

FLOWERING PHENOLOGY OF ALPINE PLANT COMMUNITIES ALONG A GRADIENT OF SNOWMELT TIMING

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Abstract: Flowering phenology of alpine plant communities was observed at seven sites (two fellfields, two alpine meadows, and three snowbeds) in 1996 and 1997 in the Taisetsu Mts., northern Japan. These sites were selected along a gradient of snowmelt time. In total, flowering phenologies of 39 species were compared across the seven sites. The length of flowering season within communities decreased with lateness of snowmelt from 88 days at the fellfield site to 32 days at the snowbed site. The onset of flowering varied among species at the early snowmelt sites, and it became concentrated within narrow periods among species at the later snowmelt sites. Interspecific overlap of anthesis was large in the late flowering season at the earliest snowmelt site, whereas it was large in the early flowering season at the snowbed sites. Such changes in flowering patterns at community level along the snowmelt gradient were considered to be induced by the difference in temperature sequence after snowmelt among the sites, *i.e.*, the increasing pattern of the effective cumulative temperature. Thus, the time of snowmelt affects not only the flowering phenology of individual species but also the flowering pattern of a whole community. Some species growing in the fellfields changed the temperature-demand for onset of flowering which was considered as an adjustment to decrease the interspecific overlap of anthesis within the community.

key words: alpine plant, anthesis, cumulative temperature, flowering phenology, snowmelt time

Introduction

Timing of snowmelt is one of the most important factors affecting the flowering phenology of alpine plants (HOLWAY and WARD, 1963, 1965; BLISS, 1971; RAM *et al.*, 1988; KUDO, 1991). Temporal differences in snow disappearance determine the time of flowering initiation and available growth period which affect reproductive success through the pollination process and the season length for fruit development (GALEN and STANTON, 1991; KUDO, 1991, 1993; STENSTRÖM and MOLAU, 1992; TOTLAND, 1994). Because air temperature changes as the season progresses, plants exposed by melting of snow cover at different seasons experience different temperature regimes through the life-cycle. For example, plants exposed in early summer begin to grow under cool temperature conditions, then the temperature increases as the season progresses. Plants exposed in mid summer, on the other hand, start to grow under mild temperature conditions, but the temperature gradually

decreases as the season progresses and they may suffer from the effect of cool temperature on seed maturation (KUDO, 1991; TOTLAND, 1997).

Flowering phenology of plants is a temperature-dependent phenomenon in most cases (RATHCKE and LACEY, 1985) and the cumulative temperature above a certain threshold value from a certain starting date is often used as an indicator of flowering traits (RATHCKE and LACEY, 1985; DIEKMANN, 1996). Flowering time of alpine plants in northern Japan can be expressed by the effective cumulative temperature, *i.e.*, the accumulation of daily mean air temperatures (degree-days) above 5°C (KUDO, 1992). In previous studies, relationships between flowering phenology of alpine plants and the time of snowmelt were mainly researched from the viewpoint of species level; phenological analysis at community level such as comparisons of flowering dynamics among communities, has scarcely been done (*e.g.* TOTLAND, 1993). In this article, we study the effects of snowmelt time on the pattern of flowering phenology on the whole community level within an area.

As a simplification, at first, we suppose that a community is composed of species having various temperature-demands for flowering (the effective cumulative temperature from snow-disappearance to onset of flowering) and the specific temperature-demands are normally distributed within the community. When a community is exposed by melting of snow in early summer, the effective cumulative temperature will increase gradually at first, then accelerate with progress of the season because air temperature increases rapidly from mid-June to mid-July. In such a case, actual flowering is expected to be distorted toward later in the season (*i.e.*, negative skewness) from the potential pattern (Fig. 1A). When a community is exposed by melting of snow in late summer when air temperature is at its maximum, the effective cumulative temperature will increase linearly with time at first, but the increase decelerates later due to the decrease in temperature. In such a case, actual flowering is expected to be distorted toward earlier in the season (*i.e.*, positive skewness) from the potential pattern (Fig. 1C). An intermediate pattern can be expected when a community is exposed by melting of snow in mid-season (Fig. 1B). This is because flowering phenology is largely determined by local climatic conditions. In an alpine environment, fellfield plant communities and snowbed plant communities correspond to the patterns A and C in Fig. 1, respectively.

Interspecific competition for acquisition of pollinator insects is considered as another important factor determining the distribution pattern of flowering times (MOSQUIN, 1971; PLEASANTS, 1980). Interspecific overlaps of anthesis may enhance competition for pollinator acquisition among entomophilous species (*i.e.*, RATHCKE 1983). It is expected that each species may regulate flowering time within a season to disperse the overlap of anthesis among species within a community (POOLE and RATHCKE, 1979). If this is true, typical fellfield plants may have different temperature-demand for flowering from typical snowbed plants. Low temperature-demand for onset of flowering will contribute to disperse the actual overlap of anthesis in fellfield communities because it enables the plants to bloom in early season. In snowbeds where the growing season is very short, high temperature-demand for the onset of flowering will contribute to disperse the actual interspecific overlap, but flowering in late season may restrict the season length for fruit development, which results in low seed production (KUDO, 1991). Thus, the late flowering traits for plants in the snowbed communities have the benefit of the small interspecific overlap of anthesis and the drawback of short available time for fruit development. For species with

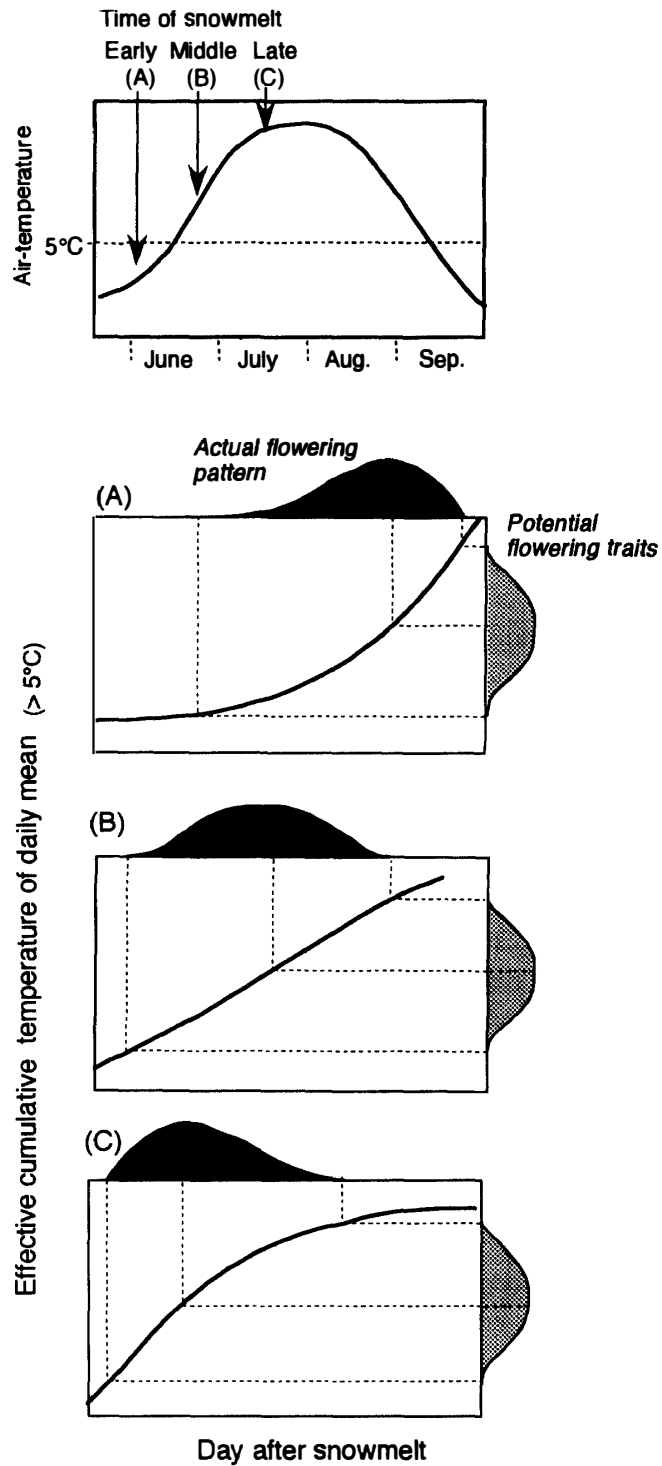


Fig. 1. Expected flowering patterns of plant communities considering the temperature effect after snowmelt. The top figure indicates seasonal change in air temperature. We consider three sites; (A) an early snowmelt site, (B) a mid-season snowmelt site, and (C) a late snowmelt site. The bottom three figures (A to C) indicate relationships between seasonal changes in effective cumulative temperature after snowmelt (see text) and flowering pattern of plant communities. In this model, we assume that each community is composed of species having normal distribution of a temperature-dependent flowering trait (in detail, see text).

wide distribution range along a snowmelt gradient, therefore, the best flowering season may differ between early-snowmelt and late-snowmelt places. If so, the temperature-demand for onset of flowering may differ between the communities even within the same species.

It is possible to compare flowering phenology among communities with different snowmelt conditions to make clear the community-level responses of flowering traits. In this study, we analyzed flowering phenologies of seven alpine-plant communities along a gradient of snowmelt time during two seasons. The purposes of this study are to answer the following questions: 1) Does flowering pattern at community level change predictably along a snowmelt gradient (Fig. 1)? 2) Does distribution of the temperature-demand for onset of flowering differ among communities with different snowmelt conditions? 3) Is there any difference in the temperature-demand for flowering within the same species among the communities?

Materials and Methods

This study was conducted in the central part of the Taisetsu Mountains, Hokkaido, northern Japan (43°33'N, 142°53'E). The annual mean temperature of this area is -1.6°C , ranging from 12.0°C in August to -14.6°C in January (average of 1990-1994). Summer precipitation during July to September is usually more than 500 mm, and annual *ca.* 1600 mm. Because of large snowfall and topographic effects, thick snow covers the south-eastern slopes in this area. The time of snow disappearance ranges from mid-May to late September, and it causes a clear gradient of snowmelt time within a narrow area. Snow begins to cover the ground again in early October (for details see KUDO, 1996).

We selected seven measurement sites along a gradient of snowmelt time; two fellfields, two alpine meadows, and three snowbeds (Table 1). Two fellfield sites (F-1 and F-2) were exposed by melting of snow in mid- to late May, and typical fellfield vegetation was common. Dwarf shrubs and lichens dominated here, and major vascular species were *Diapensia lapponica* var. *obovata*, *Arctous alpinus*, *Vaccinium uliginosum*, *Arctericia nana*, *Bryanthus gmelinii*, and *Loiseleuria procumbens*. Two alpine meadow sites (M-1 and M-2) were exposed from snow-cover in mid to late June, where dwarf shrubs and herbs, such as *Rhododendron aureum*, *Phyllodoce caerulea*, *Sieversia pentapetala*, *Anemone*

Table 1. Description of research sites which were selected along a snowmelt gradient.

Site	Vegetation type	Altitude	Time of snowmelt	
			1996	1997
F-1	Fellfield	1700 m	< May 20	< May 20
F-2	Fellfield	1910 m	May 25	May 28
M-1	Meadow	1910 m	June 13	June 13
M-2	Meadow	1890 m	June 28	June 18
S-1	Snowbed	1880 m	July 27	July 1
S-2	Snowbed	1790 m	August 7	July 23
S-3	Snowbed	1790 m	August 12	August 2

Table 2. List of species observed in this study at each site.

Sp. no.	Species	Site						
		F-1	F-2	M-1	M-2	S-1	S-2	S-3
1	<i>Rhododendron camtschaticum</i>	0						
2	<i>Dicentra peregrina</i>	0						
3	<i>Artemisia arctica</i> var. <i>villosa</i>	0						
4	<i>Patrinia sibirica</i>	0						
5	<i>Pennelianthus frutescens</i>	0						
6	<i>Campanula chamissonis</i>	0						
7	<i>Spiraea betulifolia</i>	0						
8	<i>Bupleurum ranunculoides</i> var. <i>triradiatum</i>	0						
9	<i>Saussurea yanagisawae</i>	0	0					
10	<i>Ledum palustre</i> ssp. <i>decumbens</i>	0	0					
11	<i>Diapensia lapponica</i> var. <i>obovata</i>	0	0	0				
12	<i>Arctous alpinus</i>	0	0	0				
13	<i>Vaccinium uliginosum</i>	0	0	0				
14	<i>Vaccinium vitis-idaea</i>	0	0	0				
15	<i>Arctica nana</i>	0	0	0				
16	<i>Bryanthus gmelinii</i>	0	0	0				
17	<i>Loiseleuria procumbens</i>	0	0	0				
18	<i>Tofieldia okuboii</i>			0				
19	<i>Rhododendron aureum</i>	0	0	0	0	0	0	
20	<i>Tilingia ajanensis</i>	0	0			0		
21	<i>Sieversia pentapetala</i>		0	0	0	0	0	0
22	<i>Potentilla matsumurae</i>	0	0		0	0	0	0
23	<i>Weigela middendorffiana</i>				0	0		
24	<i>Anemone soyensis</i>			0	0			
25	<i>Arnica unalaschkensis</i>				0	0		
26	<i>Vaccinium ovalifolium</i>				0	0		
27	<i>Solidago virga-aurea</i> ssp. <i>leiocarpa</i>			0	0	0	0	
28	<i>Heloniopsis orientalis</i>				0			
29	<i>Viola alliariaefolia</i>				0			
30	<i>Anemone narcissiflora</i> var. <i>nipponica</i>			0	0			
31	<i>Pedicularis chamissonis</i> var. <i>japonica</i>			0		0		
32	<i>Phyllodoce aleutica</i>			0	0	0	0	0
33	<i>Phyllodoce caerulea</i>			0	0	0	0	0
34	<i>Veronica stelleri</i> var. <i>longistyla</i>			0	0	0	0	0
35	<i>Peucedanum multivittatum</i>			0	0	0	0	0
36	<i>Gentiana nipponica</i>			0	0	0	0	0
37	<i>Primula cuneifolia</i>				0	0	0	0
38	<i>Harrimanella stelleriana</i>					0	0	0
39	<i>Sanguisorba canadensis</i> ssp. <i>latifolia</i>						0	

narcissiflora var. *nipponica*, *Arnica unalaschkensis*, *Solidago virga-aurea* ssp. *leiocarpa*, were common. Three snowbed sites (S-1, S-2 and S-3) were exposed by melting of snow cover after early July, where the timing of snow disappearance was highly variable from year to year but melting order was stable among sites. Herbs and evergreen shrubs dominated in the snowbeds. Major species were *Phyllodoce aleutica*, *Harrimanella stelleriana*, *Primula cuneifolia*, and *Peucedanum multivittatum*.

In 1996 and 1997, we observed the time of first flowering and duration of the anthesis in each entomophilous species at each site from the time of snow disappearance to the end of the growing season (late September). Observations were conducted once or twice a week within about a 30×30 m area at each site. In total, flowering phenologies of 39 species were recorded across the sites in both years (Table 2). The numbers of observed species were 20 at F-1, 13 at F-2, 19 at M-1, 17 at M-2, 16 at S-1, 12 at S-2, and 9 at S-3. From the phenological data of each species, we constructed phenological diagrams in each species as shown in Fig. 2. Then, seasonal changes in overlaps of anthesis among species were obtained from the phenological diagram at each site. We calculated the overlaps of anthesis at 5-day intervals through the flowering season.

In order to measure the temperature-demand for onset of flowering (the effective cumulative temperature above 5°C) in each species, ambient air temperature at a height of 40 cm above the soil surface was measured at F-1 and S-1 in 1997. Measurements were taken at one hour intervals with automatic recording thermometers (KADEC-U II, Kona System Co. Ltd., Sapporo Japan) and thermistor sensors from early May to the end of September. The effective cumulative temperature (K) of daily mean for first flowering from snow disappearance was calculated for each species at each site in 1997 as follows: K (degree-days) = $\sum(t_5 - 5)$, where the threshold temperature for plant growth was set at 5°C, and t_5 means daily mean air temperature above 5°C (KUDO, 1992). We categorized species into three classes with reference to the K-values: early flowering species having less than 100 degree-days, intermediate flowering species having 100–200 degree-days, and late flowering species having more than 200 degree-days for the first flowering after snow disappearance (see Fig. 2). When the K-values differed among sites within the same species, the K-value at the most dominant site for the species was used for the classification.

Results

Summer in 1996 was relatively cool in comparison with that in 1997. Monthly mean temperatures at F-1 were 10.1°C in June, 13.4°C in July and 12.6°C in August in 1996, and 10.7°C, 15.7°C and 13.1°C in 1997, respectively. Snow disappeared at the same time within the early snowmelt sites in 1996 and 1997 (Table 1). At the late snowmelt sites, the times of snow disappearance were late in 1996, especially in the snowbeds (10–26 days delay).

The length of the flowering season within a community decreased with lateness of snowmelt (Fig. 3), from 75 days at F-2 to 32 days at S-3 in 1996, from 88 days at F-1 to 52 days at S-3 in 1997. Even at the same sites, flowering season length extended 13 days at M-2, 25 days at S-1, 12 days at S-2, and 20 days at S-3 in 1997 due to early snowmelt. Flowering finished by the end of August at the fellfield sites, while it lasted until the end of September at the snowbed sites (S-2 and S-3).

The overlaps of anthesis among species were large in the late flowering season at F-1,

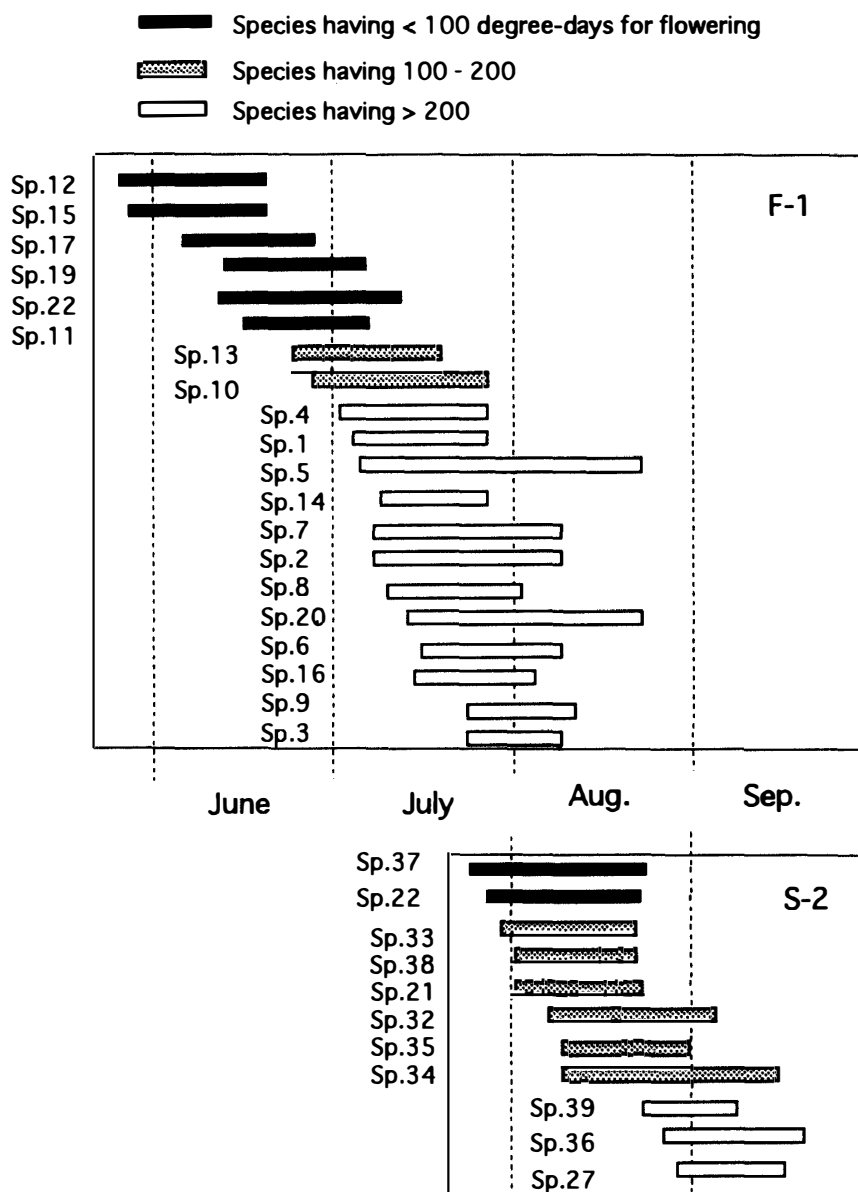


Fig. 2. Example of flowering phenology data at sites F-1 and S-2 in 1997. For each site, we constructed the diagrams in 1996 and 1997, and calculated the interspecific overlap of anthesis. Species are categorized into three classes with reference to the temperature-demand for onset of flowering: early flowering species having less than 100 degree-days for flowering since snowmelt, intermediate flowering species having 100-200 degree-days, and late flowering species having more than 200 degree-days. See Table 2 for species number.

but the time of the overlapping peak shifted toward early season at the alpine meadow and snowbed sites (Fig. 3). Such patterns agree with the prediction in Fig. 1. Mean values of the overlaps through a season within the communities were significantly large at the late snowmelt sites in 1996 with a late snowmelt and a cool summer (Table 3). In 1997, with early snowmelt and a warm summer, there was no significant difference in the overlaps of anthesis among sites. In comparisons between the years within the same sites, interspecific

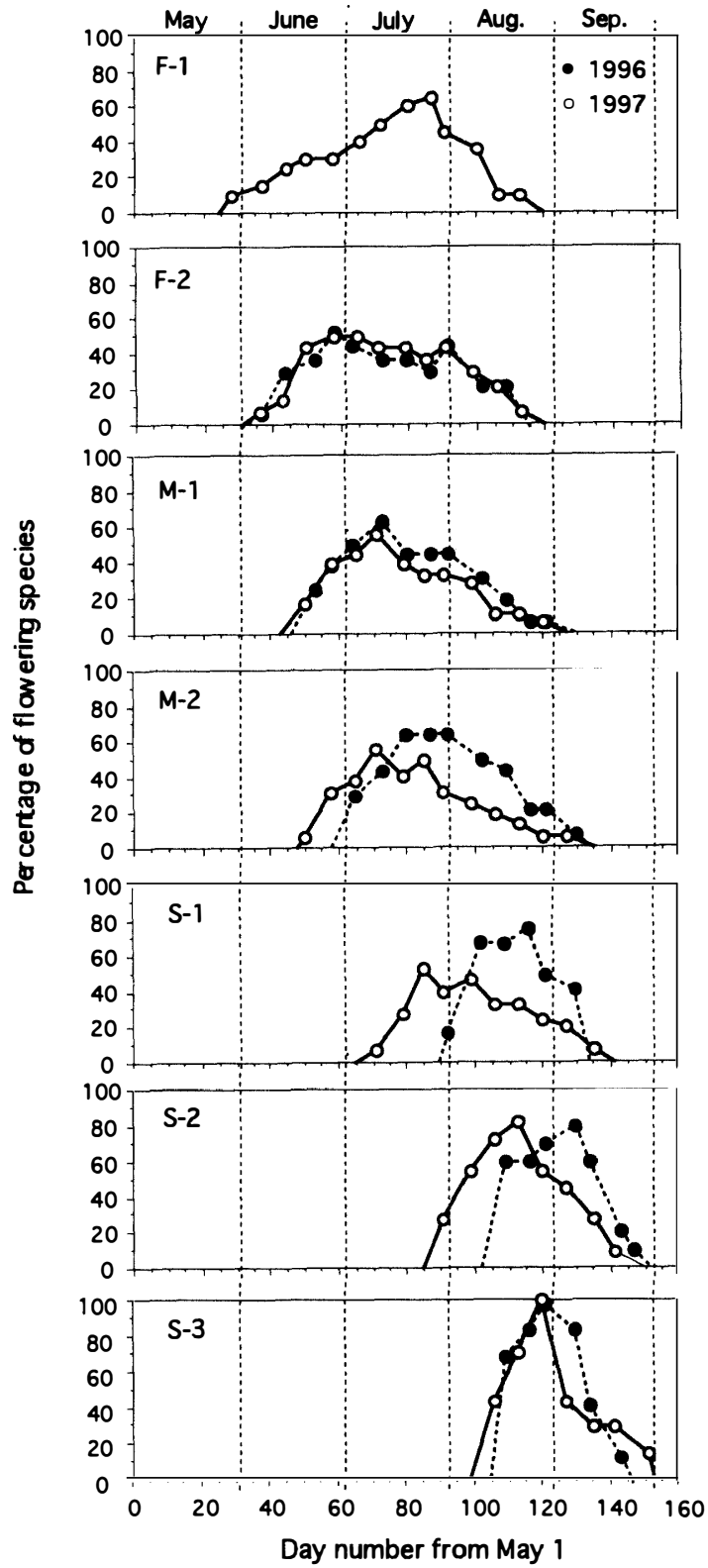


Fig. 3. Seasonal changes in interspecific overlap of anthesis (%) within communities in 1996 and 1997. One-hundred percent means full overlap of all species that bloomed in that year.

Table 3. Mean (\pm SD) values of the overlap of anthesis (%) during the flowering season at each site in 1996 and 1997. Sample sizes are shown within parentheses.

Year	F-1	F-2	M-1	M-2	S-1	S-2	S-3	P-value*
1996	No data	34 \pm 13% (11)	34 \pm 18% (11)	41 \pm 20% (10)	53 \pm 21% (6)	51 \pm 26% (7)	67 \pm 32% (6)	<0.01
1997	33 \pm 19% (13)	32 \pm 16% (12)	29 \pm 16% (11)	27 \pm 17% (12)	29 \pm 15% (10)	47 \pm 29% (8)	47 \pm 29% (7)	>0.05
P-value**		>0.05	>0.05	<0.05	<0.05	>0.05	>0.05	

*One-Way ANOVA after arcsin-transformation; ** Welch's *t*-test.

overlaps of anthesis were significantly high in 1996 at M-2 and S-1 with moderate snowmelt times. In the snowbed communities having short flowering season length, the overlaps of anthesis were large in the peak flowering season, especially at S-3 anthesis of all species which overlapped at the peak season in the both years (Fig. 3).

Patterns of the effective cumulative temperatures of species for onset of flowering differed among communities (Fig. 4). A bimodal pattern, having peaks at very low and high K-values, was observed in the fellfield communities (F-1 and F-2). Ranges of the K-values decreased with lateness of snowmelt, and many of the species had 50–200 degree-days in the snowbeds.

For 18 species which were distributed at three or more sites (see Table 2), the effective cumulative temperatures were compared among sites. Seven of the species were categorized as early flowering, six were intermediate, and five were late flowering plants (Fig. 5). In the early flowering species, the K-values in *Diapensia lapponica* var. *obovata*, *Loiseleuria procumbens*, *Rhododendron aureum*, and *Potentilla matsumurae* were much lower at the fellfield sites (F-1 and F-2) than at other sites. This indicates that these species change the temperature-demands for flowering among habitats. There were no clear tendencies in the K-values among sites in the intermediate flowering species. In the late flowering species, *Vaccinium vitis-idaea* and *Peucedanum multivittatum* showed gradually decreased K-values from the early to the late snowmelt sites. *Gentiana nipponica* growing at S-3 showed a much lower K-value than at other sites. Thus, these plants decreased the temperature-demand for flowering at the habitats with a short growing season. This tendency in the late flowering species was opposite from that in the early flowering species.

Discussion

To a considerable extent, predicted flowering patterns were detected among communities along the snowmelt gradient. But the pattern changed even within the same sites between the years. Time of snowmelt fluctuates highly from year to year in this area (KUDO, 1996), and the flowering seasons of individual species are highly influenced by the snow condition of the year even at the same place (KUDO, 1991, 1992). The results of this study indicate that time of snowmelt and temperature conditions affect not only the species-level flowering phenology but also the community-level flowering pattern. Although a normal distribution for flowering traits was assumed within a community in the model (Fig. 1), each community was composed of species having various temperature-

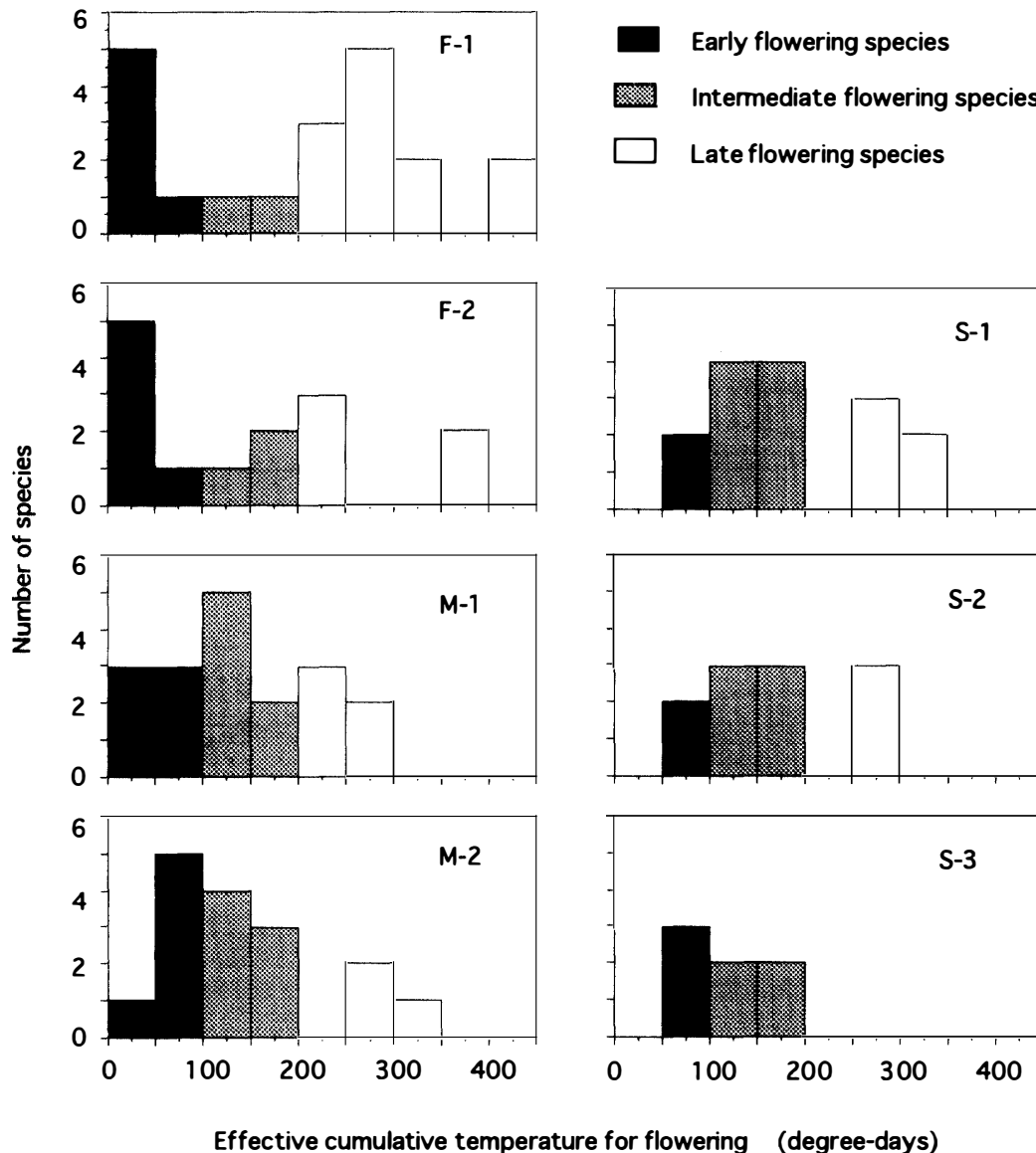


Fig. 4 Frequency distribution of the temperature-dependent flowering traits at each site. See Fig. 2 for the classification of species.

demands for flowering. In the fellfields, the range of the temperature-demand was wide, which contributed to lengthening of the flowering season of the communities. Several species had very low temperature-demand for flowering in the fellfield communities, which bloomed in very early season, resulting in decreasing overlap of anthesis among species within a community. The range of the temperature-demand was narrow in the snowbeds, and the overlap of anthesis among species was high at the peak flowering season.

Season length available for plant growth directly influences the time of flowering (RATHCKE and LACEY, 1985; PRIMACK, 1987). Flowering of alpine and arctic plants generally tends to converge in early season (BLISS, 1971; HOLWAY and WARD, 1965; INOUE and PYKE, 1988). Early flowering is an important trait to complete the reproductive cycle (flowering to seed maturation) during a short growing period for alpine plants (BLISS, 1971;

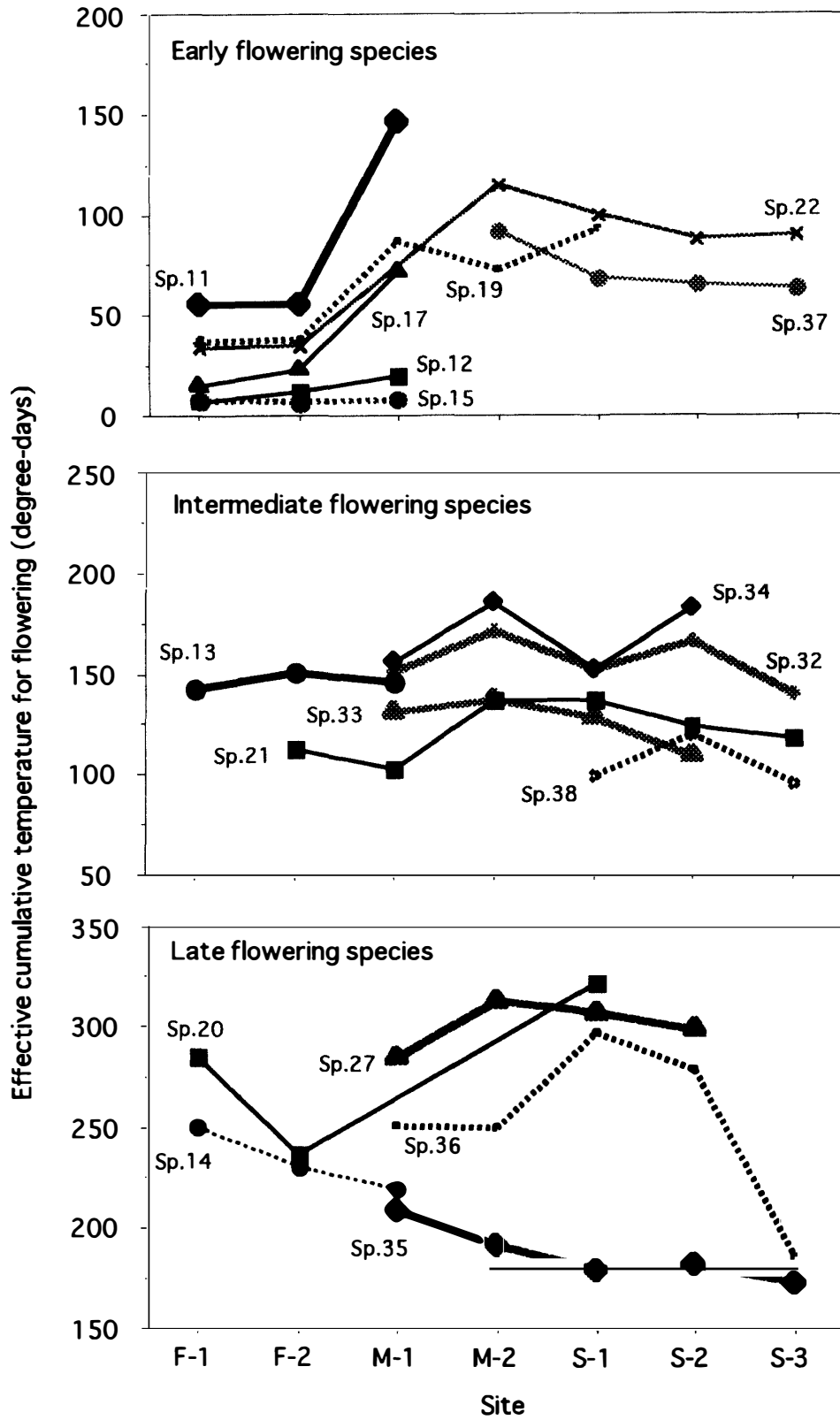


Fig. 5. Intraspecific variations of the temperature-dependent flowering traits among sites. Only species occurring at three or more sites are shown. See Table 2 for species number.

KUDO, 1991). Early flowering is more crucial for snowbed plants than for fellfield plants, and even snowbed plants having early flowering traits can mature seeds only in an extremely warm and long summer, which occurs unpredictably, in very late-snowmelt locations (KUDO, 1991).

Variations of the flowering traits were observed also within the same species among communities. The temperature-demand for flowering in *Diapensia lapponica* var. *obovata*, *Loiseleuria procumbens*, *Rhododendron aureum*, and *Potentilla matsumurae* showed very low values in the fellfield communities compared to those in other communities. Although such intraspecific variations of flowering traits contribute to decrease the overlap of anthesis among species within a community, effects of the flowering shift toward early season on reproductive success of these species are unclear. Activity of pollinator insects is low in early season due to cool temperature, and bumblebee queens usually appear around mid June in this area. Thus, the seed-sets of early flowering plants are often restricted by pollen limitation (KUDO, 1993). MOLAU (1993) compared relationships between flowering phenology and reproductive traits of 137 tundra species, and showed that insect pollinated outbreeders were predominantly early-flowering and generally had low seed/ovule ratios due to pollen limitations in early season. In some studies of intraspecific comparisons, on the other hand, higher seed-sets in early flowering plants were observed in some species (GALEN and STANTON, 1991; STENSTRÖM and MOLAU, 1992; TOTLAND, 1994).

All four of the early flowering species which changed flowering traits in this study were visited by flies in the fellfields (G. KUDO, personal observation). Dipteran insects are most common flower visitors in arctic and alpine regions; they are considered to be inefficient pollen vectors compared to bumblebees because of low mobility and the less persistent flower visiting behavior (HOCKING, 1968; KEVAN, 1972; YUMOTO, 1986; INOUE and PYKE, 1988; MCCALL and PRIMACK, 1992; TOTLAND, 1993). Comparison of reproductive success in each species is necessary to evaluate the ecological significance of the intraspecific variation of flowering traits.

Three of the late flowering species decreased the temperature-demand for flowering at late snowmelt sites. This may be an adaptation to complete seed production under restricted growing season length. KUDO (1992) compared the temperature demand for reproductive phenology of several snowbed plants in the same area, but clear intraspecific variations were not detected along a snowmelt gradient in a snowbed. This might be because the comparison was conducted along a narrower environmental gradient than that in this study.

This study proved that flowering patterns of alpine plant communities were largely controlled by climatic factors, but each community was composed of species having different flowering traits, and some species had different flowering traits among communities. It is believed that phenological variations of plants are highly controlled by phylogenetic constraints (KOCHMER and HANDEL, 1986). When sharing of flower visitors among species might benefit the pollination success of each plant species because the presence of one species results in an increase in visitation rate to the other species (WASER and REAL, 1979; MCGUIRE and ARMBRUSTER, 1991), large overlaps of anthesis among species may act as a positive effect. For these reasons, there are debates as to whether phenological regulation occurs by selective forces in nature (OLLERTON and LACK, 1992;

FOX and KELLY, 1993). More information about reproductive traits in each species and interactions among species is needed to evaluate the ecological significance of the phenological variations observed along the snowmelt gradient.

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