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Plant distribution in relation to the length of the growing season in a snow-bed in the Taisetsu Mountains, northern Japan

G. Kudo & K. Ito
Graduate School of Environmental Science, Hakkaido University, Sapporo, Japan, 060

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Abstract

The distribution pattern of plants was studied in an alpine snow-bed in six plots along a snow-melting gradient. Each plot consisted of two habitats with respect to the microtopography; the flat habitat and the mound habitat. The number of species per plot decreased with the shortened snow-free period. In the flat habitat, the dominant growth forms changed from the early exposed plots to the late exposed ones as follows; lichens ↔ evergreen and deciduous shrubs ↔ forbs ↔ graminoids ↔ bryophytes. In the mound habitat, evergreen and deciduous shrubs prevailed widely along the gradient because of the ability to exploit new habitat by creeping over exposed rocks. For shrubs, the existence of mounds contributed to the expansion of the distribution ranges. Forbs and graminoids shifted their distribution modes to the late exposed plots where shrubs decreased in cover. Deciduous shrubs and forbs completely disappeared in the latest exposed plot.

Nomenclature: Ohwi, J. 1975. Flora of Japan. Shibundo, Tokyo; Shimizu, T. 1982. The new alpine flora of Japan in color. I, II. Hoikusha, Tokyo; Yoshimura, I. 1974. Lichen flora of Japan in color. Hoikusha, Tokyo.

Introduction

In alpine and arctic environments, which are characterized by low temperature, short growing season and intense solar radiation, evergreen dwarf shrubs, graminoids, bryophytes and lichens are dominant. This distribution pattern related with the growth forms is a result of an adaptation to severe growing conditions (Grulke & Bliss 1985; Sohlberg & Bliss 1984).

One of the important factors controlling the distribution of alpine vegetation is the duration of snow cover (Billings & Bliss 1959; Gjaerevoll 1956). Snow cover protects plants from extremely low temperatures and strong wind during winter (Bamberg & Major 1968; Bliss 1962a; Johnson & Billings 1962; Karrasch 1973; Okitsu & Ito 1983). The time of snow-melt directly affects the growth, life cycle, and the existence of plants by determining the length of growing season (Billings & Bliss 1959; Isard 1986; Johnson & Billings 1962). Thus, all alpine species have established their distribution ranges along the snow-depth and/or snow-melting gradients, and vegetational microzonations reflect the preference of plants to the depth and duration of snow cover (Billings & Bliss 1959).

In snow-beds, where snow remains until summer because of a large snow accumulation during winter, there is a steep gradient in time of snow-melt within a narrow area. This gradient provides good opportunities to study the ecological responses of plants to the length of growing season. Three questions are considered in this study; (1) How are the each species distributed along a snow-melting gradient? (2) Are there similar patterns of distribution among species belonging to the same growth form? (3) Are there any interactions between species?

Plant distribution is influenced not only by snow conditions but also by microtopography and edaphic factors such as soil moisture, pH and organic content (Bliss 1962b; Eddleman & Ward 1984; Weir & Wilson 1987). We investigated vegetation and soil conditions in association with the length of snow-free period and the effect of microtopography in an alpine snow-bed on a block field slope.

Study area

The Taisetsu Mountains (43°13′–45′N, 142°32′–143°19′ E) are located in central Hokkaido, northern Japan. The central part of the mountains is composed of volcanic domes and lava plateaux of augite hypersthene andesite of Early to Late Pleistocene period (Ishikawa 1963). Although altitude is not so high (a large part of the area is less than 2000 m), there are patterned grounds and permafrosts in some places (Takahashi & Sone 1988), indicating a periglacial environment in the area.

Climatically, the Taisetsu Mts. have cold and snowy winters, and warm, wet and foggy summers. The annual mean temperature at an altitude of 2000 m was −3.8 °C, and monthly mean temperatures ranged from −21.3 °C (January) to 13.9 °C (August) in 1985 (Sone & Takahashi 1988). Summer precipitation (July to September) is usually more than 500 mm.

Because of prevailing north-west winds during the winter, large snow drifts (2–20 m) are built up on the south-east slope. The time of snow-melt is from late May to late September; partly snow remains for several years. Snow begins to cover the ground again in early October.

Our study was carried out in the snow-bed communities developing on a block-field slope at elevations between 1790 and 1910 m, in the central part of the Taisetsu Mts. (Fig. 1). Many rocks of the block field are covered with trailing dwarf shrubs. These plant-covered mounds physiognomically characterize the snow-bed

Photo 1. General view of study site. Many rocks are covered with trailing dwarf shrubs and forming the mound habitat.

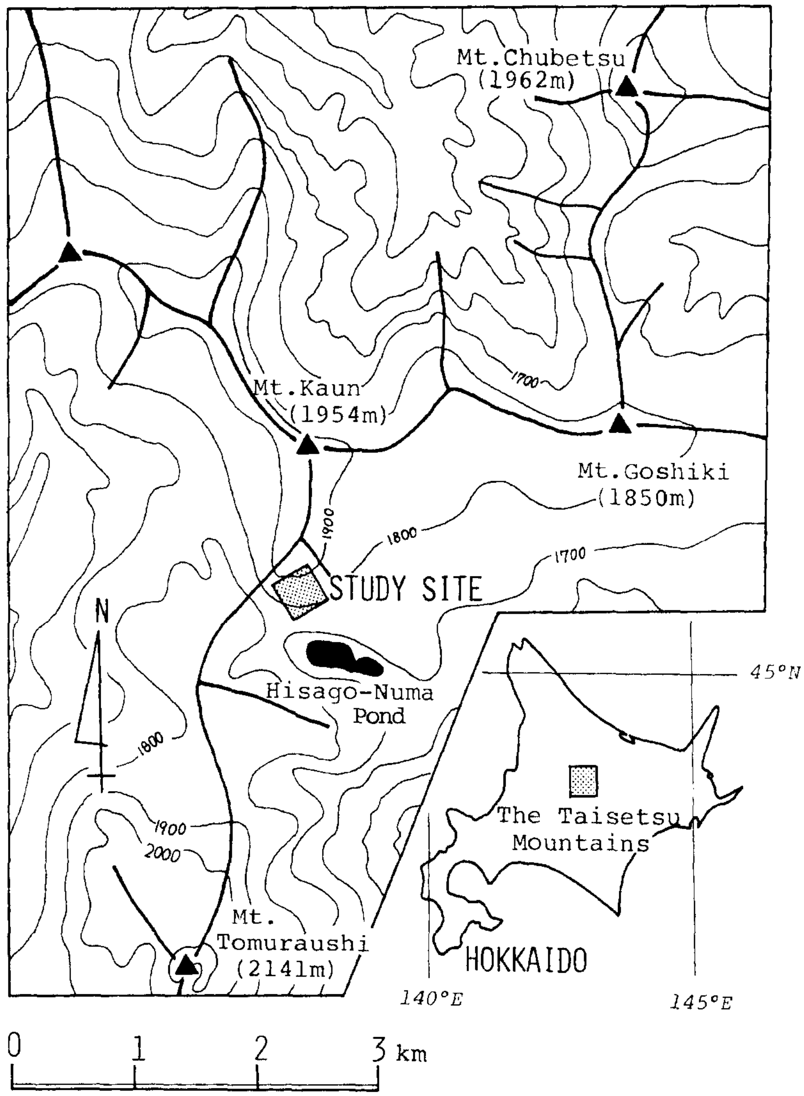

Fig. 1. Map showing the study area in the central part of the Taisetsu Mountains. Survey plots were set up on a southeast facing slope on block-field.

(Photo. 1). The study site consists of two habitat types. One is the 'flat habitat', which is the level ground between rocks with a deep soil layer (20 to 40 cm). The other is the 'mound habitat', consisting of rocks of various sizes (30 x 30 cm to more than 1 x 1 m, and 5 to 40 cm in height) with a relatively thin layer of soil. A large part of this snow-bed is covered by dwarf shrubs and herbs. In places with late snow-melt, where snow remains until late August, moss carpets develop partly and large parts are exposed as bare land.

Methods

In 1988, six 20 x 20 m plots (A to F) were selected in consideration of the time of snow-melt, from early June in plot A to mid August in plot F (Table 1). Although the snow-free period fluctuated from year to year in each plot, depending on the amount of snow accumulation in the previous winter and weather conditions in the current spring, the snow regularly disappeared first in plot A and last in plot F during three years

Table 1. Topographical and snow conditions of the study plots. For snow-free period, error range is ±5 days.

Plot	A	B	C	D	E	F
Altitude (m)	1910	1900	1880	1790	1790	1880
Slope direction	SE	SE	SSE	SSE	SE	SE
Inclination (°)	5	16	18	11	11	14
Snow-free period (day)						
1988	120	105	90	70	60	50
1989	95	80	70	60	55	45
1990	130	115	95	85	80	60

(1988–90). The time of snow-melt is directly correlated with the length of the plant growing season.

After 30 to 40 days from snow disappearance, 20 quadrats (50 × 50 cm) were randomly set up both in the flat and the mound habitats in plots A to E. In plot F the mound habitat was bare and 20 quadrats were located in the flat habitat only. In each quadrat, plants were measured quantitatively by the cover-abundance scale of Braun-Blanquet (1964). Thereafter, these values were replaced by the combined transformation of van der Maarel (1979) which was the combination of a cover scale in angular transformation with a weighting based on abundance. In addition, total plant cover and the cover of each growth form were measured in each quadrat. The growth forms were divided into six groups: (1) evergreen dwarf shrubs, (2) deciduous dwarf shrubs, (3) perennial forbs, (4) perennial graminoids, (5) lichens, and (6) bryophytes. The number of vascular species per quadrat, the relative cover of each growth form, and the mean values of the van der Maarel scale of vascular species were calculated for each habitat in every plot.

In 1989, five soil samples (depth 0–5 cm) were obtained at random locations in each habitat of plots A to E. Since the distribution of vascular plants in plot F was limited to moss carpets, 2 to 10 cm thick, the samples for soil analysis were taken from both moss carpets and bare ground. Ignition loss (burning at 700 °C for 40 min) and soil pH (1:4 mixture of dry soil and distilled water in weight) were measured. Although soil moisture is an important factor affecting plant distribution, the wet summer weather in this area seems to reduce the inter-plot differences in water supply. The soil water conditions were compared between the flat and the mound habitats by measuring pF values (log tension of soil water suction expressed in centimeter of water column), using a soil pF meter and a data logger (KADEC-UV). The measurements were made at a depth of 5 cm in plot D from 3 August to 23 September in 1990, at one hour intervals. The soil depths at the measurement points were 10 cm in the mound habitat and 30 cm in the flat habitat.

Results

Number of species

The number of vascular species per plot decreased with the shortened snow-free period, from plot A to F (Table 2). The average number of species per quadrat also gradually decreased from plot B to F in the flat habitat ($p < 0.01$, Duncan's multiple range test). In the mound habitat, the number of species was larger in plots A and B, whereas there were no significant differences between plots C, D and E ($p > 0.10$). Although the number of species per quadrat was larger in the flat habitat in plots A to D, it was larger in the mound habitat in plot E. Thus, species density was maintained in the mound habitat in spite of the short growing season. Then, the number of species sharply decreased to zero in plot F.

The species numbers of evergreen and deciduous shrubs gradually decreased with the shortened snow-free period. The number of forb species was the largest of all growth forms in plots A to E, but zero in plot F. That of graminoid species was largest in plot C and decreased towards both end of the gradient.

Distribution pattern

For the comparison of distribution pattern of species along the snow-melting gradient, species with

Table 2. Number of vascular species per plot. Number of quadrats is 20 at each habitat. Plot size was 20 x 20 m and quadrat size was 50 x 50 cm. Ev: evergreen shrubs, De: deciduous shrubs, Fo: forbs, Gr: graminoids. a to d: indicating a statistical significant difference ($p<0.01$, Duncan's multiple range test) between plots in each habitat. Mean ± SD.

Plot	A	B	C	D	E	F
No. species per plot:						
Total	36	36	33	24	21	5
Ev	11	8	7	6	4	2
De	4	4	3	2	2	0
Fo	14	16	13	9	9	0
Gr	7	8	10	7	6	3
Average no. species per quadrat:						
Flat habitat	12.0 ± 1.3^{ab}	13.0 ± 2.7^{a}	10.1 ± 2.4^{b}	7.3 ± 1.9^{c}	6.2 ± 1.6^{c}	2.9 ± 1.2^{c}
Mound habitat	11.5 ± 1.3^{a}	10.0 ± 2.0^{a}	7.1 ± 1.5^{b}	6.6 ± 1.9^{b}	7.8 ± 2.0^{b}	0

a value of at least one on the van der Maarel scale and having at least 60% frequency in at least one plot, were selected. In Figure 2, the values of the van der Maarel scale of 22 selected species are shown. Nos. 1 to 8 are evergreen dwarf shrubs, nos. 9 and 10 are deciduous dwarf shrubs, nos. 11 to 16 are perennial forbs and nos. 17 to 22 are perennial graminoids.

In evergreen shrubs, *Empetrum nigrum* var. *japonicum*, *Loiseleuria procumbens*, *Arcterica nana* and *Vaccinium vitis-idaea* occurred only in the early exposed plots. *Rhododendron aureum*, *Phyllodoce caerulea* and *P. aleutica* showed wide distribution ranges. Although *R. aureum* and *P. caerulea* grew in both habitats in the early exposed plots, they were restricted to the mound habitat in the late exposed plots. *Harrimanella stelleriana* was found in the intermediate to the late exposed plots. *P. aleutica* and *H. stelleriana* grew well in the mound habitat in plot E. The evergreen shrubs seemed to show a preference for the mound habitat, particularly in the late exposed plots.

Deciduous shrubs, such as *Arctous alpinus* var. *japonicus* and *Sieversia pentapetala* preferred the mound habitat. *S. pentapetala* extended its distribution range to the late exposed plots mainly by inhabiting the mound habitat.

Some forbs, such as *Anemone narcissiflora* and *Coptis trifolia* occurred mainly in the early exposed plots. *Solidago virga-aurea* var. *leiocarpa*, *Gentiana nipponica* and *Peucedanum multivittatum* showed wide distribution ranges. *P. multivittatum* was limited to the flat habitat. *Potentilla matsumurae* appeared in the intermediate to the late exposed plots. It seemed to prefer the flat habitat to the mound habitat but increased its cover in the mound habitat in plot E. Generally, the forbs seemed to have a preference for the flat habitat with the exception of *A. nacrissiflora* in plot B and *C. trifolis* in plot A.

Among graminoids, *Carex blepharicarpa* inhabited the early exposed plots. *Deschampsia flexuosa* and *C. pyrenaica* showed wide distribution ranges. *D. caespitosa* var. *festucaefolia*, *C. flavocuspis* and *Juncus beringensis* appeared in the intermediate to the late exposed plots. The preference of graminoids with respect to habitat type was ambiguous.

The relative cover of the growth forms in the flat and the mound habitats is shown in Figure 3. Of the flat habitat, plot A was dominated by lichens and evergreen shrubs. The dominant lichen species were *Cladonia rangiferina*, *C. stellaris*, *C. nigripes* and *Cetraria ericetorum*. Plot B showed a considerable amount of deciduous shrubs, mostly *Sieversia pentapetala*. However, the cover of deciduous shrubs drastically decreased so as to almost disappear in plot D. The cover of fobs and graminoids increased from plot C to E. In plot F, forbs disappeared, and bryophytes (mainly *Polytrichum sexangulare* Flock.ex Brid.) constituted most of the plant cover.

In the mound habitat, the relative cover struc-

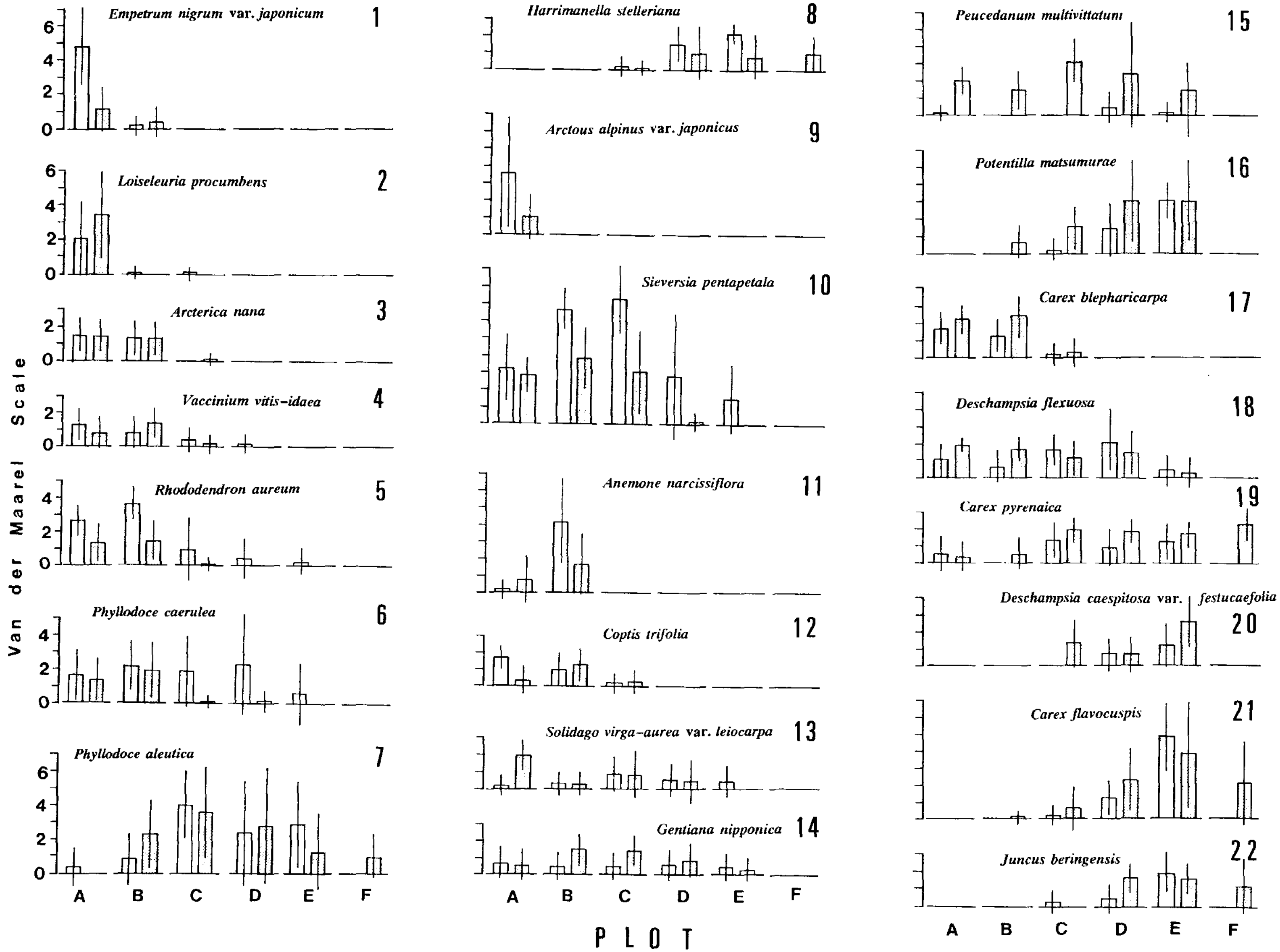

Fig. 2. Transitions of distribution patterns of the 22 major vascular species using the van der Maarel's combined transformation value. Clear column: mound habitat, dotted column: flat habitat. Vertical bars indicate standard deviation. Nos. 1–8: evergreen dwarf shrubs, 9–10: deciduous dwarf shrubs, 11–16: perennial forbs, and 17–22: perennial graminoids.

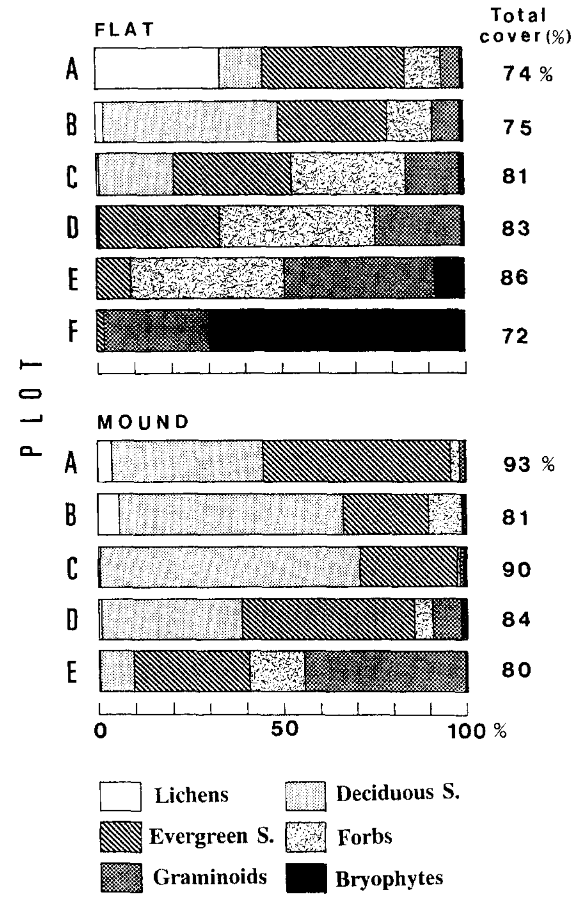

Fig. 3. Relative plant cover of each growth form in the flat and the mound habitats, and total plant cover in each plot.

tures were rather simple; evergreen and deciduous shrubs were generally dominant in plots A to D, and the cover of graminoids increased considerably in plot E. The cover of lichens and bryophytes was rather small throughout the plots.

The total cover of plants was relatively large (72–93%) in both habitats throughout the plots (Fig. 3), although the data in plot F was obtained only at moss carpets.

Thus, each growth form was composed of species having various distribution ranges along the snow-melting gradient but certain tendencies were recognized between growth form and distribution pattern; (1) The mound habitat had very different growth form structure in comparison with the flat one. (2) Forbs and graminoids prevailed in the relatively late exposed plots (D and E). (3) Deciduous shrubs and forbs completely disappeared in plot F. (4) Lichens prevailed in the earliest exposed plot, whereas bryophytes in the latest exposed plot.

Soil environmental factors

In the flat habitat, organic content in the soil was 15–32% throughout the plots and there were no significant differences among the plots ($p > 0.05$, Kruskal-Wallis's test), excepting bare ground in plot F where it was only 7.3%. In the mound habitat, the soil had more organic matter throughout the plots (35–53%) than in the flat one. The soil of the mound habitat was composed of organic matter which was directly accumulated on the substrate rocks by litter fall from plants growing in the mound habitat. The differences in organic matter among the plots were not significant ($p > 0.05$) also in the mound habitat.

The soil pH was 4.8–5.4 in the flat habitat, and there were no significant differences among the plots ($p > 0.05$) with the exception of bare ground in plot F (pH 5.5–5.6). High pH value of the bare ground seemed to reflect that of the parent material. In the mound habitat, the soil pH was much lower (4.1–4.4) than in the flat one, while the differences among the plots were not significant ($p > 0.05$). It is considered that the lower pH in the mound habitat is strongly related to the high content of organic matter.

Although the pF values of soil water in the mound habitat fluctuated more than those in the flat one, the pattern was very similar between habitats throughout the measurement period. In the greater part of the period, the values were below 2.0 in both habitats, indicating that the soil water condition was usually on the status of gravitational water (pF 0–1.8). The maximal pF value was 2.4 in the mound habitat and 2.1 in the flat one throughout the period. Those values were much lower than the incipient wilting point of plants (pF 3.8), indicating that there was no soil water shortage in either habitat during the summer. Thus, soil moisture was not a limiting factor for plant distribution in this snow-bed.

Discussion

Mound formation begins with shrubs, such as *Sieversia pentapetala*, *Phyllodoce aleutica* or *P. caerulea*, creeping over exposed rocks by layering of stems (Photo. 2). Shrubs continue to grow and branch densely over rocks. According to the increase in litter accumulation, organic soils are gradually formed on the mounds. By creeping over exposed rocks, the plants obtain more light because they can expand their leaves in open spaces. This seems to be especially advantageous in places of short snow-free period. Another advantage of the mound habitat is considered to be the escape from cold water flow during snow-melt since low soil temperature restricts plant growth (Bamberg & Major 1968; Bliss 1971). Owing to the existence of mounds throughout the gradient, trailing dwarf shrubs can expand their distribution ranges toward late exposed places. Consequently, evergreen and deciduous shrubs, which have an ability to exploit new habitat, are considered to be an adaptive form in a snowy block field environment.

Although the mound habitat is formed and dominated mainly by evergreen and deciduous shrubs, the cover of shrub species decreases in plot E. Here, some graminoid and forb species such as *Carex flavocuspis*, *Juncus beringensis*, *Deschampsia caespitosa* var. *festucaefolia* and *Potentilla matsumurae* increase their cover. Because graminoid and forb species cannot creep over mounds, it is considered that they invade after the mound formation by shrubs through the establishment of seedlings. Thus, species diversity in short snow-free places is maintained due to the advantage of the mound habitat mentioned above. However, *Peucedanum multivittatum* having deep root system does not grow well in the mound habitat, because of thin and/or acid soil (Ito & Nishikawa 1976). Under very short snow-free conditions, the shoot growth of shrubs (e.g. *Phyllodoce aleutica*) is so restricted that they have highly dwarfed forms and cannot creep up mounds, hence rocks remain to be exposed.

The increase in cover of forbs and graminoids in the relatively late exposed plots (D and E) may be related to interspecific competition. Ostler *et al.* (1982) reported that some forbs (e.g. *Erigeron*, *Lewisia* and *Viola* species) and graminoids (e.g. *Carex*, *Deschampsia* and *Juncus* species) increased in cover in late exposed places, because of the reduced biotic competition. Shrubs, which form dense clonal patches, are effective competitors to forbs and graminoids. In this study, *Potentilla matsumurae* among the forbs, *Carex*

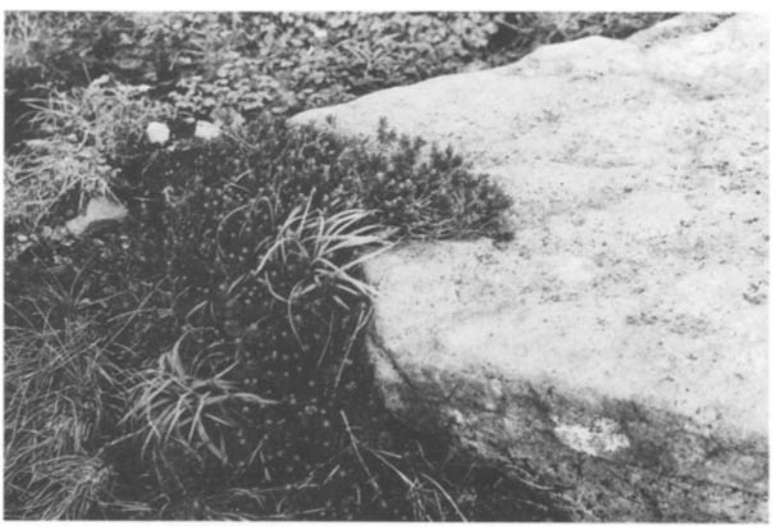

Photo 2. Exploitation of new habitat by *Phyllodoce aleutica*. Mound habitat is formed by the creeping of dwarf shrubs over bare rocks.

flavocuspis, *C. pyrenaica*, *Deschampsia caespitosa* var. *festucaefolia* and *Juncus beringensis* among the graminoids increased in cover in the late exposed plots where some shrubs (such as *Sieversia pentapetala*, *Rhododendron aureum* and *Phyllodoce caerulea*) decreased. Only one evergreen shrub species, *Harrimanella stelleriana* having a highly dwarfed form increased its cover in the late exposed plots.

There were no forbs and deciduous shrubs in plot F. This means that evergreen shrubs and graminoids are physiologically more tolerant to extremely short growing condition than deciduous shrubs and forbs. It is known that the evergreen habit is more advantageous than the deciduous habit in tundra regions, because the cost of seasonal leaf turnover is reduced by having evergreen leaves (Bell & Bliss 1977; Bliss 1971; Johnson & Tieszen 1976). Moreover, evergreen leaves are used as a storage organ for nutrients during winter (Moore 1980). Graminoids can photosynthesize more effectively than deciduous shrubs and forbs during a short period, because graminoids can efficiently utilize the carbon and nutrient resources and adjust the leaf production in accordance with the length of growing season (Callaghan 1974; Tieszen *et al.* 1981). Thus, the potential distribution range of plants may be determined by physiological characteristics which are common within plants having a same growth form.

Lichens and bryophytes inhabited the plots having diametrically opposite snow conditions; this pattern is well known in alpine vegetation (Ellenberg 1988). In extremely late exposed places, plant growth was restricted to the moss carpets of *Polytrichum sexangulare*. The soil temperature under moss carpets maintains warmth (Matsuda 1964), while moisture is relatively constant (Bell & Bliss 1980), and bryophytes contribute to nutrient cycling (Chapin *et al.* 1987). Thus, the moss carpets play a significant role in seedling establishment and growth of vascular plants in alpine snow-beds, as well as in arctic areas (Bliss & Svoboda 1984; Sohlberg & Bliss 1984). Viewed from various aspects as mentioned above, consequently, vegetation transition along the snow-melting gradient in a local snow-bed is considered to be similar to the vegetation change along the latitude where the length of growing season decreases toward higher latitudes.

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