

Variations in floral traits of sympatric alpine shrubs, *Phyllodoce caerulea* and *Phyllodoce aleutica*, along snowmelt gradients

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Abstract: Floral traits (corolla length, corolla shape, anther-stigma distance, and corolla color) of sympatric alpine shrubs, *Phyllodoce caerulea* and *Phyllodoce aleutica*, were compared among three populations having different snowmelt timing selected along snowmelt gradients (*i.e.*, early-, middle-, and late-snowmelt population) at three snowbeds in the Taisetsu Mountains, northern Japan. The corolla of *P. caerulea* was longer and more oblong than that of *P. aleutica*. The anther-stigma distance of *P. caerulea* was longer than that of *P. aleutica*. These morphological differences suggest that flowers of *P. caerulea* are more suitable for outcrossing than those of *P. aleutica*. The anther-stigma distance of *P. aleutica* tended to increase in the late-snowmelt populations. This supports our previous results that *P. aleutica* increased outcrossing success but decreased selfing ability by autodeposition in late-snowmelt populations. The corolla color of both species varied considerably among populations within each snowbed, however, directional trends in changing patterns were not detected along the snowmelt gradients. Coefficients of variation in corolla length, corolla shape, and anther-stigma distance did not show any directional patterns along the snowmelt gradients in either species. Although clear directional trends in most floral traits were not detected along the snowmelt gradients, these traits were more variable among populations within each site than among sites in both species. Thus, differences in snowmelt timing may be an important factor maintaining genetic variations within a local area.

key words: anther-stigma distance, corolla color, corolla shape, phenotypic variation, snowmelt timing

Introduction

In alpine snowbeds, steep snowmelt gradients may create variations in biotic and abiotic environments which affect various reproductive traits of plant species. For example, pollination efficiency varies considerably among plant populations selected along the snowmelt gradients because flowering phenology is directly affected by the snowmelt timing (Kudo, 1993; Totland, 1993, 1994a). Low availability of insect pollination often accelerates the selfing ability of plants (Arroyo *et al.*, 1985; Eriksen *et al.*, 1993). Likewise, when several species compete with each other for pollinator acquisition, less-competitive species sometimes show high selfing rates (Wyatt, 1986). In this context, comparison of closely related sympatric plant species along the snowmelt gradients is a very interesting approach to reveal biological interactions in an alpine

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ecosystem, for instance consequences of competition for pollinator acquisition and reproductive success of plants.

Phyllodoce caerulea (L.) Babington and *Phyllodoce aleutica* (Spreng.) A. Heller are ericaceous evergreen dwarf shrubs. They often coexist in snowbeds of the Taisetsu Mountains, northern Japan, and are mainly pollinated by bumblebees. These shrubs are distributed widely along snowmelt gradients, and the antheses of both species overlap in the same places (Kudo, 1991). We have investigated competition for pollinator acquisition, foraging behavior of bumblebees, and reproductive systems of these species at the Hisagonuma research site, central Taisetsu Mountains (Kasagi and Kudo, unpublished data). Although bumblebee visitation to *P. caerulea* was common in early- to middle-snowmelt places, bumblebees shifted their preference from *P. caerulea* to *P. aleutica* in late-snowmelt places. This is because nectar production per unit area (*i.e.*, a reward for bumblebees) was larger in *P. caerulea* than in *P. aleutica* in early- to middle-snowmelt places, but vice versa in late-snowmelt places. Furthermore, we estimated the extent of outcrossing success and autodeposition efficiency along the snowmelt gradient by comparing the seed set between the intact control and net-bagging plants. *Phyllodoce caerulea* showed successful outcrossing in the early- to middle-snowmelt places and low autodeposition ability, but failed in successful seed-setting in late-snowmelt places because of its decrease in pollinator attractiveness. On the other hand, *P. aleutica* showed high autodeposition ability in early- to middle-snowmelt places, but it showed high outcrossing success and abrupt decrease in autodeposition ability in late-snowmelt places. We suppose that these differences in reproductive characteristics between species might be caused by bumblebees' behavior as a strong selective pressure acting on pollination efficiency.

Plants pollinated by bumblebees sometimes express characteristic floral morphs, such as changes in corolla tube length related to the proboscis lengths of specific bumblebee species (Suzuki, 1992). If the populations of both *Phyllodoce* species are genetically isolated along the snowmelt gradients, corolla morphology may vary between and/or within species by the extent of efficiency of bumblebee pollination. The distance between anther and stigma often affects the selfing efficiency (Jacquemart and Thompson, 1996; Karron *et al.*, 1997; Affre and Thompson, 1998; Paillet *et al.*, 1998). Thus, the following hypothesis can be presented in the light of previous results: *P. caerulea*, an effective outcrosser, may have long anther-stigma distance in all populations. On the other hand, *P. aleutica* may have short distance in early- to middle-snowmelt populations where selfing by autodeposition is predominant, but it may increase the distance in late-snowmelt populations where frequent bumblebee visitation is expected.

Flower color is an important characteristic that affects the visitation preferences of pollinators (Real *et al.*, 1982; Stanton, 1987; Meléndez-Ackerman and Campbell, 1998). Generally, the corolla color of *P. caerulea* is pinkish, and that of *P. aleutica* is whitish-yellow. Although we concluded that the shift of bumblebees' preference from *P. caerulea* to *P. aleutica* was affected by changes in nectar production per unit area along the snowmelt gradient (Kasagi and Kudo, unpublished data), it is also important to quantify the variation of corolla color for both species.

Variations in mating systems sometimes affect genetic structures of plant popula-

tions (Sun *et al.*, 1998; Jones and Gliddon, 1999). Therefore, variations in reproductive situations caused by pollinators may affect the phenotypic variations in floral characteristics among populations. Some parameters of floral traits, including flower color, flower size, and arrangement of anthers and stigma have been compared in previous studies (*e.g.*, Tourjee *et al.*, 1995; Campbell, 1996; Odasz and Savolainen, 1996). In this study we compare the coefficients of variation of the corolla morphology and anther-stigma distances of both *Phyllodoce* species among populations selected along the snowmelt gradients.

Our major objective in this study is to answer the following questions: Do floral characters differ between the species, among sites, and among populations along the snowmelt gradients? If so, do such variations reflect the general trends of reproductive systems of both species, namely, the contrastive outcrossing success between the species along the snowmelt gradients and the abrupt decrease in autodeposition ability of *P. aleutica* in the late-snowmelt places?

Materials and methods

Phyllodoce caerulea is widely distributed throughout Arctic regions, whereas *P. aleutica* is distributed only around the North Pacific region. Both species are common and cooccur in the Taisetsu Mountains (43°33'N, 142°53'E, peak altitude: 2290 m). Both species in this area are pollinated mostly by bumblebees, *Bombus hypocrita sapporensis* Cockerell and *Bombus beaticola moshkarareppus* Sakagami et Ishikawa. *Bombus hypocrita* was dominant, and appeared earlier than *B. beaticola* (Kasagi and Kudo, unpublished data).

We selected three sites for replication, in the central part of the Taisetsu Mts., Hisagonuma, Goshikigahara, and Mt. Pon-kaun (Fig. 1; hereafter, HIS, GOS, and

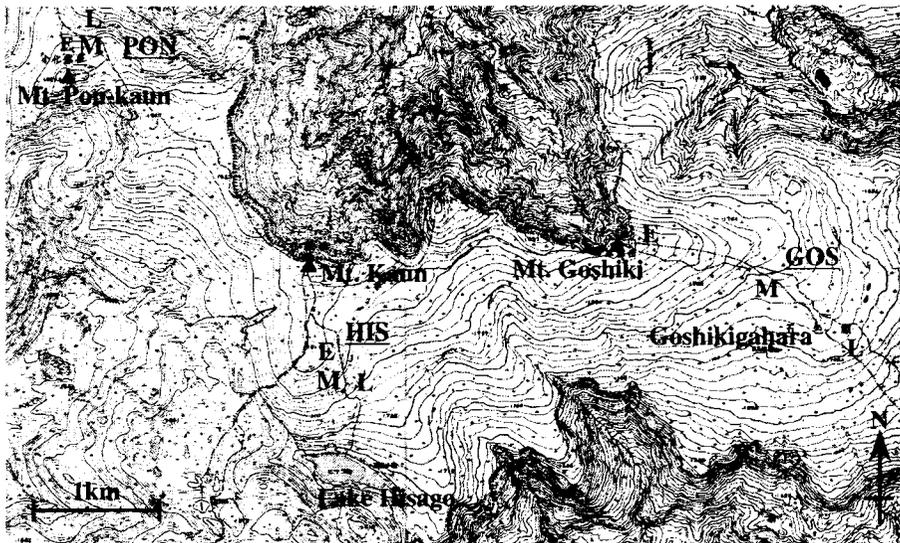


Fig. 1. Locations of three study sites (HIS, GOS, and PON) and quadrats arranged along the snowmelt gradients (E, M, and L). 'E' was set at the earliest snowmelt place, 'L' was the latest one, and 'M' was the intermediate one in each site.

PON, respectively). The HIS site is located on a south-east facing slope at 1800 to 1880 m a.s.l. near Lake Hisago. GOS is located on a south facing gentle slope at 1700 to 1840 m a.s.l., about 3–4.5 km east of HIS. PON is located on a north-east facing slope at 1800 to 1850 m a.s.l., about 3.5 km north-west of HIS. Three quadrats were established in order of snowmelt time at each site (hereafter, HIS-early, HIS-middle, and HIS-late in HIS; GOS-early, GOS-middle, and GOS-late in GOS; PON-early, PON-middle, and PON-late in PON, respectively). All quadrats were 20×20-m. Snow melted in mid-June at early melting quadrats, in early-July at middle ones, and in late-July at late ones. Onset of flowering of *Phyllodoce* species started about two weeks after snowmelt, and anthesis was continued about a week at each quadrat. Both species need about a month for seed maturation (Kudo, 1991).

At each quadrat, one flower from each 100 individual plants was randomly collected soon after corolla opening for each species in 1999. Corolla length, corolla width, and the distance between anthers and stigma (hereafter, anther-stigma distance) were measured with a digital caliper in the field. We defined the corolla shape as corolla length/corolla width. Corolla color was measured by a spectrophotometer (NF-777, Nippon Denshoku Kogyo Co., Japan), which measures color numerically and nondestructively through a 3 mm diameter sensor, in the field. Corolla color was recorded by an a*-b* unit which records hue and saturation. The a* and b* can be expressed as numerical values on dimension (see Appendix); a* expresses a situation between red direction (+) and green direction (-), and b* expresses a situation between yellow direction (+) and blue direction (-).

Two-way ANOVAs, factored with site and species, were conducted to compare the species for corolla length, corolla shape, and anther-stigma distance using pooled data from all three quadrats at each site. Thereafter, frequency distributions of corolla length, corolla shape, and anther-stigma distance were compared between the species using pooled data from all sites. In intraspecific comparisons, two-way ANOVAs factored with site and quadrats were conducted for corolla length, corolla shape, and anther-stigma distance for each species. As a post-hoc test, a Bonferroni test was conducted among quadrats at each site for both species, for corolla length, corolla shape, and anther-stigma distance.

Coefficients of variation (CV) of corolla length, corolla shape, and anther-stigma distance were compared among quadrats of every site for each species. To confirm whether directional trends occur along the snowmelt gradient in CV data, a Friedman test, factored with site and snowmelt order (*i.e.*, quadrat), was conducted for each trait in each species. Averages and standard deviations (s.d.) of a* and b* were compared between the species at each site, and among quadrats of every site for each species.

Results

In the interspecific comparisons, significant differences were detected in corolla length, corolla shape, and anther-stigma distance between the species and among sites, although interactions between species and sites existed in all variables (Table 1). The corolla length of *P. caerulea* was longer than that of *P. aleutica* (Fig. 2A). The average corolla length at each site of *P. caerulea* (7.6–8.2 mm) was apparently longer than that

Table 1. Two-way ANOVA table of corolla length, corolla shape, and anther-stigma distance among study sites (HIS, GOS, PON) and between species (*P. caerulea* and *P. aleutica*).

Source of variation	df	MS	F	P
Corolla length				
site	2	72.89	137.81	< 0.0001
species	1	696.26	1316.45	< 0.0001
site x species	2	6.13	11.59	< 0.0001
residual	1791	0.52		
Corolla shape				
site	2	0.88	44.32	< 0.0001
species	1	10.40	520.63	< 0.0001
site x species	2	0.20	10.15	< 0.0001
residual	1791	0.20		
Anther-stigma distance				
site	2	2.29	9.17	< 0.0001
species	1	756.73	3025.38	< 0.0001
site x species	2	2.51	10.05	< 0.0001
residual	1791	0.25		

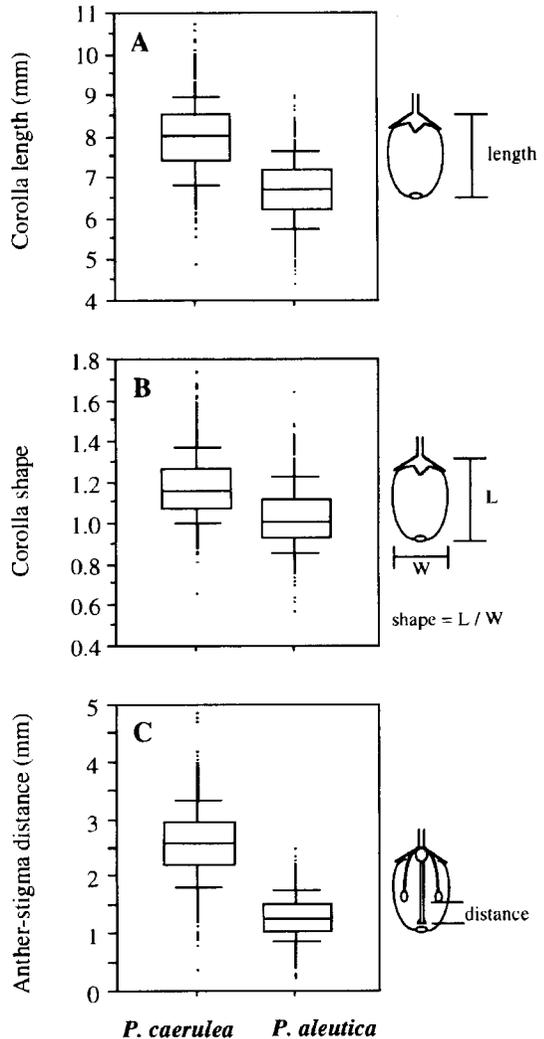


Fig. 2. Boxplots of corolla length (A), corolla shape (B), and anther-stigma distance (C) in each species. The top of a box represents the 75th percentile and the bottom the 25th percentile, and a box thus contains the middle 50% of the values, the line in the box represents the median. The top whisker ranges from the 75th to the 90th percentile and the bottom whisker from the 25th to the 10th percentile. The circles represent outliers.

of *P. aleutica* (6.4–7.1 mm). The corolla shape of *P. caerulea* was more oblong than that of *P. aleutica* (Fig. 2B). The average value of corolla shape at each site ranged from 1.1 to 1.2 in *P. caerulea*, and 1.0–1.1 in *P. aleutica*. The anther-stigma distance of *P. caerulea* was twice as long as that of *P. aleutica* (Fig. 2C). The average value of anther-stigma distance at each site of *P. caerulea* ranged from 2.5 to 2.7 mm, whereas that of *P. aleutica* was a uniform 1.3 mm at all sites. These results suggest that *P. caerulea* flowers, having large corolla and distinct separation of anthers and stigma, are morphologically more suitable for outcrossing than *P. aleutica* flowers.

In the intraspecific comparisons, corolla length, shape, and anther-stigma distance of *P. caerulea* were significantly different among sites and populations, although interactions between site and population were detected in all variables (Table 2). The corolla length and shape of *P. aleutica* significantly differ among sites and among populations. The anther-stigma distance of *P. aleutica* did not differ significantly among sites, but it was significantly different among quadrats. The changing patterns of each trait among populations were not consistent along the snowmelt gradients throughout the sites (Fig. 3), but these traits were more variable among quadrats within sites than among sites. Although the corolla length of *P. caerulea* decreased in the late-snowmelt populations at GOS and PON, that of *P. aleutica* increased in the middle- and late-snowmelt populations at GOS (Fig. 3A). Corolla shape became oblong in the later snowmelt populations at PON for both species and at GOS for *P. aleutica* (Fig. 3B). Trends in anther-stigma distance along the snowmelt gradients were opposite between the species (Fig. 3C). At GOS and PON, the anther-stigma distance of *P. caerulea* decreased, while that of *P. aleutica* increased in the later snowmelt populations. Corolla length (x) and anther-stigma distance (y) of *P. caerulea* were correlated positively ($y = 0.32x + 0.04$, $R^2 = 0.20$, $n = 898$, $P < 0.0001$). Correlation between corolla length and anther-

Table 2. Two-way ANOVA table of corolla length, corolla shape, and anther-stigma distance among study sites and quadrats for each species.

Source of variation	<i>P. caerulea</i>				<i>P. aleutica</i>			
	df	MS	<i>F</i>	<i>P</i>	df	MS	<i>F</i>	<i>P</i>
Corolla length								
site	2	35.57	93.62	< 0.0001	2	43.49	121.87	< 0.0001
quadrat	2	26.26	69.13	< 0.0001	2	1.96	5.50	0.0042
site x quadrat	4	42.20	111.08	< 0.0001	4	16.56	46.41	< 0.0001
residual	890	0.38			890	0.36		
Corolla shape								
site	2	0.29	16.94	< 0.0001	2	0.80	60.02	< 0.0001
quadrat	2	0.53	31.18	< 0.0001	2	0.88	66.12	< 0.0001
site x quadrat	4	0.63	37.02	< 0.0001	4	0.86	64.63	< 0.0001
residual	890	0.02			890	0.01		
Anther-stigma distance								
site	2	4.79	15.44	< 0.0001	2	0.01	0.12	0.8988
quadrat	2	5.16	16.63	< 0.0001	2	4.11	31.84	< 0.0001
site x quadrat	4	7.60	24.49	< 0.0001	4	1.96	15.18	< 0.0001
residual	890	0.31			890	0.13		

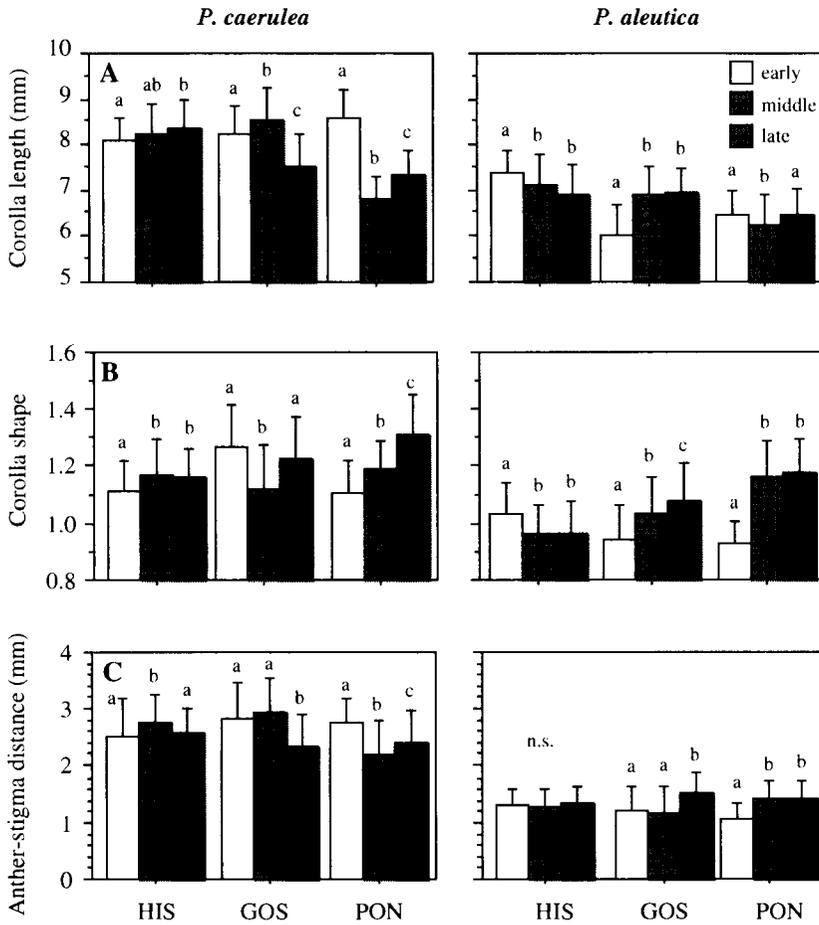


Fig. 3. Intraspecific comparisons of corolla length (A), corolla shape (B), and anther-stigma distance (C) between the species among sites and quadrats. Vertical bars indicate s.d. Different letters indicate significant differences among quadrats in each site according to Bonferroni test at $P < 0.0167$.

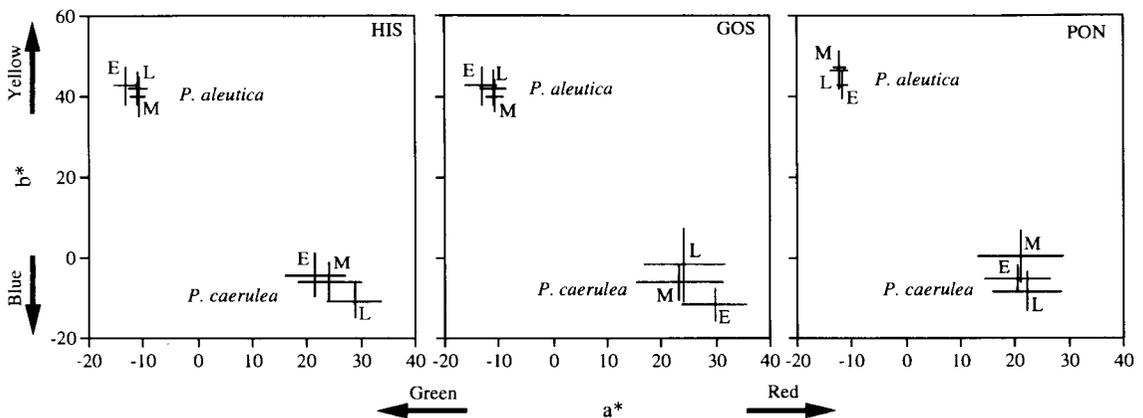


Fig. 4. Numerical values of corolla color, expressed by a^* (direction to red or green) and b^* (direction to yellow or blue) dimensions in each site. Horizontal bars indicate s.d. of a^* , vertical bars indicate s.d. of b^* . Crossing point of each bar is value of a^* and b^* . See appendix for actual color distribution.

Table 3. CVs of corolla length, corolla shape, and anther-stigma distance of all populations. *P. c* means *P. caerulea*, and *P. a* means *P. aleutica*.

	Corolla length		Corolla shape		Anther-stigma distance		
	<i>P. c</i>	<i>P. a</i>	<i>P. c</i>	<i>P. a</i>	<i>P. c</i>	<i>P. a</i>	
HIS	E	5.9	6.9	9.5	9.9	26.7	21.3
	M	8.3	9.3	11.0	10.6	18.6	27.6
	L	7.6	9.8	12.3	12.3	16.2	23.7
GOS	E	7.7	10.7	12.0	12.5	21.7	37.8
	M	8.3	9.0	14.0	15.6	20.3	40.1
	L	9.4	7.4	12.4	12.0	23.8	25.2
PON	E	7.9	8.4	10.6	8.8	15.1	26.0
	M	7.2	10.1	8.9	11.4	28.1	24.5
	L	7.2	8.6	10.9	10.1	23.0	22.8
P-level*	> 0.1	> 0.1	> 0.1	> 0.1	> 0.1	> 0.1	

* Friedman test factored with site and quadrat in each variable for each species.

stigma distance of *P. aleutica* was weakly positive ($y=0.14x+0.39$, $R^2=0.07$, $n=900$, $P<0.0001$).

The corolla color of *Phyllodoce* species differed largely among quadrats within every site (Fig. 4). However, directional trends in changing patterns were not detected along the snowmelt gradients.

The CV of anther-stigma distance showed wider ranges than that of corolla length and corolla shape in both species (Table 3). CVs of all traits did not show any directional trends along the snowmelt gradients in either species ($P>0.10$, Friedman test).

Discussion

The anther-stigma distance of *P. caerulea* was twice as long as that of *P. aleutica*. Although pollen of bagged *P. caerulea* flowers was mainly deposited around the middle part of the style, stigma surfaces of bagged *P. aleutica* flowers were covered with a considerable amount of self pollen. Therefore the difference in anther-stigma distance between species observed in this study, though slight, was enough to affect the auto-deposition efficiency and outcrossing success. In addition to high attractiveness for pollinators, spatial separation of anthers and stigma in *P. caerulea* should increase the outcrossing efficiency. On the other hand, flower productivity and nectar secretion of *P. caerulea* were sensitively reduced by the short growing season in the late-snowmelt places (Kasagi and Kudo, unpublished data). Thus, reduction of corolla length of *P. caerulea* at the late-snowmelt quadrats in GOS and PON might be caused by the short growing season. Because there was a positive correlation between corolla length and anther-stigma distance, the decrease in anther-stigma distance observed in *P. caerulea* at the late-snowmelt quadrats was supposed to be affected by the restriction of resources for reproduction. On the other hand, the anther-stigma distance of *P. aleutica* in-

creased at the late-snowmelt quadrats at GOS and PON, although physiological activities of *P. aleutica* as well as *P. caerulea* were also reduced by the short growing season (Kasagi and Kudo, unpublished data). In our previous study, enhanced bumblebee visitation due to decreasing the attractiveness of competitive species (*i.e.*, *P. caerulea*), high seed production by outcrossing, and the decrease in selfing rate by autodeposition were revealed in *P. aleutica* in the late-snowmelt populations (Kasagi and Kudo, unpublished data). The acceleration of anther-stigma separation in *P. aleutica* in the late-snowmelt populations may be concerned with modification of the reproductive system (Fenster and Ritland, 1994).

Corolla color variations of both *Phyllodoce* species did not show any directional patterns along the snowmelt gradients. This fact supports our finding that the shift of bumblebees' preference from *P. caerulea* to *P. aleutica* did not reflect the changes in corolla color, but those in nectar production. Distinct separation of corolla color between the species throughout the snowmelt gradients (Fig. 4) may make it easy for bumblebees to identify the species, depending on the nectar content.

Values of each floral trait measured in this study were more variable among quadrats (populations) within each site than those among sites. It is necessary to clarify the extent to which these phenotypic variations reflect genetic variations. If these phenotypic variations partly reflect genetic variations among populations along the snowmelt gradient, this would demonstrate that variations in flowering phenology caused by differences in snowmelt timing act as a selective force preventing gene flow among populations. In a previous study (Stanton *et al.*, 1997), clear genetic separation was not detected in the snow buttercup (*Ranunculus adoneus*) within a very narrow area (50×100-m) across a snowmelt gradient. It was speculated that effective seed and/or pollen movements across the snowmelt gradient occurred. Further research should be conducted by using species having different reproductive systems and/or at a different scale of the snowmelt gradients.

Genetic variations sometimes differ among populations due to differences in pollination effectiveness (Andersson and Widén, 1993). If the modification of autodeposition efficiency observed in *P. aleutica* was a general phenomenon, genetic variation within populations may change along the snowmelt gradients. However, clear directional trends were not detected in CVs of corolla length, corolla shape, and anther-stigma distance, and in s.d. of corolla color along the snowmelt gradients in this study. The flowering timing of each population is highly variable among years because of yearly fluctuation of snowmelt timing in snowbeds (Kudo, 1991). Since pollinator activity is highly influenced by climatic conditions (Bliss, 1971; Heinrich, 1975; Inouye and Pyke, 1988; Corbet, 1990; Corbet *et al.*, 1993; Totland, 1994b), the efficiency of pollination success depends on local climate during the flower season in each year. Moreover, the floral density of these *Phyllodoce* species extensively fluctuates from year to year, especially in late-snowmelt places (Kasagi and Kudo, unpublished data). These yearly fluctuations of biotic and abiotic factors should affect the seed production and selfing rates of each population. Therefore, any directional trend of floral characteristics might be difficult to develop in this system. More extensive studies of genetic structure, phenotypic variation, and mating system of alpine plants are needed with reference to environmental fluctuation both in space and time.

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Appendix Actual color distribution of a^* and b^* , copied from the brochure of the spectrophotometer (NF-777, Nippon Denshoku Kogyo Co., Japan).

