prefer warm or cool climate, suggesting that

Table 1. Species groups associating to forest types, represented the fidelity more than 20% of total stands of each forest type, and commodal groups with number of species per associating group. Dot means the fidelity more than 20% stands of each forest type.

Species group	I		II					III		
Subgroup	a	b	a	b	c	d	e	a	b	c
Forest type										
Spruce-fir forest	•	•						•	•	•
Mixed forest		•				•	•		•	•
Oak-maple forest				•	•	•	•		•	•
Beech forest			•		•		•	•		•
Commodal group										
CSR	1						2	2		6
COr	2	3					4			1
COO	2	1					5			6
csr				1		2	1			
csO				1		2			2	
cOr						1	1			
cOO						3	2		1	1
WSR			3		4	1			2	1
WSO					3	2	1		4	
WsR					2	1			1	
Wsr				3		1				
WsO				5	1	11	1		1	
WOR					1	1			5	2
WOr						4				
WOO				1	5	5	2		5	3
OSO								1		2
OsO				4			1			1
OOO				1		5	4	1	2	7
Total	5	4	3	16	16	39	24	4	23	30

their normal home ranges are in the temperate forests. Of these species, IIa and IIc were often found in beech forest and were mostly distributed in snowy and rainy regions: all of them were S, and half of them were R. In contrast, IIb and IId being absent in beech forest required little snowfall climate: the 87.5% species of IIb and the 43.6% of IId were s. Though most species of IIIa were closely related to snowy conditions and those of IIIb to cold or cool climate, those of IIIc showed a great variation of distribution and seemed indifferent to the three environmental gradients examined.

Relationship between phytogeography and life forms

Although southern plants (S) mostly required a 'warm' climate, a few of them required a 'cold' climate as tabulated in Table 2. Since most of them belong to the group CSR, their expansion to the north seemed to be made possible by deep snow cover and much rainfall. Most northern plants (N) were nearly indifferent to snowfall. Species endemic to Hokkaido and its vicinity (H) numbered as few as eight.

Trees and woody vines did not have a particular center of preference along snowcover and rainfall gradients, while those of shrubs and herbs are apparently biased: S and R are 64% and 46%, respectively in shrubs, and 7% and 8% in herbs, suggesting that the distribution of understory species of forests is more strongly affected by the snowfall or rainfall. All species of evergreen trees were conifers, and the shrubs other than *Cephalotaxus harringtonia* var. *nana* in WSO were broad-leaved. Evergreen herbs in COO included many pteridophytes such as *Lycopodium serrata*, *L. obscurum*, *Polypodium virginianum*, *Pyrrosa tricuspis* and *Lepisorus ussuriensis* var. *distans* and a few flowering plants such as *Carex sachalinensis*. Evergreen shrubs particularly preferred deep-snow regions, while evergreen trees and herbs were indifferent to snow conditions; all

Table 2. Commodal groups with number of species per phytogeographical group and life form category. Abbreviations are given in the Terminology section.

	Phytogeographical group				Life form category							
	H	S	N	O	Te	Ts	Ve	Vs	Se	Ss	He	Hs
Commodal group												
CSR	1	7	3			1			2	6		2
COr	1	1	8		3	1				1	3	2
COO	1	1	8	4		1		2	1		5	5
csr		1	2	1		1				2		1
csO		4		1		2				1	1	1
cOr	1		1							1		1
cOO		2	4	1	1	2				1	1	2
WSR		10		1		2			4	3	2	
WSO		9		1		1			4		3	2
WsR		4				2				1		1
Wsr		4				2						2
WsO	1	12	1	5		11			1	1	1	5
WOR		8		1		5		2				2
WOr		3		1		2						2
WOO		10	4	7		9		3			2	7
OSO	1	2								2	1	
OsO		2	1	3						1	2	3
OOO	2	5	10	3		2	1		1		5	11
Total	8	85	42	29	4	43	1	8	13	20	26	49

of the former and 83% of the latter were indifferent. Summergreen plants showed a variety of climatic preference without any particular tendencies.

Behavior of trees dominating mixed forests

The distribution patterns of three boreal conifers and three temperate hardwoods dominating many of the mixed conifer-hardwood forests are respresented in Fig. 3. Boreal conifers such as *Abies sachalinensis*, *Picea jezoensis* and *P. glehnii* were classified into the COr group, preferring cold and little rainfall regions with indifference to snow conditions (Fig. 3A). *Abies sachalinensis* and *Picea jezoensis* sometimes expanded their distribution into the warm regions where *WI* was 55 °C or more. On the other hand, temperate hardwoods such as *Quercus mongolica* var. *crispula*, *Acer mono* and *Tilia japonica* belonged to the WOO group (Fig. 3B). Both the boreal conifers and the temperate hardwoods frequently occurred together over a wide thermal range of 35 °C$\leq$ *WI* $<$ 65 °C where rainfall was low.

Behavior of some isolated southern species

If most of the southern plants had immigrated into Hokkaido from Honshu in the postglacial period, they might be expected to be found frequently in the southernmost area of Hokkaido, i.e. Oshima Peninsula. However, such southern species as *Acer cissifolium*, *Stephanandra incisa*, *Cacalia delphiniifolia*, *Asperella longe-aridstata* and *Pourthiaea villosa* were never or rarely found in Oshima Peninsula but almost exclusively in Hidaka District.

The direct gradient analysis of *Acer cissifolium*, *Stephanandra incisa* and *Cacalia delphiniifolia* demonstrated that their distributional modes were situated in relatively warm and dry zones. As shown in Fig. 3C, however, they appeared potentially tolerant to cooler areas where snowfall and rainfall were relatively scarce. Since the precipitation including snowfall during the full glacial age in Hidaka District is considered to have been very restricted (Nogami *et al.* 1980; Ono 1984), this region may have been covered by mixed forests consisting of *Quercus mongolica* var. *crispula*, *Tilia japonica*, and *Acer mono*, whose freezing re-

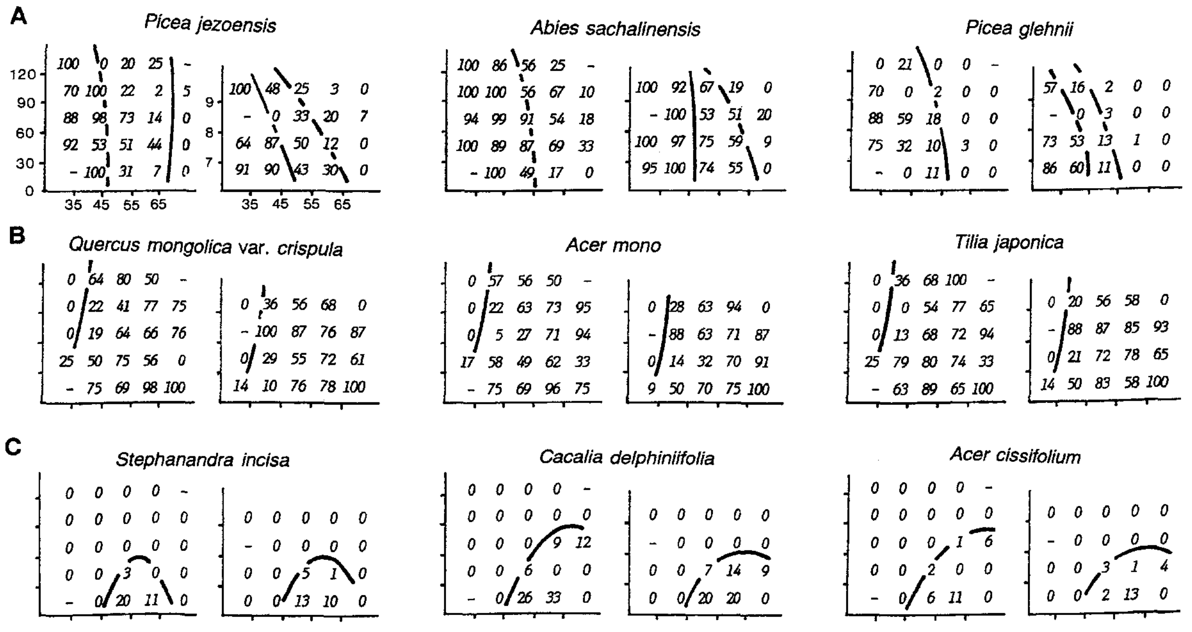

Fig. 3. Distribution patterns of three boreal conifers (A) and three temperate hardwoods (B) predominating mixed conifer-hardwood forest, and those patterns of three southern species isolated in Hidaka District (C). The axes in each graph are explained in Fig. 2.

sistances are adequate to withstand the estimated minimum temperature (ca. 5–7 °C below the present) in the last glacial age (Sakai 1975).

Evenness between northern and southern plants

Of the 164 species analysed, 47 tree species formed overstories of summergreen or coniferous forests: i.e. 30 southern species (S), 6 northern species (N), 4 endemics to Hokkaido and its vicinity (H) and 7 widespread species (O). Of these 47 species, 44 were also found in mixed conifer-hardwood forest (Fig. 4A). In fact, most of the overstory species participated in the co-occurrence of southern and northern floras in the forests, except three specific species, *Fagus crenata*, *Quercus serrata* and *Acer cissifolium*, which are restricted to the southwestern or eastern part of southern central regions and are absent in mixed conifer-hardwood forest.

Understory plants totalled 113 species: i.e. 52 southern species, 32 northern species, 7 endemics and 22 widespread species. As shown in Fig. 4A, the floral make-up of the understory was similar among the forests except beech forest. Almost all of the northern species were able to inhabit each type of forest. The slight difference noted was due in large part to a slightly smaller number of southern species in the mixed conifer-hardwood forest and spruce-fir forest. In addition, the evenness scores in understory are significantly higher than those in the overstory (P < 0.01 in the Mann-Whitney *U*-test). The evenness was nearly equal among these three types of forest, ca. 0.7 of the evenness score (Fig. 4B). Beech forest was relatively poor in northern species (19 species), producing an evenness score of ca. 0.5, significantly lower than that of other forests (P < 0.001 in the Mann-Whitney *U*-test). Thus, the floral mixture in the forest understories was notable in that it exceeded that in the overstories.

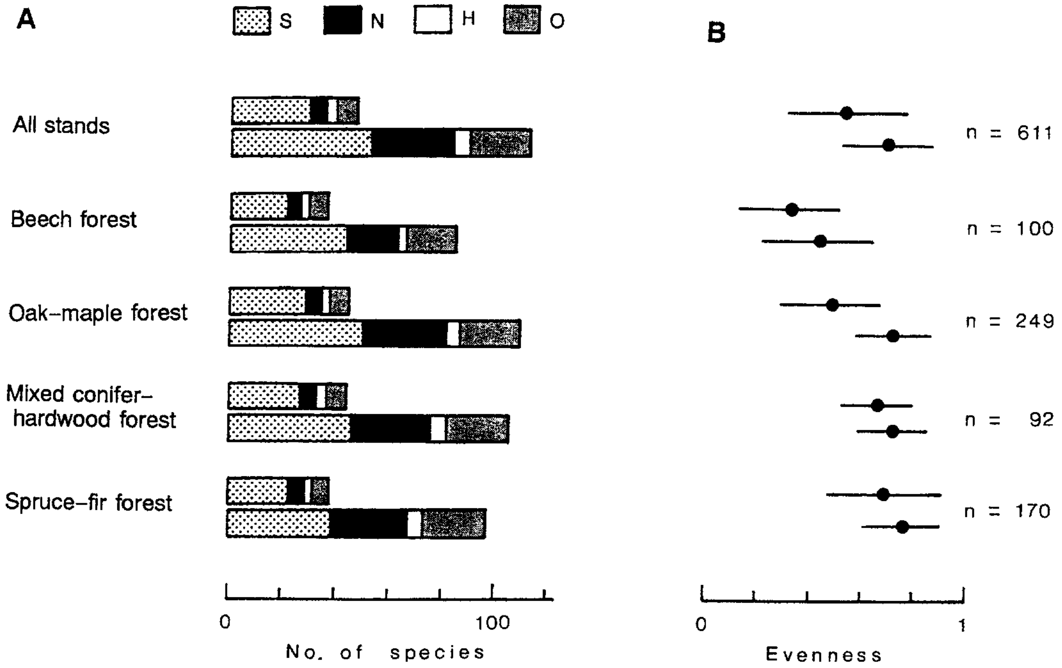

Fig. 4. Phytogeographical composition (A) and evenness J' (B: mean ± SD) between southern and northern plants in the overstory (upper) and understory (lower) of each forest type. S, southern plants; N, northern plants; H, endemics to Hokkaido and its vicinity; O, widespread plants.

Life form, climatic preference and floral mixture

The co-occurrence of understory plants is due to the distributional expansion of northern species into summergreen forest and of southern species into spruce-fir forest. Table 3 shows the life form and climatic preference of southern plants and northern plants frequently found in spruce-fir forest and oak-maple forest, respectively. The relationships between leaf habit and the occurrence frequency are depicted in Fig. 5. Many of the southern plants frequently found in spruce-fir forest have overwintering leaves and are tolerant to cold winter if thick snowcover is provided. In contrast, most of the northern plants often inhabiting oak-maple forest are summergreen herbs.

Of the northern plants, evergreen species such as *Carex sachalinensis* did not inhabit oak-maple forest, while such summergreen species as *Maianthemum dilatatum*, *Cardamine leucantha*, *Cacalia hastata* var. *orientalis* and *Cimicifuga simplex*, etc. inhabited more than 40% of the stands of oak-maple forest. Of the southern species, however, more than 75% of the summergreen plants were absent or quite rare in spruce-fir forest, while such evergreen species as *Sasa kurilensis*, *S. senanensis*, *Skimmia japonica* var. *intermedia*, *Ilex rugosa* and *Rhododendron brachycarpum* were frequently found in spruce-fir forest. The distribution patterns of evergreen plants and summergreen plants shown in Fig. 5 were statis-

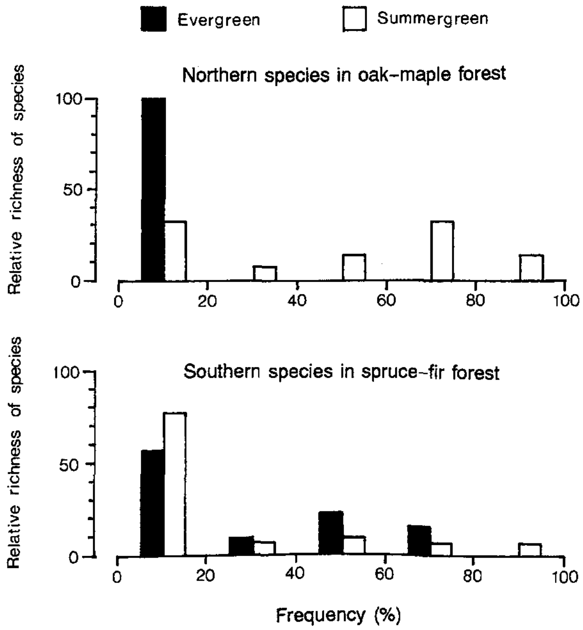

Fig. 5. Relative species richness for summergreen plants (open) and evergreen plants (solid) for each 20% frequency class.

Table 3. Life form (LF) and climate preference (CP) of southern plants and northern plants frequently found (≥20% stands) in spruce-fir forest and oak-maple forest, respectively. Abbreviations are given in the Terminology section.

Southern species	LF	CP	Northern species	LF	CP
Sasa senanensis	Se	OOO	*Acanthopanax senticosus*	Ss	Csr
Skimmia japonica v. *intermedia*	Se	WSR	*Actinidia kolomikta*	Vs	COO
Rhododendron brachycarpum	Se	COO	*Maianthemum dilatatum*	Hs	OOO
Sasa kurilensis	Se	CSR	*Cardamine leucantha*	Hs	cOr
Ilex rugosa	Se	CSR	*Cimicifuga simplex*	Hs	cOO
Sasa megalophylla	Se	WSO	*Cacalia hastata* v. *orientalis*	Hs	cOO
Menziesia pentandra	Ss	CSR	*Cirsium kamtschaticum*	Hs	OOO
Viburnum furcatum	Ss	OSO	*Polygonatum odoratum* v. *thunbergii*	Hs	OOO
Vaccinium smallii	Ss	CSR	*Cacalia auriculata* v. *kamtschatica*	Hs	WsO
Rhodondendron albrechtii	Ss	CSR	*Angelica ursina*	Hs	WOO
Vaccinium hirtum	Ss	CSR	*Angelica sachalinensis*	Hs	OOO
Hydrangea petiolaris	Ve	OOO	*Lilium cordatum* v. *glehnii*	Hs	OOO
Schizophragma hydrangeoides	Vs	WOR	*Calamagrostis hakonensis*	Hs	OOO
Plagiogyria matsumureana	He	OSO	*Circaea quadrisullata*	Hs	COO
Tripterospermum japonicum	He	OOO	*Anemone debilis*	Hs	COr
Tiarella polyphylla	He	COr	*Clintonia udensis*	Hs	CSR

tically different from each other both in oak-maple forest and in spruce-fir forest ($P<0.01$ in the *G*-test).

Discussion

Although beech forest is the typical and dominant forest in the temperate zone of Japan (Sasaki 1970), the distribution in Hokkaido has not been sufficiently explained by any thermal factors. Certain hypotheses for the limiting factors have been proposed, e.g. disturbance by wildfire, short distance of seed dispersal, etc. Another speculation is that the moisture conditions of the northern margin where less annual precipitation is provided has been charging the migration: i.e. their northward expansion is not in equilibrium with the drastic rise of temperature in the postglacial period (Tsukada 1983). This hypothesis appears to be supported by the climatic preference of *Fagus crenata*, whose distribution is biased to regions where much snowfall and rainfall are provided. In Hokkaido, many temperate hardwood trees seem to be expanding their distribution toward the north and east by replacing boreal conifers. This suggests that the distribution of forests is more dependent on the geo-historical background than on the present conditions of climate. In the process of northward expansion of temperate hardwoods during the postglacial age, they have established mixed forest with boreal conifers, especially in regions where the rainfall is lower. As observed in northeastern Europe, eastern North America and eastern Eurasia, regions where mixed conifer-hardwood forest is normally distributed are characterized by relatively less precipitation (Walter 1979). However, the climatic preference of individual plant species is one of the proximate factors for the establishment of mixed conifer-hardwood forest.

In general, deciduous plants usually have a high efficiency of photosynthesis to accumulate enough carbohydrate resources during a short active season (Chabot & Hicks 1982). During this short season, they are less tolerant to shade stress but more competitive in exposed habitats than evergreen plants (Kikuzawa, 1984). In contrast, evergreen plants are generally successful in shaded and less competitive habitats. Therefore, it is reasonable to postulate that the frequent co-occurrence of northern and southern plants is mostly promoted by the expansion of southern evergreen plants into the understories of evergreen spruce-fir forest and of northern summergreen plants into the understories of deciduous oak-maple forest. Because the Strait of Sohya isolating Hokkaido from Sakhalin is only 60 m deep (maximum), these islands have been frequently connected to each other in glacial periods (Ohshima 1982). During the last glacial maximum, Hokkaido was largely dominated by boreal conifers including the deciduous conifer *Larix* (Tsukada 1983). The understory of larch forest was probably composed of many summergreen herbs, as the present vegetation of eastern Siberia where forest of the deciduous conifer *Larix dahurica* is the most dominant, and many summergreen herbs frequently occur in the understory (Uemura *et al.* 1990).

On the other hand, it is still controversial when or under what circumstances southern species immigrated into Hokkaido over the Strait of Tsugaru. Based on the fossils of pollen, Tsukada (1983) suggested that most of the southern plants simultaneously immigrated to Hokkaido in the postglacial age. As pointed out by Prentice (1986), however, the absence of pollen does not always imply the absence of the species concerned. This is especially likely in vegetatively expanding plant species like *Sasa*, which is monocarpic and rarely effloresces, or in local and small relicts, which are very restricted in distribution (Davis *et al.* 1986). These plant species markedly contributed to the floral mixture. The Strait of Tsugaru is deeper than 140 m, and Hokkaido has been isolated from Honshu for the last 70 000 years at least (Ohshima 1982). Moreover, this barrier has been widened with the rise of temperature throughout the postglacial age. The present frequent mixture of southern plants and northern plants suggests the long-term co-existence of these plant species in Hokkaido.

How and where could the southern species survive in the glacial age? Unlike in Europe and

North America, most areas of Hokkaido were not covered by glacier ice even in the coldest period of the last glacial age. Furthermore, the southwestern part of Hokkaido was covered by snow in winter (Ono 1984), which enabled the survival of the snow-tolerant southern species such as *Sasa kurilensis*, *S. cernua*, *Cephalotaxus harringtonia* var. *nana*, *Daphniphyllum macropodum* var. *humile*, *Ilex crenata* var. *paludosa*, *Skimmia japonica* var. *intermedia*, *Rhododendron brachycarpum*, etc. The present study further revealed that some snow-intolerant southern species could withstand a cool climate if the precipitation was low, indicating their survival during the last glacial in drier regions such as Hidaka District (Uemura & Takeda 1987). Overall, the present study strongly suggests that the postglacial recovery of southern species in Hokkaido is not due to their immigration from Honshu but rather due to the expansion of snow-tolerant species from the Sea of Japan side, especially from Oshima Peninsula, and the expansion of snow-intolerant species from their dry refuges such as the Hidaka District.

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Appendix

Commodal species groups of Hokkaido forest plants distinguished on the basis of common modes along the *WI*, *D50* and *Ra* gradients. Group indications refer to gradient positions, and attributions in parentheses show its phytogeography, life form and associated forest type, as explained in the text.

CSR: Cold, deep-snow, much rainfall.

Sasa kurilensis (S, Se, IIIc); *Streptopus amplexifolius* var. *papillatus* (N, Hs, IIIc); *Clintonia udensis* (N, Hs, IIe); *Ilex rugosa* (S, Se, IIIc); *Euonymus tricarpus* (H, Ss, IIe); *Acer tschonoskii* (S, Ts, IIIa); *Menziesia pentandra* (S, Ss, IIIc); *Rhododendron albrechtii* (S, Ss, IIIc); *Vaccinium ovalifolium* (N, Ss, IIIa); *Vaccinium hirtum* (S, Ss, Ia); *Vaccinium smallii* (S, Ss, IIIc).

COr: Cold, snow-indifferent, little rainfall.

Polypodium virginianum (N, He, Ia); *Abies sachalinensis* (N, Te, IIIc); *Picea jezoensis* (N, Te, IIe); *Picea glehnii* (H, Te, Ia); *Anemone debilis* (N Hs IIe); *Tiarella polyphylla* (S He, IIe); *Ribes sachalinense* (N, Ss, IIe); *Oxalis acetosella* (N, He, Ib); *Cornus canadensis* (N, Hs, Ib); *Acer ukurunduense* (N, Ts Ib).

COO: Cold, snow-indifferent, rainfall-indifferent.

Lycopodium obscurum (O, He, IIIc); *Arachniodes mutica* (N, He, Ia); *Thelypteris connectilis* (O, Hs, IIe); *Dryopteris austriaca* (O, Hs, IIIc) *Carex sachalinensis* (N, He Ib); *Paris verticillata* (O, Hs, IIe); *Betula ermanii* (N, Ts, IIe); *Rubus pseudojaponicus* (H, Vs, IIe); *Actinidia kolomikta* (N, Vs, IIe); *Circaea alpina* (N, Hs, IIIc); *Pyrola renifolia* (N, He, IIIc); *Rhododendron brachycarpum* (S, Se, IIIc); *Galium kamtschaticum* (N, Hs, Ia); *Peracarpa carnosa* var. *circaeoides* (N, He, IIIc).

csr: Cool, shallow-snow, little rainfall.

Adiantum pedatum (O, Hs, IIc); *Schisandra chinensis* (N, Vs, IIc); *Stephanandra incisa* (S, Ss, IIa); *Acanthopanax senticosus* (N, Ss, IIe).

csO: Cool, shallow-snow, rainfall-indifferent.

Pyrrosia tricuspis (S, He, IIa); *Carex siderosticta* (O, Hs, IIc); *Cercidiphyllum japonicum* (S, Ts, IIc); *Fraxinus lanuginosa* (S, Ts, IIIb); *Viburnum wrightii* (S, Ss, IIIb).

cOr: Cool, snow-indifferent, little rainfall.

Cardmine leucantha (N, Hs, IIc); *Ribes latifolium* (H, Ss, IIe).

cOO: Cool, snow-indifferent, rainfall-indifferent.

Polystichum tripteron (O, He, IIc); *Taxus cuspidata* (S, Te, IIe); *Cimicifuga simplex* (N, Hs, IIIb); *Hydrangea paniculata* (S, Ss, IIIc); *Prunus ssiori* (N, Ts, IIe); *Phellodendron amurense* (N, Ts, IIc); *Cacalia hastata* var. *orientalis* (N, Hs, IIc).

WSR: Warm, deep-snow, much rainfall.

Leptorumohra miqueliana (O, He, IIIb): *Sturthiopteris niponica* (S, He, IId); *Corylus sieboldiana* (S, Ts, IIc); *Fagus crenata* (S, Ts, IIb); *Lindera umbellata* var. *membranacea* (S, Ss, IIb); *Hydrangea macrophylla* var. *megacarpa* (S, Ss, IId); *Skimmia japonica* var. *intermedia* (S, Se, IIIc); *Daphniphyllum macropodum* var. *humile* (S, Se, IIIb); *Ilex crenata* var. *paludosa* (S, Se, IId); *Ilex leucoclada* (S, Se, IIb); *Vaccinium japonicum* (S, Ss, IId).

WSO: Warm, deep-snow, rainfall-indifferent.

Arachniodes standishii (S, He, IId); *Athyrium vidalii* (S, Hs, IIIb); *Leptogramma pozoi* subsp. *mollissima* (S, Hs, IIIb); *Asplenium scolopendrium* (O, He, IIc); *Cephalotaxus harringtonia* var. *nana* (S, Se, IId); *Sasa cernua* (S, Se, IId); *Sasa megalophylla* (S, Se, IIe); *Carex foliosissima* (S, He, IV); *Acer mono* var. *mayrii* (S, Ts, IIc); *Euonymus alata* f. *dentatus* (S, Se, IIIb).

WsR: Warm, shallow-snow, much rainfall.

Disporum smilacinum (S, Hs, IId); *Picrasma quassioides* (S, Ts, IIc); *Acer palmatum* var. *matsumurae* (S, Ts, IIIb); *Viburnum dilatatum* (S, Ss, IId).

Wsr: Warm, shallow-snow, little rainfall.

Tilia maximowicziana (S, Ts, IIc); *Acer cissifolium* (S, Ts, IIa); *Spuriopimpinella calycina* (S, Hs, IIa); *Cacalia delphiniifolia* (S, Hs, IIa).

WsO: Warm, shallow-snow, rainfall-indifferent.

Lunathyrium pycnosorum (O, Hs, IId); *Sasa nipponica* (S, He, IIc); *Chloranthus serratus* (S, Hs, IIa); *Carpinus cordata* (S, Ts IIc); *Ostrya japonica* (S, Ts, IIc); *Quercus serrata* (S, Ts, IIa); *Ulmus davidiana* var. *japonica* (O, Ts, IIc); *Morus bombycis* (S, Ts, IIc); *Magnolia kobus* var. *borealis* (H, Ts, IIc); *Prunus sargentii* (S, Ts, IIc); *Prunus maximowiczii* (O, Ts, IIc); *Maackia amurensis* var. *buergeri* (S, Ts, IIa); *Desmodium oxyphyllum* (S, Hs, IIa); *Pachysandra terminalis* (S, Se, IIc); *Euonymus oxyphylus* (S, Ss, IV); *Acer palmatum* var. *amoenum* (S, Ts, IIc); *Styrax obassia* (O, Ts, IIa); *Phryma leptostachya* var. *asiatica* (O, Hs, IIc); *Cacalia auriculata* var. *kamtschatica* (N, Hs, IIe).

WOR: Warm, snow-indifferent, much rainfall.

Dryopteris monticola (O, Hs, IIIb); *Paris tetraphylla* (S, Hs, IIIb); *Magnolia obovata* (S, Ts, IIIb); *Schizophragma hydrangeoides* (S, Vs, IIIa); *Rhus ambigua* (S, Vs, IIIb); *Rhus trichocarpa* (S, Ts, IId); *Acer japonicum* (S, Ts, IIIb); *Acanthopanax sciadophylloides* (S, Ts, IIIa); *Cornus controversa* (S, Ts, IIc).

wOr: Warm, snow-indifferent, little rainfall.

Juglans ailanthifolia (S, Ts, IIc); *Laportea bulbifera* (S, Hs, IIc); *Caulophyllum robustum* (O, Hs, IIc); *Syringa reticulata* (S, Ts, IIc).

WOO: Warm, snow-indifferent, rainfall-indifferent.

Matteuccia orientalis (O, Hs, IId); *Arisaema Angustatum* var. *peninsulae* (N, Hs, IIc); *Smilacina japonica* (N, Hs, IId); *Disporum sessile* (S, Hs, IIIb); *Calanthe tricarinata* (S, He, IId); *Chloranthus japonicus* (O, Hs, IIc); *Betula maximowicziana* (S, Ts, IIIb); *Betula platyphylla* var. *japonica* (S, Ts, IId); *Alnus hirsuta* (N, Ts, IIc); *Quercus mongolica* var. *crispula* (S, Ts, IIIa); *Actaea asiatica* (O, Hs, IIe); *Sorbus alnifolia* (O, Ts, IIIb); *Acer mono* (O, Ts, IIIb); *Vitis coignetiae* (S, Vs, IIIb); *Tilia japonica* (S, Ts, IIIc); *Actinidia arguta* (O, Vs, IId); *Actinidia polygama* (S, Vs, IIe); *Kalopanax pictus* (S, Ts, IIIc); *Angelica ursina* (N, Hs, IIa); *Fraxinus mandshurica* var. *japonica* (S, Ts, IIc); *Asperula odorata* (O, He, IIc).

OSO: Deep-snow, and temperate and rainfall indifferent. *Plagiogyria matsumureana* (S, He, IIIa); *Leucothoe grayana* var. *oblongifolia* (H, Ss, IIIc); *Viburnum furcatum* (S, Ss, IIIc).

OsO: Shallow-snow, and temperature and rainfall indifferent. *Dryopteris crassirhizoma* (O, He, IIIc); *Athyrium yokoscense* (O, Hs, IIa); *Sasa chartacea* (S, He, IIa); *Zanthoxylum piperitum* (S, Ss, IIa); *Sanicula chinensis* (O, Hs, IIa); *Senecio cannabifolius* (N, Hs, IIe).

OOO: Indifferent species.

Lycopodium serratum (O, He, IIIc); *Lepisorus ussuriensis* var. *distans* (N, He, IIIb); *Sasa senanensis* (S, Se, IIIc); *Calamagrostis hakonensis* (N, He, IIe); *Carex caryophyllea* var. *microtricha* (N, Hs, IIc); *Carex pilosa* (N, He, IIc); *Allium victorialis* var. *platyphyllum* (O, Hs, IIIb); *Lilium cordatum* var. *glehnii* (N, Hs, IIc); *Polygonatum odoratum* var. *maximowiczii* (N, Hs, IIc); *Maianthemum dilatatum* (N, Hs, IIIc); *Epipactis papillosa* (N, Hs, IIIc); *Ulmus laciniata* (O, Ts, IIc); *Asarum heterotropoides* (H, Hs, IIe); *Diphylleia grayi* (H, Hs, IIIc); *Hydrangea petiolaris* (S, Ve, IIIc); *Sorbus commixta* (S, Ts, IIIc); *Osmorhiza aristata* (S, Hs, IIe); *Angelica anomala* (N, Hs, IIa); *Tripterospermum japonicum* (S, He, IIIa); *Cirsium kamtschaticum* (N, Hs, IIe).

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