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Performance and phenology of alpine herbs along a snow-melting gradient

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Responses of plants to the length of the growing season were studied in an alpine snow-bed by setting five plots along a snow-melting gradient. Performance and phenology were compared between the plots for five herbaceous species (*Peucedanum multivittatum, Primula cuneifolia, Veronica stelleri* var. *longistyla, Solidago virga-aurea* var. *leiocarpa* and *Potentilla matsumurae*). Performance characteristics measured were flower height, leaf height, leaf number, flower number and fruit number. In the late exposed plots with short snow-free periods, fruit-set was reduced in many species due to the decrease in flower number and/or the short growing season for fruit development. *Veronica stelleri* var. *longistyla* and *Solidago virga-aurea* var. *leiocarpa*, which decreased in flower and leaf numbers due to the short snow-free period, were sensitive to the short growing season. *Peucedanum multivittatum* was vigorous in the late exposed plots, but its slow flowering and fruiting prevented the fruit-set from developing in the last exposed plot. *Primula cumeifolia* and *Potentilla matsumurae*, quick flowering species that maintained their flower number throughout the snow-melting gradient, were considered the most successful species in late exposed habitats.

Key words: alpine snow-bed; flower number; fruit number; phenology; plant height; snow-free period.

INTRODUCTION

One of the most important characteristics of alpine environments is the duration of snow cover which varies largely from site to site. The time of snow-melt significantly affects the appearance and life-cycle of plants; directly through the length of the growing season (Billings & Bliss 1959; Johnson & Billings 1962; Callaghan 1974; Kudo 1991) and indirectly through soil moisture or low soil temperature as affected by melting water (Billings & Bliss 1959; Johnson & Billings 1962; Scott & Billings 1964). Many studies have indicated that distribution patterns (Helm 1982; Eddleman & Ward 1984; Isard 1986; Weir & Wilson 1987; Kudo & Ito 1992) and phenologies (Holway & Ward 1963, 1965; Ostler *et al.* 1982; Ram *et al.* 1988; Kudo 1991) of alpine plants are controlled to a great extent by the time of snow-melt. Such being the case, do the species having similar distribution ranges respond in the same way to snow-melt conditions? Little is known about the growth and reproductive activity of alpine plants with reference to the snow conditions (*cf.* Wijk 1986a).

The aim of this study was to determine the effect of the length of the growing season on the performance and reproductive activity of herbaceous plants, which are widely distributed along a gradient at the time of snow-melt. Because plants are affected by various environmental factors such as temperature, moisture, nutrient status, microtopography and competition, the details in comparative studies of growing conditions are necessary in order to make clear the response of plants to snow-melt. In this study, the performances (heights of flowers and leaves, and the numbers of leaves, flowers and fruits) and phenologies of five herbaceous species were compared with reference to the snow-free period, soil moisture, soil nutrient level and vegetation cover along a snow-melting gradient.

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STUDY AREA

This study was conducted on a gentle slope (5°–18°) situated at an elevation of 1790–1910 m, near Mt Kaun (43°43′N, 142°52′E) in the central part of the Taisetsu Mountains of Hokkaido, northern Japan (Fig. 1). The mountains are composed of a lava plateau of augite hypersthene andesite of the early to late Pleistocene period. As this area is exposed to northwesterly winds during the winter, large snow deposits form on the southeast facing slopes. Snow depth varies from 2 to 20 m in early spring. The snow-melting season lasts from early May to late September, and snow begins to cover the vegetation again from early October. A large part of the study area is snow-bed plant communities, which are composed of dwarf shrubs, forbs and graminoids, and sites where snow disappears in late August are sparsely covered by a bryophyte carpet and bare soil (Kudo & Ito 1992).

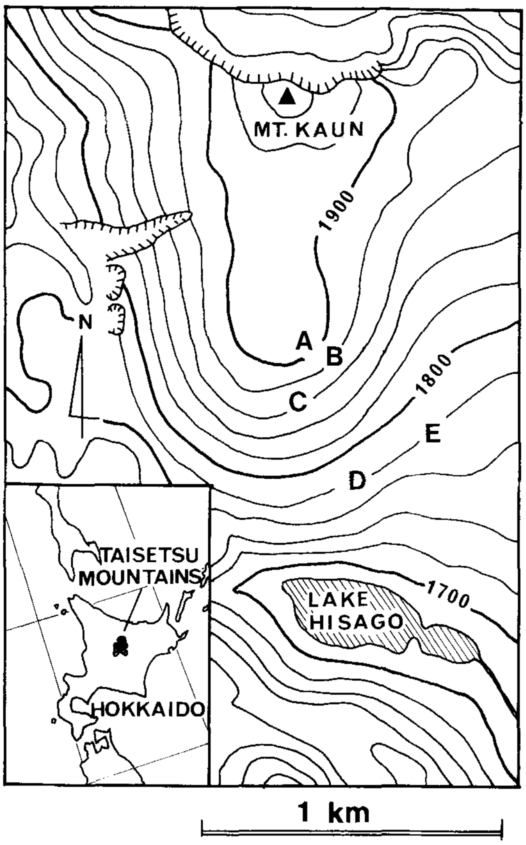

Fig. 1. Map of study site. Survey plots (A to E) were arranged along a snow-melting gradient on a slope.

The Taisetsu Mountains are characterized by rainy and foggy summers and cold winters with heavy snowfalls. Summer precipitation (July to September) is usually more than 500 mm. The annual mean temperature in this study site was − 0.9°C, while monthly mean temperatures ranged from − 16.2°C (January) to 12.1°C (August) in 1990 (Y. Kodama & T. Yamada, pers. comm. 1991).

METHODS

Peucedanum multivittatum Maxim. (Umbelliferae), *Primula cuneifolia* Ledeb. (Primulaceae), *Veronica stelleri* Pall. ex Link var. *longistyla* Kitagawa (Scrophulariaceae), *Solidago virga-aurea* Linn. var. *leiocarpa* (Benth.) Miq. (Compositae) and *Potentilla matsumurae* Th. Wolf (Rosaceae) are deciduous perennial herbs that occur in places with various snow-free periods in this area (Kudo 1991). *Peucedanum multivittatum* and *P. matsumurae* have several radical leaves with petiole and a flower stalk. *Primula cuneifolia* has several rosette leaves and a flower stalk. *Veronica stelleri* var. *longistyla* and *Solidago virga-aurea* var. *leiocarpa* are erect herbs with inflorescences on the upper part of the shoot.

In 1989, five plots (A to E) were set on a southeast facing slope (Fig. 1) along a snow-melting gradient, from late June (plot A) to early August (plot E). Each plot was *ca* 20 m × 20 m in size. *Peucedanum multivittatum, V. stelleri* var. *longistyla* and *S. virga-aurea* var. *leiocarpa* were distributed in all plots (A to E), and *P. cuneifolia* and *P. matsumurae* in plots B to E.

The following abiotic environmental factors were measured for each plot; the length of the snow-free period (in days) in 1989, the per cent of soil moisture on a dry weight basis and the total nitrogen content of the soil. For soil moisture measurements, five samples were collected from the 0–5 cm layer at random locations within each plot with a soil sampler (100 mL in volume), 20 to 30 days after the snow had disappeared. After measuring of wet weight, samples were dried at 105°C for 48 h and the dry weight was measured. Per cent soil moisture was obtained using the following formula: (weight of soil water/solid dry weight) × 100(%). Total nitrogen content of the topsoil (0–5 cm in depth) was analyzed for nine samples per plot, collected at random locations within each plot using a C-N analyzer (Yanaco MT-3). Statistical comparisons of soil moisture and nitrogen content were made between plots using the non-parametric Kruskal-Wallis test.

To determine if species grew under different conditions of plant cover, the per cent cover of plants was obtained for each plot. Forty quadrats (50 m × 50 cm in size) were set at random locations within each plot, 15–30 days after the snow disappeared, and the vegetation cover was measured. The frequency of appearance of the five species was obtained in each plot as follows: (number of quadrats where the species occurs/40 which is the number of arranged quadrats per plot) × 100(%).

In the performance survey, the heights of flowers and the uppermost leaf from soil surface, the numbers of leaves, flowers and ripe fruits were measured for 40 adult individuals of each species chosen at random within each plot in 1989. The measurements of the plant heights and the numbers of leaves and flowers were obtained during the flowering season, and that of the fruit number during the fruiting season for each species. When there were less than 40 flowering or fruiting individuals within a plot, measurements were made on all plants within that plot. For *S. virga-aurea* var. *leiocarpa* and *V. stelleri* var. *longistyla*, the number of flower buds was used as a measure of the potential number of flowers, because flowering advanced gradually from the lower part to the upper part within an inflorescence. For *P. multivittatum*, the number of umbels per individual was regarded as a flower number as their flowers were numerous. Statistical comparisons of each measurement variable between plots were made using the Kruskal-Wallis test followed by the Mann-Whitney *U*-test if the variable had a non-normal distribution, or if the variable had normal distribution, using ANOVA followed by Duncan's multiple range test.

Phenological phases were recorded for 50 individuals chosen at random for each species from each plot, at 5–10 day intervals during the summer of 1989. When there were less than 50 flowering or fruiting individuals within a plot, observations were made on all plants within the plot. The number of flower buds, open flowers, developing fruits and ripe fruits were counted for each individual. Then, cumulative percentages of flowering (CFL) and fruiting (CFR) were regularly obtained in each plot through the season for each species as follows:

$$\mathrm{CFL}(\%) = [(\mathrm{FL} + \mathrm{DF} + \mathrm{RF})/(\mathrm{FB} + \mathrm{FL} + \mathrm{DF} + \mathrm{RF})] \times 100$$

$$\mathrm{CFR}(\%) = [\mathrm{RF}/(\mathrm{FB} + \mathrm{FL} + \mathrm{DF} + \mathrm{RF})] \times 100$$

(FB: total flower-bud number of observed individuals in a plot, FL: total flower number, DF: total developing-fruit number, and RF: total ripe-fruit number).

RESULTS

Environmental factors and frequency of each species

A late snow-melt means a shortened snow-free period and growing season for the plants. The snow-free period varied from 95 days in plot A to 55 days in plot E (Table 1). Although the snow-free period fluctuated from year to year within a plot, the snow regularly disappeared first in plot A and last in plot E every year (Kudo & Ito 1992).

Table 1 Environmental conditions of survey plots in 1989

Plot	Altitude (m)	Snow-free period (days)	Time of snow-disappearance	Soil moisture (%)	N content in soil (%)
A	1910	95	Late June	71 ± 29	0.79 ± 0.38
B	1890	80	Early July	88 ± 33	1.07 ± 0.40
C	1880	70	Mid July	75 ± 19	0.77 ± 0.30
D	1790	60	Late July	89 ± 14	0.89 ± 0.34
E	1790	55	Early Aug.	87 ± 11	0.84 ± 0.39

Soil moisture is weight of soil water/soil dry weight ($\bar{x} \pm$ SD). Sample sizes were five for soil moisture and nine for nitrogen content in each plot. There were no significant differences ($P > 0.05$) in soil moisture and nitrogen content among plots.

Soil moisture and soil nitrogen content were highly variable within plots, and showed no statistical significance between plots ($P > 0.05$). Soil moisture ranged from 71 to 89%, and total nitrogen content was 0.77–1.07% throughout the plots (Table 1).

Vegetation cover was more than 80% throughout the plots and was not statistically different ($P > 0.05$) between plots (Table 2). Frequencies of *V. stelleri* var. *longistyla* and *S. virga-aurea* var. *leiocarpa* in 40 quadrats were highest in plot A and decreased in the later exposed plots; whereas frequencies of *P. cuneifolia* and *P. matsumurae* were highest in plot E, those of *P. multivittatum* were highest in plot C and obviously decreased in the later exposed plots.

Performances for each species

Flower height and leaf height showed similar patterns of change in each species (Table 3). Three patterns were recognized in flower and leaf heights. *Veronica stelleri* var. *longistyla* was highest in plot C and decreased toward both edges of the snow-melting gradient, plots A and E. The heights of *P. multivittatum* and *S. virga-aurea* var. *leiocarpa* varied between plots; they were lowest in plot A, increased in plots B and C, then decreased in plot D, and increased again in plot E. The heights of *P. cuneifolia* and *P. matsumurae*, inhabiting plots B to E, were largest in plot B, then decreased in plots C, D and E.

Species were classified into three groups from the patterns of leaf number (Table 3). Leaves of *P. multivittatum* increased with the lateness of the snow-melt, from plots A to E. Those of *P. cuneifolia*, *V. stelleri* var. *longistyla* and *S. virga-aurea* var. *leiocarpa* decreased in the later exposed plots. *Potentilla matsumurae* had a constant leaf number throughout the plots.

The numbers of umbels in *P. multivittatum* and flowers in *P. cuneifolia* and *P. matsumurae* were relatively constant throughout the plots, while those in *V. stelleri* var. *longistyla* and *S. virga-aurea* var. *leiocarpa* decreased with the shortened snow-free period (Table 3).

Fruit-set was apparently limited by frost in September: aboveground parts of plants with developing fruits died from freezing injury or snow cover by late September. Fruit number did not differ significantly throughout the plots for *P. cuneifolia*, but decreased with the lateness of snow-melt in *V. stelleri* var. *longistyla* due to the decrease in flower number (Table 3). The fruits of *P. multivittatum* were scarcely able to mature in plot E, as were the fruits of *S. virga-aurea* var. *leiocarpa* in plots C, D and E. For *P. matsumurae*, the fruit number was not affected by the shortened snow-free period.

Effect of the time of snow-melt on reproductive phenology

The later the snow-melt, the later flowering and fruiting began in all species (Fig. 2). *Peucedanum multivittatum*, *P. cuneifolia*, *V. stelleri* var. *longistyla* and *P. matsumurae* attained full flowering (100% CFL) in every plot, while *S. virga-aurea* var. *leiocarpa*, which took longer to flower, did not attain full flowering in plots D and E. *Primula cuneifolia* and *P. matsumurae* bloomed simultaneously within a plot, which attained full flowering within 2 weeks of the beginning of flowering. In contrast, the flowering of *V. stelleri* var. *longistyla* and *S. virga-aurea* var. *leiocarpa* gradually advanced within a plot, and it took more than 20 days for full flowering to occur. The flowering pattern of *P. multivittatum* fell in between the above two patterns. The durations needed to attain 50% CFL after the snow disappeared ranged from

Table 2 Vegetation cover (%) and frequency (%) in 40 quadrats for each species in each plot

Plot	Vegetation cover (%)	Frequency (%) *Peucedanum multivittatum*	*Primula cuneifolia*	*Veronica stelleri* v. *longistyla*	*Solidago virga-aurea* v. *leiocarpa*	*Potentilla matsumurae*
A	81 ± 12	45	—	28	43	—
B	80 ± 12	33	13	20	15	18
C	86 ± 10	50	35	25	15	33
D	83 ± 9	23	25	13	13	40
E	83 ± 10	13	38	13	13	43

n = 40 quadrats; $\bar{x} \pm$ SD in vegetation cover.

Table 3 Performance characteristics of the five species in each plot

Plot	Flower height (cm)	Leaf height (cm)	Leaf no.	Flower no. (Umbel no.)	Fruit no.
Peucedanum multivittatum					
A	9.0 ± 2.8^a (40)	6.5 ± 2.6^a (40)	2.3 ± 0.8^a (40)	16.6 ± 6.6^a (40)	22.9 ± 15.0^a (40)
B	16.8 ± 5.1^b (40)	14.0 ± 4.5^b (40)	2.5 ± 0.7^a (40)	16.5 ± 6.8^a (40)	21.3 ± 10.4^a (40)
C	22.2 ± 4.3^c (40)	15.9 ± 4.3^c (40)	2.8 ± 0.5^b (40)	18.0 ± 5.8^a (40)	24.2 ± 9.6^a (40)
D	17.6 ± 5.4^{bd} (40)	10.9 ± 3.8^d (40)	3.3 ± 0.6^c (40)	17.5 ± 5.6^a (40)	27.5 ± 13.9^a (40)
E	20.8 ± 8.2^{cd} (30)	13.1 ± 5.6^{bd} (30)	3.3 ± 0.7^c (30)	19.5 ± 0.7^a (30)	—
Primula cuneifolia					
B	10.7 ± 2.0^a (40)	3.9 ± 0.8^a (40)	10.3 ± 2.2^a (40)	2.0 ± 0.8^a (40)	1.4 ± 0.5^a (10)
C	6.9 ± 2.4^{bc} (40)	3.1 ± 1.0^b (40)	10.9 ± 1.9^a (40)	1.6 ± 0.6^a (40)	1.4 ± 0.6^a (40)
D	6.4 ± 2.3^c (40)	1.9 ± 0.8^c (40)	8.4 ± 2.6^b (40)	1.6 ± 0.8^a (40)	1.3 ± 0.5^a (30)
E	7.6 ± 1.9^b (40)	2.0 ± 0.6^c (40)	8.4 ± 1.4^b (40)	1.8 ± 0.8^a (40)	1.7 ± 0.7^a (28)
Veronica stelleri var. *longistyla*					
A	8.2 ± 1.7^a (40)	7.0 ± 1.7^a (40)	12.4 ± 2.2^a (40)	10.7 ± 3.4^a (40)	3.5 ± 2.1^a (40)
B	11.1 ± 2.0^b (40)	9.7 ± 2.2^b (40)	12.2 ± 2.2^a (40)	9.2 ± 3.8^a (40)	3.8 ± 2.3^a (40)
C	13.6 ± 2.7^c (40)	12.4 ± 2.6^c (40)	12.7 ± 2.4^a (40)	7.3 ± 3.7^b (40)	2.0 ± 1.3^b (40)
D	11.1 ± 1.9^b (40)	9.9 ± 1.9^b (40)	13.2 ± 2.0^a (40)	7.7 ± 3.2^b (40)	2.1 ± 1.0^b (26)
E	9.7 ± 2.3^d (30)	8.3 ± 2.0^d (30)	10.8 ± 2.3^b (30)	4.4 ± 2.0^c (30)	1.5 ± 0.6^c (15)
Solidago virga-aurea var. *leiocarpa*					
A	16.0 ± 4.0^a (40)	14.8 ± 3.8^a (40)	17.8 ± 3.0^a (40)	14.1 ± 5.5^a (40)	9.7 ± 5.7^a (31)
B	25.7 ± 5.6^b (40)	24.4 ± 5.8^b (40)	17.9 ± 4.1^a (40)	18.4 ± 7.5^b (40)	9.6 ± 6.1^a (30)
C	25.4 ± 4.4^b (40)	23.1 ± 4.5^{bc} (40)	15.2 ± 2.4^b (40)	14.8 ± 4.0^a (40)	—
D	18.3 ± 5.0^c (40)	16.6 ± 4.9^a (40)	16.3 ± 4.0^b (40	9.7 ± 3.0^c (40)	—
E	23.0 ± 5.9^d (23)	21.4 ± 5.9^c (23)	13.5 ± 3.3^c (23)	10.7 ± 2.9^c (23)	—
Potentilla matsumurae					
B	14.0 ± 3.1^a (30)	9.9 ± 3.4^a (30)	4.3 ± 0.8^a (30)	2.2 ± 0.8^a (30)	1.2 ± 0.4^a (20)
C	10.2 ± 1.9^b (40)	8.3 ± 1.4^b (40)	4.6 ± 1.2^a (40)	2.0 ± 0.9^a (40)	1.6 ± 0.7^{ab} (40)
D	9.3 ± 2.5^b (40)	5.8 ± 1.7^c (40)	4.4 ± 1.1^a (40)	2.0 ± 0.8^a (40)	2.0 ± 0.6^b (40)
E	9.1 ± 2.3^b (40)	6.1 ± 1.7^c (40)	5.0 ± 1.3^a (40)	2.2 ± 1.1^a (40)	1.6 ± 0.6^{ab} (40)

Values are $\bar{x} \pm$ SD. Sample numbers are given in parentheses. Values in each column with superscripts of different letters are significantly different from each other ($P < 0.05$).

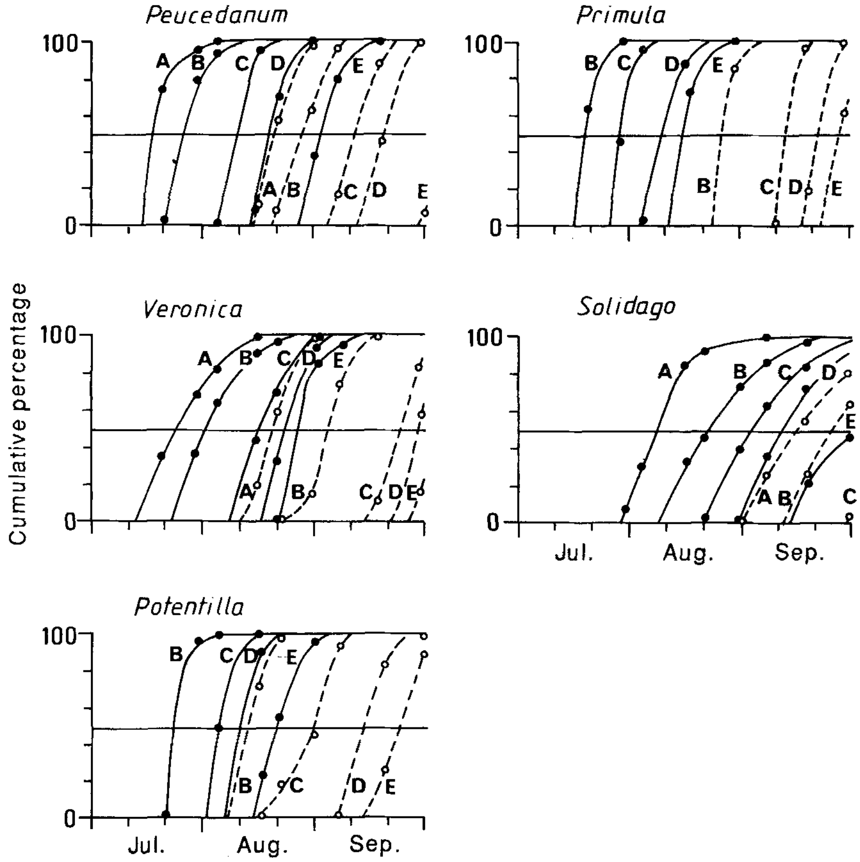

Fig. 2. Cumulative percentages of flowering (——) and fruiting (– – –) for each species in each plot (A to E).

8 days in *P. cuneifolia* to 40 days in *S. virga-aurea* var. *leiocarpa* (Table 4). Within a plot, flowering advanced as follows: *P. cuneifolia* → *P. matsumurae* → *P. multivittatum* → *V. stelleri* var. *longistyla* → *S. virga-aurea* var. *leiocarpa*.

No species succeeded in full fruit maturation (100% CFR) in the latest exposed plot E, due to the decreased snow-free period. Thus, the seed-set for every species was more or less influenced by the length of the snow-free period. *Potentilla matsumurae* and *P. cuneifolia* attained more than 50% CFR even in plot E, whereas *S. virga-aurea* var. *leiocarpa* did not attain full fruit maturation in any plot and fruit-set hardly occurred in plots C, D

Table 4 Duration (days) from snow disappearance to 50% flowering, and from 50% flowering to 50% fruiting for each species

	Peucedanum multivittatum	*Primula cuneifolia*	*Veronica stelleri* v. *longistyla*	*Solidago virga-aurea* v. *leiocarpa*	*Potentilla matsumurae*
50% Flowering	19	8	23	40	12
	(17–23)	(7–9)	(21–25)	(38–42)	(11–13)
50% Fruiting	32	43	32	36	28
	(31–32)	(37–45)	(25–36)	(35–37)	(21–33)

Ranges are shown in parentheses. Data obtained from Fig. 2.

and E. The durations required for 50% CFR from 50% CFL ranged from 28 days in *P. matsumurae* to 43 days in *P. cuneifolia* (Table 4).

DISCUSSION

Responses of plant performance to the time of snow-melt varied among species in this study. Because soil moisture and nitrogen content did not differ between plots (Table 1), edaphic effects on plant performance were considered to be negligible. Plant heights of the three species inhabiting all plots were lower in plot A, but this may be independent of the onset of snow-melt. Plot A was on an upper slope near the ridge, and seemed to be more exposed to the wind than the other plots. Wind affects the net assimilation and shoot growth rates of plants by reducing the leaf temperature (Warren Wilson 1959). Since wind speed is drastically reduced near ground level, low plant height is an advantageous form in windy places (Warren Wilson 1959; Bliss 1966).

In the late exposed plots, small stature (observed in *P. cuneifolia*, *P. matsumurae* and *V. stelleri* var. *longistyla*) and the decreases in leaf number (*P. cuneifolia, V. stelleri* var. *longistyla* and *S. virga-aurea* var. *leiocarpa*) and flower number (*V. stelleri* var. *longistyla* and *S. virga-aurea* var. *leiocarpa*) may be related to the limited growing season. A short growing season limits the plant's ability to store resources for shoot elongation at the beginning of the next season (Billings & Bliss 1959; Mooney & Billings 1960; Wijk 1986b). In particular, *V. stelleri* var. *longistyla* and *S. virga-aurea* var. *leiocarpa* were less vigorous in the late exposed plots, indicating that these species are sensitive to the short period of snow-free conditions.

Peucedanum multivittatum, *P. cuneifolia* and *P. matsumurae*, whose flower number was constant throughout the plots, maintained the same level of reproductive activity under the short snow-free period. Actual seed-set is determined not only by potential reproductive output (i.e. flower number) but also by phenological traits, which are the time of flowering and duration for fruit maturation. Because the growing season is limited by lingering snow cover and because flowering time is controlled by the onset of snow-melt, fruit maturation is restricted by the limited growing season in late exposed places (Kudo 1991). Thus quick flowering species such as *P. matsumurae* and *P. cuneifolia* are at a greater advantage in such environments than slow flowering species like *S. virga-aurea* var. *leiocarpa* and *V. stelleri* var. *longistyla*. Although *P. cuneifolia* takes a long time to achieve fruit maturation, its trait of flowering quickly enables a high fruit-set in places that are free of snow for only short periods. Thus the high frequencies of *P. cuneifolia* and *P. matsumurae*, and the low frequencies of *V. stelleri* var. *longistyla* and *S. virga-aurea* var. *leiocarpa* in the late exposed plots (Table 2) reflect the reproductive success of each species under short snow-free periods.

Wijk (1986a) mentioned that *Salix herbacea* increased plant cover, biomass and shoot density in late exposed places in comparison with early exposed ones because interspecific competition decreased in places with short snow-free periods. In this snow-bed, shrub species such as *Sieversia pentapetala*, *Phyllodoce aleutica* and *Rhododendron aureum* dominate in the early to mid exposed plots and they decrease their cover toward the late ones; in exchange some forb and graminoid species increase their cover in the later exposed plots (Kudo & Ito 1992). The vigor of *P. multivittatum* in the later exposed plots may be due to the decrease in intensity of interspecific competition with the shortened snow-free period. It indicates the physiological adaptability of this species to the short growing conditions. However, fruit-set was restricted in the latest exposed plot due to the limited fruit developing period, and this seems to explain the low frequency of this species in the late exposed plots.

In summary, the species having similar distribution ranges along the snow-melting gradient respond differently to the short growing period. Under a given snow condition, the frequency of appearance of a species is determined by the interaction between physiological traits, phenological constraints and interspecific relationships.

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REFERENCES

BILLINGS W. D. & BLISS L. C. (1959) An alpine snowbank environment and its effects on vegetation, plant development, and productivity. *Ecology* **40**: 388–97.

BLISS L. C. (1966) Plant productivity in alpine micro-environments on Mt Washington, New Hampshire. *Ecol. Monogr.* **36**: 125–55.

CALLAGHAN T. V. (1974) Intraspecific variation in *Phleum alpinum* L. with specific reference to polar populations. *Arc. Alp. Res.* **6**: 361–401.

EDDLEMAN L. E. & WARD R. T. (1984) Phytoedaphic relationships in alpine tundra of north-central Colorado, USA. *Arc. Alp. Res.* **16**: 343–59.

HELM D. (1982) Multivariate analysis of alpine snow-patch vegetation cover near Milner Pass, Rocky Mountain National Park Colorado, USA. *Arc. Alp. Res.* **14**: 87–95.

HOLWAY J. G. & WARD R. T. (1963) Snow and meltwater effects in an area of Colorado Alpine. *Am. Mid. Nat.* **69**: 189–97.

HOLWAY J. G. & WARD R. T. (1965) Phenology of alpine plants in northern Colorado. *Ecology* **46**: 73–83.

ISARD S. A. (1986) Factors influencing soil moisture and plant community distribution on Niwot Ridge, Front Range, Colorado, USA. *Arc. Alp. Res.* **18**: 83–96.

JOHNSON P. L. & BILLINGS W. D. (1962) The alpine vegetation of cryopedogenic processes and patterns. *Ecol. Monogr* **32**: 105–35.

KUDO G. (1991) Effects of snow-free period on the phenology of alpine plants inhabiting snow patches. *Arc. Alp. Res.* **23**: 436–43.

KUDO G. & ITO K. (1992) Plant distribution in relation to the length of the growing season in a snow-bed in the Taisetsu Mountains, northern Japan. *Vegetatio* **98**: 165–74.

MOONEY H. A. & BILLINGS W. D. (1960) The annual carbohydrate cycle of alpine plants as related to growth. *Am. J. Bot.* **47**: 594–8.

OSTLER W. K., HARPER K. T., MCKNIGHT K. T. & ANDERSON D. C. (1982) The effects of increasing snowpack on a subalpine meadow in the Uinta Mountains, Utah, USA. *Arc. Alp. Res.* **14**: 203–14.

RAM J., SINGH S. P. & SINGH J. S. (1988) Community level phenology of grassland above treeline in central Himalaya, India. *Arc. Alp. Res.* **20**: 325–32.

SCOTT D. & BILLINGS W. D. (1964) Effects of environmental factors on standing crop and productivity of alpine tundra. *Ecol. Monogr.* **34**: 243–70.

WARREN WILSON J. (1959) Notes on wind and its effects in arctic-alpine vegetation. *J. Ecol.* **47**: 415–27.

WEIR D. A. & WILSON J. B. (1987) Micro-pattern in an area of New Zealand alpine vegetation. *Vegetatio* **73**: 81–8.

WIJK S. (1986a) Performance of *Salix herbacea* in an alpine snow-bed gradient. *J. Ecol.* **74**: 675–84.

WIJK S. (1986b) Influence of climate and age on annual shoot increment in *Salix herbacea*. *J. Ecol.* **74**: 685–92.