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Scientific note

Pattern of seedling emergence of alpine plants: Comparisons between fellfield and snowbed habitats

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Abstract: We observed the germination pattern of alpine plants at a fellfield (three species) and a snowbed (four species) in relation to environmental differences between the habitats. Emergence patterns of seedlings varied among species within each habitat, especially at the fellfield, which has a relatively long growing season. At the fellfield, the peak of seedling emergence occurred early in the growing season for *Potentilla matsumurae*, mid-season for *Patrinia sivirica*, and late season for *Bupleurum ranunculoides*. At the snowbed, germination of *Peucedanum multivittatum* started immediately after snowmelt, germination of *P. matsumurae* and *Primula cuneifolia* were concentrated in early July, and germination of *Arnica unalaschcensis* was common in mid-July in 1998. Species which produced large seeds tended to have a short period for seedling growth, while species which produced small seeds tended to continue seedling growth as long as they could. Temperature requirements for germination of *P. matsumurae* differed between the habitats. Seeds in the snowbed population needed a warmer temperature regime for germination than seeds in the fellfield population. These results indicate that germination traits may differ between habitats even within the same species.

1. Introduction

Because the young seedling stage is most sensitive to various environmental stresses for establishment of most plants, timing of seed germination crucially affects subsequent survivorship of seedlings under seasonal climates where growing conditions fluctuate throughout the year (Baskin and Baskin, 1979; Kachi and Hirose, 1990; Marks and Prince, 1981; Maruta, 1976). Various factors are related to the timing of seed germination: *e.g.* life form (Baskin and Baskin, 1988), seed size (Gross, 1984; Stanton, 1985), and environmental conditions such as water availability (Swagel *et al.*, 1997) and winter severity (Meyer *et al.*, 1995; Meyer and Monsen, 1991). It has been reported that the germination pattern varies among co-occurring species within a moist grassland community in a warm temperate region (Masuda and Washitani, 1990). This means that there are several choices of germination schedules for plants under conditions of relatively long growing season.

Arctic and alpine environments are characterized by short growing season (Billings and Mooney, 1968; Bliss, 1971), where current year seedlings must rapidly grow to larger than a certain critical size for survival during winter (Maruta, 1983, 1994). Therefore, variation of seed germination timing among co-occurring species may be much smaller there than in temperate environments.

Generally, growing conditions in alpine environments are not uniform but heterogeneous even within a local area. This is mainly caused by differences in the time of snowmelt (Billings, 1974; Miller, 1982). Fellfields and snowbeds are contrasting habitat types within the alpine ecosystem. Fellfields are located on ridges or around mountaintops, snowbeds on leeward slopes. Little snow accumulation at fellfields results in freezing soil during winter, frost in spring, and soil drought in the growing season. On the other hand, thick snow cover at snowbeds protects soil and plants from freezing and frost, and lingering snow provides water in summer. Because of such differences in soil conditions, factors that threaten seedling establishment should differ between the habitats.

In alpine environments, soil drought and needle ice activity are considered to be the most important environmental stresses for seedling establishment during the first growing season (Bliss, 1971). This is especially applicable to fellfield plants. At snowbeds, plants are not exposed from snow cover until the middle of the season when frost is not common, and water supply from lingering snow and developed organic soil retain soil moisture throughout the growing season. On the other hand, the growing season is extremely short due to the lateness of snowmelt. Therefore, germination of snowbed plants should occur as early as possible after snowmelt so that seedlings can extend the growing period until winter. At fellfields, simultaneous germination in early season may result in complete failure in seedling establishment due to spring frost or unexpected snowfall. On the other hand, germination too late in the season may cause insufficient growth, which makes it difficult to overwinter. Furthermore, drought stress may prevent seedling establishment through the summer season. Therefore, a scattered germination pattern thorughout the growing season may be adaptive for risk dispersal at fellfields.

We observed germination patterns of several alpine plant species at a fellfield and a snowbed. The purpose of this study is to confirm whether there is any variation of germination timing among co-occurring species within habitats, and whether expected patterns of seedling emergence occur between the habitats, by comparing germination timing and survival during a summer season in the field.

2. Materials and methods

2.1. Study sites

This study was conducted at a fellfield and a snowbed situated in the central part of the Taisetsu Mountains (43°13′–45′N, 142°32′–143°19′E), Hokkaido, northern Japan. The sites are located 1500 m apart from each other.

The fellfield site is located on a terrace at 1700 m above sea level. There is little snow accumulation during winter due to strong wind, and ground temperatures sometimes fall to -15°C in winter. Dwarf shrubs such as *Empetrum nigrum* var. *japonicum*, *Diapensia lapponica* ssp. *obovata*, *Loiseleuria procumbens*, and *Bryanthus gmelinii* dominate, lichens (mainly *Cladonia* and *Cetraria* species) commonly cover the ground. Because of poor vegetation cover, the soil surface temperature becomes extremely high on fine days even in early spring, but frost can occur unexpectedly. Soil moisture is generally low throughout the summer due to less-organic gravelly soil (Y. Shimono, unpublished data).

The snowbed site is located on a southeast-facing slope at 1880 m a.s.l. Because of thick snow cover, the soil surface temperature remains constant at 0℃ during winter. Snow usually disappears sometime in July. Dwarf shrubs such as *Phyllodoce caerulea*, *P. aleutica*, and *Sieversia pentapetala*, and herbs such as *Primula cuneifolia*, *Peucedanum multivittatum*, and *Veronica stelleri* var. *longistyla*, dominate there. Because of development of organic soil and dense plant cover at the snowbed, soil moisture remains moderate (Y. Shimono, unpublished data).

The time of snow disappearance was recorded in 1998 and 1999 at the snowbed, and soil surface temperature was recorded at one hour intervals by Optic StowAway (Onset Co., U.S.A.) from May to September in 1998 and 1999 at both sites. Precipitation and solar radiation accumulation at one-hour intervals were also recorded by automatic data loggers (KADEC UP, Kona Systems, Japan) during summer at the fellfield in 1998 and 1999.

2.2. Observation of seedling emergence

On 3 June 1998, six 100×100 cm quadrats were set on places where some seedlings just started to emerge at the fellfield. On 9 June 1998, six 40×40 cm quadrats were placed at the snowbed similarly. Thereafter, emergence and survival of current-year seedlings were recorded at 10-day intervals until 27 September 1998, and the species of each seedling was identified. The current-year seedlings were distinguished by the presence of cotyledons. Species of which more than 40 seedlings were observed at each site were used for analysis in this study. The temperature requirement for germination of each species was quantified by measuring mean soil surface temperature during 10 days before germination among cohorts observed at 10-day intervals.

Only seedlings of *Potentilla matsumurae*, one of the identified species, were observed commonly at both habitats. We continued the observation of *P. matsumurae* the next year by using the same quadrats to compare the effect of yearly fluctuation of snowmelt timing on germination patterns. Emergence and survival of current-year seedlings were recorded at 10-day intervals from 10 June to 28 August 1999 in the same quadrats.

2.3. Comparisons of seed size

It is known that variation of seed size influences germination rate (Stanton, 1984; Winn, 1985) and subsequent survivorship (Galen *et al*., 1991; Maruta, 1994; Vera, 1997). To grasp seed size variations among observed species and other co-occuring species within each community, seed weights of dominant species (total 28 species, listed in Table 2) were measured at the fellfield and the snowbed. Fully mature seeds were collected from more than 20 individuals in each species at each habitat, dried at room temperature for about one month, and then seed weights without any attachments such as pappus were measured (20 replications).

3. Results

3.1. Environmental conditions

Timing of snowmelt at the snowbed fluctuated between the years. Spring of 1998 was characterized by very little snow and warm conditions which resulted in very early snowmelt. Snow disappeared on 8 June in 1998 at the snowbed, 42 days earlier than in 1999.

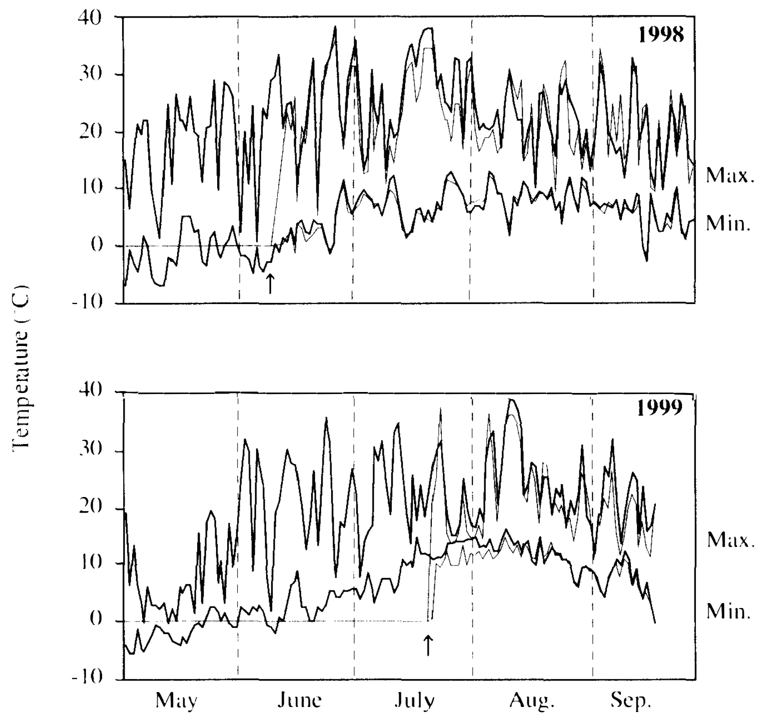

Fig. 1. *Seasonal transition of daily maximum and minimum soil surface temperatures at the fellfield (thick lines) and the snowbed (thin lines). Arrows show the time of snowmelt at the snowbed. Until snowmelt, soil surface temperature remained at 0°C at the snowbed.*

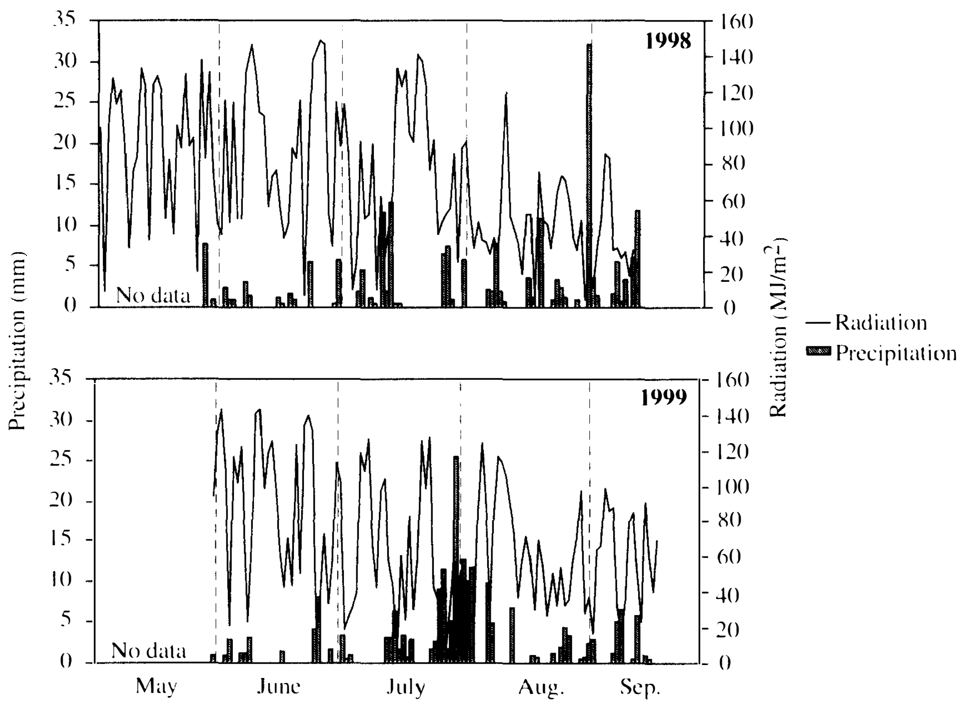

Fig. 2. *Seasonal transition of daily accumulation of solar radiation and precipitation. Measurements were done at the fellfield in 1998 and 1999.*

Soil surface temperature sometimes increased to more than 20℃ in May, but frost occurred nearly every night (Fig. 1). Soil surface temperature highly fluctuated in June when daily maximum temperature was sometimes higher than 30℃ on fine days, while daily minimum temperature sometimes decreased below zero at night. Because of little rainfall and strong solar radiation (Fig. 2), June corresponded to a dry season in this area. Starting in July, daily minimum temperature increased to more than 5℃. Daily maximum temperature at the snowbed was lower than that at the fellfield in both years (Fig. 2, Two group t-test, $P<.0001$, 1.4℃ difference in 1998 and 2.1℃ difference in 1999). Similarly, daily minimum temperature at the snowbed was slightly lower than that at the fellfield ($P<.001$, 0.3℃ difference in 1998 and 0.9℃ difference in 1999).

3.2. Patterns of seedling emergence in 1998

Among seedlings observed in the quadrats, three herbaceous species (*Potentilla matsumurae*, *Patrinia sibirica*, and *Bupleurum ranunculoides* var. *alpinum*) were identified as common species at the fellfield, and four herbaceous species (*Peucedanum multivittatum*, *Potentilla matsumurae*, *Arnica unalaschcensis* var. *tschonoskyi*, and *Primula cuneifolia* var. *cuneifolia*) at the snowbed (Table 1). Densities of current-year seedlings were higher at the snowbed (5016 seedlings/m^2) than at the fellfield (38 seedlings/m^2).

Emergence patterns of seedlings varied among the species at both habitats, especially at the fellfield (Fig. 3). At the fellfield, the peak of seedling emergence occurred in early growing season for *P. matsumurae*, mid-season for *P. sivirica*, and late season for *B. ranunculoides*. Because seed dispersal of these species occurred later than the peak emergence time of each species, current year seedlings were derived from overwintered seeds. At the snowbed, germination of *P. multivittatum* started immediately after snowmelt, and new emergence of seedlings stopped by the middle of July. Seedlings of *P. matsumurae* and *P. cuneifolia* showed similar emergence patterns. Germination of both species was concentrated at the beginning of July in 1998. Germination of *A. unalaschcensis* was common in

Table 1. Total number of seedlings observed in six quadrats, and survival rate during the first summer. Quadrate size was 100×100 cm at the fellfield and 40×40 cm at the snowbed.

	Total number of seedlings	Living seedlings at the end of summer	Survival rate
Fellfield			
Potentilla matsumurae (98)	63	44	0.70
(99)	24	20	0.83
Patrinia sibirica	56	31	0.55
Bupleurum ranunculoides	74	66	0.89
Other species	10		
Snowbed			
Potentilla matsumurae (98)	183	163	0.89
(99)	160	139	0.87
Primula cuneifolia	62	50	0.81
Peucedanum multivittatum	299	139	0.46
Arnica unalaschcensis	44	30	0.68
Other species	88		

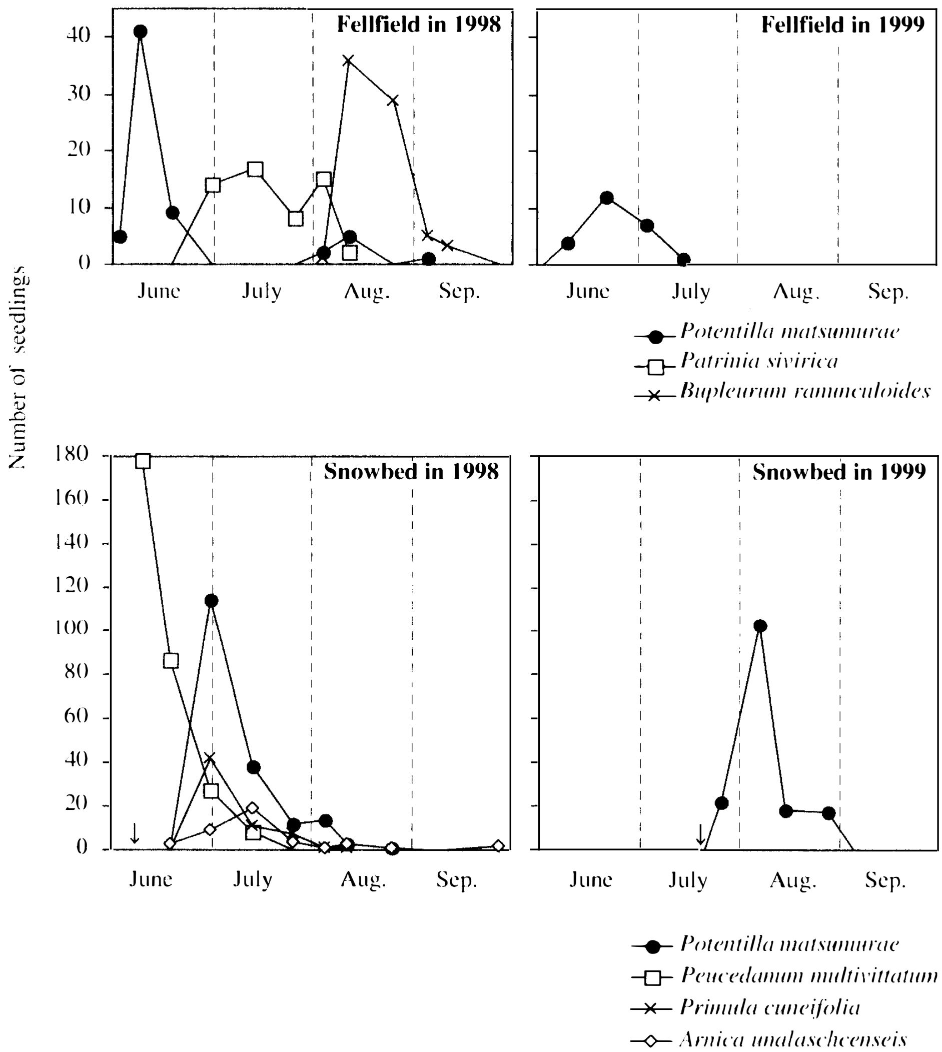

Fig. 3. The number of new seedlings of each species at the fellfield and the snowbed. In 1999, seedlings of Potentilla matsumurae *were observed. Arrows show the time of snowmelt at the snowbed.*

mid-July. All of these seedlings were derived from overwintered seeds.

Distributions of daily mean temperature just before seedling emergence showed that temperature demand for germination significantly differed among the species within each habitat (Fig. 4, Kruskal-Wallis H = 109.66, df = 2, $P < .0001$ at the fellfield, and H = 378.23, df = 3, $P < .0001$ at the snowbed). At the fellfield, *P. matsumurae* germinated at a significantly lower temperature, and *P. sivirica* needed higher temperature for germination than other species (Steel-Dwass multiple comparisons test for nonparametric analysis, $P < .01$). At the snowbed, *P. multivittatum* germinated at a significantly lower temperature than other species (Steel-Dwass multiple comparisons test for nonparametric analysis, $P < .01$).

Leaf senescence of *P. multivittatum* seedlings, the earliest emerging species, began in mid-August, while seedlings of other species retained green leaves until mid-September. The

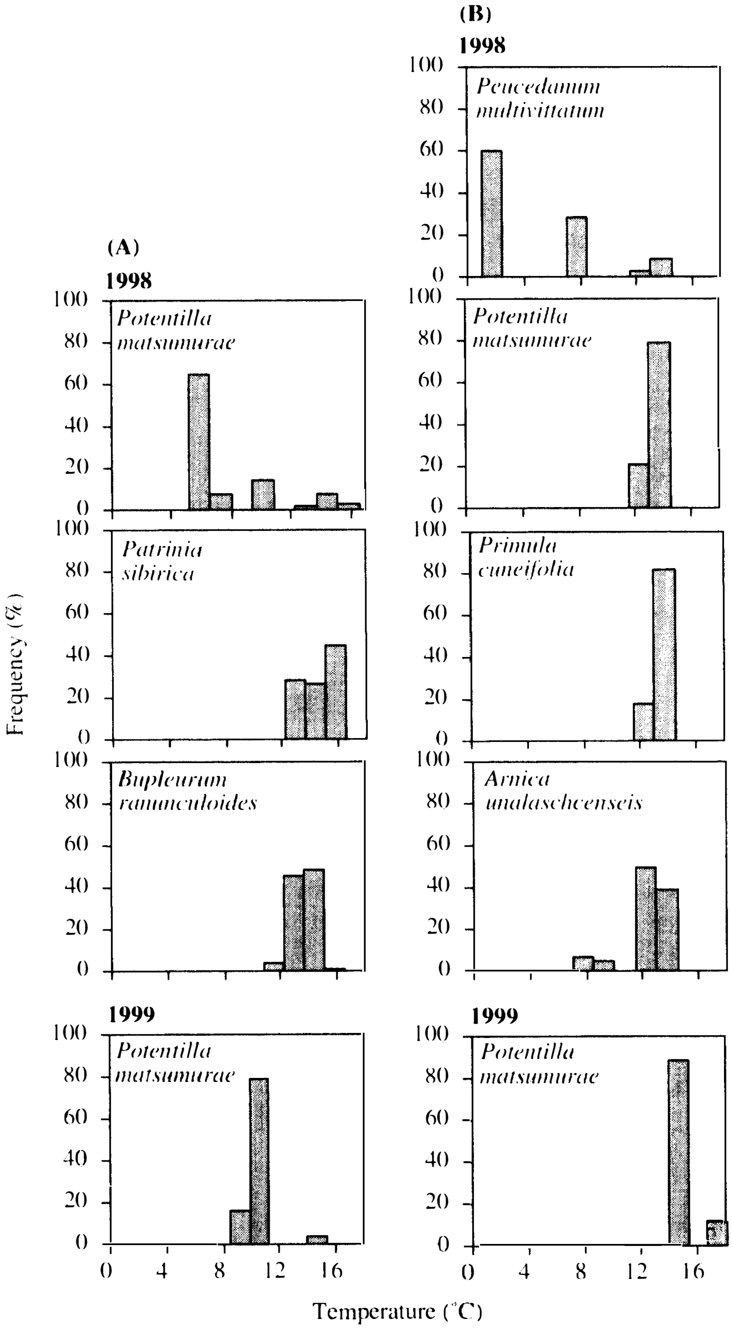

Fig. 4. Emergence of new seedlings with reference to the daily mean soil surface temperature during 10 days before germination of each species in both years at the fellfield (A) and the snowbed (B). When seedlings emerged within 10 days after snowmelt, mean temperature from snowmelt to emergence is used.

survival rate during the 1998 season was low in *P. sivirica* and *P. multivittatum* (Table 1). There was no rainfall during about 10 days in mid-July 1998 when *P. sivirica* germinated vigorously, therefore many seedlings seemed to die of desiccation. Two other species which germinated in months other than July at the fellfield showed high survival rates ranging from 0.70 to 0.89. At the snowbed, there was little effect of no rainfall, therefore three species, though not *P. multivittatum*, showed relatively high survival rates ranging from 0.68 to 0.89. In the case of *P. multivittatum*, germination occurred when snowmelt water was supplied in the quadrate, therefore many seedlings were washed away outside the quadrates before rooting.

The growing period of each species was obtained from the peak time of germination to leaf senescence in late September (but mid-August for *P. multivittatum*). At the fellfield, seedlings of *P. matsumurae* had the longest growing period (about 16 weeks in 1998 and 14 weeks in 1999), and *B. ranunculoides* had the shortest growing period (6 weeks). *Patrinia sivirica* germinated vigorously for one month, so seedlings that germinated in early July had a 13-week growing period, and seedlings that germinated in early August had 8 weeks. At the snowbed, seedlings of *P. matsumurae* and *P. cuneifolia* had the longest growing period (about 13 weeks), and seedlings of *A. unalaschcensis* had 11 weeks. The growing period of *P. multivittatum* seedlings was the shortest (9 weeks). In 1999, lingering snow shortened the growing period of *P. matsumurae* to only 8 weeks.

3.3. Comparison of P. matsumurae germination between habitats and years

At the snowbed, *P. matsumurae* did not germinate until more than 10 days after snowmelt in 1998 when snow disappeared in early June; however, it took only one week after snowmelt to germinate in 1999 when snow disappeared in mid-July. Daily mean soil surface temperature was below 8℃ when snow melted in 1998, and 14℃ in 1999. Because no seeds germinated when the daily mean temperature of the soil surface was lower than 12℃ (Fig. 4), the time of seedling emergence at the snowbed was determined not only by snowmelt timing but also by seasonal temperature changes. Interestingly, fellfield seeds could germinate under cooler conditions than snowbed seeds, *i.e.*, about 5℃ in 1998, and 8℃ in 1999 (Fig. 4). Distribution of germination temperature significantly differed between the habitats (Kolmogorov-Smirnov test, $P < .0001$ in both years). The yearly difference in peak germination times between 1998 and 1999 was 10 days at the fellfield, whereas it was more than one month at the snowbed.

3.4. Seed weight of dominant species

Most alpine species produced small seeds. Seed weights of 10 of the 15 species at the fellfield and 12 of the 15 species at the snowbed were less than 1 mg (Table 2). Seeds of *P. sibirica*, *B. ranunculoides*, *P. multivittatum*, and *A. unalaschcensis* were larger than 1 mg. Especially, seeds of *P. multivittatum* were largest among alpine species. Seed sizes of *P. matsumurae* (0.3–0.5 mg) and *P. cuneifolia* ($<$0.2 mg) were relatively small.

4. Discussion

Although several species are compared in this study, patterns of seedling emergence varied among the species within habitats, especially at the fellfield, which has a relatively long growing season. Maruta (1994) reported that final seedling size at the end of the first growing season is correlated with seed size, and that large seedling size is advantageous for the winter survival of two *Polygonum* species growing in an alpine region. At the fellfield, *Potentilla matsumurae* germinated early in the growing season. Because of small seed size,

Table 2. List of species and habitats in which seed weights were measured. Mean value and SD of individual seed weight of each species are shown.

Family	Species	Habitat	Seed weight (mg)
Compositae	*Saussurea yanagisawae*	Fellfield	3.47±0.72
	Arnica unalaschcensis var. *tschonoskyi*	Snowbed	0.91±0.08
	Solidgo virga-aurea var. *leiocarpa*	Snowbed	0.68±0.03
Cyperaceae	*Carex stenanta* var. *taisetsuensis*	Fellfield	0.75±0.10
	Carex pyrenaica	Snowbed	0.61±0.03
Diapensiaceae	*Diapensia lapponica* ssp. *obovata*	Fellfield	0.061±0.002
Empetraceae	*Empetrum nigrum* var. *japonicum*	Fellfield	0.86±0.11
Ericaceae	*Arctous alpinus* var. *japonicus*	Fellfield	5.01±0.92
	Bryanthus gmelinii	Fellfield	0.016±0.001
	Loiseleuria procumbens	Fellfield	0.026±0.001
	Therorhodion camtschaticum	Fellfield	0.028±0.001
	Vaccinium uliginosum var. *alpinum*	Fellfield	0.20±0.01
	Vaccinium vitis-idaea	Fellfield	0.24±0.01
	Phyllodoce aleutica	Snowbed	0.016±0.001
	Rhododendron aureum	Snowbed	0.084±0.004
	Vaccinium ovalifolium	Snowbed	0.140±0.005
Gentianaceae	*Gentiana nipponica*	Snowbed	0.13±0.01
Primulaceae	*Primula cuneifolia* var. *cuneifolia*	Snowbed	0.11±0.01
Ranunculaceae	*Anemone narcissiflora* var. *nipponica*	Snowbed	6.47±1.21
Rosaceae	*Potentilla matsumurae*	Fellfield	0.46±0.09
		Snowbed	0.40±0.07
	Sieversia pentapetala	Snowbed	0.46±0.06
Scrophulariaceae	*Penstemon frutescens*	Fellfield	0.26±0.02
	Pedicularis chamissonis var. *japonica*	Snowbed	0.91±0.03
	Veronica stelleri var. *longisyla*	Snowbed	0.11±0.01
Umbelliferae	*Bupleurum ranunculoides* var. *alpinum*	Fellfield	1.87±0.15
	Tilingia ajanensis	Fellfield	2.06±0.07
		Snowbed	1.95±0.15
	Peucedanum multivittatum	Snowbed	5.60±0.93
Valerianaceae	*Patrinia sibirica*	Fellfield	2.02±0.11

P. matsumurae probably needs a long growing season to accumulate enough reserves before the onset of winter. However, June is the driest season, when daily ground temperature fluctuates intensely. Therefore, seedlings are required to tolerate both freezing temperature and drought stress in this period. The relatively high survival rate during the first summer of *P. matsumurae* (0.70) seems to be evidence of tolerance. On the other hand, *Patrinia sibirica* and *Bupleurum ranunculoides*, having relatively large seed sizes, germinated later than *P. matsumurae*, resulting in a shorter growing season. Due to larger amounts of storage in seeds, these seedlings may not need a long growing period to reach critical size during the first summer, in comparison with species having smaller seeds. In fellfields, later germination may be advantageous to escape frost damage and desiccation stress early in the season. The high survival rate of *B. ranunculoides* may reflect this advantage. Although the temperature requirement for germination was higher in *P. sibirica* than that in *B. ranunculoides*, as shown in Fig. 4, actual emergence of seedlings of *P. sibirica* was earlier than that of *B. ranunculoides* (Fig. 3). Other environmental factors than simple mean temperature, such as day length, may act as important stimuli for germination in these species. For example, the germination of *Betula pubescens* was enhanced as the day length increased (Bewley and Black, 1982). In contrast, the germination of *Tsuga canadenses* was increased under the short day length condition (Stearns and Olsen, 1958).

At the snowbed, *Peucedanum multivittatum* showed simultaneous germination soon after snow disappearance. We observed that germination of *P. multivittatum* started soon after snowmelt, indicating that this species could germinate under very cool conditions, around 0℃ to 4℃. *P. matsumurae* and *Primula cuneifolia* did not germinate below 12℃, even when snowmelt occurred earlier than usual. Large seeds of *P. multivittatum* are hard to trap in the soil (Chambers *et al*., 1991), and remain on the soil surface where water content reduces quickly (Maruta, 1976). The soil surface absorbs snowmelt water soon after snowmelt. Therefore, very quick germination after snowmelt may be important for seedling establishment of *P. multivittatum*. A previous study reported that most tundra species require nearly water-saturated soils for germination and seedling establishment (Oberbauer and Miller, 1982).

Because *P. multivittatum* stopped growing by mid-August, the leaf life-span of *P. multivittatum* was shortest among the species at the snowbed. If leaf senescence of this species is determined by stimulus of day length or cool temperature, seedlings occurring in late snowmelt years would have an extremely short growing period. Large amounts of resource storage in seeds would make such a life cycle possible. Also, *Arnica unalaschcensis*, having relatively large seeds, tended to germinate slowly, resulting in a short growing season. Therefore, species having larger seeds can get along with a relatively short growing period even in snowbed environments, in comparison with species having smaller seeds. Masuda and Washitani (1990) also reported that interspecific variation of emergence timing seemed to be associated with mean seed weight among the species, *i.e.,* larger seeds tended to emerge later than smaller seeds.

Germination temperature requirements of *P. matsumurae* varied between the habitats. These results indicated that physiological traits of germination in this species may differ between the fellfield and snowbed populations. Snowbed seeds could not germinate when daily mean temperature of soil surface was lower than 12℃. At the snowbed, snow usually disappears in July when mean temperature is more than 10℃, therefore, populations at the snowbed may not have the ability to germinate under cooler conditions than 10℃.

Species specific patterns of emergence at the fellfield varied more than that at the snowbed. At the fellfield, the growing period for plant growth is about 4 months from June to September in every year. On the other hand, the growing period at the snowbed fluctuated unpredictably from about 4 months in 1998 to 2 months in 1999, depending on the snowmelt timing. Germination timing of *P. matsumurae* fluctuated between the years, especially at the snowbed. In fact, the growing period of *P. matsumurae* at the snowbed in 1999 was almost the same as that of *B. ranunculoides*, which was late germination species at the fellfield. Thus, variations of snowmelt timing strongly determined the actual timing of germination of snowbed plants.

Although many species showed concentrated germination patterns with narrow ranges, germination of *P. sivirica* lasted constantly beyond one month at the fellfield. In addition, most seedlings of *P. matsumurae* at the fellfield emerged in June, but some seedlings also emerged in August. We hypothesize that simultaneous germination immediately after snowmelt would be an advantage for seedling establishment in snowbeds, and scattered germination through the growing season would be an advantage in fellfields. As we expected, snowbed species showed simultaneous germination after snowmelt, and fellfield species which emerged early in the growing period, when environmental conditions fluctuated considerably, may have a wider range of germination timing. Measurements of overwintering survival pattern are necessary to confirm whether such differences in emergence patterns are advantageous.

This study indicates that germination patterns vary among species within a community even in an alpine environment having a short growing season, and such variation partly reflects the variation of seed size. Although we compared only herbaceous species in this study, alpine shrubs such as *Loiseleuria procumbens*, *Bryanthus gmelinii*, *Phyllodoce caerulea*, and *P. aleutica* are important component species at this site, which produces very small seeds ranging from 0.01 to 0.02 mg. The germination timing of these species is an interesting subject for further study.

Acknowledgments

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