Title	Environmental Factors Controlling the Distribution of Forest Plants with Special Reference to Floral Mixture in the Boreo-Nemoral Ecotone, Hokkaido Island
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Citation	Environmental science, Hokkaido University : journal of the Graduate School of Environmental Science, Hokkaido University, Sapporo, 15(2), 1-54
Issue Date	1993-03-25
Doc URL	http://hdl.handle.net/2115/37276
Type	bulletin (article)
File Information	15(2)_1-54.pdf

Environ, Sci., Hokkaido University	15 (2)	1 ~54	Dec. 1992

Environmental Factors Controlling the Distribution of Forest Plants with Special Reference to Floral Mixture in the Boreo-Nemoral Ecotone, Hokkaido Island

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Abstract

Effects of climatic factors on the plant distribution were examined by means of direct gradient analysis, and the relationship of forest flora with life form and phytogeographical distribution was examined. Subsequently, leaf phenology of forest plants were analyzed to evaluate the adaptive significance in relation to the environments in forest understory. In the boreo-nemoral forest ecotone, Hokkaido Island, northern Japan, co-occurrence of northern and southern plants in a certain forest site is more notable in the understory than in the crown, and this dates back to the late-Quaternary period, where the decrease in temperature associated with the glacial period forced the understory plants to adapt their life forms or leaf habits to snowcover and to light conditions of the interior forests.

Key words : Direct gradient analysis; Floral mixture; Leaf phenology; Mixed forest; Phytogoegraphy; Snowcover; Understory

Intoroduction

In the upper-middle latitudes of Europe, eastern Asia and eastern North America, the boreal coniferous forest formation confronts to the temperate hardwood forest formation. These areas are called as "pan-mixed forest zone" (Tatewaki 1958), "hemi-boreal forest zone" (Hämet-Ahti et al. 1974), or "boreonemoral zonoecotone" (Walter 1979). The general properties of the forest area are : (1) mosaic arrangements of pure stands of boreal forest and those of 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 conifer-hardwood forests, in which boreal trees and temperate trees concurrently grow, where their interactions are competitive (Woods and Whittaker 1981) or are in dynamically equilibrium due to the frequent occurrence of catastrophic disturbance (Falinski 1986 ; Ishikawa and 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 extensively dominant. The boreal plants of Hokkaido have undoubtedly come from the northeastern Eurasian Continent, migrating mostly through Sakhalin Island and/or Kurile Islands, while the temperate Asian plants and some Japanese endemics have come from Honshu Island through Oshima Peninsula, which is the southernmost area of Hokkaido (Kawano 1971 ; Maekawa 1974). During the postglacial periods, many temperate hardwood species have immigrated from Honshu and rapidly taken the place of 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 latitudinal distribution is expected to be outlined by their altitudinal distribution. However, precipitation often distorts the effects of temperature (Austin et al. 1984). Especially in Japan, the distribution of many forest plants is usually influenced by snowfall and/or rainfall : e.g., thermal tolerance ranges of many plants appear to vary among regions of different snowfall or rainfall conditions (Kure and Yoda 1984 ; Hattori and Nakanishi 1985 ; Tanaka 1986). Snowcover is considered to influence the distribution of plants. For instance, in deep-snow regions where plants were well protected from the frost damage by deep snowcover, some evergreen broad-leaved shrubs are occasionally found in summergreen forests (Sakai 1968). "Heteroptic" shrubs have evergreen leaves on creeping stems in addition to summergreen leaves on arborescent stems ; then, they can inhabit summergreen forests of Hokkaido (Kikuzawa 1984, 1989). In order to examine the process of floral mixture in boreo-nemoral forest ecotone, therefore, the inter- and intra-specific variation of distribution should be analyzed 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 and Hall 1987). The flora of the Japanese Archipelago also has a unique background of geo-histories, because this chain of islands has been frequently isolated from the Eurasian Continent or neighboring islands (Ohshima 1982 ; Tsukada 1983). In particular, Hidaka District of Hokkaido is isolatedly inhabited by some temperate plant species, which are common on the southern island Honshu (Tatewaki 1960 ; Uemura and Takeda 1987).

The distribution of plants is controlled by micro environmental factors such as light conditions, soil moisture and nutrients of their habitat. In particular, the light conditions of the habitat ecologically and physiologically affects the plants in photosynthetic activity, leaf number, leaf lifespan, timing of leaf emergence and shedding, etc (Chabot and Hicks 1982 ; Chapin and Shaver 1985). For forest plants, therefore, shade stress is considered as a fatal factor which determines whether they can establish themselves in a given habitat (Baruah and Ramakrishnan 1989 ; Woodward 1990). In the boreo-nemoral forest ecosystems, the distribution and establishment of forest plants are affected by the light conditions of forest understory. Hence, the shade tolerance of plants is a key factor for the ecological succession and regeneration of the ecosystems of boreo-nemoral forests.

In Hokkaido, the emergence and survivorship of leaves have been studied frequently for deciduous woody plants (Kikuzawa 1983, 1984 ; Koike 1988) and ferns (Sato and Sakai

1980), but rarely for understory species. The evolution of plants is a history of their adaptation to environmental stresses including low temperature, drought and shading, and the present distribution of plants is the result of the long-term interactions between plants and environments. Therefore, the floral mixture in boreo-nemoral forest ecotone should be investigated on the basis of physiological and ecological abilities for the establishment of each species.

The aims of the present study are : (1) to analyze the climatic preference of forest plant species for determining the factors controlling the distribution and those facilitating the speciation, (2) to elucidate the co-occurrence of southern and northern plants in Hokkaido, which has a wide dispersion of climate and a particular history of frequent paleogeographical isolation, and (3) to evaluate the leaf phenology in relation to seasonal changes of light conditions in forest understory.

First, effects of proximal climate factors on the distribution of forest plants are revealed in Chubu District, central Japan, where the vertical zonation of forests is well developed and the distribution of temperate or subalpine forests occasionally overlaps with each other, and in Hokkaido : that is, the distribution of forest plant species along three climatic gradients, temperature, snowfall and rainfall were analyzed. In order to evaluate the climatic preference of individual species and the relationship with the life form or floral make-up of forest vegetation, and at the same time the properties of distribution of plants are compared between these regions.

Subsequently, the co-existence of boreal and temperate floras are discussed with reference to the influence of those climatic variables and the history of immigration in the interglacial period. Moreover, the leaf phenology of understory vascular species is analyzed in order to examine the relationship of leaf habit and growth form with shade stress, competition and some other selective factors. Finally, significance of leaf habit as an aspect of the long-term dynamics of forest vegetation is discussed.

Areas studied

Hokkaido Island

Hokkaido Island (79,000 km^2) is one of the latitudinally lowest boreo-nemoral forest ecotone in the northern Hemisphere, being situated within the range of 41°24′-45°31′N and 139°45′-145°50′E (Figure 1). According to the Köppen's classification of climate, Hokkaido belongs to the humid microthermal climate Df, where the mean temperature is less than -3°C in the coldest month but exceeds 10°C in the warmest month, and precipitation is provided sufficiently for forest formation (Trewartha 1957).

The climate of this island is primarily controlled by : (1) the front of polar air masses which often cross the northern parts 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 parts 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 four climatic divisions (Kojima 1979) : the southwestern region, facing the Sea of Japan, which is warm and heavy

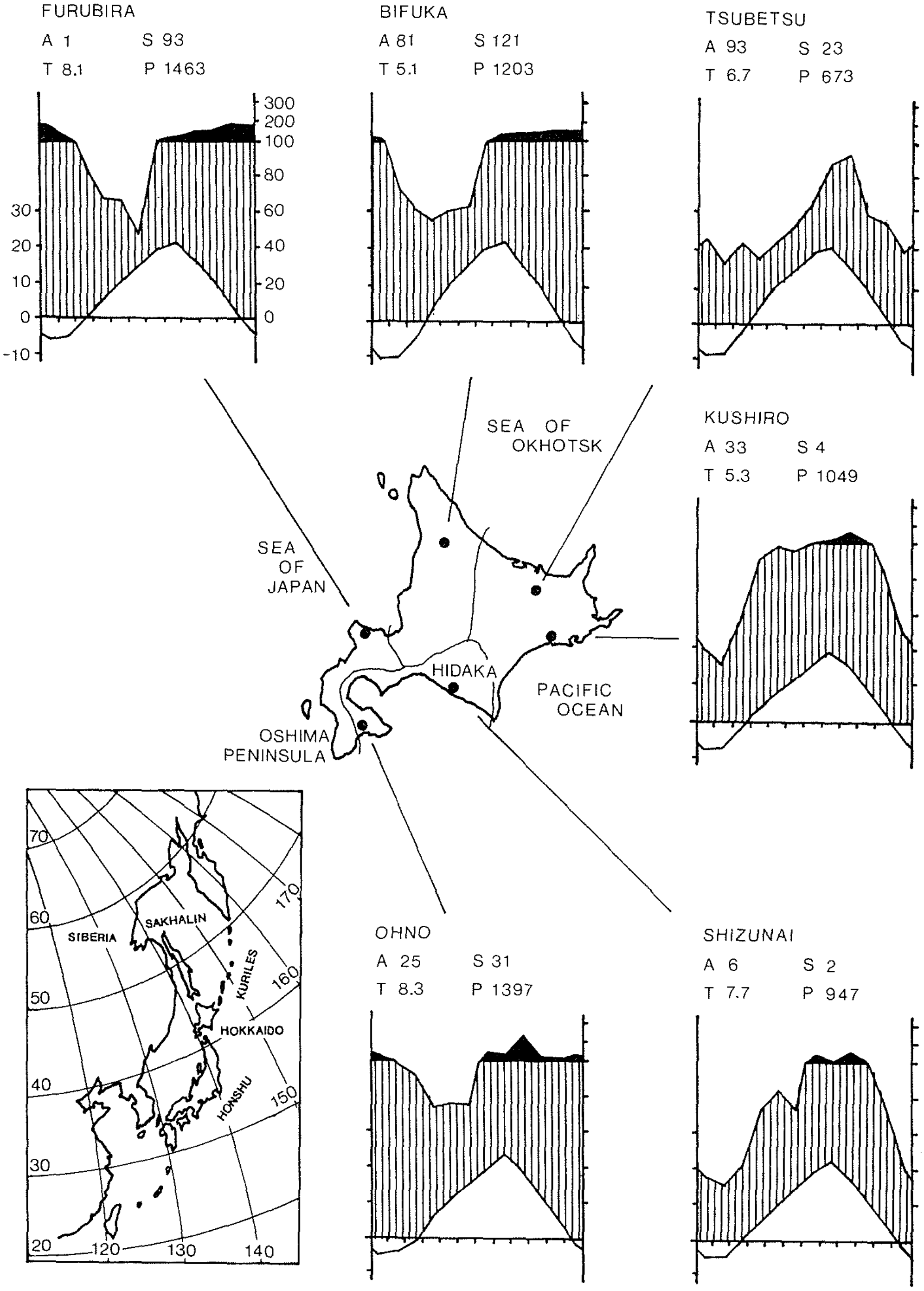


Figure 1. Climatic diagrams of some selected weather stations in Hokkaido Island. A, altitude of station (m) ; S, 50 cm or more deep snow days of per year ; T, mean annual temperature (℃) ; P, mean annual precipitation (mm).

snowfall ; 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 snowy ; and the eastern region facing the Pacific Ocean and the Sea of Okhotsk and being cool with little snowfall and minimal rainfall (Figure 1).

In flora of forests Hokkaido is similar to the other boreo-nemoral ecotone of Europe and North America. However, there are some particular features in Hokkaido : for instance, higher score of species richness, well-developed vertical structure, and distribution of many vine species such as *Vitis coignetiae* Pulliat, *Actinidia arguta* Miq., *Actinidia polygama* Maxim., *Hydrangea petiolaris* Sieb. et Zucc., *Schizophragma hydrangeoides* Sieb. et Zucc., etc. (Tatewaki 1958 ; Kojima 1979). Some genera endemic to Japan such as *Cercidiphyllus, Taxus* and *Kalopanax* also characterize the forests of Hokkaido. Another feature is the forest floor broadly predominated by dwarf bamboos, e.g., *Sasa kurilensis* Makino et Shibata, *Sasa senanensis* Rehd., *Sasa cernua* Makino, *Sasa magacarpa* Makino et Uchida, *Sasa nipponica* Makino et Shibata, *Sasa chartacea* Makino, etc.

The outline of natural forest vegetation is as follows. Boreal coniferous forests composed of *Abies sachalinensis* Masters, *Picea jezoensis* Carr. and *Picea glehnii* Masters, are dominant in the eastern region, summergreen forests predominated by boreal hardwood *Betula ermanii* Cham. are occasionally established. Temperate hardwood forests are classified into two types, i.e., beech forest and oak-maple forest. Beech forests largely dominated by *Fagus crenata* Blume are restricted to the southwestern region, particularly to the Oshima Peninsula. Oak-maple forests are dominant in the southern central region and eastern region, consisting of *Quercus mongolica* Fischer var. *crispula* Blume in association with *Acer mono* Maxim., *Acer mono* var. *mayrii* Koidz., *Acer japonica* Thunb., *Tilia japonica* Simonkai, *Tilia maximowicziana* Thunb., *Kalopanax pictus* Nakai, *Betula maximowicziana* Regel, *Prunus sargentii* Rehder, *Magnolia obovata* Thunb., *Ostrya japonica* Sarg., *Cercidiphyllum japonicum* Sieb. et Zucc., *Carpinus cordata* Blume, etc. In some cases, there are summergreen forests without *Quercus mongolica* var *crispula,* where *Quercus serrata* Murr., *Acer mono, Ulmus davidiana* Planch. var. *japonica* Nakai, etc. are instead dominant. Another conspicuous type of forest ecosystem is mixed forests composed of boreal conifers and many temperate hardwoods except *Fagus crenata.*

Though mixed forests are the transitional ecosystems between boreal and temperate forest formations, the community has been identified as Fagetea crenatae Miyawaki, Ohba et Murase 1964, simply due to the species richness of the temperate flora being more abundant than the boreal flora.

Chubu District

The Chubu District (65,000 km^2), situated in central Japan, has a particular climate ; thus, in winter, the very cold Siberian air mass is blown over the warm Sea of Japan current and brings the deepest snowfall of the world (up to 10 m) to the Sea of Japan side of the area, while in summer the hot Pacific air mass brings about 3000 mm rainfall to the Pacific side. In contrast, the inland regions are surrounded by many mountains of over 3000 m (including Mt. Fuji, the highest in Japan, 3776 m), and hence they have only about 1000 mm of annual precipitation (Figure 2).

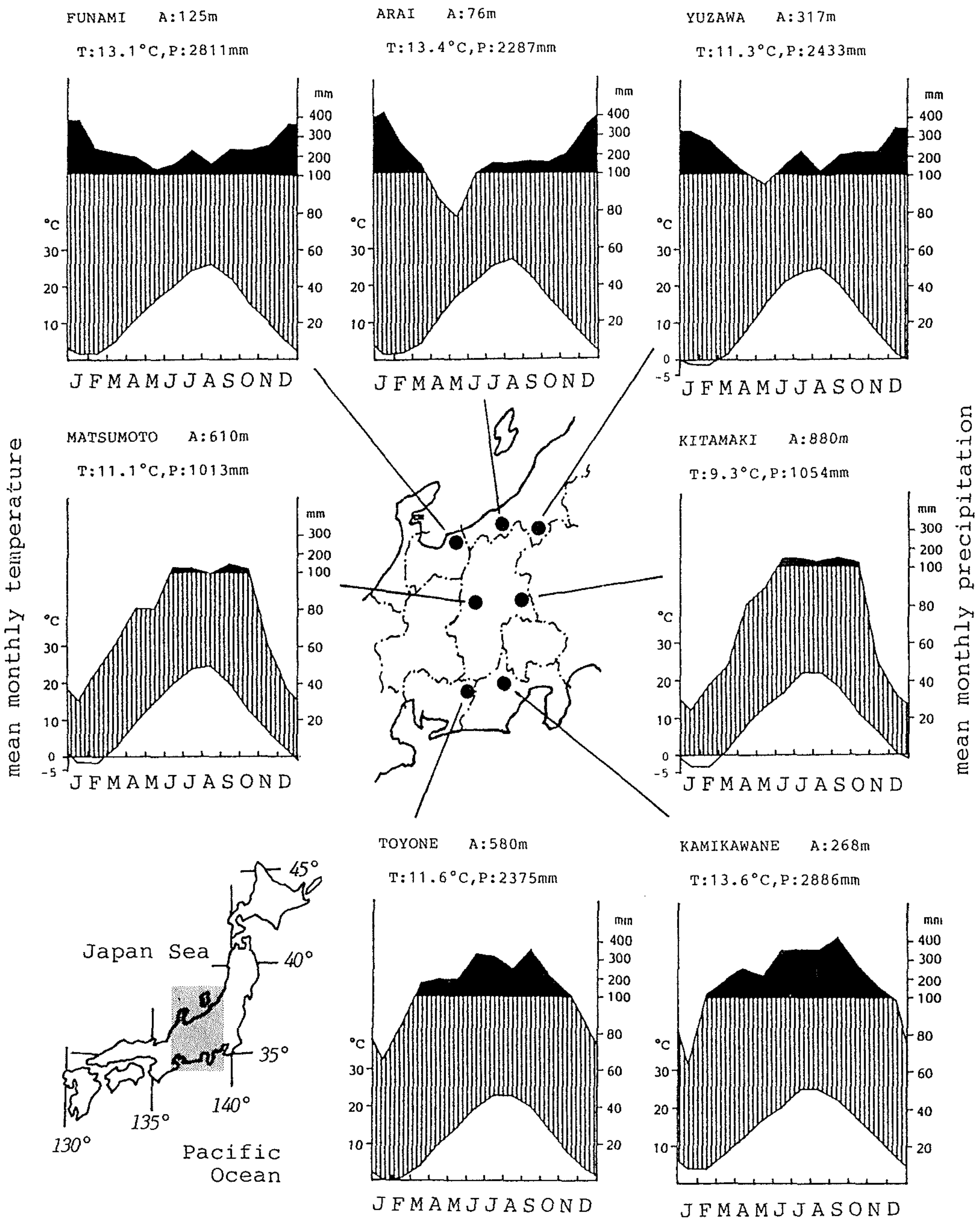


Figure 2. Climatic diagrams of some selected weather stations in Chubu District. A, altitude of station (m) ; T, mean annual temperature (°C) ; P, mean annual precipitation (mm).

Phytogeographically, this district is a most unusual area in Japan with about 3700 vascular plant species, corresponding to ca 70% of all Japanese species (Maekawa 1974 ; Shimizu 1985). High endemic ratio is another obvious feature on the flora : e.g., 73 flowering plant species are endemics to this district (Shimizu 1985). The main natural vegetation of this district is summergreen forests, which are largely. predominated by *Fagus crenata* associating with *Fagus japonica* Maxim., *Quercus mongolica* var. *crispula, Magnolia obovata, Acer japonica, Acer sieboldii* Miq., *Aesculus turbinata* Bl., *Kalopanax pictus,* etc. In these forests, some temperate coniferous species are occasionally distributed, e.g., *Abies homolepis* Sieb. et Zucc., *Tsuga sieboldii* Carr. and *Cryptomeria japonica* D. Don. The forest floor is completely dominated by dwarf bamboos such as *Sasa* and *Sasamorpha.* Laurel (evergreen broad-leaved) forests composed by *Castanopsis cuspidata* Schottky, *Quercus salicina* Bl. and *Quercus myrsinaefolia* Bl. are occasionally found in the lowlands (Miyawaki and Itow 1960; Miyawaki and Sasaki 1985) ; the subalpine-coniferous forests of *Abies mariesii* Masters, *Abies veitchii* Lindle., *Tsuga diversifolia* Masters, *Picea jezoensis* var. *hondoensis* Rehder, often dominated the highlands between 1500 and 2500 m in altitude (Miyawaki and Itow 1960 ; Nakamura 1986) ; mountain tops over 2500 m are covered by alpine heath or meadows including many circumpolar plant species (Nakamura 1987).

The arrangement of these vegetation zones is primarily controlled by the thermal factor (kira 1977). However, the distribution of many plant species which belong to a particular forest zone is rather complicated. For instance, on the Sea of Japan side some evergreen shrubs, e.g., *Cephalotaxus harringtonia* K. Koch var. *nana* Rehder and *Sasa kurilensis* are altitudinally widespread and frequently found in the different forest zones, presumably because of the effects of snow (Hotta 1974). Moreover, the altitudinal boundaries of the various vegetation zones are dependent on rainfall, snowfall, wind exposure and topography ; the thermal conditions at the border of each vegetation zone vary from region to region (Kure and Yoda 1984 ; Tanaka 1986).

Methods

1. Direct gradient analysis for climatic preference of plants

Chubu District

As shown in Figure 3, the vegetation was surveyed at 375 stands in 40 areas. The quadrats were set on closed and undisturbed sites in primary forests, size ranging from 15 x 15 m to 20 x 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 430 stands in 31 regions reported in the literature, e.g., Miyawaki et al. (1974) and Miyawaki (1977). Of the total of 805 analyses, 378 were from summergreen forests, 413 from subalpine-coniferous forests, and 14 from transitional mixed forests, defined by the 20-80% of the proportion of temperate hardwoods in the canopy coverage.

To evaluate their correlation to proximal climatic factors, direct gradient analysis proposed by Whittaker (1967) was performed on these plant species, in order to determine

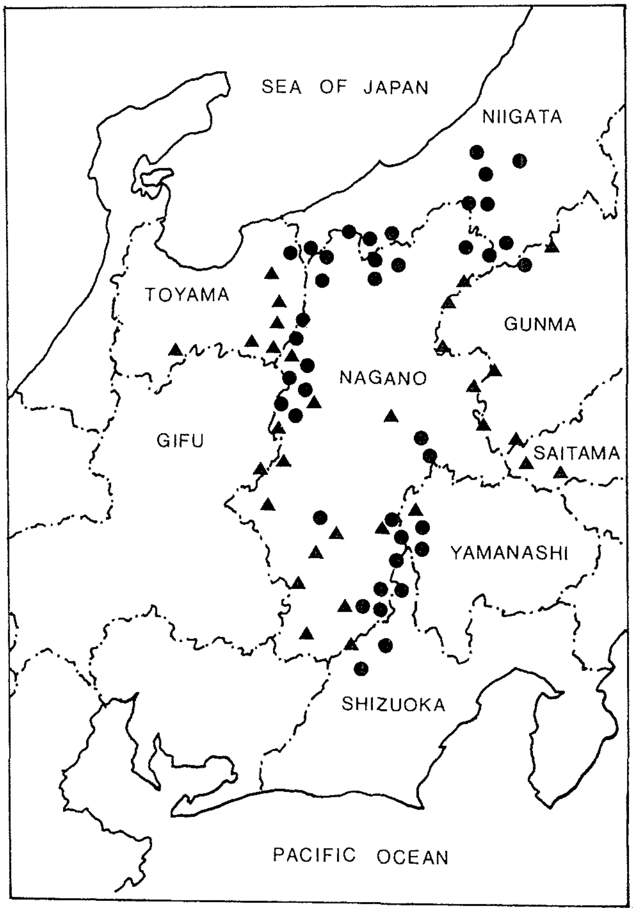


Figure 3. Location of area in the Chubu District surveyed. Circles, regions surveyed by the author ; triangles, cited from research reports (e.g., Miyawaki et al. 1974 ; Miyawaki 1977).

the habitats they would normally be found in. The following variables were calculated for the analysis :

Climatic data for each stand were estimated from the 1916-1950 records of the Japan Meteorological Agency at 88 weather stations in central Japan. Mean monthly temperature (T) was given by :

$$T = Tw - 0.6 \times 10^{-2} \ (As - Aw),$$

where Tw is the mean monthly temperature at the nearest weather station, As and Aw are the altitudes of the stand concerned and the nearest weather station, respectively. 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 estimated 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 ; winter precipitation *Pw* (mm), amount from December to March. As a snow index, 50 cm or more deep days of snow 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 :

$$D50 = 43.0 \ \ln \mid CI \ Pw \ 10^{-3} \mid - 58.0, \ (r = 0.848, \ P < 0.001).$$

Table 1 shows the correlation coefficients between each pairing of *WI, D50* and *Ra,* which were used for the direct gradient analysis. The correlations between *WI-D50* and *D50-Ra* are low in spite of statistical significance and that between *WI-Ra* is not significant, and hence it is realistic for the Chubu District to analyze the effects of these climatic factors on the plant distribution. Table 2 shows the distribution of values *WI* against *D50* and *WI* against *Ra.*

Table 1. Correlation (r) between *WI, D50* and *Ra* (n=88).

	r	t test
WI-D50	−0.288	$p < 0.01$
WI-Ra	0.093	$p > 0.1$
D50-Ra	0.276	$p > 0.01$

Table 2. Distribution of values of *WI* against *D50* and *WI* against *Ra* for 805 stands.

	WI (°C month) <25≤ <35≤ <45≤ <55≤ <65≤ <75≤								*WI* (°C month) <25≤ <35≤ <45≤ <55≤ <65≤ <75≤						
D50(days)								*Ra*(mm)							
120≤	23	29	19	11	0	0	0								
90≤ <120	45	73	48	68	34	21	2	1800≤	50	47	35	25	15	9	4
60≤ <90	58	32	68	42	21	3	28	1500≤ <1800	7	18	8	6	6	5	19
30≤ <60	9	21	21	35	37	16	10	1200≤ <1500	49	40	58	69	39	16	11
0≤ <30	0	0	1	7	16	2	5	<1200	29	50	57	63	48	12	11

Hokkaido Island

The vegetation was surveyed at 506 stands in 120 areas chosen over the entire island of Hokkaido (Figure 4). To complement this, additional vegetation records from 105 stands in 31 areas reported in the literatures, e.g., Kojima (1982, 1983). Of the total of 611 stands combined, 170 were grouped into boreal coniferous forests, 100 into beech forests, 249 into oak-maple forests, and 92 into mixed forests. On their localities, 101 stands were

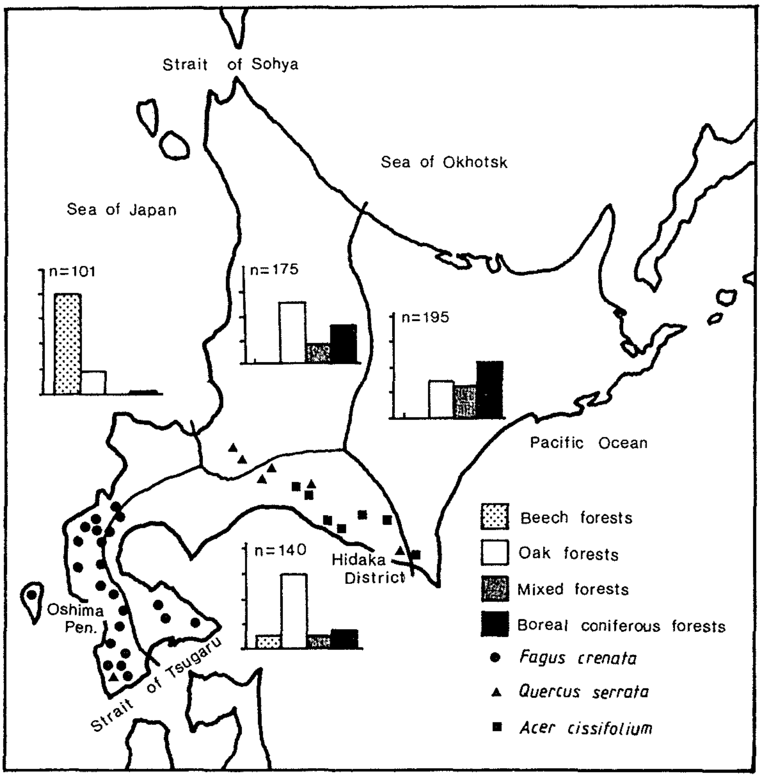


Figure 4. Forest distribution in the four climatic divisions. Histograms show frequency of each forest community. Distribution of three tree species being absent in mixed conifer-hardwood forest is also shown.

chosen from the southwestern region of this island ; 140 from the southern central region ; 175 from the northern region ; and 195 from the eastern region.

The climate at each stand was estimated from the climatic records at 79 weather stations, by the same method previously described in the analysis of Chubu District. In Hokkaido, the regression formula for *D50* value is :

$$D50 = 84.0 \ln \mid CI\ Pw\ 10^{-3} \mid -148.1, (r=0.884, P<0.001).$$

As shown in Table 3, the correlations of *WI, D50* and *Ra* with each other are not statistically significant indicating that these factors are considered to be independent of each other. Table 4 shows the distribution of values *WI* against *D50* and *WI* against *Ra.*

2. Co-occurrence of northern and southern plants

The co-occurrence of northern and southern plants was analyzed by using 164 vascular plant species whose climatic preferences have been revealed. As an index of floral mixture, the following evenness J' proposed by Pielou (1975) was used :

Table 3. Correlation (r) between *WI, D50* and *Ra* (n=79).

	r	t test
WI-D50	−0.097	$p > 0.1$
WI-Ra	0.084	$p > 0.1$
D50-Ra	0.141	$p > 0.1$

Table 4. Distribution of values of *WI* against *D50* and *WI* against *Ra* for 611 stands.

	WI (°C month)						*WI* (°C month)				
	<35≤ <45≤ <55≤ <65≤						<35≤ <45≤ <55≤ <65≤				
D50(days)						*Ra*(mm)					
120≤	1	14	25	4	0						
90≤ <120	10	8	41	45	20	900≤	7	25	53	31	1
60≤ <90	17	81	21	79	17	800≤ <900	0	8	34	55	16
30≤ <60	12	18	62	39	30	700≤ <800	11	87	61	99	22
0≤ <30	0	9	35	46	4	<700	12	10	36	28	5

$$J' = -\Sigma\ (p_n \ln p_n + p_s \ln p_s)\ (p_n + p_s)/\ln 2,$$

where p_n and p_s are relative richness of northern species and southern species, respectively.

3. Leaf phenology

The investigation was conducted in thirty-one 20 m × 20 m quadrats chosen from the closed primary forests in Hokkaido (Figure 5) : 9 quadrats from beech forests, 6 from oak-maple forests, 10 from coniferous forests, and 6 from mixed forests. In each quadrat, canopy coverage of all trees taller than 2 m was measured in midsummer, and concurrently, those of understory plants including tree saplings smaller than 2 m were measured in five 2 m × 2 m blocks randomly chosen. Dominance of understory species were represented by mean coverage in the five blocks. Other than epiphytes, a total number of vascular species *NS* was also recorded in each quadrat. In spring, the leaf habit of understory plants was examined by observing coverage and leaf age in the five blocks in 13 of the 31 quadrats. Of these 13 quadrats, 3 were chosen from each of beech, oak-maple and mixed forests, and 4 from coniferous forests.

The Shannon-Weaver diversity index *H'* (Peilou, 1975) was used as the index of tree diversity in the overstory :

$$H' = -\Sigma p'_i \ln p'_i,$$

where p'_i is proportion of species i in the canopy coverage.

Attenuation of light intensity within a plant community varies directly with extinction ratio, that is a function of time. As schematically represented in Figure 6, solar radiation penetrating through a crown of species i at time t is expressed by weighting the coverage of the species :

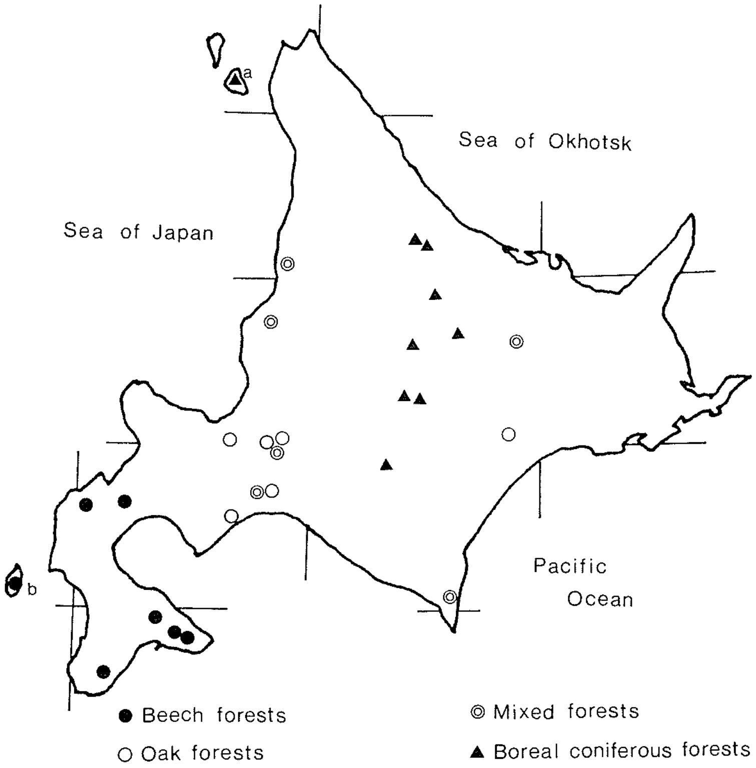


Figure 5. Localities of the 31 stands surveyed the leaf phenology of understory plants. Sites of a and b in the map include two and three stands, respectively.

$$L_i(t)' = p_i \ r_i(t) \ L_0(t),$$

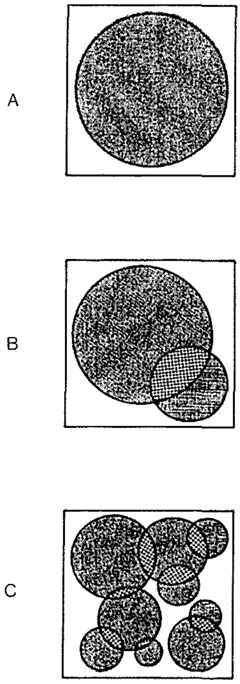
where $L_0(t)$ is incident solar radiation and p_i and $r_i(t)$ are area and the light extinction ratio of the species, respectively, while solar radiation which is not intercepted by the crown is :

$$L_i(t)'' = (1 - p_i) \ L_0(t).$$

Thus, the average solar radiation passing through each tree species is :

$$L_i(t) = L_i(t)' + L_i(t)''.$$

In the case of canopy composed of n species, occurrence of overlapping by three or more species is rare since the spatially exclusive spreading of crowns in mature forest (Ishizuka 1984), and additionally, solar radiation penetrating through such areas is nearly zero because of the attenuation by multiplied extinction ratios. Then, solar radiation penetrating through the canopy is approximately given by the amount of solar radiations through each patch with single, double and no species :



$$L = p_i r_i L_0 + p_0 L_0$$

$$L = \{\sum_{i=1}^{2} (p_i - k_i) r_i\} L_0 + (k_i r_1 r_2) L_0 + p_0 L_0$$

$$L = \{\sum_{i=1}^{n} (p_i - k_i) r_i\} L_0 + \{\sum_{i=1}^{n} k_i \sum_{i=1}^{n-1} \sum_{j=i+1}^{n} r_i r_j / n(n-1)\} L_0 + p_0 L_0$$

Figure 6. Schematic representation of solar radiation penetrating through a canopy attenuated by a canopy composed of a species (A), two species (B) and n species (C), respectively. L, transmitted solar radiation ; L_0, incident solar radiation ; p, coverage of a crown ; p_0, area covered by no crown ; k, area covered by two crowns ; r, light transmission ratio. For detail explanation, see text.

$$L(t) = \{\Sigma(p_i - k_i) r_i(t) + \Sigma k_i \sum_{i=1}^{n-1} \sum_{j=i+1}^{n} r_i(t) r_j(t) / n(n-1) + p_0\} \ L_0(t),$$

where k_i is overlapped area in the crown of species i, $\Sigma\Sigma\ r_i(t)\ r_j(t)$ is average extinction ratio of double-species patches and p_0 is the area covered with no crown. If light extinction ratio of a deciduous tree is in direct proportion to attached leaves, $r_i(t)$ can be approximately obtained from such leaf events as budbreak, end of leaf emergence, commencement of leaf fall and end of leaf fall. For the deciduous broad-leaved trees, dates of these leaf events were estimated from the leaf survival curves represented in Kikuzawa (1983) as being irrespective of sites, and the maximum and minimum extinction ratios of all species were assumed to be 0.9 and 0.4, respectively. For evergreen conifers, the extinction ratios were conjectured to be 0.9 throughout a year. To evaluate the efficiency of light transmission of each species, transmitted solar radiation TSR was calculated as :

$$TSR = \int L_i(t)\ dt / \int L_0(t)\ dt.$$

Unlike canopy trees, understory plants are also have a limited photosynthesis due to snowcover, hence, the only light resource available is during snow-free season. As the light resource in spring, relative solar radiation (RSR, viz., a ratio to the annual amount on the canopy surface) was integrated from the thawing of continuous snowcover (tt) to 30 June ($t=181$) :

$$RSR=\int_{tt}^{181} L(t)\ dt / \int_{0}^{365} L_0(t)\ dt,$$

and likewise, RSR in summer was integrated from 1 July ($t=182$) to 30 September ($t=273$), and RSR in autumn was from 1 October ($t=274$) to the commencement of continuous snowcover (tc). For the values of $L_0(t)$, the 1981-1990 observation record of solar radiation (MJ/m^2) at the Experimental Farms, Hokkaido University, Sapporo, was used.

Predicted dates of tt and tc in each site were estimated from the records at the nearest weather station by using the 1951-1980 records of the Japan Meteorological Agency of 23 weather stations :

$$tt=-3.1\ \Sigma\ T_i+0.22\ \Sigma\ P_i-2,\ (R=0.650,\ P<0.01)\ ;$$
$$tc=4.8\ T_{12}-1.60\ P_{12}+364,\ (R=-0.809,\ P<0.01),$$

where $\Sigma\ T_i$ and $\Sigma\ P_i$ are respectively accumulations of mean monthly temperature (°C) and precipitation (mm) from January to the last month of which mean monthly temperature was below 0°C, and T_{12} and P_{12} are those in December. The snow-cover duration per year at each quadrat (CS, days) was obtained by :

$$CS=tt+(365-t_c).$$

To reveal the correlation of leaf habits to light resources, cluster analysis was conducted based on the similarity of understory vegetation. Available information for samples was obtained by Mountford's average linkage clustering which was performed by Gleason's index of community similarity PS :

$$PS=2\ \Sigma\ \min\ (x_i,\ y_i)/\Sigma\ (x_i+y_i),$$

where x_i and y_i are the amounts of coverage of species belonging to leaf phenological group i at each quadrat, respectively.

Terminology

To indicate the thermal and snowfall conditions, the following criteria were adopted : "cold (C)" means $WI<35$ °C month ; "cool (c)", 35 °C month $\leq WI<65$ °C month ; "warm (W)", 65 °C month $\leq WI$; "deep-snow (S)", 90 days $\leq D50$; "shallow-snow (s)", $D50<$ 30 days. The rainfall conditions were classified as follows : in Chubu District, "much rainfall (R)" means 1500 mm $\leq Ra$; "little rainfall (r)", $Ra<1200$ mm ; and in Hokkaido, "much rainfall (R)", 900 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. Hultén 1972 ; Kawano 1971 ; Nakaike 1975 ; Ohwi and Kitagawa 1984). In Chubu District, those plants were divided into the following five groups : southern plants (S), with their northern margin located in central Japan ; northern plants (N), with their southern margin located in central Japan; plants endemic to Chubu District and its vicinity (EE) ; endemic from central to northern Japan (E) ; and otherwise widespread plants (O). In Hokkaido, 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, those forms were divided into nine 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) ; summergreen herbs (Hs) ; and non-green leaved herbs (Hn), i.e., saprophagous plants. In these divisions, plant species with overwintering leaves are clustered into evergreen categories.

Results

1. Climatic preference of forest plants in central Japan

Commodal groups

Out of 731 vascular plant species found in the present study, 151 species occurring in 30 or more stands were used for the analysis of commodal groups. For each species their occurring stands were arranged along the three climatic factors *WI, D50* and *Ra*. According to the similarity of the stand distribution, the 151 species were divided into 16 commodal groups (see Appendix 1). Some typical species of each group are represented in Figure 7. These groups were distinguished on the basis of their distribution modes along the three climatic gradients in order. Number of species for the commodal groups are tabulated in Table 5.

As a whole, the distribution of 142 of the 151 species appeared to be controlled by temperature (Cxx + cxx + Wxx ; 94.0%) ; 76 by snowcover (xSx+xsx ; 50.3%) ; 27 by rainfall (xxR + xxr; 17.9%) ; and 6 to neither factors (OOO ; 4.0%). This suggests that the behavior of the forest plants is controlled primarily by temperature and partly by snowcover. Especially, *Sasa kurilensis, Heloniopsis orientalis* C. Tanaka and *Tripterospermum japonicum* Maxim. preferred snow regardless of the thermal conditions (OSO). Rainfall factor is considered nearly ineffective to the distribution of many plant species.

Occurrence of commodal groups in forest ecosystems

According to the occurrence frequency in forest ecosystems, those species were arranged in the following three ecological groups (Mueller-Dombois and Ellenberg 1974) : **I**, species of subalpine-coniferous forests ; **II**, species of summergreen forests; and **III**, species common to both forest ecosystems. As shown in Table 5, species of Wxx group are associated with summergreen forests while those of Cxx group are combined with subalpine-coniferous forests, supporting that the species make-up of forest communities are primarily controlled by the thermal factor.

The WS group consists exclusively of summergreen forest components (I), involving many shrub taxa which are varieties having become differentiated from the parent populations of the species. For instance, *Lindera umbellata* Thunb. var. *membranacea* Momiyama is a variety of *Lindera umbellata* belonging to the WsO group. Most of the

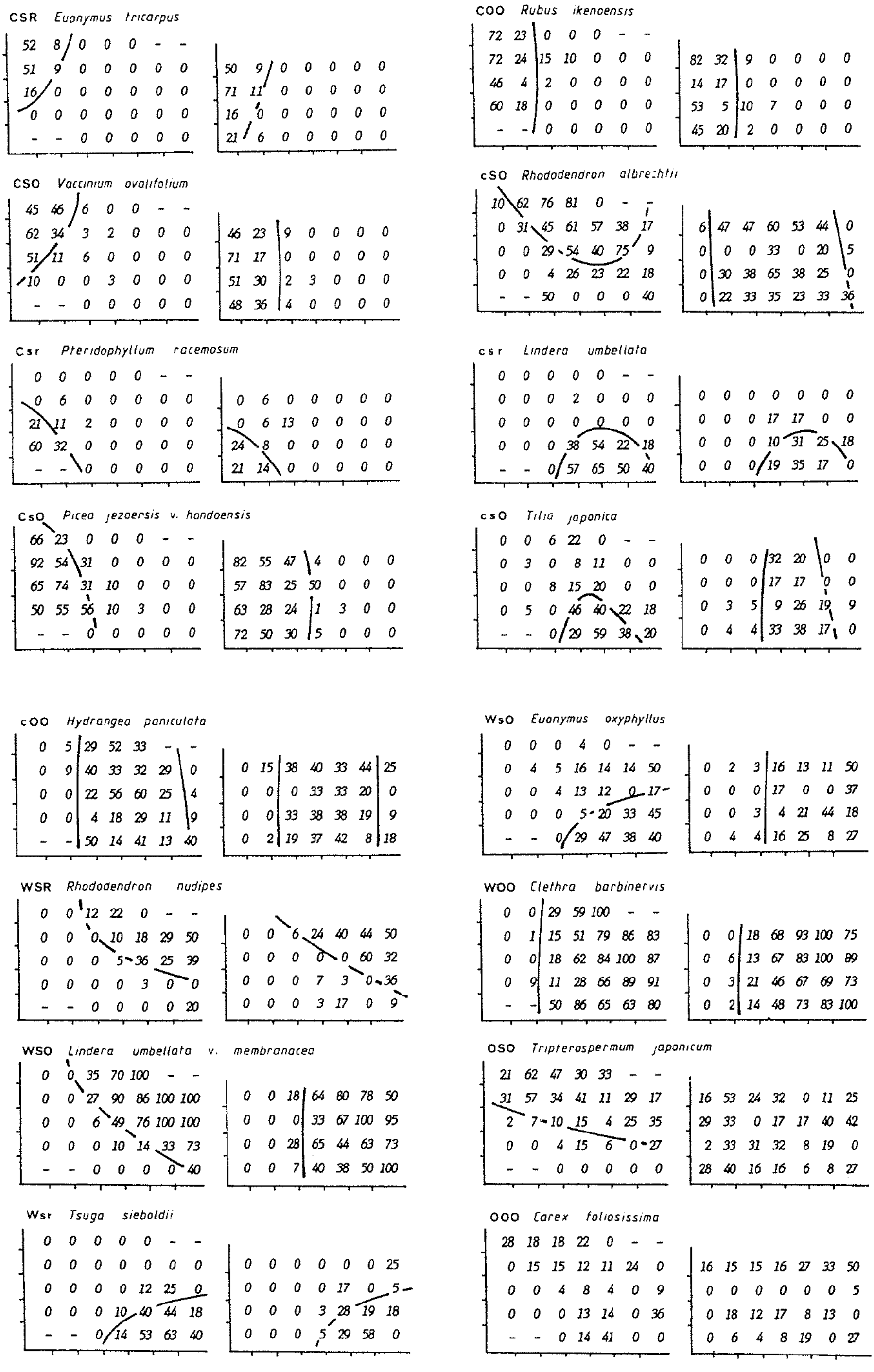


Figure 7 Distribution of representative species of 16 commodal groups along *WI* and *D50* (left side) and *WI* and *Ra* (right side). Values given are 100 × *Fs* / *Ft*, where *Fs* and *Ft* are the numbers of stands inhabited by a given species and total stands in the whole data set (Table 2), respectively. Isolines are also shown by solid lines.

Table 5. *Commodal species groups with total number of species and number of species per* phytogeographical group, life form and forest type. Commodal groups were represented by the modes along *WI, D50* and *Ra,* in order (cf. Appendix 1). Abbreviations are given in the Terminology section.

Commodal group	Phytogeographical group					Life form category									Ecolog group		
	EE	E	S	N	O	Te	Ts	Ve	Vs	Se	Ss	He	Hs	Hn	I	II	III
CSR		3		1	1						2	1	2		4		1
CSO	1	4		1	1	1	1			1	2	1	1		4		3
Csr	2				1								3		3		
CsO	5	3				3	1				1	1	2		8		
COO	5	8		11	4	3	4			3	4	2	12		19		9
cSO		7		2	1		1		1	3	2	1	2			4	6
csr		2	1		1	1					2	1				3	1
csO		3			4	1	1		1		2	1	1			6	1
cOO	4	5	2	2	5		4	1			3	1	9			13	5
WSR	1	6	1		3		3			2	4	2				11	
WSO	1	7	1		2		1		1	5	1	3				1	
Wsr		3			1	1	1			1		1				4	
WsO					3		2				1					3	
WOO	2	11	1		9		15		3		2	1	2			23	
OSO		1	1	1						1		2					3
OOO	1	2			3						1	4		1			6
Total	22	65	7	18	39	10	34	1	6	16	27	22	34	1	38	78	35

varieties are endemic to central Japan and its vicinity (EE). All the species of groups OSO and OOO, which do not respond to *WI*, are commonly distributed in summergreen and subalpine-coniferous forests (**III**).

Relationship with phytogeography and life forms

As shown in Figure 8, none of the northern species (N) requires "warm" conditions ; most of them require "cold" conditions irrespective of their response to the snow factor. In contrast, the southern plants (S) do not require "cold" conditions, as predicted from the importance of temperature as a primary factor. However, the distribution of endemic plants seems to depend on snowfall as well as on temperature. The snow-independent species, O make up 52.4% of the total of EE species, 39.1% in E, 42.8% in S, 72.2% in N and 58.5% in O. The values for the southern and endemic group are lowest, suggesting that many such species are influenced by snowfall, which prevents their northward expansion. In particular, the endemic plants limited to the Chubu District and its vicinity (EE) are characterized by many Cs species (33.3%), which cannot advance to northwards because of the heavy snowfall and neither southward because of high temperatures ; the widely distributed Japanese endemics (E) require deep-snow conditions. This suggests that among the endemics, snow-tolerant taxa are most likely to be distributed towards the north of Japan.

Also Figure 8 shows the relationship with life form categories. Evergreen coniferous trees (Te) preferred the cold climate while avoiding deep snow : the ratio of species requiring "cold" conditions is 70.0%, and that of "shallow-snow" is 60.0%. Summergreen

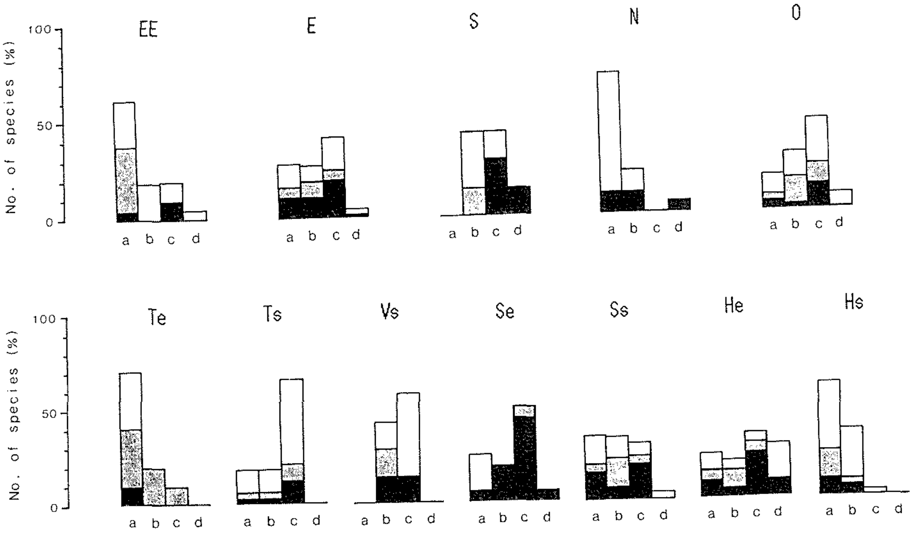


Figure 8. Frequency of distribution of species in each warmth index commodal group (as %) for phytogeographical categories (A) and life form (B). The solid blocks represent species which require snow-rich conditions, the shaded ones refer to snow-poor conditions, and the open to snow-indifference. Abbreviations are given in the Terminology section. a, Cxx ; b, cxx ; c, Wxx ; d, Oxx.

broad-leaved trees (Ts) are dominant in "warm" or "cool" regions, but rather independent of the influence of snow: the ratio of snow-independent species is 67.6%. Even for the shrubs the ratio of snow-independent species was higher in the summergreen group (37.0% in Ss) than in the evergreen group (18.8% in Se). All the woody vines required "cool" or "warm" conditions. However, their distribution was not overly affected by the snow : the ratio of snow-independent species is 57.0%. Herbs were not concentrated in a special range of temperature and, like woody vines, they seemed to be less influenced by snow. These facts indicate that the snow exerts more influence on evergreen trees and shrubs than on summergreen trees and shrubs, and on woody vines and herbs.

Life forms and forest types of endemic species

Table 6 shows the number of endemic species (E and EE) and the other broadly distributed plants (S, N, and O) in each life form group. The endemic ratio, (E + EE) / total number of species, was higher in evergreen groups than in deciduous groups, and higher in trees and shrubs than in herb species. However, 6 endemics in Te (66.7%) prefer shallow-snow stands irrespective of their response to thermal factors, and 9 endemics in Se (75.0%) prefer deep-snow stands. Thus, regarding snow conditions evergreen trees are different from evergreen shrubs.

Of the evergreen shrubs, all plants which require 'cold' conditions are endemics, i.e., *Rhododendron brachycarpum* D. Don. of CSO, and *Rhododendron metternichii* Sieb. et Zucc. var. *pentamerum* Maxim., *Epigaea asiatica* Maxim. and *Ilex rugosa* Fr. Schm. of COO. The three ericaceous species commonly have thick curly leaves with numerous trichomes, and

Table 6. Number of plants endemic to central Japan, E, and to the Chubu District, EE, in each life form category. Abbreviations are given in the Terminology section.

Life form	No. of endemics		No. of non-endemics	Endemic ratio
	EE	E	S+N+O	
Te	4	5	1	0.90
Ts	2	21	11	0.68
Ve	0	0	1	0
Vs	0	1	5	0.17
Se	2	12	2	0.88
Ss	2	14	11	0.59
He	3	7	12	0.45
Hs	9	5	20	0.41
Hn	0	0	1	0

Table 7. A 3×3 contingency table showing the association between phytogeographical categories and ecological groups combined with forest types. Expected values are given in parentheses. The association is significant at $P<0.05$ ($\chi^2=12.6$).

Phytogeographical group	EE	E	S+N+O	Total
Ecological group				
I	11 (5)	13 (16)	14 (16)	38
II	5 (11)	39 (34)	34 (34)	78
III	5 (5)	13 (15)	17 (15)	35
Total	21	65	65	151

the remaining species *Ilex rugosa* is a creeping dwarf shrub. Other evergreen shrubs requiring "cool" or "warm" conditions prefer deep-snow stands ; they cannot tolerate low temperatures without snowcover.

Table 7 shows the distribution of those plants in each ecological group combined with particular forest types. The Chubu District endemics (EE) are significantly concentrated in group I, which is associated with subalpine-coniferous forest. Many of those species are the postglacial relict.

Behavior of main tree species

Summergreen forests are usually predominated by *Fagus crenata, Fagus japonica* and *Quercus mongolica* var. *crispula.* As shown in Figure 9, *Fagus crenata* preferred warm, deep-snow and much rainfall conditions (WSO), but its distribution range was so wide that it was sometimes present in regions as cold as *WI* < 45°C month if snowfall or rainfall was high. In contrast, *Fagus japonica* was restricted to a narrow range of *WI* and *D50* (Wsr) and was absent from cold regions, also if there was little snowfall. *Quercus mongolica* var. *crispula* was classified into the WOO group ; however, it can survive even in the cold regions where *WI* = 35°C month if the snowfall was as much as 60-120 days of *D50*.

In subalpine-coniferous forest *Tsuga diversifolia, Abies veitchii* and *Abies mariesii* are usually dominant. However, the two former species, belonging to group CsO, occur

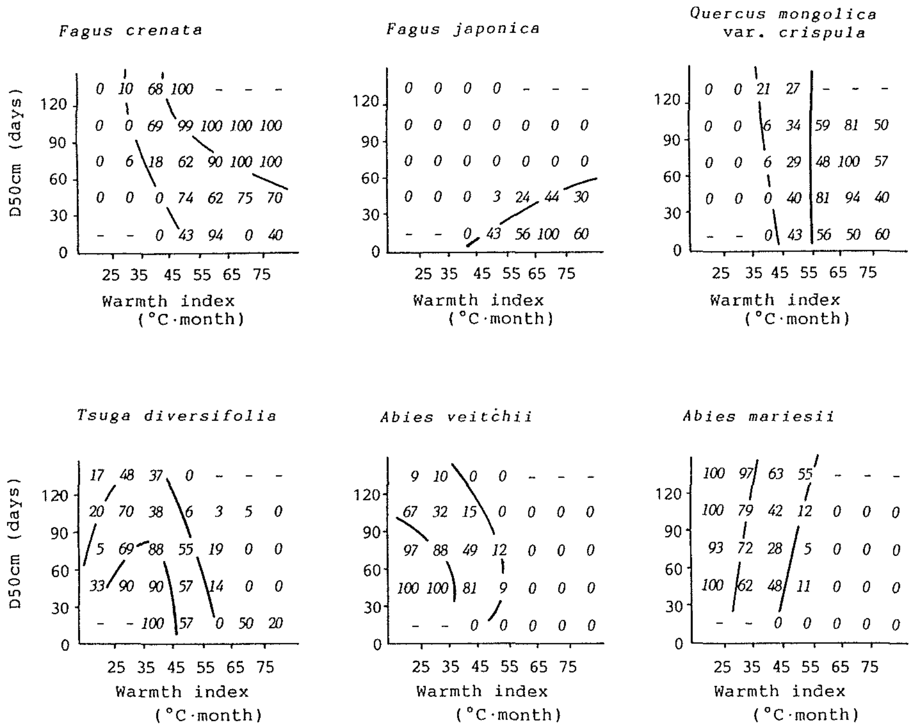


Figure 9. Behavior of tree species belonging mainly to the summergreen forests or the subalpine-coniferous forests along the primary factors *WI* and *D50*.

occasionally in warm regions where *WI* = 55-75°C month, if there is provided a limited snowfall or rainfall. The distribution of the third species, classified as COO, was completely restricted to the regions with *WI* < 45°C month.

2. Climatic preferences of Hokkaido forest plants

Commodal groups

A total of 537 vascular plant species were identified, and 164 species found in more than 24 stands were used for analysis. According to the similarity of the stand-distribution along *WI, D50* and *Ra,* the 164 species were divided into 18 commodal groups (see Appendix 2). Figure 10 represents the stand-distribution of typical species in each group.

Table 8 shows the number of species in each commodal group. As a whole, the distribution of 135 of the 164 species appeared to be controlled by temperature (Cxx + cxx + Wxx = 82.3%, where arbitrary modes along snowcover and rainfall refer to x, orderly), 77 by snowcover (xSx + xsx = 47.0%), and 59 by rainfall (xxR + xxr = 36.0%). That is the behavior of the forest plant species in Hokkaido are primarily controlled by temperature, but snowcover and rainfall are additional factors affecting their behavior. The comparison with Chubu District demonstrates that the distribution of plant species is more strongly dependent on rainfall, but more weakly on temperature in Hokkaido, thus, fewer species preferring "cool" regions (cxx) and the larger number of species being

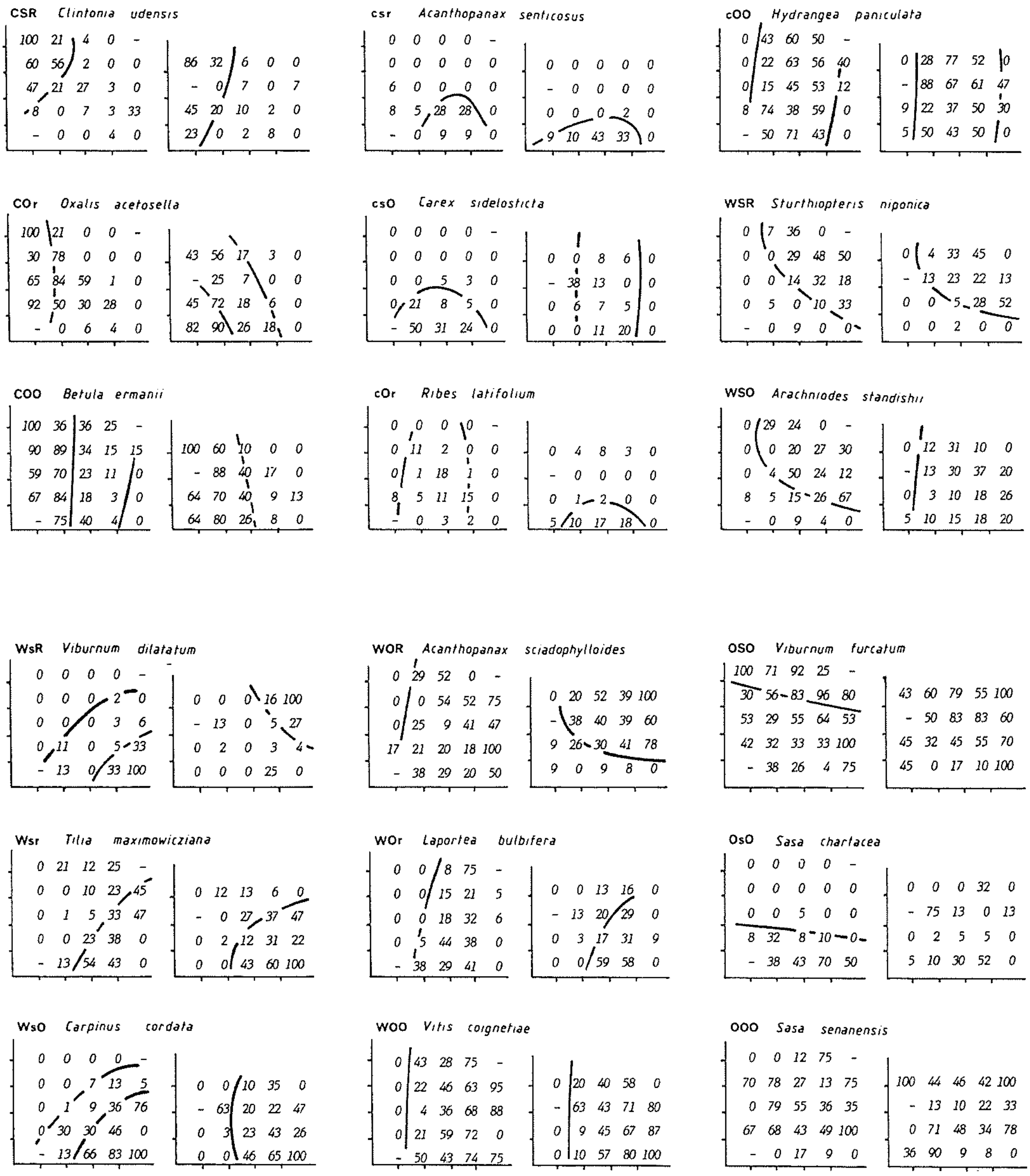


Figure 10. Distribution of representative species of 18 commodal groups along *WI* and *D50* (left side) and *WI* and *Ra* (right side). Values given are 100 × *Fs* / *Ft*, where Fs and *Ft* are the numbers of stands inhabited by a given species and total stands in the whole data set (Table 4), respectively. Isolines are also shown by solid lines.

Table 8. Number of species per each gradient commodal group in Hokkaido and in Chubu District. Commodal groups are represented by mode. By chi-square contingency test, significance of differences in both districts are also shown.

		along *WI*		along *D50*		along *Ra*
Hokkaido						
	C	35 (21.3%)	S	35 (21.3%)	R	35 (21.3%)
	c	18 (11.0%)	s	42 (25.6%)	r	24 (14.6%)
	W	82 (50.0%)	O	87 (53.0%)	O	105 (64.2%)
	O	29 (17.7%)				
Chubu District						
	C	51 (33.8%)	S	47 (31.1%)	R	16 (10.6%)
	c	39 (25.8%)	s	29 (19.2%)	r	11 (7.3%)
	W	52 (34.4%)	O	75 (49.7%)	O	121 (80.1%)
	O	9 (6.0%)				
χ^2		23.3 ($P<0.01$)		4.8 ($P<0.05$)		12.6 ($P<0.01$)

indifferent to temperature (Oxx).

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 following three groups (Figure 11) : **I** species mainly distributed in boreal coniferous forests. They were subdivided into two types : **Ia,** found exclusively in boreal coniferous forests and **Ib** found also in mixed forests. **II** species mainly distributed in summergreen forests, with five subgroups, i.e., **IIa** species found only in beech forests, **IIb** found only in oak-maple forests, **IIc** common to beech and oak-maple forests, **IId** common to oak-maple and mixed forests, and **IIe** found in beech, oak-maple and mixed forests. **III** species common to boreal coniferous forests and summergreen forests, with three subgroups, i.e., **IIIa** common to boreal coniferous and beech forests, **IIIb** common to boreal coniferous, mixed and oak forests, and **IIIc** common to all forest ecosystems. No species group was exclusively associated with mixed forests. The relationship between commodal groups and forest types is shown in Table 9.

Many species of group **I** preferred cold climate and little rainfall : Cxx = 100% and xxr = 55.6%. The difference between **Ia** and **Ib** is merely dependent on the thermal range. Species of group **II** prefer warm or cool climate, suggesting that their normal home ranges are in the temperate forests. Of these species, **IIa** and **IIc** often found in beech forests were mostly distributed in snowy and rainy regions : xSx and xxR were 100% and 100% in **IIa** and 43.8% and 43.8% in **IIc**, respectively. In contrast, **IIb** and **IId** being absent in beech forests were biassedly distributed in regions where snowfall and rainfall were little : xsx and xxr were 87.5% and 25.0% in **IIb** and 43.6% and 20.5% in **IId**, respectively. The climatic preferences of **IIc**, **IId** and **IIe** were varied among species. The species of group **IIIa** were closely related to snowy conditions, xSx constituting 75.0%. Most of the species of group **IIIb** preferred cold or cool climate, Wxx consisting of only 16.7%. The species of group **IIIc** showed a great variation of distribution and seemed indifferent to the three environmental gradients examined.

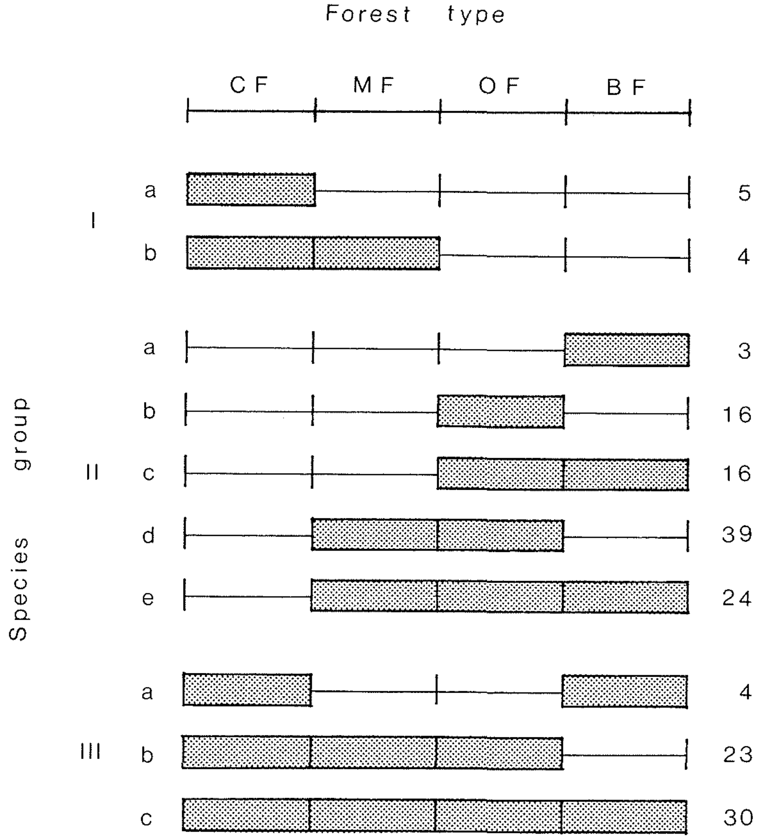


Figure 11. Species groups associating to forest types, represented by the fidelity more than 20% of total stands of each forest type. For abbreviations of each species group, see text.

The number of summergreen forest species (**IIa** + **IIb** + **IIc**) was small (35 species), which was less than a half of that in central Japan presented in Uemura (1989), though the ratio of summergreen forest stands to all stands surveyed was higher in Hokkaido (57%) than in central Japan (47%). Species exclusively inhabiting boreal coniferous forests was fewer in Hokkaido (**Ia** constituing 5 species) than in central Japan (38 of 164 species analysed), suggesting that the altitudinal distribution of forest plants is not completely identical to their latitudinal distribution.

Relationship between phytogeography and life forms

Although southern plants mostly required 'warm' climate (Wxx = 70.6%), a few of them required "cold" climate, Cxx = 10.6% (Table 10). Since most of them belong to the group CSR, their expansion to the north seemed to be made possibly by heavy snowfall and much rainfall. Most of northern plants were nearly indifferent to snowfall, xOx = 83.3%. Endemics to Hokkaido and its vicinity (H) were as few as only eight species.

Trees and woody vines did not have a particular center of preference along snowcover

Table 9. Commodal groups with total number of species and number of species per species group classified by the frequency of distribution which were over than 20% of quadrats in each forest type. Commodal groups were represented by the modes along *WI, D50* and *Ra,* in order (cf. Appendix 2). For abbreviations of ecological groups, see Figure 11.

Commodal	Ecological group									
group	Ia	Ib	IIa	IIb	IIc	IId	IIe	IIIa	IIIb	IIIc
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

and rainfall gradients, while those of shrubs and herbs are apparently biassed : xSx and xxR are respectively 64% and 46% in shrubs and, 7% and 8% in contrast with herbs, suggesting that the distribution of understory species of forests is more strongly affected by the snowcover or rainfall.

All species of evergreen tree plant were coniferous and the shrubs other than *Cephalotaxus harringtonia* var. *nana* in WSO are broad-leaved. Evergreen herbs included many pteridophytes such as *Lycopodium serrata* Thunb., *Lycopodium obscurum* Linn., *Polypodium virginianum* Linn., *Pyrrosa tricuspis* Tagawa and *Lepisorus ussuriensis* Ching var. *distans* Tagawa and a few flowering plants such as *Carex sachalinensis* Fr. Schm. Evergreen shrubs particularly preferred snowy regions (xSx = 75%), while evergreen trees and herbs were indifferent to snow conditions, xOx constituting 100% of evergreen trees and 83% of evergreen herbs. Summergreen plants showed a variety of climatic preference without showing any particular tendencies.

Behavior of trees predominating mixed forests

Figure 12 represents the three boreal conifers and three temperate hardwoods dominating many of mixed forests. Boreal conifers such as *Abies sachalinensis, Picea jezoensis* and *Picea glehnii* were classified into COr group, preferring cold and little rainfall regions with indifference to snow conditions. *Abies sachalinensis* and *Picea jezoensis* sometimes expanded their distribution into the warm regions where *WI* was 55°C month or more. On

Table 10. Commodal groups with number of species per phytogeographical group and life form category. Commodal groups were represented by the modes along *WI*, *D50* and *Ra*, in order (cf. Appendix 2). Abbreviations are given in the Terminology section.

Commodal	Phytogeographical group						Life form category					
group	H	S	N	O	Te	Ts	Ve	Vs	Se	Ss	He	Hs
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

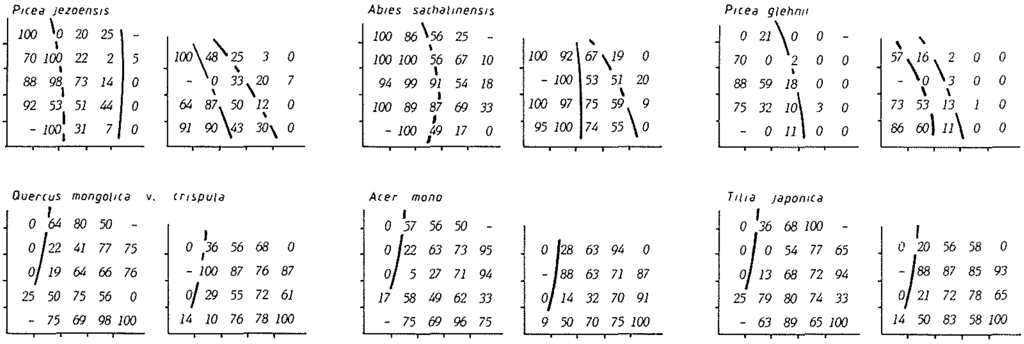


Figure 12. Behavior of six tree species largely predominating the mixed forests.

the other hand, temperate hardwoods such as *Quercus mongolica* var. *crispula, Acer mono* and *Tilia japonica* belonged to the WOO group. Both the boreal conifers and the temperate hardwoods frequently occurred together over a wide thermal range of 35°C month $\leqq$ *WI* $<$ 65°C month where rainfall was little.

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 in the southernmost area of

Hokkaido, i.e., Oshima Peninsula. However, such southern species as *Acer cissifolium* K. Koch, *Stephanandra incisa* Zabel, *Cacalia delphiniifolia* Sieb. et Zucc., *Asperella longe-aridstata* Ohwi and *Pourthiaea villosa* Decne 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 Figure 13, however, they appeared potentially tolerant to cooler areas where snowfall and rainfall were relatively scarce. Since the precipitation including snowfall during the fullglacial age in Hidaka District is considered to have been very limited (Nogami et al. 1980 ; Ono 1984), this region may have been covered by mixed forests consisting of *Quercus mongolica* var. *crispula, Tilia japonica, Acer mono,* whose freezing resistances are adequate to withstand estimated minimum temperature (ca 5-7°C below the present) in the last glacial age (Sakai 1975).

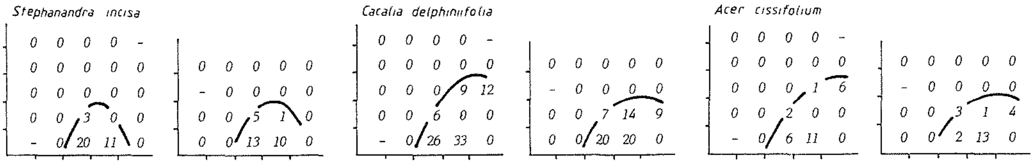


Figure 13. Behavior of three southern plant species isolated in Hidaka District.

Preferences of species common to Chubu District

A total of 70 species were found both in Hokkaido and Chubu District. Of these common species, 58 (82.9%) show a different modality between the two districts surveyed. Along *WI,* 16 species (72.7%) preferring "cool" climate in Chubu District shift their mode in Hokkaido : 4 species to "cold", 7 to "warm", and 5 to temperature-indifferent. Their climatic preferences in Hokkaido and Chubu District are shown in Table 11. Modes of the species immigrated to Hokkaido from Honshu (S) shift to the warm side ; in contrast, those of northern species (N) were shifted to the cold side. Along the *D50* gradient, most of mode-shifted species are southern plants or the Japanese endemics, and no northern species change their modes. Along the gradient of *Ra,* many species being indifferent to rainfall in Chubu District, including *Fagus crenata,* prefer much rainfall areas of Hokkaido (24 species ; 80.0%) : Chubu District is provided much rainfall even in the "little rainfall" regions such as about 1000 mm. However, there are three abnormal species such as *Oxalis acetosella* Linn., *Acer ukurunduence* Trautv. et Mey. and *Cornus canadensis* Linn. preferring little rainfall regions in Hokkaido (COr) while they are rainfall-indifferent in Chubu District (COO). All of them are northern species, suggesting that there are some factors limiting their expansion into the much rainfall regions of Hokkaido.

Table 11. Climatic preference of speices common to Hokkaido and Chubu District. Commodal groups were represented by the modes along *WI, D50* and *Ra,* in order (cf. Appendix 2).

Hokkaido	Chubu	Species
CSR	CSO	*Acer tschonoskii, Vaccinium ovalifolium*
CSR	COO	*Ilex rugosa, Menziesia pentandra*
CSR	cSO	*Rhododendron albrechtii, Clintonia udensis*
CSR	OSO	*Sasa kurilensis*
CSR	OOO	*Vaccinium hirtum*
COr	COO	*Oxalis acetosella, Acer ukurundense, Cornus canadensis*
COO	CSO	*Rhododendron brachycarpum*
COO	cOO	*Galium kamtschaticum, Peracarpa carnosa* var. *circaeoides*
WOO	csO	*Fraxinus lanuginosa*
WSR	csO	*Skimmia japonica* var. *intermedia* f. *repens*
WSR	WSO	*Leptorumohra miqueliana, Sturthiopteris niponica, Fagus crenata, Lindera umbellata* var. *membranacea, Daphniphyllum macropodum* var. *humile, Ilex crenata* var. *paludosa, Ilex leucoclada*
WSR	WOO	*Corylus sieboldiana*
WSO	cOO	*Athyrium vidalii*
WSO	WOO	*Euonymus alatus* f. *dentatus*
WsO	WOO	*Acer palmatum* var. *matsumurae*
WOR	cSR	*Paris tetraphylla, Acanthopanax sciadophylloides*
WOR	WSR	*Rhus tricarpa*
WOR	WOO	*Magnolia obovata, Schizophragma hydrangeoides, Rhus ambigua, Acer japonicum, Cornus controversa*
WOO	csO	*Tilia japonica, Actinidia arguta*
WOO	cOO	*Smilacina japonica*
OSO	cSO	*Plagiogyria semicprdata* subsp. *matsumureana, Viburnum furcatum*
OSO	WSR	*Leucothoe grayana* var. *oblongifolia*
OsO	csr	*Dryopteris crassirhizoma*
OsO	csO	*Athyrium yokoscense*
OOO	COO	*Maianthemum dilatatum, Diphylleia grayi, Sorbus commixta*
OOO	cSO	*Sasa senanensis*
OOO	cOO	*Hydrangea petiolaris*
OOO	OSO	*Tripterospermum japonicum*

3. Floral mixture in forest ecosystems of Hokkaido

Evenness between northern and southern plants

Of the 164 species analyzed, 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 forests. In fact, most of the overstory species participated in the co-occurrence of southern and northern floras in the forests, except three specific species such as *Fagus crenata, Quercus serrata* and *Acer cissifolium* which are restricted to southwestern or eastern part of southern central regions and are absent in mixed forests.

Understory plants totalled 113 species : i.e., 52 southern species, 32 northern species, 7 endemics and 22 widespread species. As shown in Figure 14, the floral make-up of the understory was similar among oak-maple forests, mixed forests and coniferous forests. Almost all of the northern species were able to inhabit each type of forest. A slight difference noted was due to large parts of a slightly smaller number of southern species in mixed forests and coniferous forests. In addition, the evenness scores in understory are significantly higher than those in overstory ($P < 0.01$ in Mann-Whitney U test). The

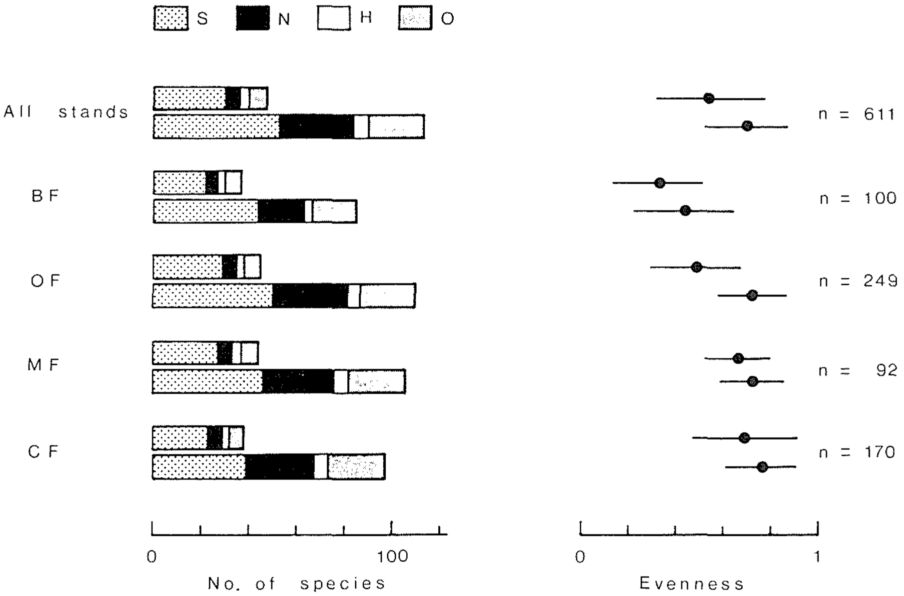


Figure 14. Phytogeographical composition and evenness J' between southern and northern plants in the overstory (upper) and understory (lower) of each forest communities. Evenness is shown by the mean and standard deviation. S, southern plants ; N, northern plants ; H, endemics to Hokkaido and its vicinity ; O, widespread plants.

evenness was nearly equal, ca 0.7 of J', to these three types of forest (Figure 14). Beech forests were relatively poor in northern species (19 species) producing an evenness score of ca 0.5, significantly lower than that of other forest types ($P < 0.001$ in Mann-Whitney U test). Thus, the floral mixture in forest understories were notable in that they exceeded in overstories.

Life form, climatic preference and floral mixture

The co-occurrence of understory plants is due to the distributional expansion of northern species into summergreen forests and of southern species into coniferous forests. Table 12 shows the life form and climatic preference of southern plants and northern plants frequently were found in coniferous forests and oak-maple forests, respectively. The relationships between leaf habit and the occurrent frequency are depicted in Figure 15. Many of the southern plants frequently found in coniferous forests have overwintering leaves and are tolerant to cold winter if thick snowcover is provided. In contrast, most of the northern plants often inhabiting oak forests are summergreen herbs.

Of the northern plants, evergreen species such as *Carex sachalinensis* did not inhabit oak forests while such summergreen species as *Maianthemum dilatatum* Nels. et Macbr., *Cardamine leucantha* O.E. Shulz, *Cacalia hastata* Linn. var. *orientalis* Ohwi and *Cimicifuga simplex* Wormsk., etc. inhabited more than 40% of the oak-maple forests. Of the southern species, however, more than 75% of the summergreen plants were absent or quite rare in coniferous forests while such evergreen species as *Sasa kurilensis, Sasa senanensis, Skimmia japonica* Thunb. var. *intermedia* Komatsu f. *repens* Hara, *Ilex rugosa* and *Rhododendron brachycarpum* were frequently found in boreal coniferous forests. The distribution patterns of evergreen plants and summergreen plants shown in Figure 15 were statistically different from each other in both the oak-maple forests and the coniferous forests ($P < 0.01$ in G test).

Table 12. Life form (LF) and climate preference of southern plants and northern plants frequently found (more than 20% stands) in coniferous forests and oak forests, respectively. Commodal groups were represented by the modes along *WI, D50* and Ra, in order (cf. Appendix 2). Abbreviations for life form categories are given in the Terminology section. Hyphen means absent.

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

4. Leaf habits as adaptive strategies in understory

Leaf phenology of understory plants

A total of 242 vascular plant species were found in the understories of the 31 quadrats surveyed. From the leaf survival patterns, the 242 species were divided into eight categories (Figure 16) : (1) perennial-leaved, with leaf lifespan of more than two years, resulting in the overwintering of different aged leaves; (2) biennial-leaved, overwintering leaves which fall after the expansion of new leaves in spring (the "semi-evergreen" type of Sato, 1982) ; (3) facultative biennial-leaved, in which the overwintering of leaves varies from plant to plant ; (4) heteroptic, as defined by Kikuzawa (1984), having two types of leaf, i.e., summergreen leaves and overwintering leaves ; (5) summergreen, leaf which emerges in spring and falls in autumn ; (6) spring-green, corresponding to the species generally called spring ephemeral, with leaf lifespan from only early spring to midsummer at latest; and (7) wintergreen, where leaves expand in late summer or early autumn and detaches before the following summer.

The first two categories are considered evergreen with no bare phase, while the last three are considered annual or deciduous with leaf lifespan shorter than one year. A few plant species belong to none of these categories but to a saprophagous group lacking green leaves. In the present study, *Monotropastrum globosum* H. Andres and *Gastrodia elata* Bl. were the species classified under this group.

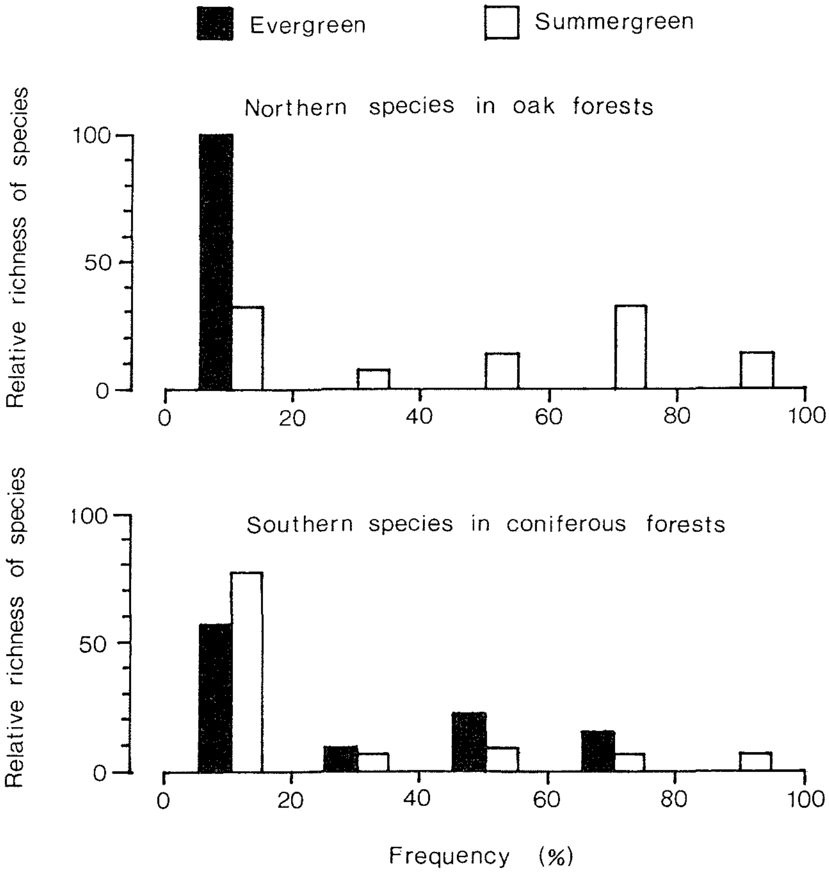


Figure 15. Relative species richness for summergreen plants (open bars) and evergreen plants (solid bars) for each 20% frequency class.

Table 13. Number of species per growth form in each leaf habit category.

Growth form	Tree	Vine	Shrub	Herb	Total
Perennial-leaved	4	2	12	8	26
Biennial-leaved				19	19
Facultative biennial-leaved			1	14	15
Heteroptosis		1	1	1	3
Summergreen	40	9	21	95	165
Winter-green			1	2	3
Spring-green				9	9
Non-assimilate				2	2

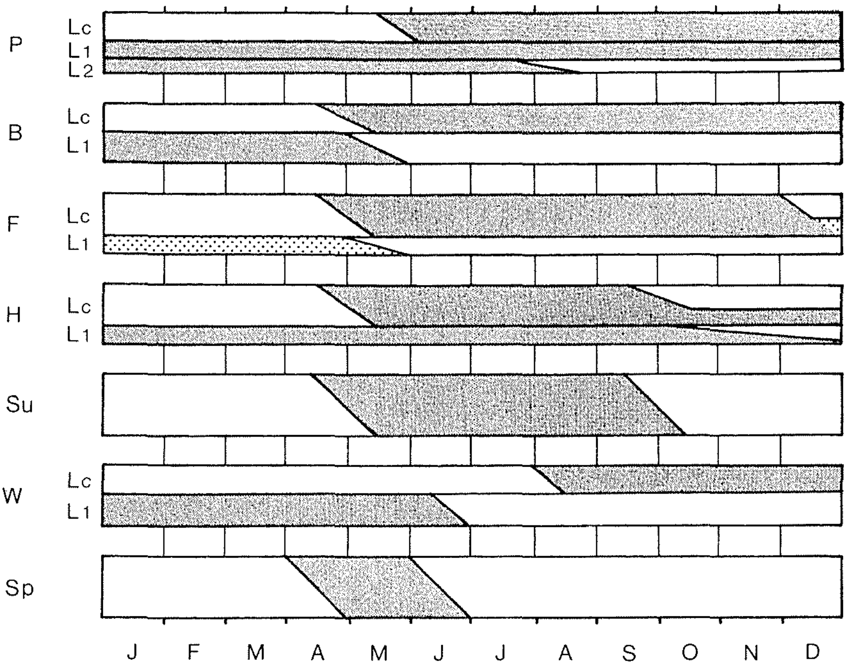


Figure 16. Leaf survival patterns of perennial-leaved (P), biennial-leaved (B), facultative biennial-leaved (F), heteroptosis (H), summergreen (Su), wintergreen (W) and spring-green (Sp). Lc, current leaf ; L_1, 1-year old leaf ; L_2, 2-years old leaf.

Relationship with growth forms

The relationship between leaf habit and growth form is shown in Table 13. All tree species were perennial-leaved or summergreen : conifers such as *Abies sachalinensis, Picea jezoensis, Picea glehnii* and *Taxus cuspidata* Sieb. et Zucc. were perennial-leaved ; and all other trees were summergreen. Woody vines were mostly summergreen with the exceptions of *Hydrangea petiolaris* Sieb. et Zucc. which is heteroptic and *Euonymus fortunei* Hand.-Mazz. var. *radicans* Rehd. which is perennial-leaved. Most of shrub species were perennial-leaved or summergreen, but some shrubs were heteroptic (*Euonymus alatus* Sieb. f. *dentatus*), facultatively biennial-leaved (*Ligstrum tschonoskii* Decaisne var. *glabrescens* Koidz.) or wintergreen (*Daphne kamtschatica* Maxim. var. *jezoensis* Ohwi).

Herbaceous species showed a great variation of leaf habit. As summergreen, for instance, *Dryopteris monticola* C. Chr., *Cornus canadensis* Linn., *Maianthemum dilatatum* Nels. et Macbr., *Trillium smallii* Maxim., *Cardamine leucantha* O.E. Shulz, *Cimicifuga simplex* Wormsk. ; as perennial-leaved, *Lycopodium serratum* Thunb., *Lycopodium obscurum* Linn., *Carex sachalinensis* Fr. Schm., *Chamaele decumbens* Makino ; as biennial-leaved, *Polystichum tripteron* Pr., *Dryopteris crassirhizoma* Nakai, *Arachniodes mutica* Ohwi, *Tiallera polyphylla* D. Don ; as facultative biennial-leaved, *Solidago virga-aurea* Linn. var. *asiatica* Nakai, *Galium trifloriforme* Komar., *Angelica edulis* Miyabe ; as heteroptic, *Geum macrophyllum* Willd. var. *sachalinense* Hara ; as wintergreen, *Gentiana zollingeri* Fawcett and *Cremastra appendiculata* Makino ; and as spring-green, *Anemone yezoensis* Koidz., *Anemone flaccia* Fr. Schm., *Corydalis ambigua* Cham. et Schlecht, *Symplocarpus nipponicus* Makino.

All the species of biennial-leaved group were chamaephytes, and most were ferns or sedges : 11 and 4 species, respectively. In summary, diversification in leaf habits was from trees to woody vines, shrubs, and herbs, i.e., vertically from higher to lower, and temporally from longer to shorter lifespan.

Table 14. Efficiency of the trasmitted solar radiation *TSR* for 41 tree species whose leaf events such as budbreak, end of leaf emergence, commencement of leaf fall, and end of leaf fall were obtained from the leaf survival curves represented in Kikuzawa (1983).

Species	*TSR*	Species	*TSR*
Salix sachalinensis	0.480	*Fraxinus mandshurica* var. *japonica*	0.347
Alnus hirsuta	0.446	*Stylax obassia*	0.345
Alnus japonica	0.436	*Kalopanax pictus*	0.330
Populus sieboldii	0.406	*Cercidiphyllum japonicum*	0.328
Salix hultenii var. *angustifolia*	0.403	*Tilia japonica*	0.328
Magnolia kobus var. *borealis*	0.401	*Ulmus davidiana* var. *japonica*	0.323
Betula maximowicziana	0.396	*Maackia amurense* var. *buergeri*	0.323
Magnolia obovata	0.393	*Sorbus commixta*	0.321
Betula platyphylla var. *japonica*	0.387	*Acanthopanax sciadophylloides*	0.321
Syringa reticulata	0.383	*Prunus ssiori*	0.310
Salix subfragilis	0.381	*Acer mono*	0.306
Ulmus laciniata	0.379	*Carpinus cordata*	0.302
Cornus controversa	0.369	*Sorbus alnifolia*	0.299
Juglans ailanthifolia	0.368	*Tilia maximowicziana*	0.297
Phellodendron amurense	0.363	*Ostrya japonica*	0.291
Betula davulica	0.360	*Aesculus turbinata*	0.285
Picrasma quossioides	0.359	*Quercus mongolica* var. *crispula*	0.281
Castanea crenata	0.358	*Acer japonicum*	0.279
Populus maximowiczii	0.354	*Acer palmatum* var. *matsumurae*	0.277
Betula ermanii	0.353	*Fagus crenata*	0.276
Prunus sargentii	0.353		

Efficiency of light transmission of canopy trees

Transmitted solar radiation (*TSR*) of 41 deciduous broad-leaved tree species was shown in Table 14. *TSR* values varied with a wide range from 0.480 in *Salix sachalinensis* Fr. Schm to 0.276 in *Fagus crenata*. Such species as *Populus sieboldii* Miq., *Salix sachalinensis, Salix hultenii* Floderus var. *angustifolia* Kimura, *Alunus hirsuta* Turcz., *Alnus japonica* Steud. and *Magnolia kobus* DC. var. *borealis* Sarg. preferring gap phases or early successional stages show higher *TSR* exceeding 0.400 while species of late successional stages such as *Fagus crenata, Quercus mongolica* var. *crispula, Acer palmatum* Thunb. var. *matsumurae* Makino, *Acer japonicum* Thunb. are characterized by lower *TSR* below 0.300. Many other species show intermadiate values of *TSR* ranging from 0.300 to 0.400.

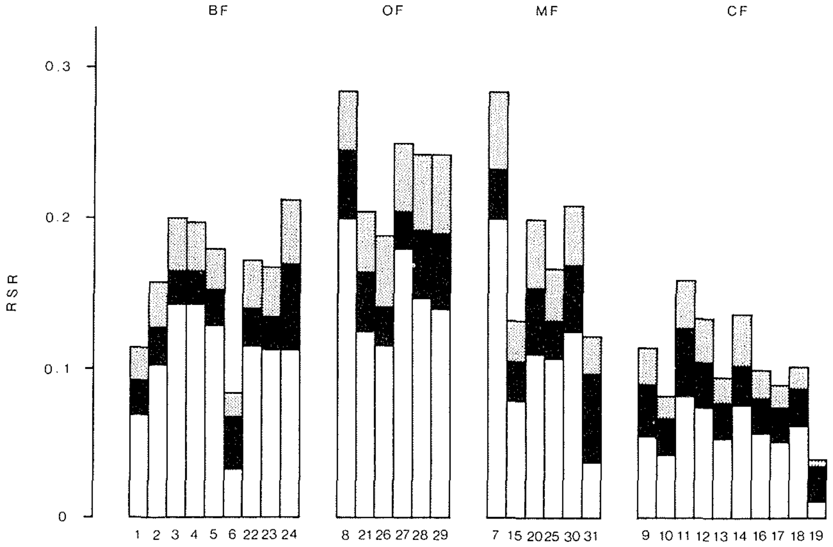


Figure 17. Histogram showing the seasonal allocation of relative solar radiation *RSR* in each stand. Open, solid and shaded blocks designate *RSR* in spring, in summer and in autumn, respectively ; BF, OF, MF and CF denote beech, oak-maple, mixed and coniferous forests, respectively. Numerals indicate quadrat code.

Environments of understory controlled by phenology of canopy

Figure 17 represents the distribution of light resources available for understory plants in each quadrat. The interior of summergreen forests generally has been considered as similarly dark during the growing season and light during canopy dormancy. However, understories were obviously darker in the beech forests than in the oak-maple forests, though both canopies are largely deciduous broad-leaved trees : the differences were significant not only in annual amount but also in each season in Mann-Whitney's U test. The differences are considered to be caused by the following : beech forests are mainly distributed in snowy regions, the leaf emergence of *Fagus crenata* occurs early and explosively and the commencement of leaf fall is the latest of all hardwood trees in Hokkaido while the ends of leaf emergence of many trees consisting of oak-maple forests and mixed forests delay the end of spring, and their commencements of leaf fall precede the end of summer. Because of the higher solar radiation in early summer, effects of timing of leaf expansion in overstory are relatively important for understory plants. Consequently, not only by the long duration with snowcover but also by the particular leaf phenology of *Fagus crenata,* the interior of beech forests is considerably oligophotic. Though solar radiation in the interior of coniferous forests is strongly restricted both in spring and in autumn, the differences between other forests in summer were not significant ($P > 0.05$ in Mann-Whitney's U test).

Table 15 shows the correlation coefficients between two of all combination of these environmental variables. The correlation was significantly positive between *RSR(annual)*

Table 15. Correlation coefficients among environmental variables in forest understory. *NS*, total number of species in understory ; *H'*, species diversity in overstory ; *CS*, number of days with continuous snowcover (days in a year) ; *RSR*, relative solar radiation in spring, in summer, in autumn and the annual amount.

	(1)	(2)	(3)	(4)	(5)	(6)
(1) *NS*						
(2) *H'*	0.648**					
(3) *CS*	−0.224	−0.277				
(4) *RSR*(spring)	0.481**	0.512**	−0.863***			
(5) *RSR*(summer)	0.303*	0.275	−0.080	0.167		
(6) *RSR*(autumn)	0.514**	0.631***	−0.782***	−0.838***	0.419*	
(7) *RSR*(annual)	−0.529**	0.569**	−0.833***	0.967***	0.398*	0.920***

Significance of correlation coefficient : $P<0.001$ (***), $P<0.01$ (**) and $P<0.05$ (*).

and each of other *RSR* and between *H'* and each of *RSR*, but negative between *CS* and *RSR* except in summer, suggesting that light resources for understory plants are primarily limited by snowcover and heterogeneity in the canopy. In consequence, the understories both of oak-maple forests and mixed forests seems to be unpredictable, competitive and euphotic, a forest interior with an abundance of solar radiation penetrating through the canopy, while those of beech and coniferous forests seems to be predictable, less competitive and oligophotic.

Cluster analysis for grouping of understory vegetation

Based on the similarity of leaf habit categories, the 31 and 13 quadrats surveyed in midsummer and in spring were clustered at the levels of 60% and 50%, respectively (Figure 18). Group **b** in summer and group **e** in spring consisted of beech and coniferous forests, and group **c** in summer and group **f** in spring were made up of oak-maple forests and mixed forests. Mean coverage of leaf categories in each clustered group were represented in Figure 19 Perennial-leaved plants largely dominated in groups **b** and **e** while they were absent or rare in groups **d** and **f** where biennial-leaved plants and summergreen plants or spring-green plants instead dominated. Group **a** consisted of various types of forests, in

Table 16. Mean values of environmental variables in each cluster group based on the percentage cover in midsummer (from **a** to **f**) and in spring (from **e** to **g**). Variables as described in Table 15. Differences of *l-m* and of *p-q* indicate significant at $P<0.05$ and of *l-n* and of *p-r* at $P<0.01$ in Mann-Whitney's *U* test.

Group code	**a** n=10	**b** n=13	**c** n=7	**d** n=1	**e** n=7	**f** n=5	**g** n=1
NS	$32.\pm+6.2^{l}$	31.2 ± 9.8^{l}	56.4 ± 12.0^{n}	51.0	35.1 ± 10.4	54.0 ± 16.0	47.0
H'	1.43 ± 0.75^{l}	1.11 ± 0.38^{l}	2.55 ± 0.38^{n}	1.90	1.18 ± 0.54^{p}	2.15 ± 0.45^{r}	2.76
CS	154.1 ± 38.1^{l}	150.2 ± 49.3^{lm}	117.6 ± 22.0^{m}	90	176.9 ± 45.5^{p}	118.6 ± 23.3^{q}	136
RSR(spring)	$.078\pm.028^{l}$	$.084\pm.040^{l}$	$.146\pm.030^{n}$	.201	$.069\pm.041^{p}$	$.126\pm.015^{r}$	.126
RSR(summer)	$.039\pm.012^{l}$	$.024\pm.001^{n}$	$.038\pm.030^{l}$	.045	$.029\pm.009^{p}$	$.043\pm.009^{q}$	.040
RSR(autumn)	$.032\pm.009^{l}$	$.023\pm.009^{l}$	$.044\pm.006^{n}$	.038	$.021\pm.010^{p}$	$.044\pm.006^{r}$	.039
RSR(annual)	$.149\pm.039^{l}$	$.130\pm.049^{l}$	$.229\pm.035^{n}$	.284	$.119\pm.052^{p}$	$.212\pm.028^{r}$	.205

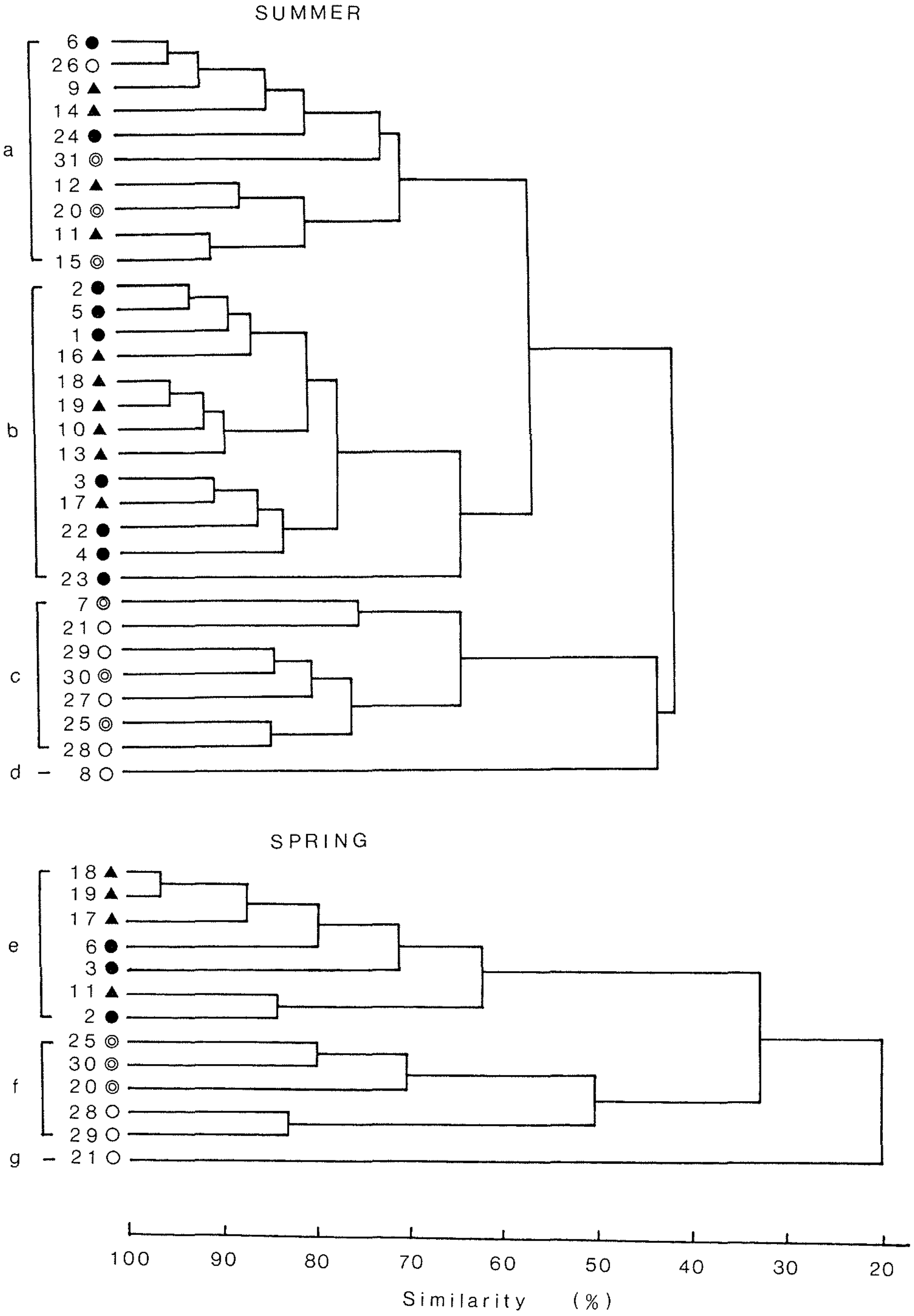


Figure 18. Clusterings among the quadrats surveyed in midsummer and in spring. Based on Gleason's similarity index using coverage, the quadrats were clustered by Mountford's average-linkage method. Numeral indicate quadrat code, and solid circles, open circles, double circles and triangles indicate beech, oak-maple, mixed and coniferous forests, respectively.

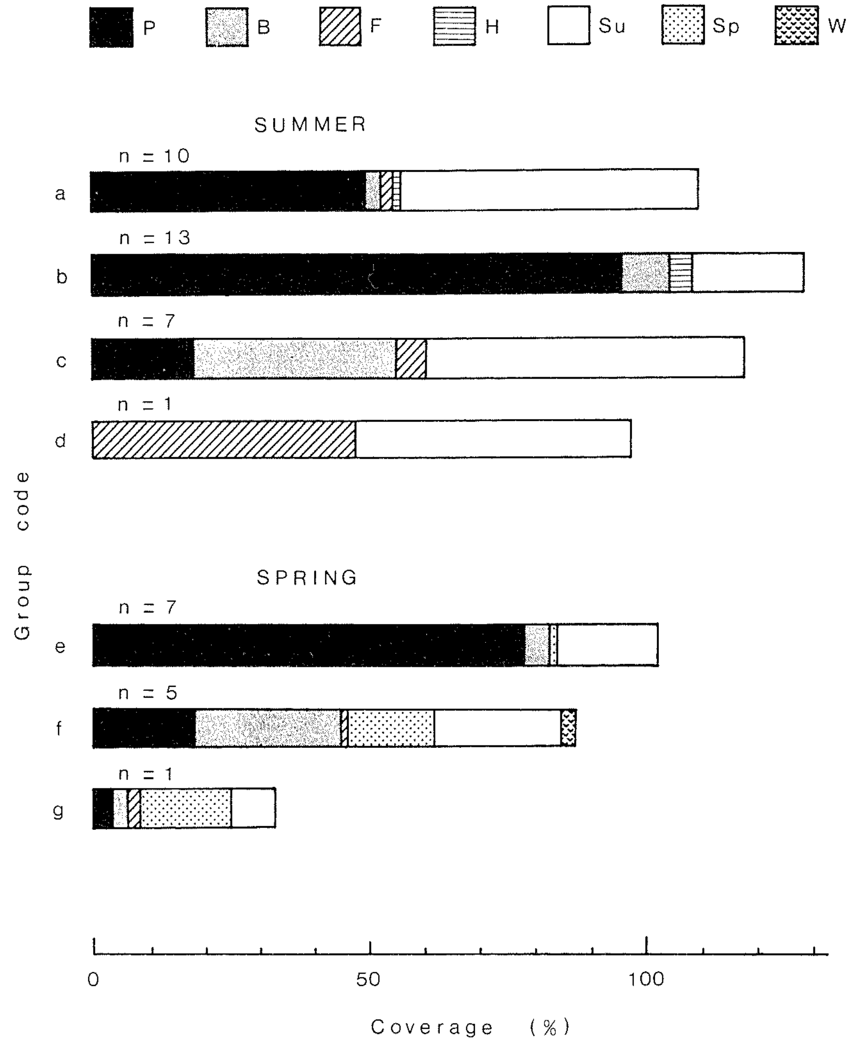


Figure 19. Mean amount of coverage of species belonging to each leaf habit category. Abbreviations for leaf habit category as legend in Figure 16.

which perennial-leaved plants and summergreen plants compete. Of the quadrats consisting of group **f**, 4 were common in group **c** (constituting 80%), suggesting that the temporal habitat segregation occurred between spring-green plants and some of summergreen plants. Group **d**, which showed lower similarity with any other quadrats, consisted of a single stand of oak forest and was dominated by facultative biennial-leaved plants *Sasa nipponica* Makino et Shibata. In group **g** consisting of a mixed forest stand, the total coverage of understory vegetation was only ca 25%, though spring-green plants dominated there as well as seen in group **f**.

Environments of each cluster group were shown in Table 16. Except for *CS* and *RSR(summer)*, all the environmental variables in group **c** were higher than those in groups

a and **b**, suggesting that the understory of group **c** is competitive, unpredictable and euphotic. Highly significant difference between **a** and **b** is found in *RSR(summer)*, indicating that the dominance of summergreen plants depends on the photosynthesis in summer other than that in spring and autumn. According to the heterogeneity of canopy trees, the oak-maple forests and mixed forests are characterized by the various patterns of seasonal change in light transmission, and this may proceed the growth of many successional plant species in the understory.

Table 17. Correlation coefficients between environmental variables and dominance of each leaf category surveyed in summer and spring. Significant levels as $P<0.001^{(***)}$, $P<0.01^{(**)}$, $P<0.05^{(*)}$. P, perennial-leaved; B, biennial-leaved ; F, Facultative biennial leaved; H, heteroptosis; Su, summergreen; W, winter-green ; Sp, spring-green.

Leaf habit	P	B	F	H	Su	W	Sp
In summer (n=31)							
NS	−0.625**	0.601***	0.319	0.073	0.424*		
H'	−0.607***	0.456**	0.236	−0.138	0.427*		
CS	0.209	−0.482**	−0.093	−0.347	0.008		
RSR (spring)	−0.399*	0.519***	0.396*	0.116	0.038		
RSR (summer)	−0.488***	0.189	0.204	−0.080	0.562***		
RSR (autumn)	−0.534***	0.567**	0.151	0.074	0.307*		
RSR (annual)	−0.503***	0.547***	0.373*	0.089	0.229		
In spring (n=13)							
NS	−0.672*	0.472	0.688**	0.464		0.481	0.674*
H'	−0.709**	0.490	0.590*	0.102		0.613*	0.656*
CS	0.390	−0.754**	−0.052	0.079		−0.381	−0.264
RSR (spring)	−0.424	0.533*	0.339	0.180		0.671*	0.605*
RSR (summer)	−0.699**	0.494*	0.296	0.436		0.376	0.691**
RSR (autumn)	−0.651*	0.720**	0.411	0.277		0.589*	0.658*
RSR (annual)	−0.562*	0.616*	0.378	0.264		0.659*	0.686*

Relationship between leaf habits and environments

Table 17 shows the correlation coefficients between environmental variables and coverage of leaf habit categories surveyed in midsummer and spring. The correlations between coverage of perennial-leaved plants and *NS, H', RSR* were negative, and in contrast, those with biennial-leaved plants were positive except for *RSR(summer)*. This suggests that the former plants prefer less competitive, predictable and oligophotic habitat while the latter plants are the opposite, though both of them have no bare phase alike. Positive correlations were shown between summergreen plants and *NS, H', RSR(summer)* and *RSR(autumn)*, suggesting that the solar radiation in summer are the limiting factor for summergreen plants while those in spring and autumn are more important for biennial-leaved plants. For wintergreen plants, a weakly significant correlation was found in *RSR(autumn)*. Facultative biennial-leaved plants showed a positive correlation with *NS* and *H'* but were indifferent to snow and light resources. Spring-green plants preferred euphotic habitats. Particular tendency was not shown in heteroptosis plants.

Discussion

Effects of snow on the plants distribution and speciation

By analyzing the occurrence of each plant species along thermal gradients in Japan, Kira and Yoshino (1967) showed that plant distribution is controlled mostly by the integrated temperature factor ; e.g., the summergreen forest species (*Fagus crenata, Abies homolepis*) and the subalpine-coniferous forest species (*Abies mariesii, Abies veitchii, Pinus koraiensis* Sieb. et Zucc.) are clearly separated from each other, with an altitudinal boundary where *WI* = 40-45°C month ; the distributions of *Abies mariesii* and *Abies veitchii* overlap each other on the thermal gradient. However, many tree species, including *Fagus crenata,* show different patterns of altitudinal distribution on the Pacific side and the Sea of Japan side of the country, suggesting an effect of snow (Kure and Yoda 1984 ; Tanaka 1986). Snowfall is highly correlated with air temperature in most districts of Japan; therefore, it has been difficult to distinguish the effect of snow from that of temperature. In the Chubu District, which is geographically and meteorologically complex, the thermal ranges over which a certain species occurs were often differentiated by snowfall conditions. Thus, the behavior of forest plants is not as simple as has previously been thought ; for example, *Fagus crenata* can extend even to cold areas if snowfall or rainfall is high, while *Tsuga diversifolia* and *Abies veitchii* occasionally occupy warm areas with little snowfall or rainfall ; *Abies mariesii* is nearly independent on the influence of snow and is often found in the snowy regions which *Abies veitchii* avoids.

Location of the polar front fluctuated north and south during the Quaternary, resulting in the great variance of total precipitation in the middle latitude regions of the Northern Hemisphere (Austin et al. 1984). In post-glacial periods warm sea currents often ran into the Sea of Japan ; and the winter air mass provided the Japanese Archipelago with much snow which proceeded the isolated plant species to expand their distribution into a broader spectrum of habitat. However, the snow-intolerant species were restricted in their distribution, enhancing the ratio of evergreen coniferous which generally speciated into endemic species of Japan. The process of isolation and the associated fluctuation of snowfall may have created an opportunity for divergence to some populations into various taxa or ecotype, and for convergence into a particular life form.

The following morphological and functional attributes are regarded adaptive in the snowy regions : (1) high capacity to sprout from shoot or rhizome (Sakai 1968, 1976) ; (2) rapid growth, especially in spring (ibid.) ; (3) shrub, stature especially procumbent or decumbent (ibid.) ; (4) evergreen, wintergreen or heteroptosis (Sato and Sakai 1980 ; Kikuzawa 1984) ; (5) longevity of leaves (Kikuzawa 1984, 1989) ; (6) large leaf area (Hagiwara 1977). The first two attributes include a capacity of recovery from serious damage by avalanche or snow pressure ; the three latter attributes are associated with effective photosynthesis especially in the interior of summergreen forests, and may be considered as stress-tolerant strategy (Grime 1979). Plants with these attributes can assimilate as soon as the snow thaws and the photosynthesis prior to the leaf-expansion in the canopy probably provides benefits which exceeds the total cost for maintaining leaves in winter (Chabot and Hicks 1982), because photosynthesis and metabolic activities of the evergreen leaves rise in spring and in autumn (Yoshie and Kawano 1986). Furthermore, the temperature at a depth of 50 cm in snow stays at around 0°C (Sakai 1976), and the snow serves as protection from frost damage for the photosynthetic organs of plants. As a consequence, the evergreen shrub life form is potentially among the most appropriate for conditions associated with heavy snowfall.

Actually, as shown in the deciduous shrubs *Lindera umbellata* (csr) and *Lindera umbellata* var. *membranacea* (WSO), of which the latter has larger leaves, differences in snow tolerance have been reported in many closely related forms such as *Cephalotaxus harringtonia*—*Cephalotaxus harringtonia* var. *nana*, *Aucuba japonica* Thunb.—Aucuba japonica var. *borealis* Miyabe et Kudo, *Ilex crenata* Thunb.—*Ilex crenata* var. *paludosa* Hara, and *Daphniphyllum macropodum* Miq.—*Daphniphyllum macropodum* var. *humile* Rosenthal (Hotta 1974 ; Sakai 1976). Of these, the parent forms are evergreen broad-leaved trees or shrubs, and are distributed in the laurel forests, and all of them tend to avoid snow ; all their varieties are evergreen decumbent plants and frequently found in the summergreen forests on the Sea of Japan side of the country. They are classified into the WSR or WSO and are invariably snow-tolerant. Unlike the tall trees or winter-withered herbs, the shrubs are frequently subject to the stress of snow, and the chance of speciation of snow-tolerant neo-endemics by adaptive radiation may be increased.

Modal shifts of climatic preference

Because of avoidance problems of uneven sample distribution, direct gradient analysis can be applied in a restricted area to examine the responses of individual species to environmental variables (Austin 1987), suggesting that it is required to compare the behavior in different regions to examine the response. At least for the thermal variable, modal positions of southern species and the Japanese endemics in Chubu District and those of northern species in Hokkaido are expected to be nearly their physiological optimum. Therefore, it is expected that there are some other factors such as moisture, topography and geo-history, skewing the ecological behaviors of southern plants in their northern frontiers and those of northern plants in their southern areas. On the other hand, niche segregation between temperate and boreal plants along thermal gradient is not so clear in Hokkaido, that is, a significantly large number of species show indifferent to temperature. One of the reasons is considered to be narrower thermal range of the forest distribution in Hokkaido. However, there are mumerous species of temperature-indifferent and fewer species preferring "cool" climate in Hokkaido, suggesting that geographical factors have a stronger effects on the horizontal distribution of plants than on the vertical distribution.

Although beech forest is the typical and dominant forest ecosystem in the temperate zone of Japan (Sasaki 1970 ; Kira 1977), its distribution in Hokkaido has not been sufficiently explained by any thermal factors such as *WI* and/or *CI* of Kira (1977). Certain hypotheses for the limiting factors have been proposed, e.g., disturbance by wildfire, short distance of seeds dispersed, niche boundary based on species interaction, etc. (Watanabe 1987). 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 disequilibrium with the drastic rise of temperature in the postglacial period

(Takeda and Nakanishi 1984). This hypothesis appears to be supported by the climatic preference of *Fagus crenata,* whose distribution is biassed to regions where much snowfall and rainfall are provided in Hokkaido.

In Hokkaido, many temperate hardwood trees seem to be expanding their distribution toward north and east by expelling boreal conifers. This suggests that the distribution of forests is more dependent on geo-historical background than on the present conditions of climate in Hokkaido. 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 rainfall is less provided. Indeed, as observed in northeastern Europe, eastern North America and eastern Asia, regions where mixed forests are normally distributed are characterized by relatively less precipitation (MacArthur and Connell 1966). However, climatic preference of individual plant species is one of the proximate factors for the establishment of mixed forests.

Co-occurrence process of northern and southern plants

In Hokkaido, co-occurrence of northern and southern floras is mostly attributed to the expansion of southern evergreen plants into the understories of boreal coniferous forests and of northern summergreen plants into the understories of oak forests. Because the Strait of Sohya isolating Hokkaido from Sakhalin is as shallow as only 60 m deep in 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 coniferous forest dominated by the deciduous conifer *Larix* (Tsukada 1985). 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* Turcz. 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 circumstance southern species immigrated into Hokkaido over the Strait of Tsugaru. Based on the fossils of pollen, Tsukada (1985) 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 rarely effloresce, or in local and small relicts, which are very restricted distributionally (Davis et al 1986). These plant species makedly 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 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 was 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, Sasa cernua, Cephalotaxus harrin-*

gtonia var. *nana, Daphniphyllum macropodum* var. *humile, Ilex crenata* var. *paludosa, Skimmia japonica* var. *intermedia* f. *repens, Rhododendron brachycarpum,* etc. The present study further revealed that some snow-intolerant southern species could withstand a cool climate if precipitation was low, indicating their survival during the last glacial in drier regions such as Hidaka District (Uemura and Takeda 1987). Overall, the present study strongly suggests 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 Hidaka District.

Patterns of leaf phenology in forest understory

In general, deciduous plants usually have a high efficiency of photosynthesis during a short active season : they are less tolerant to shade stress but competitive in exposed habitats since the little investment for leaf maintenance (Bazzaz 1979 ; Chabot and Hicks 1982). In contrast, evergreen plants are generally successful in shaded habitat but less competitive, because the total benefit cannot exceed the cost even if they have ability of high assimilation. The distribution analysed in this study supports the generalized theory : summergreen and spring-green plants are dominant in habitat where abundant of solar radiation is provided while perennial-leaved plants are opposite. However, biennial-leaved plants are rather dominant in euphotic habitat, though they have no bare phase in perennial-leaved plants, indicating such physiognomic criteria as "deciduous" or "evergreen" are not so appropriate to evaluate the leaf phenology of forest plants sufficiently.

Unlike spring-green plants which can be considered ruderal in the sense of Grime (1979), summergreen plants correspond to the competitive-ruderal strategy (Grime 1979) can effectively assimilate in summer. This makes it possible to grow in forest understory where solar radiation is restricted by snowcover in spring. In addition, sunflecks occasionally streaming through the canopy are considered to be more important for the photosynthesis of understory plants than the average light intensity (Woodward 1990). For instance, 10-80% of solar radiation in a forest floor and 30-60% of daily carbon fixation of saplings are dependent on the sunflecks (Chazdon 1988), suggesting that summergreen plants are not always severely shaded throughout summer, and the major carbon gain seems to depend on sunflecks.

The wintergreen habit has been considered another strategy to adapt to less shaded habitats : the leaf habit seemed to be one of the ecological factors for seasonally effective use of the light resources (Kikuzawa 1989). In the present study, however, their distribution was not correlated to the light resources, suggesting that the overwintering leaves are not always adaptive to euphotic habitat in winter, where they should often risk themselves to frost and drought damage.

Perennial-leaved habit is considered as the stress-tolerant strategy of Grime (1979). Potentially, the overwintering leaves can assimilate throughout winter, hence, they are most suitable for effective use of light resources in summergreen forests from late autumn to early spring (Kikuzawa 1989). If the defense cost against frost damage was reduced, the benefit obtained in winter should be relatively greater. In fact, shade-tolerance in sapling of an evergreen oak compensated by effective use of such seasonal gap in deciduous forest, where the net production in winter exceeds that in summer resulting their positive growth (Takenaka 1986). For evergreen plants, an adaptation to avoid frost damage is found on a procumbent form, because snowcover serves as a protector for the overwintering leaves (Sakai and Larcher 1987). In Hokkaido such temperate shrubs preferring snowy climate are frequently found in boreal coniferous forest (Uemura, unpublished), suggesting that the snow-tolerance is highly correlated to the shade-tolerance and snowcover has played some roles to raise their fitness. Hence, the shade-tolerance is considered as preadaptation to environment long covered by snow. However, extended snowcover would not be disadvantageous, because their carbon fixation must largely depend on the assimilation in the snow-free duration but never exceed those of summergreen plants.

Biennial-leaved plants nearly correspond to the group designated "evergreen II" type in Kawano (1985), of which productive substance assimilated by current leaf is consumed for the reproductive performance. For many of them, the shedding of overwintering leaves and emergence of new leaves occur rapidly and simultaneously likewise the "flush type" categorized for deciduous woody plants (Kikuzawa 1983). According to the prediction based on the model of Iwasa and Cohen (1989), leaf emergence of a flush typed fern is optimal for species growing in a habitat where phenotypic tolerances exceed environmental variability (Hamilton 1990). Between photosynthetic efficiency and leaf lifespan, a trade-off relationship is known (Chabot and Hicks 1982 ; Koike 1988), and the timing of leaf emergence and fall is considered to maximize the net gain in a growing season (Harada and Takada 1988). However, less interest has been focused on the role of overwintering leaves to date. The overwintering leaves can serve as storage organs guaranteeing quick expansion of new leaves in the next spring, and additionally, their rapid leaf-emergence seems to give damage to the neighboring plants by shading. If so, an temporal differentiation in leaf function is expected to have occurred, and plants with such leaf habits could be selected in habitats being competitive in spring and euphotic in autumn.

Phenology of facultative biennial-leaved plants is basically similar with biennial-leaved plants. For some monocarpic herbs found on coastal dunes or old fields, the critical conditions as to whether overwintering leaves should be attached or shed is controlled by reproductive events depending on the size, age or environments (Hirose and Kachi 1982 ; Couvet et al. 1990). Among the forest plants, *Sasa* species are rare examples of monocarpic plants. Of these, *Sasa nipponica* and *Sasa chartacea* Makino were facultative biennial-leaved, but the behavior is flexible depending neither on size nor on reproduction. Their flowering is believed to occur once about 60 years or more, and the critical condition is considered to be determined by the environments, i.e., snowcover to escape from frost damage, suggesting that the leaf habit may be preadaptation for unpredictable snow conditions of the habitat.

The heteroptic habit found in *Euonymus alatus* f. *dentatus* was considered as a form of developmental plasticity (Kikuzawa 1984), because individual plants will experience different environments throughout the life history and such developmental plasticity is generally found in many species (Bazzaz 1979 ; Bazzaz and Pickett 1980). As shown in *Geum macrophyllum* which has overwintering rosette leaves and summergreen stem leaves, however, the morphologically differentiated leaves seem to be determined by the genetic constraints, and such dimorphism cannot be considered as the plastic variance. Moreover, even the phenotypic plasticity in plants is controlled genetically (Bradshaw 1965). Probably, the leaves of these types differ in function from each other since the environments that each of them will experience would be certainly different. Benefit by the overwintering leaves will occasionally exceed the maintenance cost in habitat where light resources are unpredictable in winter, indicating that the habit is considered as bet-hedging strategy which will be favored by risk-spreading in unpredictable environments.

Leaf phenology as a key factor facilitating the floral mixture in boreo-nemoral ecotone

On the temperate forest plants, differentiation from the evergreen ancestors and the adaptive radiation in leaf habits were facilitated by the establishment of apparent cyclic regularity of illumination in the understory of deciduous forests, where dark period and light period reciprocally occur in a year (Axelrod 1966). However, direction of evolution in leaf lifespan is not always to shorten, and the optimal longevities and timing of emergence and shedding are expected to be selected by stress or available resources (Harada and Takada 1988 ; Iwasa and Cohen 1989). The divergence of leaf phenology occurred over many phylogenetic taxa, and it is more notable in plants growing in vertically lower niches in forest ecosystems, especially in herbaceous plants which are generally considered to be subject to the extreme influence of shade stress (Grime 1979 ; Bierzychudek 1982). Unlike in woody plants, frequent adaptive evolution to the seasonal change in light resources occurred in herbaceous plants because of the plasticity and flexibility both in morphology and in function, and the genetic variation will expand easily and rapidly in their gene pools.

Various patterns of leaf survivor were distinguished in the forest plants of Hokkaido where divergence occurred over many phylogenetic taxon as shown in the present study, and the adaptive significance of each habit was discussed above. In the boreo-nemoral forest ecotone, leaf habits have played an important role on the process of floral mixture especially in the forest understory besides the climatic preference of individual plant species. Even for canopy trees, for instance, their distribution is strongly controlled by environments of understory through the early stages of their seedling and sapling growth.

Though boreal forest formation is largely predominated by such evergreen conifers as *Picea* and *Abies* (Larsen 1980), northern plants species are not always associated with evergreen forests. Especially in eastern Asia, deciduous larch forests are rather superior, with occasionally distributed by boreal deciduous broad-leaved forests composed of *Betula, Populus* or *Salix* (Larsen 1980). Northern species contributing to the floral mixture in Hokkaido is considered to be associated with these boreal deciduous forests. Consequently, postglacial changes in climate including seasonality in precipitation, must have controlled the distribution of individual plant species through the interaction between understory and overstory, and the floral mixture visually observed now in Hokkaido has been just a synthetic outcome of such individual vectors of migration and evolutionary histories of adaptation.

Acknowledgements

I wish to express my sincere thanks to Prof. K. Ito for his useful suggestion and encouragement in the course of this study, Dr. S. Higashi for his helpful comments and valuable discussion. Cordial thanks are also due to Drs. K. Kikuzawa, T. Tsujii, K. Tsutsui, T. Igarashi, and H. Fukuda, for their useful suggestions on the manuscript. Special gratitude is due to the late Prof. S. Nakanishi and Prof. Emeritus N. Yano for their useful advice and pertinent guidance on plant ecology.

Summary

1. In the Chubu District, central Japan, the distribution of many forest plant species was controlled not only by temperature but also by snowfall. *Sasa kurilensis, Heloniopsis orientalis* and *Tripterospermum japonicum* preferred snow regardless of thermal conditions. The snow seemed to exert more influence on endemics than on the more widespread plants, on evergreen plants than on summergreen plants, and on trees or shrubs more than on herbs or woody vines. Thus, the snow contributes to the high endemic ratio of central Japan. Among the snow-tolerant evergreen shrubs there were many neo-endemics derived from snow-intolerant parent populations of the species which have restricted distribution in the laurel forests. They could occupy habitats in the summergreen forests, where their life form can withstand heavy snowfall. Because of the heavy snowfall on the Sea of Japan side of central Japan in the postglacial age, evergreen coniferous trees have lost many of their previous habitats since most of them are intolerant of heavy snowfall.

2. In Hokkaido, the northernmost island of Japan, where boreal plants and temperate plants frequently co-occur with each other, distribution of forest plants is exerted more influence by rainfall than that in Chubu District, and many species common to central Japan shift their modal positions along the temperature gradient. From the behavior of predominating tree species, mixed forests are distributed with a wide thermal range, especially in regions where little rainfall was provided. However, co-occurrence in a certain forest site is more notable in the understory than in the crown. A particular case of this is where southern evergreen shrubs and herbs in boreal coniferous forests. Another is the presence of northern summergreen herbs in temperate hardwood forests. It is speculated that the co-occurrence dates back at least to the late-Quaternary period, where the decrease in temperature associated with the glacial period forced understory plants to adapt their life form or leaf habit to snowcover and light conditions of interior forests. Recent geographical evidences suggest that the island has been isolated from the southern island Honshu at least for 70,000 years. Thus postglacial reexpansion of southern species in Hokkaido does not appear to be due to their immigration but rather due to their expansion from refuges on the island such as Oshima Peninsula for snow-tolerant southern species and HidaKa District for the snow-intolerant species.

3. Forest plant species in Hokkaido were categorized by the leaf phenological patterns, and the adaptive significance of the leaf habits was evaluated in relation to the environments of forest understory seriously controlled by the phenology of canopy species.

Perennial-leaved plants are dominant in such intensively shaded habitat as beech or coniferous forest while both of summergreen and spring-green plants are more successful in weakly shaded habitat, e.g., oak-maple forest or mixed forest. The shade-tolerance of some perennial-leaved plants is considered as preadaptation to snow-tolerance. Despite of attaching overwintering leaves likewise perennial-leaved plants, biennial-leaved plants are assumed to be adaptive to grow in less shaded habitats. Such leaf habit is expected to be an adaptive trait through the competition in spring, probably because of the quick emergence of current leaves by effective use of the previously accumulated resources. Heteroptosis attaching summergreen leaves and overwintering leaves concurrently are considered as a bet-hedging strategy. Not only by the seasonal change in light conditions related to the phenology of canopy trees but also by the duration of snowcover, divergence of phenological leaf habit of understory plants has been facilitated, therefore, leaf phenology is considered as a key factor facilitating the floral mixture in Hokkaido.

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Appendix 1

Commodal species groups of Chubu District 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'.

Thelypteris quelpaertensis Ching (O, Hs, II), *Smilacina yesoensis* Fr. et Sav. (E, Hs, II), *Coptis trifolia* Salisb. (N, He, II), *Euonymus tricarpus* Koidz. (E, Ss, II), *Vaccinium smallii* A. Gray (E, Ss, III).

CSO : 'Cold, deep-snow, rainfall-indifferent'.

Thuja standishii Carr. (EE, Te, II), *Shortia soldanelloides* Makino (E, He, III), *Acer tschonoskii* Maxim. (E, Ts, III), *Tripetaleia bracteatus* Sieb. et Zucc. (E, Ss, II), *Rhododendron brachycarpum* D. Don (E, Se, II), *Vaccinium ovalifolium* J. E. Smith (N, Ss, II), *Trientalis europaea* Linn. (O, Hs, III).

Csr : 'Cold, shallow-snow, little rainfall'.

Pteridophyllum racemosum Sieb. et Zucc. (EE, Hs, II), *Pternopetarum tanakae* Hand.-Mazz. (O, Hs, II), *Pedicularis keiskei* Fr. et Sav. (EE, Hs, II).

CsO : 'Cold, shallow-snow, rainfall-indefferent'.

Abies veitchii Lindl. (EE, Te, II), *Picea jesoensis* Varr. var. *hondoensis* Rehder (EE, Te, II), *Tsuga diversifolia* Masters (E, Te, II), *Platanthera ophrydioides* Fr. Schm. (E, Hs, II), *Betula corylifolia* Regel et Maxim. (EE, Ts, II), *Coptis quinquefolia* Miq. (E, He, II), *Vaccinium yatabei* Makino (EE, Ss, II), *Cacalia adenostyloides* Matsum. (EE, Hs, II).

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

Arachniodes mutica Ohwi (N, He, III), *Athyrium melanolepis* Christ (O, Hs, II), *Dryopteris austriaca* Fraser-Jenkins et Jermy (O, Hs, III), *Thelypteris connectilis* Watt (O, Hs, II), *Abies mariesii* Masters (EE, Te, II), *Pinus koraiensis* Sieb. et Zucc. (N, Te, II), *Pinus parviflora* Sieb. et Zucc. var. *pentaphylla* Henry (E, Te, II), *Veratrum stamineum* Maxim. (E, Hs, II), *Streptopus streptopoides* Frye et Rigg var. *japonicus* Fassett (EE, Hs, II), *Maianthemum dilatatum* Nels. et Macbr. (N, Hs, III), *Listera cordata* R. Br. (N, Hs, II), *Ephippianthus schmidtii* Reichb. (N, Hs, II), *Betula ermanii* Cham. (N, Ts, II), *Diphylleia grayi* Fr. Schm. (N, Hs, II), *Rubus pedatus* Smith (N, Hs, II), *Rubus ikenoensis* Lev. et Van. (EE, Hs, II), *Prunus nipponica* Matsum. (E, Ts, II), *Sorbus matsumurana* Koehne (E, Ss, II), *Sorbus commixta* Hedl. (E, Ts, III), *Oxalis acetosella* Linn. (N, He, II), *Ilex rugosa* Fr. Schm. (E, Se, III), *Acer ukurunduense* Trautv. et Mey. (N, Ts, III), *Oplopanax japonicus* Nakai (E, Ss, II), *Cornus canadensis* Linn. (N, Hs, II), *Menziesia pentandra* Maxim. (O, Ss, III), *Rhododendron metternichii* Sieb. et Zucc. var. *pentamerum* Maxim. (EE, Se, III), *Epigaea asiatica* Maxim. (E, Se, II), *Viburnum urceolatum* Sieb. et Zucc. f. *procumbens* Nakai (EE, Ss, III).

cSO : 'Cool, deep-snow, rainfall-indifferent'.

Plagiogyria semicordata subsp. *matsumureana* Nakaike (E, He, III), *Sasa senanensis* Rehd. (E, Se, III), *Clintonia udensis* Trautv. et Mey. (N, Hs, III), *Paris tetraphylla* A. Gray (E, Hs, III), *Skimmia japonica* Thunb. var. *intermedia* Komatsu f. *repens* Hara (E, Se, III), *Ilex sugerokii* Maxim. var. *brevipedunculata* S.Y. Hu (E, Se, I), *Tripteygium regelii* Sprague et Takeda (N, Vs, I), *Acanthopanax sciadophylloides* Fr. et Sav. (E, Ts, I), *Rhododendron albrechtii* Maxim. (E, Ss, I), *Viburnum furcatum* Blume (O, Ss, III).

csr : 'Cool, shallow-snow, little rainfall'.

Dryopteris crassirhizoma Nakai (O, He, III), *Abies homolepis* Sieb. et Zucc. (E, Te, I), *Euonymus melananthus* Fr. et Sav. (E, Ss, I).

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

Athyrium yokoscense Christ (O, Hs, III), *Chamaecyparis obtusa* Sieb. et Zucc. (E, Te, I), *Carex conica* Boott (O, He, I), *Lindera umbellata* Thunb. (S, Ss, I), *Tilia japonica* Simonkai (E, Ts, I), *Actinidia arguta* Planch. (O, Vs, I), *Enkianthus campanulatus* Nichols. (E, Ss, I), *Viburnum wrightii* Miq. (O, Ss, I).

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

Athyrium vidalii Nakai (O, Hs, I), *Smilacina japonica* A. Gray (O, Hs, I), *Smilacina hondoensis* Ohwi (EE, Hs, I), *Betula grossa* Sieb. et Zucc. (E, Ts, I), *Cimicifuga simplex* Wormsk. (O, Hs, I), *Rodgersia podophylla* A. Gray (N, Hs, I), *Hydrangea petiolaris* Sieb. et Zucc. (O, Ve, I), *Hydrangea paniculata* Sieb. (O, Ss, I), *Hydrangea macrophylla* Ser. var. *acuminata* Makino (S, Ss, I), *Oxalis griffithii* Edgew. et Hook. (S, Hs, I), *Acer distylum* Sieb. et Zucc. (E, Ts, I), *Acer micranthum* Sieb. et Zucc. (E, Ts, I), *Acer nipponicum* Hara (E, Ts, I), *Menziesia multiflora* Maxim. (E, Ss, III), *Galium kamtschaticum* Steller (N, Hs, III), *Peracarpa carnosa* Hook. var. *circaeoides* Makino (O, He, III), *Ainsliaea acerifolia* Schulz Bipont. var. *subapoda* Nakai (EE, Hs, III), *Cacalia nikomontana* Matsum. (EE, Hs, III).

WSR : 'Warm, deep-snow, much rainfall'.

Carex morrowii Boott var. *temnolepis* Kükenth. (EE, He, I), *Fagus crenata* Blume (E, Ts, I), *Magnolia salicifolia* Maxim. (E, Ts, I), *Hamamelis japonica* Sieb. et Zucc. var. *obtusata* Matsum. (E, Ts, I), *Daphniphyllum macropodum* Miq. var. *humile* Rosenthal (E, Se, I), *Rhus tricarpa* Miq. (O, Ts, I), *Tripetaleia peniculata* Sieb. et Zucc. (E, Ss, I), *Rhododendron nudipes* Nakai (E, Ss, I), *Leucothoe grayana* Maxim. var. *oblongifolia* Ohwi (E, Ss, I), *Vaccinium japonicum* Miq. (O, Ss, I), *Ardisia japonica* Blume (S, Se, I), *Mitchella undulata* Sieb. et Zucc. (O, He, I).

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

Leptorumohra miqueliana H. Ito (O, He, I), *Leptogramma posoi* subsp. *mollissima* Nakaike (O, He, I), *Struthiopteris niponica* Nakai (E, He, I), *Cephalotaxus harringtonia* K. Koch var. *nana* Rehder (E, Se, I), *Smilax nipponica* Miq. (S, Vs, I), *Lindera umbellata* Thunb. var. *membranacea* Momiyama (E, Ss, I), *Ilex crenata* Thunb. var. *paludosa* Hara (E, Se, I), *Ilex leucoclada* Makino (E, Se, I), *Camellia rusticana* Honda (EE, Se, I), *Aucuba japonica* Thunb. var. *borealis* Miyabe et Kudo (E, Se, I).

Wsr : 'Warm, shallow-snow, little rainfall'.

Tsuga sieboldii Carr. (E, Te, I), *Sasamorpha borealis* Nakai (O, Se, I), *Carex reinii* Fr. et Sav. (E, He, I), *Fagus japonica* Maxim. (E, Ts, I).

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

Carpinus cordata Blume (O, Ts, I), *Euonymus oxyphyllus* Miq. (O, Ss, I), *Styrax obassia* Sieb. et Zucc. (O, Ts, I).

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

Dryopteris sabaei C. Chr. (E, Hs, I), *Disporum smilacinum* A. Gray (O, Hs, I), *Corylus sieboldiana* Blume (O, Ts, I), *Quercus mongolica* Fischer var. *crispula* Blume (E, Ts, I), *Magnolia obovata* Thunb. (S, Ts, I), *Schizophragma hydrangeoides* Sieb. et Zucc. (O, Vs, I), *Prunus grayana* Maxim. (E, Ts, I), *Sorbus alnifolia* C. Koch (O, Ts, I), *Rhus ambigua* Lavallee (O, Vs, I), *Euonumus alatus* Sieb. f. *dentatus* Hiyama (O, Se, I), *Acer palmatum* Thunb. var. *matsumurae* Makino (E, Ts, I), *Acer sieboldianum* Miq. (E, Ts, I), *Acer japonicum* Thunb. (E, Ts, I), *Acer mono* Maxim. (O, Ts, I), *Acer rufinerve* Sieb. et Zucc. (EE, Ts, I), *Aesculus turbinata* Blume (E, Td, I), *Vitis coignetiae* Pulliat (E, Vs, I), *Kalopanax pictus* Nakai (O, Ts, I), *Cornus controversa* Hemsley (O, Ts, I), *Shortia uniflora* Maxim. (EE, He, I), *Clethra barbinervis* Sieb. et Zucc. (E, Ts, I), *Fraxinus lanuginosa* Koidz. (E, Ts, I), *Rhododendron kaempferi* Planch. (E, Ss, I).

OSO : 'Deep-snow, temperate and rainfall indifferent'.

Sasa kurilensis Makino et Shibata (N, Se, III), *Heloniopsis orientalis* C. Tanaka (E, He, III), *Tripterospermum japonicum* Maxim. (S, He, III).

OOO : Indifferent species.

Lycopodium serratum Thunb. (O, He, III), *Carex dolichostachya* Hayata var. *glaberrima* T. Koyama (E, He, III), *Carex foliosissima* Fr. Schm. (O, He, III), *Shortia soldanelloides* Makino var. *magna* Makino (EE, He, III), *Monotropastrum globosum* H. Andr. (O, Hn, III), *Vaccinium hirtum* Thunb. (E, Ss, III).

Appendix 2

Commodal species groups of Hokkaido forest plants. For detail information, see Appendix 1.

CSR : 'Cold, deep-snow, much rainfall'.

Sasa kurilensis Makino et Shibata (S, Se, IIIc) ; *Streptopus amplexifolius* DC. var. *papillatus* Ohwi (N, Hs, IIIc) ; *Clintonia udensis* Trautv. et Mey. (N, Hs, IIe) ; *Ilex rugosa Fr.* Schm. (S, Se, IIIc) ; *Euonymus tricarpus* Koidz. (H, Ss, IIe) ; *Acer tschonoskii* Maxim. (S, Ts, IIIa) ; *Menziesia pentandra* Maxim. (S, Ss, IIIc) ; *Rhododendron albrechtii* Maxim. (S, Ss, IIIc) ; *Vaccinium ovalifolium* J. E. Smith (N, Ss, IIIa) ; *Vaccinium hirtum* Thunb. (S, Ss, Ia) ; *Vaccinium smallii* A. Gray (S, Ss, IIIc).

COr : 'Cold, snow-indifferent, little rainfall'.

Polypodium virginianum Linn. (N, He, Ia) ; *Abies sachalinensis* Masters (N, Te, IIIc) ; *Picea jezoensis* Carr. (N, Te, IIe) ; *Picea glehnii* Masters (H, Te, Ia) ; *Anemone debilis* Fischer (N, Hs, IIe); *Tiarella polyphylla* D. Don (S, He, IIe) ; *Ribes sachalinense* Nakai (N, Ss, IIe) ; *Oxalis acetosella* Linn. (N, He, Ib) ; *Cornus canadensis* Linn. (N, Hs, Ib) ; *Acer ukurunduense* Trautv. et Mey. (N, Ts, Ib).

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

Lycopodium obscurum Linn. (O, He, IIIc) ; *Arachniodes mutica* Ohwi (N, He, Ia) ; *Thelypteris connectilis* Watt (O, Hs, IIe) ; *Dryopteris austriaca* Fraser-Jenkins et Jermy (O, Hs, IIIc), *Carex sachalinensis* Fr. Schm. (N, He, Ib) ; *Paris verticillata* M. v. Bieb. (O, Hs, IIe) ; *Betula ermanii* Cham. (N, Ts, IIe) ; *Rubus pseudo-japonicus* Koidz. (H, Vs, IIe) ;

Actinidia kolomikta Maxim. (N, Vs, IIe) ; *Circaea alpina* Linn. (N, Hs, IIIc) ; *Pyrola renifolia* Maxim. (N, He, IIIc) ; *Rhododendron brachycarpum* D. Don (S, Se, IIIc) ; *Galium kamtschaticum* Steller (N, Hs, Ia) ; *Peracarpa carnosa* Hook. var. *circaeoides* Makino (N, He, IIIc).

csr : 'Cool, shallow-snow, little rainfall'.

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

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

Pyrrosia tricuspis Tagawa (S, He, IIa) ; *Carex siderosticta* Hance (O, Hs, IIc) ; *Cercidiphyllum japonicum* Sieb. et Zucc. (S, Ts, IIc) ; *Fraxinus lanuginosa* Koidz. (S, Ts, IIIb) ; *Viburnum wrightii* Miq. (S, Ss, IIIb).

cOr : 'Cool, snow-indifferent, little rainfall'.

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

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

Polystichum tripteron Pr. (O, He, IIc) ; *Taxus cuspidata* Sieb. et Zucc. (S, Te, IIe) ; *Cimicifuga simplex* Wormsk. (N, Hs, IIIb); *Hydrangea paniculata* Sieb. (S, Ss, IIIc) ; *Prunus ssiori* Fr. Schm. (N, Ts, IIe) ; *Phellodendron amurense* Rupr. (N, Ts, IIc) ; *Cacalia hastata* Linn. var. *orientalis* Ohwi (N, Hs, IIc).

WSR : 'Warm, deep-snow, much rainfall'.

Leptorumohra miqueliana H. Ito (O, He, IIIb) ; *Sturthiopteris niponica* Nakai (S, He, IId) ; *Corylus sieboldiana* Blume (S, Ts, IIc) ; *Fagus crenata* Blume (S, Ts, IIb) ; *Lindera umbellata* Thunb. var. *membranacea* Momiyama (S, Ss, IIb) ; *Hydrangea macrophylla* Ser. var. *megacarpa* Ohwi (S, Ss, IId) ; *Skimmia japonica* Thunb. var. *intermedia* Komatsu f. *repens* Hara (S, Se, IIIc) ; *Daphniphyllum macropodum* Miq. var. *humile* Rosenthal (S, Se, IIIb) ; *Ilex crenata* Thunb. var. *paludosa* Hara (S, Se, IId) ; *Ilex leucoclada* Makino (S, Se, IIb) ; *Vaccinium japonicum* Miq. (S, Ss, IId).

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

Arachniodes standishii Ohwi (S, He, IId) ; *Athyrium vidalii* Nakai (S, Hs, IIIb) ; *Leptogramma pozoi* subsp. *mollissima* Nakaike (S, Hs, IIIb) ; *Asplenium scolopendrium* Linn. (O, He, IIc) ; *Cephalotaxus harringtonia* K. Koch var. *nana* Rehder (S, Se, IId) ; *Sasa cernua* Makino (S, Se, IId) ; *Sasa megalophylla* Makino et Uchida (S, Se, IIe) ; *Carex foliosissima* Fr. Schm. (S, He, IV) ; *Acer mono* Maxim. var. *mayrii* Koidz. (S, Ts, IIc) ; *Euonymus alata* Sieb. f. *dentatus* Hiyama (S, Se, IIIb).

WsR : 'Warm, shallow-snow, much rainfall'.

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

Wsr : 'Warm, shallow-snow, little rainfall'.

Tilia maximowicziana Shirasawa (S, Ts, IIc) ; *Acer cissifolium* K. Koch (S, Ts, IIa) ; *Spuriopimpinella calycina* Kitagawa (S, Hs, IIa) ; *Cacalia delphiniifolia* Sieb. et Zucc. (S, Hs, IIa).

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

Lunathyrium pycnosorum Koidz. (O, Hs, IId) ; *Sasa nipponica* Makino et Shibata (S, He, IIc) ; *Chloranthus serratus* Roem. et Schult. (S, Hs, IIa) ; *Carpinus cordata* Blume (S, Ts, IIc) ; *Ostrya japonica* Sarg. (S, Ts, IIc) ; *Quercus serrata* Thunb. (S, Ts, IIa) ; *Ulmus davidiana* Planch. var. *japonica* Nakai (O, Ts, IIc) ; *Morus bombycis* Koidz. (S, Ts, IIc) ; *Magnolia kobus* DC. var. *borealis* Sarg. (H, Ts, IIc) ; *Prunus sargentii* Rehder (S, Ts, IIc) ; *Prunus maximowiczii* Rupr. (O, Ts, IIc) ; *Maackia amurensis* Rupr. et Maxim. var. *buergeri* C.K. Schn. (S, Ts, IIa) ; *Desmodium oxyphyllum* DC. (S, Hs, IIa) ; *Pachysandra terminalis* Sieb. et Zucc. (S, Se, IIc); *Euonymus oxyphylus* Miq. (S, Ss, IV) ; *Acer palmatum* Thunb. var. *amoenum* Ohwi (S, Ts, IIc) ; *Styrax obassia* Sieb. et Zucc. (O, Ts, IIa) ; *Phryma leptostachya* Linn. var. *asiatica* Hara (O, Hs, IIc); *Cacalia auriculata* DC. var. *kamtschatica* Matsum. (N, Hs, IIe).

WOR : 'Warm, snow-indifferent, much rainfall'.

Dryopteris monticola C. Chr. (O, Hs, IIIb) ; *Paris tetraphylla* A. Gray (S, Hs, IIIb) ; *Magnolia obovata* Thunb. (S, Ts, IIIb); *Schizophragma hydrangeoides* Sieb. et Zucc. (S, Vs, IIIa) ; *Rhus ambigua* Lavallee (S, Vs, IIIb) ; *Rhus trichocarpa* Miq. (S, Ts, IId) ; *Acer japonicum* Thunb. (S, Ts, IIIb) ; *Acanthopanax sciadophylloides* Fr. et Sav. (S, Ts, IIIa) ; *Cornus controversa* Hemsley (S, Ts, IIc).

WOr : 'Warm, snow-indifferent, little rainfall'.

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

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

Matteuccia orientalis Trev. (O, Hs, IId) ; *Arisaema Angustatum* Fr. et Sav. var. *peninsulae* Nakai (N, Hs, IIc) ; *Smilacina japonica* A. Gray (N, Hs, IId) ; *Disporum sessile* D. Don (S, Hs, IIIb) ; *Calanthe tricarinata* Lindl. (S, He, IId) ; *Chloranthus japonicus* Sieb. (O, Hs, IIc) ; *Betula maximowicziana* Regel (S, Ts, IIIb) ; *Betula platyphylla* Sukatchev var. *japonica* Hara (S, Ts, IId) ; *Alnus hirsuta* Turcz. (N, Ts, IIc) ; *Quercus mongolica* Fischer var. *crispula* Blume (S, Ts, IIIa) ; *Actaea asiatica* Hara (O, Hs, IIe); *Sorbus alnifolia* C. Koch (O, Ts, IIIb) ; *Acer mono* Maxim. (O, Ts, IIIb) ; *Vitis coignetiae* Pulliat (S, Vs, IIIb) ; *Tilia japonica* Simonkai (S, Ts, IIIc) ; *Actinidia arguta* Planch (O, Vs, IId); *Actinidia polygama* Maxim. (S, Vs, IIe) ; *Kalopanax pictus* Nakai (S, Ts, IIIc) ; *Angelica ursina* Maxim. (N, Hs, IIa) ; *Fraxinus mandshurica* Rupr. var. *japonica* Maxim. (S, Ts, IIc) ; *Asperula odorata* Linn. (O, He, IIc).

OSO : 'Deep-snow, temperate and rainfall indifferent'.

Plagiogyria semicordata subsp. *matsumureana* Nakaike (S, He, IIIa); *Leucothoe grayana* Maxim. var. *oblongifolia* Ohwi (H, Ss, IIIc); *Viburnum furcatum* Blume (S, Ss, IIIc).

OsO : 'Shallow-snow, temperature and rainfall indifferent'.

Dryopteris crassirhizoma Nakai (O, He, IIIc) ; *Athyrium yokoscense* Christ (O, Hs, IIa) ; *Sasa chartacea* Makino (S, He, IIa); *Zanthoxylum piperitum* DC. (S, Ss, IIa) ; *Sanicula chinensis* Bunge (O, Hs, IIa) ; *Senecio cannabifolius* Less. (N, Hs, IIe).

OOO : Indifferent species.

Lycopodium serratum Thunb. (O, He, IIIc) ; *Lepisorus ussuriensis* var. *distans* Tagawa (N, He, IIIb) ; Sasa *senanensis* Rehd. (S, Se, IIIc) ; *Calamagrostis hakonensis* Fr. et Sav. (N, He, IIe) ; *Carex caryophyllea* Latour. var. *microtricha* Kükenth. (N, Hs, IIc) ; *Carex pilosa* Scop. (N, He, IIc) ; *Allium victorialis* Linn. var. *platyphyllum* Makino (O, Hs, IIIb) ; *Lilium* *cordatum* Koidz. var. *glehnii* Woodcock (N, Hs, IIc) ; *Polygonatum odoratum* Druce var. *maximowiczii* Koidz. (N, Hs, IIc) ; *Maianthemum dilatatum* Nels. et Macbr. (N, Hs, IIIc) ; *Epipactis papillosa* Fr. et Sav. (N, Hs, IIIc) ; *Ulmus laciniata* Mayr (O, Ts, IIc) ; *Asarum heterotropoides* Fr. Schm. (H, Hs, IIe) ; *Diphylleia grayi* Fr. Schm. (H, Hs, IIIc); *Hydrangea petiolaris* Sieb. et Zucc. (S, Ve, IIIc) ; *Sorbus commixta* Hedl. (S, Ts, IIIc) ; *Osmorhiza aristata* Makino et Yabe (S, Hs, IIe) ; *Angelica anomala* Lallemant (N, Hs, IIa) ; *Tripterospermum japonicum* Maxim. (S, He, IIIa) ; *Cirsium kamtschaticum* Ledeb. (N, Hs, IIe).