Scientific Paper

EFFECTS OF SNOWMELT TIMING ON REPRODUCTIVE PHENOLOGY AND POLLINATION PROCESS OF ALPINE PLANTS

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Abstract: Comparative studies on alpine plants along a snowmelt gradient bring us good information about the selective force of short growing season acting on plants. Flowering and fruiting phenologies of each species are potentially determined by temperature, and actual flowering and fruiting times are influenced by the timing of snow disappearance. Snowmelt pattern within an area is rather stable, but actual time of snowmelt at the same place is highly variable from year to year. Early flowering induced by early snowmelt often reduces pollination success because activity of pollinating insects is low in early cool conditions. On the other hand, delay of flowering restricts the length of the fruit developing season, and plants in late snowmelt habitats sometimes fail to set seeds even if pollination is successful. Steep snowmelt gradient causes variations of flowering pattern within and among species and visitation pattern of pollinators. This may accelerate inter-specific competition for pollinator acquisition among plants which affects reproductive success in each species. Thus, the distribution pattern of plants along a snowmelt gradient should be explained not only by abiotic environments (snow depth, snow-free period, soil condition and micro-topography) and physiological traits of each species (tolerance for short growing season and temperature dependent phenological traits), but also by biotic interactions (plant-plant interaction and plant-insect interaction).

1. Introduction

One of the most important factors causing heterogeneity of alpine environments is timing of snowmelt. Deep snow cover effectively protects the plants from low temperature and desiccation by strong wind during the winter; lingering snow constantly provides water to plants during the growing season. Moreover, snow cover has been suggested to be a principal factor controlling the length of the growing season and lifecycle of alpine plants (BILLINGS and BLISS, 1959; ISARD, 1986; JOHNSON and BILLINGS, 1962; OBERBAUER and BILLINGS, 1981; KUDO, 1991). The timing of flowering and dormancy of alpine plants is considerably controlled by the time of snow disappearance and/or beginning of snowfall (BLISS, 1971; HOLWAY and WARD, 1963, 1965; RAM *et al.*, 1988; KUDO, 1991, 1992). In early summer, the alpine region is spotted by lingering snow, called snow-beds. A steep gradient of snowmelt time is formed within a narrow area in the snow-bed environment. This gradient provides a good research field to study the ecological responses of plants to the length of growing season.

There is a view that biological interaction is not so remarkable in the tundra ecosystem because adaptation to harsh weather conditions is most important for survival in tundra plants. This may be true, but we should evaluate the functional role of the bio-

logical interaction for complete understanding of the tundra ecosystem. It is known that, for example, many alpine and arctic plants depend on insects for pollen transfer and fertilization in spite of low activity and diversity of pollinating insects in the tundra environment (HOCKING, 1968; KEVAN, 1972; PETERSEN, 1977). There are many alpine and arctic species producing extraordinarily large and remarkable flowers in comparison with the small plant size, suggesting the importance of pollinator attraction for outcrossing. I have studied various ecological events of alpine plants along a snowmelt gradient in the Taisetsu Mountains, northern Japan. In this paper, I briefly summarize my works and present some perspectives on alpine plant ecology, especially with respect to the phenological characteristics and pollination process of alpine plants.

2. Snowmelt Gradient

My research field is in the Taisetsu Mountains in Hokkaido, northern Japan (43°13′–45′N, 142°32′–143°19′E). The monthly mean temperature at 2000 m altitude ranged from –21.3°C (January) to 13.9°C (August), with an annual mean of –0.9°C in 1985 (SONE and TAKAHASHI, 1988). Summer precipitation during July to September is usually more than 500 mm, and annual precipitation *ca.* 1600 mm. Because of large snowfall and topographic effects, thick snow covers the south-eastern slopes in this area. Melt-off times range from mid-May to late September, and there is a clear gradient of time of snowmelt within a narrow area. Snow begins to cover the ground again in early October.

The study site was chosen in snow-bed communities developed on a block field slope (1910–1790 m a.s.l.) near Lake Hisago in the central part of the Taisetsu Mountains. I set six plots on the slope in 1987, plots A to F arranged by snowmelt order. Each plot was 20 × 20 m in area, and all plots were located within 800 m of one another. The pattern of snowmelt among plots was very stable; snow always disappeared from plots A to F (Table 1). Annual snow-free periods ranged from 114 days at plot A to 42 days at

Table 1.   Annual snow-free period (day) and time of snow disappearance at each plot in the Taisetsu Mountains during 1988–1995. The altitude of each plot is shown in parenthesis.

		1988	1989	1990	1991	1992	1993	1994	1995	Mean	SD
Plot A	Snow-free days	120	95	130	124	117	90	120	117	114	14.1
(1910 m)	Melt-off time	Jun 6	Jul 1	May 31	Jun 8	Jun 15	Jul 5	Jun 7	Jun 11		
Plot B	Snow-free days	105	80	115	116	97	80	105	97	99	13.9
(1890 m)	Melt-off time	Jun 20	Jul 10	Jun 14	Jun 16	Jun 28	Jul 15	Jun 23	Jul 1		
Plot C	Snow-free days	90	70	95	99	75	55	85	69	80	15
(1880 m)	Melt-off time	Jul 5	Jul 20	Jul 5	Jul 3	Jul 15	Aug 10	Jul 13	Jul 28		
Plot D	Snow-free days	70	60	85	84	55	30	67	61	64	17.5
(1790 m)	Melt-off time	Jul 25	Jul 28	Jul 14	Jul 18	Aug 5	Sep 3	Jul 30	Aug 5		
Plot E	Snow-free days	60	55	80	81	45	20	55	59	57	19.4
(1790 m)	Melt-off time	Aug 5	Aug 8	Jul 19	Jul 21	Aug 15	Sep 15	Aug 10	Aug 7		
Plot F	Snow-free days	50	45	60	63	35	0	40	43	42	19.5
(1800 m)	Melt-off time	Aug 16	Aug 15	Aug 6	Aug 8	Aug 25		Aug 25	Aug 23		

plot F (average of the last 8 years). The actual time of snow disappearance fluctuated from year to year within each plot. For example, there was a 35-day range in the melt-off time at plot A. Thus, the fixed pattern of snowmelt order within an area and the yearly fluctuation of actual available days at the same point characterizes the snow-bed environment.

3. Plant Distribution

Time of snowmelt (or the length of the growing season) greatly affects the distribution of plant species (Fig. 1). Where snow melts early, plants have a long growing season, but these plants needs cold tolerance for survival. Where snow melts late, plants are protected from low temperature during the cold season by thick snow cover, but the length of the growing season is highly restricted and plants have to complete the life cycle during a short period. Thus, each species has its own physiologically determined range of distribution along a snowmelt gradient. The number of vascular plant species
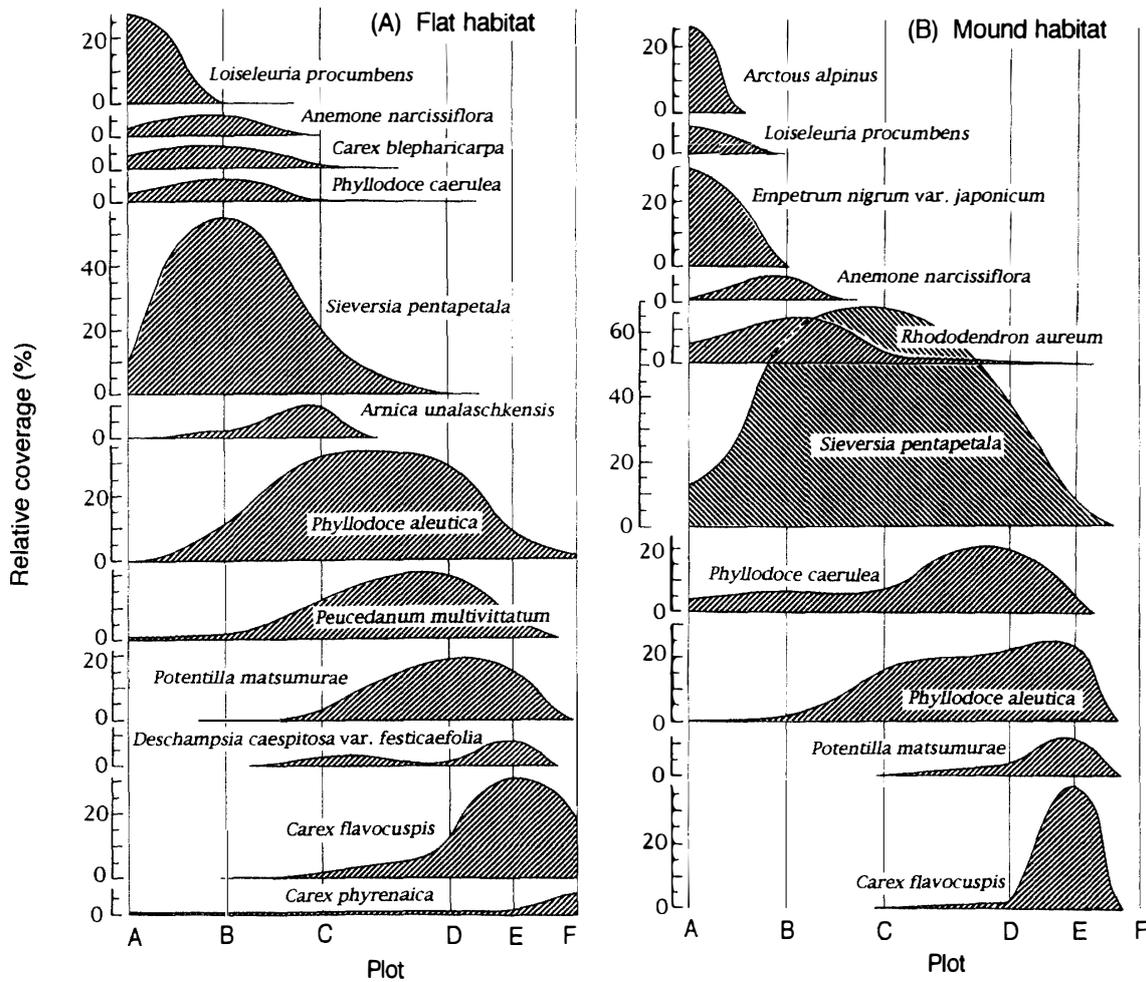

Fig. 1. Distribution pattern of major plant species along the snowmelt gradient on a flat habitat and a mound habitat. Snow disappears from plot A to plot F every year. For details see KUDO and ITO (1992).

within each plot decreased from plot A (36 spp.) to plot F (5 spp.), indicating the increasing selective force along the snowmelt gradient (KUDO and ITO, 1992).

At this site, many rocks were covered with trailing dwarf shrubs which physiognomically characterize the snow-bed vegetation (KUDO and ITO, 1992). Two micro habitats were recognized: a "flat habitat", level ground between rocks with a deep soil layer, and a "mound habitat", consisting of rocks of various sizes (30 × 30 cm to more than 1 × 1 m, and 5–40 cm in height) with a relatively thin soil layer. On the flat habitats, lichens (*Cladonia* and *Cetraria* spp.) and evergreen shrubs such as *Loiseleuria procumbens* and *Empetrum nigrum* var. *japonicum* dominated at the early snowmelt plot A. Deciduous shrubs, mostly *Sieversia pentapetala*, showed considerable cover at plot B. The cover of forbs and graminoids increased from plots C to E where shrub species decreased in cover. At plot F, forbs suddenly disappeared, and mosses (mainly *Polytrichum sexangulare*) constituted most of the plant cover.

On the mound habitats, the pattern of vegetation change along the snowmelt gradient was rather simple; evergreen (*Phyllodoce aleutica* and *P. caerulea*) and deciduous shrubs (*Sieversia pentapetala*) were generally dominant at plots A to D, and graminoids drastically increased at plot E. Covers of lichens and mosses were rather small throughout the plots. Thus, the existence of micro topography increased the species diversity along the snowmelt gradient.

Distribution of plant species has often been explained by only physical factors such as soil condition, topography and air temperature (BLISS, 1962; EDDLEMAN and WARD, 1984; WEIR and WILSON, 1987), and fundamental factors decide the potential distribution range of each species. But the actual range and mode of each species along an environmental gradient may also be affected by biological factors such as competition among plant species or plant-insect interaction through pollination or herbivory processes. Analyses of species distribution considering biological effects are rare in tundra regions (*e.g.*, WIJK, 1986).

4. Phenology

The phenological response of alpine species against the shortened growing season is determined primarily by (1) growth form, (2) the span of pre-flowering from the beginning of the growing season, and (3) the term of the seed maturation after flowering in each species (KUDO, 1991). Shrub species, especially evergreen shrubs, take longer for maturing their seeds, and they often abandon sexual reproduction and reproduce vegetatively by layering in late snowmelt habitats. Forb and graminoid species, on the other hand, bloom even in the late snowmelt habitats, because many of these species tend to rapidly complete their reproductive phenology.

In alpine environments having a short growing season, early flowering and fruiting is considered to be advantageous to finish their reproductive phenology during the short summer (RAM *et al.*, 1988). Hence, if a population inhabiting a place with a short growing season is able to reduce the period of pre-flowering and/or fruiting after fertilization, reproductive success of the population may be enhanced. I measured pre-flowering and fruiting periods of nine plant species at each plot during two seasons, and found that phenological events of each species were determined by the temperature regime and
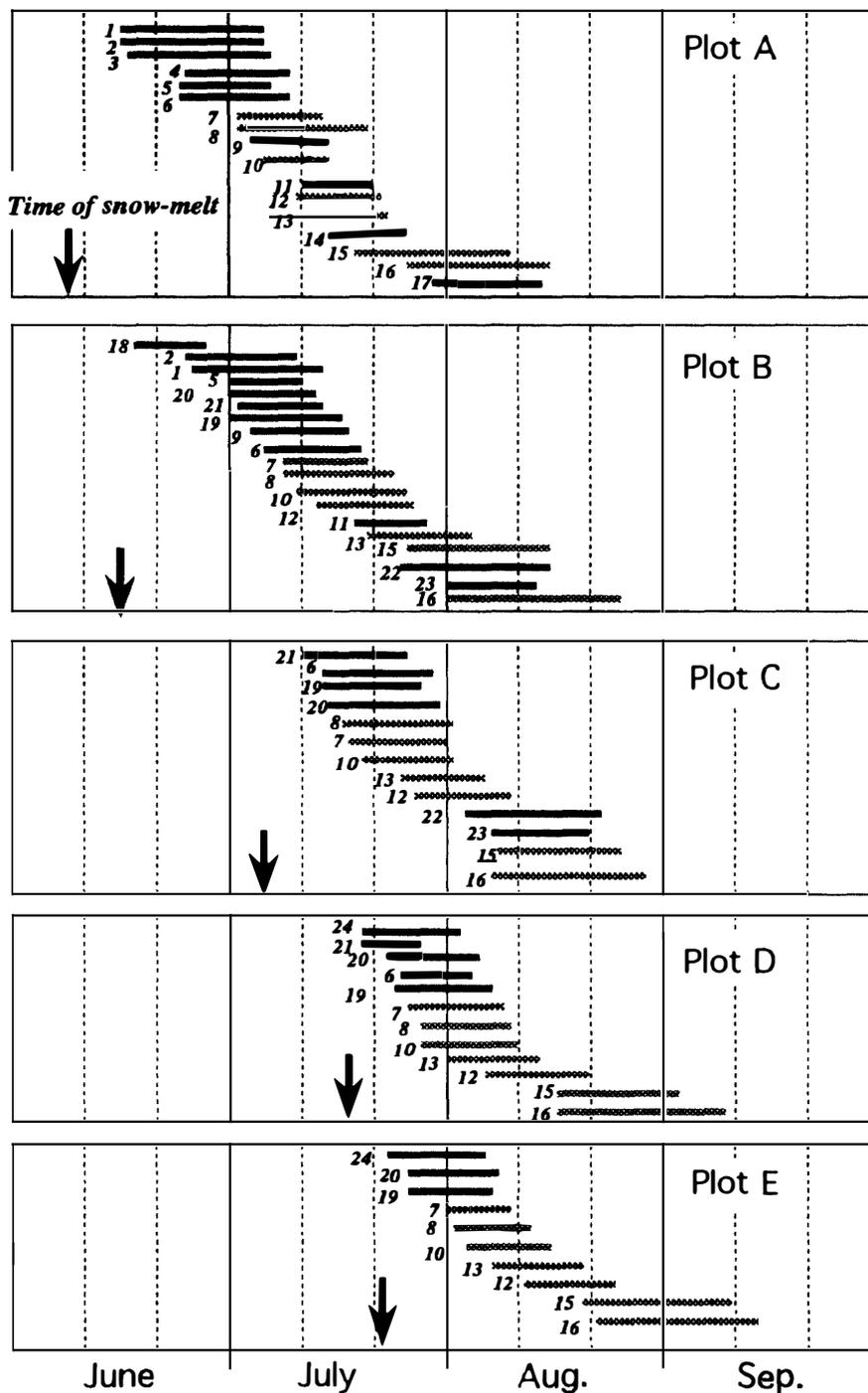
Fig. 2. *Flowering season of major entomophilous species on each plot in 1991. Bright bars mean species occurring at every plot. 1:* Arctous alpinus *var.* japonicus, *2:* Anemone soyensis, *3:* Arctous alpinus *var.* japonicus, *4:* Loiseleuria procumbens, *5:* Vaccinium uliginosum, *6:* Rhododendron aureum, *7:* Phyllodoce caerulea, *8:* Sieversia pentapetala, *9:* Anemone narcissiflora, *10:* Phyllodoce aleutica, *11:* Vaccinium vitis-idaea, *12:* Peucedanum multivittatum, *13:* Veronica stelleri *var.* longistyla, *14:* Pedicularis chamissonis *var.* japonica, *15:* Solidago virgaurea *var.* leiocarpa, *16:* Gentiana nipponica, *17:* Bryanthus gmelinii, *18:* Heloniopsis orientalis, *19:* Primula cuneifolia, *20:* Potentilla matsumurae, *21:* Vaccinium ovalifolium, *22:* Tilingia ajanensis, *23:* Arnica unalaschcensis, *24:* Harrimanella stelleriana.*

there was no evidence of plastic adjustment of reproductive phenology between populations of the same species growing under different snowmelt conditions (Kudo, 1992). This result indicates that difference of snowmelt timing directly causes variation of the flowering season among populations.

Differences in flowering season may affect the pollination success of insect-pollinated species. The sequence of flowering period of major entomophilous species at each plot in 1991 is shown in Fig. 2. With late snowmelt, time of flowering became later within and between species. Although species composition differed among plots, some species (indicated with bright bars) were distributed through the plots. There was about a one month difference for flowering season of same species between plots A and E in this year. Such a large difference in flowering season complicates the patterns of pollinator visitation and seed-set among and within species at a local site. In such a system, plants may compete for pollinator acquisition not only with plants blooming in the same place, but also with plants blooming in other places, because visiting insects can easily choose the best plants by moving a short distance along the snowmelt gradient.

5. Activity of Visiting Insects and Pollination Success

In alpine and arctic environments, the out-crossing rate is lowered by low temperature, strong wind and short growing season which reduce the activity of pollinators, and the importance of vegetative propagation or self-fertilization is often enhanced (Bliss, 1971; Callaghan and Collins, 1981; Johnson, 1969; Mooney and Billings, 1960). Nevertheless, many alpine and arctic plant species depend on pollinators for fertilization (Hocking, 1968; Kevan, 1972; Petersen, 1977). Out-crossing is important for increase in gene-flow, heterozygosity and population diversity also in plants growing in alpine and arctic areas (Bliss, 1962; Savile, 1964). Even in self-compatible species, the fruiting rate increases by insect rummaging around the inside of flowers (Estes and Brown, 1973; Kudo, 1993; Petersen, 1977). Thus, it is expected that seasonal changes in pollinator activity greatly affect the possible seed-set of alpine plants.

What vectors do alpine plants use for pollen transfer? Of 75 species growing in this area, about 75% species are considered to be pollinated by insects. Major available pollinators in this area are dipteran insects, flies and syrphid-flies, and bees (mainly bumble-bees). Flies appear from early June, then syrphid-flies and bumble-bee queens begin to occur around mid June. The most active pollinators, bumble-bee workers, appear from late July. Because activity of these insects much depends on temperature (Levesque and Burger, 1982; Totland, 1994), the most active season for pollinating insects is from late July to mid-August in this area, so blooming in this season increases pollinating success.

I studied the relationships between flowering phenology, pollinator visitation and fruit-set success of *Rhododendron aureum* along the snowmelt gradient (Kudo, 1993; Fig. 3). The flowering period of *R. aureum* varied from mid-June to late July among plots. Although *R. aureum* is physiologically self-compatible, pollinator visitation was necessary to set fruits due to lack of autodeposition, and fruit-set was highly restricted by pollen limitation on early snowmelt plots. With lateness of flowering, frequency of pollinator visitation highly increased, and both control and emasculated flowers increased
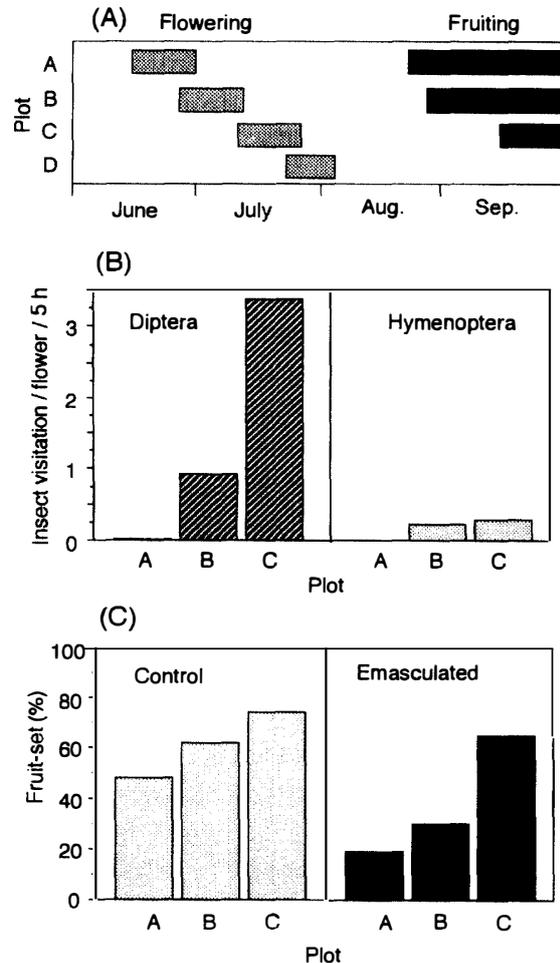
Fig. 3. Flowering and fruiting phenology (A), frequency of flower visitors (B) and fruit-set of intact and emasculated flowers (C) of Rhododendron aureum *along the snowmelt gradient in 1991. For details see* Kudo *(1993).*

the fruit-set. On the other hand, later-flowering plants often failed to set fruits because of the onset of autumn frost and snow before maturation because it took about two months to mature the fruits after flowering. Thus, a best place for reproductive success exists on the snowmelt gradient, and it may fluctuate from year to year because of the variation of snowmelt time.

A similar tendency was obtained by other species such as *Peucedanum multivittatum* and *Primula cuneifolia* along the snowmelt gradient (Kudo, unpublished data). Seed-set of these plants increased with delay of flowering from early to middle season, but plants failed to set seeds when flowering occurred in late season because of lack of a seed-developing period. Such a pattern of seed-set success is considered to be fundamental in the snow-bed environment. Difference in seed-set among plots may affect the distribution pattern of the species along the snowmelt gradient, but the relationship between seed-set success and distribution has not yet been studied.

6. Inter-specific Competition for Pollinator Acquisition

Finally, I consider the modification of distributions of two plant species through the process of insect-plant interaction. Let's assume that two species, *sp A* and *B* are competing with each other for pollinator acquisition under a pollen-limited condition,

and *sp A* is more attractive than *sp B*. When both species evenly grow along a snowmelt gradient, phenological regulation to reduce the flowering overlap between the species may not be effective for avoidance of competition, because pollinating insects can visit *sp A* throughout the flowering season within the site by moving a short distance along a snowmelt gradient (Fig. 4A). On the other hand, when flowering activity of *sp A* decreases in a later snowmelt habitats due to short photosynthetic period but that of *sp B* does not, pollinating insects come to visit *sp B* at later snowmelt habitats (Fig. 4B). In such case, the distribution mode of *sp B* may shift to later snowmelt habitats.

I try to explain the difference in distribution pattern of two relative evergreen shrub species, *Phyllodoce caerulea* and *Phyllodoce aleutica*, along a snowmelt gradient. Both species are common in the snow-bed environment. *P. caerulea* has pink flowers and *P. aleutica* has whitish-yellow flowers, and both species are pollinated by bumble-bees. Although these species often coexist, *P. caerulea* generally dominates in earlier snowmelt habitats and *P. aleutica* dominates in later snowmelt habitats in this area. This distribution pattern seems to be common also on other mountains.

If *P. aleutica* prefers a late snowmelt habitat to an early one in comparison with *P. caerulea*, biological interaction may be less important to explain the distribution difference. So, it is necessarily to compare the tolerance to a short growing season in each species. As an index of reproductive activity, I compared number of flowers per shoot and the flowering interval of each stem between species along the snowmelt gradient. The number of flowers produced on a shoot decreased from 3.3 to 2.8 in *P. caerulea* (14% decrease) and from 5.9 to 5.2 in *P. aleutica* (13% decrease). Flowering intervals on each stem were clearly extended with lateness of snowmelt from 3.0 to 6.9
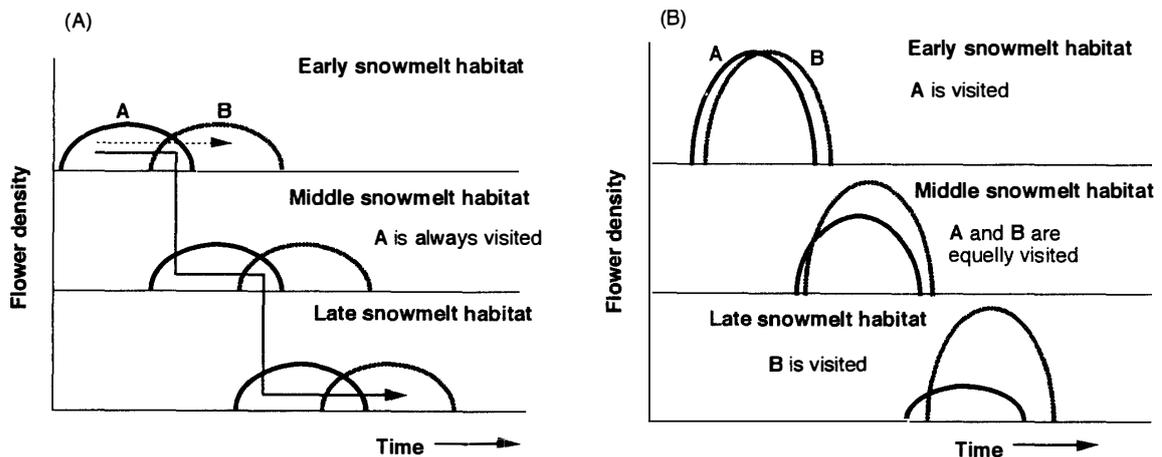

Fig. 4.   Visitation pattern of pollinating insects when two species are competing for pollinator attraction. Species A is postulated to be more attractive than species B in this schema. (A) When two competitive species equally occur among habitats, changes in anthesis for one species is not effective in avoiding competition for pollinator acquisition because the pollinators can visit another (more attractive) species at neighboring later snowmelt habitats. (B) When a competitively superior species decreases flower density at a later snowmelt habitats, pollinators are likely to visit, the other, less attractive species having higher flower density in later snowmelt habitats. In such case, a shift of the less attractive species to later snowmelt habitats may be accelerated under pollinator-limited conditions. Thus, the actual distribution mode may be affected by inter-specific competition.
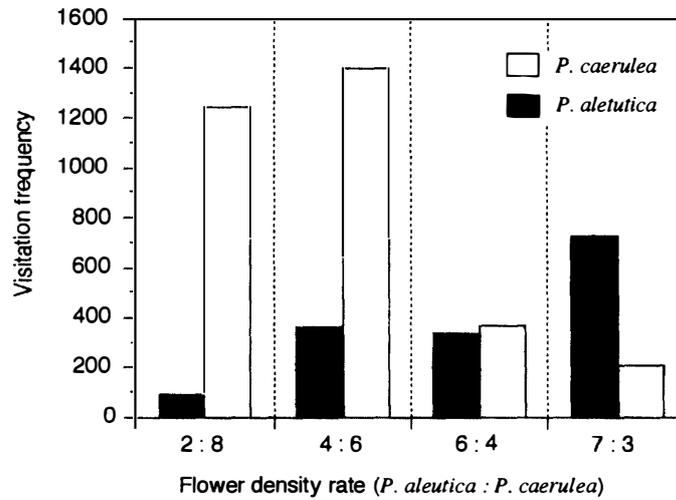
Fig. 5. *Number of inflorescences visited by bumblebees at four quadrats (5 × 5 m) having different flower density rates of* Phyllodoce caerulea *and* P. aleutica. *The quadrats were arranged from an early snowmelt place (2 : 8 in* P. aleutica *:* P. caerulea*) to a later snowmelt place (7 : 3).*
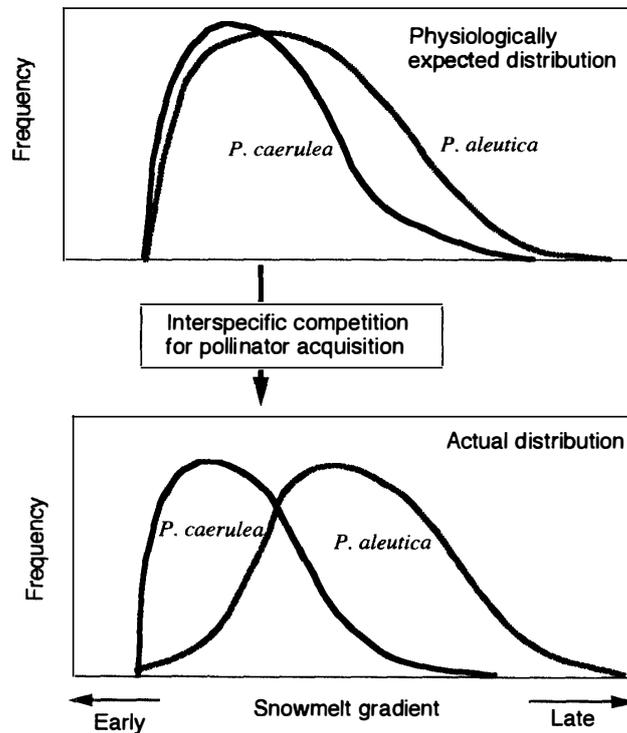

Fig. 6. *Shift of distribution modes of* Phyllodoce caerulea *and* P. aleutica *mediated by inter-specific competition for pollinator acquisition estimated from field observation.*

year in *P. caerulea* (2.3-fold extension) and from 4.1 to 6.9 year in *P. aleutica* (1.7-fold extension). These results indicate that both species potentially prefer early snowmelt habitats, and *P. caerulea* is more susceptible to a short growing season than *P. aleutica*.

Then, I observed bumble-bee visitations to *P. aleutica* and *P. caerulea* at four stands with various flower density ratios of both species (Fig. 5). Many bumble-bees chose *P. caerulea* even where *P. aleutica* was denser than *P. caerulea*, and only when flower density of *P. aleutica* was much higher than that of *P. caerulea* at later snowmelt places, *P. aleutica* was more visited by bumble-bees than *P. caerulea*. This visitation pattern indicates that *P. caerulea* is more attractive than *P. aleutica*. This result seems to support the prediction that the shift of distribution mode of *P. aleutica* to later snowmelt habitats may be because of inter-specific competition for pollinator acquisition (Fig. 6), although we have to assess quantitatively the effects of pollinator visitation on reproductive success in these species.

7. Conclusions

In order to make clear the mechanism determining the distribution pattern, we have to determine the contribution of each component to reproductive success (Fig. 7). The distribution pattern of a given species reflects the result of sexual and asexual (including vegetative growth) reproductive success. Sexual reproduction can be expressed as a product of seed production and survival through dispersal, germination and growth processes. Seed production can be expressed as a product of flowering activity, pollination success and maturation success after fertilization. Many biotic and abiotic factors affect each component, and biological interactions and strategies of plants are expected in each component.

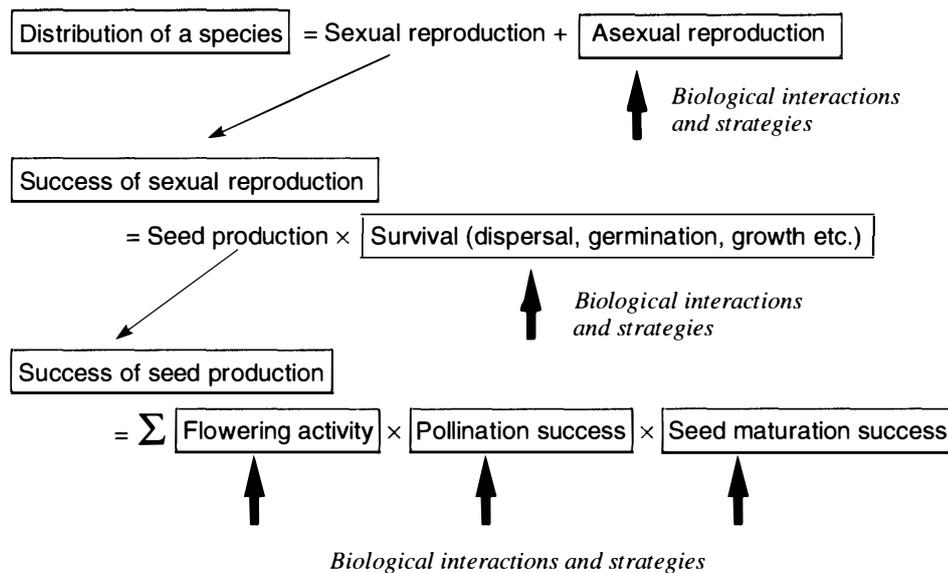In this paper I have stressed the importance of biological factors affecting the pol-

Fig. 7. *Component factors affecting distribution pattern of plant species. In each component constructing reproductive success, some biological interactions and adaptive strategies are expected.*

lination process in an alpine environment. Timing of snowmelt directly controls the length of the growing season and phenological events of plants, and the species distribution along a snowmelt gradient is potentially determined by the snow condition. On the other hand, flowering timing and seasonal changes in activity of pollinating insects greatly affect the fertilization success of plants. Under pollinator-limited conditions, increase of fertilization success directly enhances reproductive success; therefore, competition for pollinator acquisition must be serious in such a system. Differences in reproductive success may bring about the modification of the physiological (potential) distribution mode of each species. I have discussed the biological interaction through only the pollination process in this paper, but there are many biological factors affecting reproductive success, survival and migration of plants, such as seed dispersal, seed predation and herbivory processes. Thus, species distribution which we recognize in the field is a result of various abiotic and biotic natural selections. We should make an effort to detect the functional connection of biological interaction in a tundra ecosystem.

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