

NATURAL SELECTION FAVORS RAPID REPRODUCTIVE PHENOLOGY IN *POTENTILLA PULCHERRIMA* (ROSACEAE) AT OPPOSITE ENDS OF A SUBALPINE SNOWMELT GRADIENT¹

KRISTINA A. STINSON²

Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544 USA and Rocky Mountain Biological Laboratory (RMBL), Gothic, Colorado 81224 USA

In high altitude plants, flowering quickly ensures reproductive success within a short snow-free period, but limits maturation time and fecundity. Natural selection on prefloration intervals may therefore vary in contrasting snowmelt environments and could influence the outcome of phenological responses to climatic change. This study investigated adaptive differentiation and plasticity of prefloration intervals in the subalpine perennial *Potentilla pulcherrima*. Three years of in situ field observations were combined with phenotypic selection analyses and a common garden experiment. Plants from high, intermediate, and low altitudes expressed similar prefloration intervals and plasticity when grown at common altitude, indicating no evidence for adaptive differentiation. Selection on the prefloration interval was negative at both low and high altitudes before and after accounting for strong positive selection on size. Environmental differences between high and low altitudes indicated that long, dry seasons and short, wet seasons both favored rapid reproduction. Therefore, quicker reproduction was adaptive in response to late snowmelt, but slower reproduction in response to earlier snowmelt appeared to be maladaptive. Selection differed marginally between late snowmelt years and dry ones. Plastic responses to future precipitation patterns may therefore have positive or negative effects on fitness within a single species, depending upon altitude and year.

Key words: phenology; plasticity; *Potentilla pulcherrima*; reproduction; selection; snowmelt; subalpine plant.

In seasonal environments, the proper timing of reproduction is critical for maximizing fitness (Reekie and Bazzaz, 1987; Kozłowski, 1992) and is therefore likely to be influenced by natural selection. By influencing the abiotic and biotic environment in which reproduction takes place, flowering phenology can strongly influence seed number (Alatalo and Totland, 1997; Totland, 1999), pollination success (Waser, 1978; Gross and Werner, 1983; Totland, 1997; Gugerli, 1998), and the likelihood of seed predation (Gross and Werner, 1983; Brody, 1997). Quick or slow flowering also determines the allocation of resources to growth vs. reproductive output (Reekie and Bazzaz, 1987; Kozłowski, 1992; Molau, 1993). While ecotypic differentiation in flowering times is common in natural plant populations (Turesson, 1922; Clausen et al., 1948; Gross and Werner, 1983; Lacey and Pace, 1983; Kudo, 1992; Pickering, 1995; Stanton et al., 1997; Gugerli, 1998; Del Pozo et al., 2002; Fitter and Fitter, 2002), little is known about variation in the underlying developmental rates that determine the chronological timing of reproduction (Diggle, 1999). During each growing season, developmental signals to switch meristem allocation from growth to reproduction may involve both genetic and environmental cues (Geber, 1990; Stratton, 1998; Simpson and Dean, 2002; Yanovsky and Kay, 2002). The duration of

the prefloration and other intervals may therefore be plastic (Aydelotte and Diggle, 1997; Luzar, 2001) or genetically fixed (Sørensen, 1941).

Rapidly changing precipitation, temperature, and other climatic factors over the next century (Houghton et al., 1996) are likely to destabilize seasonal and genetic cues for developmental shifts between growth and reproduction each year (e.g., Inouye et al., 2002). Altered maturation rates may in turn affect reproductive output, interactions among species, and the overall functioning of ecosystems. It is therefore important to understand the extent of environmental and evolutionary processes governing variation in the prefloration interval.

Temperate mountain and polar regions may be particularly susceptible to a rapidly changing environment because of the sensitivity of plant phenology to the timing of snowmelt (e.g., Galen and Stanton, 1995; Price and Waser, 1998; De Valpine and Harte, 2001; Theurillat and Guisan, 2001; Inouye et al., 2002). Spatial and temporal patterns of snow pack, rather than photoperiod, strongly influence the date and abundance of flowering in these systems (Inouye and McGuire, 1991; Walker et al., 1995; Inouye et al., 2002). Variation among arctic and alpine species suggests that trade-offs between growth and reproduction have led to divergent strategies for ensuring reproductive success in early and late melting sites (Molau, 1993; Prock and Körner, 1996; Theurillat and Schlüssel, 2000). “Pollen-risk” species flower quickly to ensure maturation of seeds within a short growing season, but they risk reduced pollination success, small size at reproduction, and/or low seed numbers (Waser, 1978; Stenstrom and Molau, 1992; Molau, 1993; Totland, 1997; Gugerli, 1998; Totland and Eide, 1999). “Seed-risk” species mature more slowly to enhance growth and fecundity, but they may lose larger numbers of seeds if the growing season ends prior to fruit maturation (Molau, 1993; Galen and Stanton, 1995).

¹ Manuscript received 2 September 2003; revision accepted 4 December 2003.

The author thanks D. Stratton, H. Horn, M. Price, N. Waser, and K. Donohue for discussions on design, results, and analyses; K. Donohue, T. Seidler, A. Wilczek, K. Woods, and two anonymous reviewers for comments on the manuscript; the Rocky Mountain Biological Laboratory for logistical support; and E. Baumgartner, S. Borges, M. Carroll, M. Lett, E. Mathai, and D. Wallace-Senft for invaluable field assistance. Financial support was provided by a Doctoral Dissertation Improvement Grant from the National Science Foundation (DEB-9520859), a graduate research fellowship from Princeton University, and the Lee Snyder Scholarship for Graduate Research at RMBL.

² Present address: Harvard Forest, PO Box 68, Petersham, MA 01366 USA.

Within a species, adaptive modifications to the prefloration interval may arise from phenotypic plasticity, genetic variation, or both. While snowmelt generally occurs later with increasing altitude, environmental conditions can also change dramatically over very short distances and from year to year within a site (Sørensen, 1941; Inouye and McGuire, 1991; Galen and Stanton, 1995; Wagner and Mitterhofer, 1998; Inouye et al., 2002). Plastic phenological responses to spatial and temporal heterogeneity in snowmelt timing have been shown to increase fecundity in alpine plants (McGraw, 1987; Emery et al., 1994; Aydelotte and Diggle, 1997; Diggle, 2002). In other species, ecotypic differentiation in reproductive dates can arise along local and altitudinal snowmelt gradients, particularly if spatial separation of reproductive events precludes gene flow among altitudes (Robertson, 1895; Turesson, 1922; Clausen et al., 1948; Bliss, 1962; Gross and Werner, 1983; Waser and Price, 1985) or contrasting microsites (Bliss, 1956; Billings and Bliss, 1959; Galen and Stanton, 1993; Wagner and Mitterhofer, 1998). The magnitude and direction of natural selection on a given trait may also vary considerably among contrasting habitats (Bennington and McGraw, 1995; Caruso, 2001) and in climatically different years (Kalisz, 1986).

The extent to which plants in high altitude systems can endure climatic changes will therefore depend upon the potential for adaptive plasticity and/or genetic changes in reproductive phenology under new environmental conditions (Geber and Dawson, 1993). An initial step towards understanding evolutionary potential within extant populations is to examine relationships between size, reproductive maturation rates, and fitness under natural and experimental conditions. It is possible to infer that a trait is adaptive when there are strong correlations between that character and a fitness estimator (Lande and Arnold, 1983; Mitchell-Olds and Shaw, 1987). For instance, strong, negative relationships between prefloration times and seed numbers would indicate that quick flowering is adaptive in a given environment. Such work can greatly enhance traditional measures of phenological variation along high altitude snowmelt gradients by directly testing hypotheses about the adaptive significance of flowering quickly or slowly in different environments. However, despite their potential importance for understanding plant responses to future selective regimes, very few studies have made direct measures of phenotypic plasticity and natural selection on the reproductive phenology within high altitude species, particularly while accounting for possible relationships between size and the timing of reproduction (Stanton et al., 1997; Totland, 1999).

In this study, I used three years of field observations, phenotypic selection-regression techniques (Lande and Arnold, 1983; Mitchell-Olds and Shaw, 1987), and a classical common garden experiment to test for ecotypic differentiation and/or adaptive plasticity in the prefloration interval of the subalpine plant *Potentilla pulcherrima* Lehmann (Rosaceae). This herbaceous, long-lived perennial plant is found primarily in open, subalpine meadows in western North American mountainous regions. *Potentilla pulcherrima* is iteroparous; it flowers and fruits each year after the first year of growth, and recruitment is usually via locally dispersed seeds (personal observation). On the western slope of the Rocky Mountain range, this species is found between 2200 and 3700 m in altitude, in sites with relatively deep soils and regular accumulation of winter snow pack (Weber and Wittmann, 1996). It tends to dominate or co-dominate in mixed perennial communities, along with occasional shrubs, grasses, sedges, and other angiosperms such

as *Delphinium nuttallianum*, *Frasera speciosa*, *Ipomopsis aggregata*, *Helianthella quinquenervis*, and *Erigeron speciosus*. Within the subalpine zone, lower altitude meadows are typically released earlier from snow cover than those at higher altitudes. As altitude increases, vegetation density and temperature tend to decrease, and soil moisture tends to increase (Billings and Bliss, 1959; Ehleringer and Miller, 1975; Bell and Bliss, 1979; Bliss, 1985; Benedict, 1990). Lower altitude meadows are therefore potentially subject to late-season droughts, whereas less densely populated, higher elevation sites retain more soil moisture yet provide a shorter snow-free period. Microtopographical exposure gradients create smaller-scale variation in snowmelt timing within each altitude that may offset the general altitudinal patterns. For instance, sparse vegetation and dry conditions can predominate on early melting slopes at the lower altitudes, whereas lush vegetation may predominate in warmer, early melting sites at higher altitudes.

Utilizing the natural variation in snowmelt timing found across *P. pulcherrima*'s altitudinal range, I asked the following: (1) Does the prefloration interval differ among altitudes, and if so, is this variation due to ecotypic differentiation, phenotypic plasticity, or both? (2) Does natural selection on the prefloration interval indicate that these differences in phenology are adaptive?

MATERIALS AND METHODS

Field observations—Fifteen natural populations of *P. pulcherrima* in west central Colorado, USA, were studied for three consecutive years (1994–1996). Study populations were located along an altitudinal gradient in the Gunnison National Forest in western Colorado. Five 20 × 5 m² plots were constructed within randomly selected subalpine meadows at each of three altitudes: 2600–2900 m (low), 2900–3200 m (intermediate), and 3200–3600 m (high). Plots were evenly divided into eight sections for environmental measurements. Date of snowmelt, percentage vegetative cover, soil temperature, and gravimetric soil moisture were measured at each section on a weekly basis. Soil cores were taken at 15–20 cm depth, to ensure sampling within the rooting zone.

At each plot, 25 adult *P. pulcherrima* plants were randomly selected and permanently tagged (125 per altitude) for weekly phenology censuses and size measurements. The following phenological variables were recorded in the field: date of first spring foliage appearance (emergence date), number of flowers, and number of fruits. Initial and peak reproduction dates and the number of days from emergence date to full flowering (prefloration interval) were derived from these data. Individual fitness was estimated as the total number of ripened fruits (number of fruits) harvested from each plant at each census. *Potentilla* is acrocarpous, producing a large number of distinct individual seeds (nutlets) per fruit. Final plant size was estimated in terms of maximum leaf area (leaf area), based on weekly measurements of rosette length and width. The estimator for leaf area, $A = \pi (0.5 \text{ rosette length} \times 0.5 \text{ rosette width})$, is strongly correlated with dry biomass (Stinson, 1998).

Common garden experiment—Three 12 × 15 m transplant gardens were constructed along an exposure gradient from approximately 2870 m to 3000 m in a subalpine meadow near the Rocky Mountain Biological Laboratory (RMBL), Gothic, Colorado. Snowmelt generally varies by ~5–7 d along this local gradient (personal observation). Ninety previously marked *P. pulcherrima* adults from each altitude were excavated prior to emergence from their native sites and were temporarily protected by a thin layer of snow. Thirty replicate plants from each altitude were then transplanted in a Latin-square design into each garden (3 gardens × 3 altitudes × 30 replicates per altitude per garden = 270 plants). All individuals were planted on a cool, rainy day (5 June 1996) and were identified by the altitude of origin with aluminum tags. During the second growing season after transplanting (May to August 1997), individual plants were monitored on a weekly basis to obtain emergence date, flowering date, prefloration interval, leaf area, and fecundity mea-

TABLE 1. *F* ratios from analyses of variance comparing environmental variables and plant variables, over 3 yr and among low, intermediate, and high altitude populations of *Potentilla pulcherrima* in Gunnison National Forest, Colorado, USA. * *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001.

Effect	Date of snowmelt	Percentage of soil moisture	Soil temperature	Percentage of plant cover	Reproductive date (julian date)	Pre-reproductive interval (d)	Seasonal live shoot interval (d)	Leaf area (cm ²)	Total fruits (number)
Year	356.73***	20.56***	2.23	51.32***	1131.809***	18356***	26.25***	33.78***	13.75***
Altitude	92.83***	1.16	4.59*	0.32	11.68**	80.67***	67.12***	30.64***	8.24*
Plot [altitude]	2.14*	3.19**	0.75	1.14	6.08***	1.54	1.56	7.28***	3.11**
Year × altitude	1.81	1.46	1.16	1.27	4.40**	2.28	16.76***	1.24	3.48*
Year × plot [altitude]	13.28***	2.36***	0.19	0.84	4.60***	4.92***	3.63***	1.46	1.66*

surements as described earlier. Snowmelt dates were recorded within each quadrant as the date of first appearance of bare ground in 1996 and 1997. Weekly gravimetric soil moisture measurements were obtained in 1997 at the rooting level at 12 designated points within each garden (three samples per quadrant).

Data analysis—Seasonal averages of all field observations (environmental and plant variables) were compared using an analysis of variance model with fixed main effects: year, altitude, and the year × altitude interaction term. Plot number was included as a nested, random effect in the model to control for environmental variability within altitudes. The effect of altitude was tested over the nested factor, plot. The model also included the random crossed effect of year × plot, which was used as the denominator mean square in the *F* test for effects of year and year × altitude. A repeated measures model was not used in this study because the considerable environmental variation among years precludes the assumption that responses of individual plants are parallel through time (Sokal and Rohlf, 1995, pp. 345–346). Large differences among years warrant the consideration of year × altitude and year × plot interactions as separate terms, rather than as error (Sokal and Rohlf, 1995, pp. 342–346). Tukey's HSD post-hoc analyses were applied to significant effects when comparisons between years, altitudes, and/or plots within each altitude were necessary. To test for direct effects of environmental variation on plant performance, all environmental variables differing within or among altitudes were regressed against each measured plant trait. Forward stepwise regression was used to determine the best fit model without establishing a priori relationships between the predictor and response variables (Sokal and Rohlf, 1996, pp. 654–657). Regression variables differing from zero in the final regression equations were considered to affect a given plant trait.

The three common gardens were ranked by snowmelt date (early, intermediate, and late) for analysis. To capture potential effects of among-garden variation in soil moisture, plant variables were analyzed with a two-way ANCOVA (altitude of origin × garden) using soil moisture as a covariate. Using this model, two comparisons were made in order to assess the role of ecotypic variation and plasticity. First, following classical common garden transplant designs (Turesson, 1922; Clausen et al., 1948), populations were tested for ecotypic variation by comparing the phenotypic expression of individuals from distinct habitats grown together in a common environment. With this approach, an effect of altitude on a given trait within the transplant gardens would demonstrate ecotypic differentiation, whereas no effect of altitude would indicate plasticity for that trait. A second measure of phenotypic plasticity was made possible by the inclusion of garden number in the model. This allowed for a measure of phenotypic variation as a function of local environmental heterogeneity among the different gardens. An effect of garden number on a given trait was thus interpreted as evidence for plasticity in response to local snowmelt and soil moisture conditions in early, intermediate, and late melting common gardens. In both cases, plasticity was measured in the broadest sense (population level) and not in the narrow sense (genotypic level) (e.g., Bradshaw, 1965). Differences within and among the common gardens were compared with Tukey's HSD post-hoc analyses.

Phenotypic selection regression analyses (Lande and Arnold, 1983) were conducted on both in situ and experimental plants to estimate the magnitude and direction of selection acting on the timing of reproduction, before and after accounting for selection on plant total leaf area. Standardized linear (directional) selection differentials (\hat{s}) were estimated as the covariance be-

tween relative fitness and the standardized values for prefloration interval and leaf area. Selection differentials estimate the total selection on a trait, including both direct selection and indirect selection acting on correlated traits. Standardized linear (directional) selection coefficients (β) were derived from multiple regressions of relative fitness on the prefloration interval and leaf area. Selection coefficients describe the direct selection on a trait, after accounting for selection on other traits included in the model.

Estimates of total and direct selection were obtained for in situ plants from 1994 to 1996. Selection differentials (\hat{s}) and selection coefficients (β) were calculated separately in each year and for each elevation. To measure selection within each altitude, relative fitness was calculated as the total number of fruits produced by an individual in a given altitude by the mean number of fruits produced by all individuals in that altitude. Because selection may occur at different spatial scales, relative fitness was also measured across the entire gradient. Relative fitness across all altitudes was calculated by dividing the total number of fruits produced by an individual by the mean number of fruits of all individuals from all altitudes within a given year. Heterogeneity of slopes tests (ANCOVA) were used to test whether relationships between relative fitness and the measured traits differed among altitudes and among years. Estimates of total and direct selection were also obtained as described for experimental plants. Within the common gardens, \hat{s} and β were calculated separately for each native altitude. The model included garden number as a fixed effect to control for environmental differences among gardens. ANCOVA models were used to test whether relationships between relative fitness and the measured traits differed among altitudes and among gardens.

RESULTS

Field observations—The main environmental differences along the altitudinal gradient were date of snowmelt and soil moisture (Table 1). High altitude plots emerged from snow cover ~13 d later than intermediate altitude plots, and intermediate plots emerged ~11 d later than low altitude plots. The average dates of snow disappearance were 12 May 1994, 13 June 1995, and 15 May 1996 at low altitude; 28 May 1994, 23 June 1995, and 29 May 1996 at intermediate altitude; and 6 June 1994, 9 July 1995, and 15 June 1996 at high altitude. The 3–4 wk delay in snowmelt date at each altitude in 1995 was due to record-high snow accumulation during the preceding winter, as reported in weather records maintained by RMBL (B. Barr, RMBL, personal communication). Interannual variation in soil moisture was due to a late season drought in 1994, which reduced the percentage soil water content in each altitude by ~5% on average compared to the other two years (Turkey's HSD, *P* < 0.05). Although altitude did not have a significant effect on mean soil moisture, percentage soil water content was lower and declined more rapidly in the intermediate and early altitudes compared to high altitudes in all years, as shown for 1996 (Fig. 1). Effects of plot on snowmelt timing and soil moisture were explained primarily by heterogeneity among intermediate altitude plots during 1995 and 1996. Soil temperatures ranged from ~5° to 22°C throughout the growing season, with slightly lower temperatures at high

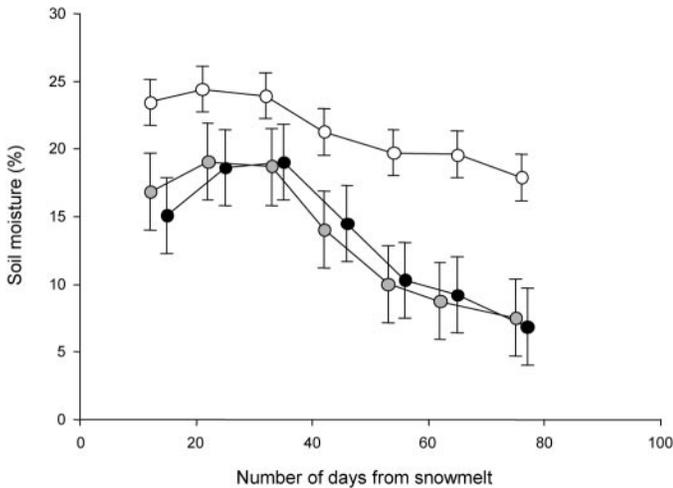


Fig. 1. Soil moisture at low, intermediate, and high altitude throughout the 1996 growing season at 20×5 m plots in Gunnison National Forest, Colorado, USA. Mean (± 1 SE) soil moisture is expressed as a percentage based on gravimetric data. The x-axis is the number of days from the mean snowmelt date at each altitude. Closed symbols correspond to low altitude; grey symbols correspond to intermediate altitude; open symbols correspond to high altitude.

altitude compared to the low and intermediate altitudes. Vegetative cover ranged from 60% to 100% and was similar across altitudes. A reduction of plant cover during the drought year was attributed to reduced foliage and early plant senescence at the time of measurement.

Field populations expressed interannual and altitudinal differences in all of the measured traits (Table 1). Tukey's HSD post-hoc analyses revealed differences ($P < 0.05$) among altitudes and among years as follows. The prefloration interval was shorter at progressively higher altitude, and these differences were conserved from year to year (Fig. 2a). Leaf area and number of fruits declined with progressively higher altitudes (Fig. 2b, c). Plants at low altitude reduced fruit production in 1994, but increased total leaf area and number of fruits during the late snowmelt year, 1995. Dates of reproduction (Fig. 2d) were later at high altitude compared to the intermediate and low altitudes. Plants from all altitudes reproduced 3–4 wk later in 1995 than in the other two years.

There were effects of plot, year \times altitude, and the three-way interaction term on number of fruits and reproductive dates. Tukey's HSD ($P < 0.05$) tests revealed that dates of reproduction differed among plots within the high altitude: earliest reproduction occurred consistently in the same two earliest melting plots every year. Plants also flowered earlier in the driest, low altitude plot compared to the other low altitude plots in 1994. The year \times altitude interaction effect on fruit number was explained by directional shifts in trait values among altitudes in the late snowmelt year: a reduction in fecundity in the intermediate and high altitudes in 1995 was accompanied by increased fecundity at low altitude.

Snowmelt date and soil moisture were the only environmental variables to affect the measured plant traits in the forward-stepwise regression analysis. Estimates for snowmelt date and soil moisture were different from zero in the final regression models for the prefloration interval and leaf area (Table 2), demonstrating that phenology and size are related to those environmental factors. Snowmelt date was the only

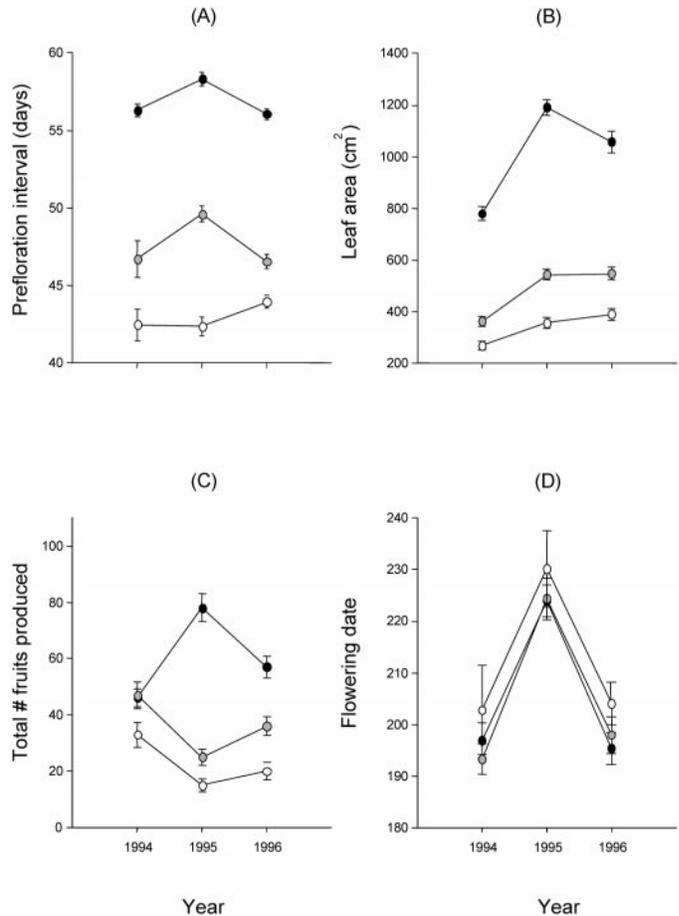


Fig. 2. Means (± 1 SE) of plant characters for *Potentilla pulcherrima* in each year of the study. Each line connects the mean value for plants at low (closed symbols), intermediate (grey symbols), and high (open symbols) altitude. The prefloration interval (panel A) is expressed in number of days; size and fecundity are shown in panels B and C; peak flowering date (D) is expressed as day of year.

parameter to affect fruiting date. None of the regression models yielded significant parameter estimates for environmental effects on total number of fruits.

Phenotypic selection within and among altitudes—Phenotypic selection analyses demonstrated strong relationships between prefloration intervals, plant size, and relative fitness in the field (Table 3a). The overall directional selection coefficient and the overall selection differential were both significantly positive when all altitudes were included in the analysis. This positive relationship between prefloration interval and relative fitness was driven by longer mean reproductive intervals and higher mean fecundity at progressively lower altitudes (Fig. 2). In contrast, the separate directional selection coefficients and differentials for each altitude were negative. Thus, selection acted in the direction of longer prefloration intervals when all altitudes were included in the model, but favored shorter prefloration intervals within each altitude separately. Selection coefficients and differentials for the prefloration interval were significantly negative in the low and high altitudes, but did not differ from zero in the intermediate altitude. Selection generally acted in the direction of larger size, irrespective of altitude. Selection coefficients and differentials

TABLE 2. Variable estimates and regression results for effects of snowmelt date (calendar day) and soil moisture (gravimetric) on the traits measured in situ for field populations of *Potentilla pulcherrima* in Gunnison National Forest, Colorado, USA. Regression results are shown for best fit models resulting from forward stepwise regression of each plant trait on all environmental data (snowmelt date, soil moisture, vegetation cover, and temperature).

Plant trait	Snowmelt date		Soil moisture		R ²	P
	Estimate	F	Estimate	F		
Prefloration interval	-0.28	16.91	+1.01	5.29	0.29	<0.001
Leaf area	-11.17	21.55	+45.13	8.36	0.34	<0.001
Flowering date	+0.69	97.97	63.86	1.51	0.80	<0.001
Number of fruits	—	0.049	—	0.25	—	NS

for total leaf area were positive overall and for each altitude analyzed separately, with the exception that β did not differ from zero at low altitude.

At each altitude, β and β for the prefloration interval were negative in 1995, but did not differ from zero during the drought year, 1994. A heterogeneity of slopes test on the 1994, 1995, and 1996 selection regression equations revealed nearly significant interannual effects on the relationship between prefloration interval and relative fecundity (ANCOVA for effects of prefloration interval, altitude, year, and all interaction terms: $F_{pre-repro} = 20.41, P < 0.001$; $F_{pre-repro \times year} = 2.33, P = 0.08$; all other effects in the model N/S). Thus, selection did not differ significantly across altitudes but was slightly different among years. Selection on size was positive at all altitudes in both the drought and late snowmelt years. Slopes of the size-fitness regression lines did not differ among years or among altitudes.

Ecotypic variation, plasticity, and natural selection in the common gardens—Snowmelt varied by 5 ± 2 d between the earliest and latest melting gardens in both years, and the rank order for mean snowmelt dates was conserved across the two years of the study. Snowmelt varied among gardens and among quads within gardens ($F_{garden} = 2.03, P < 0.01$; $F_{quad[garden]} = 2.05, P < 0.01$). Soil moisture ranged from 5% to 19% in all gardens throughout the season and varied within and among gardens ($F_{garden} = 1.58, P < 0.01$; $F_{quad[garden]} = 8.16, P < 0.01$). Total leaf area was the only plant trait for which there was an effect of native altitude. Plants from low altitude were consistently larger than those from higher alti-

tudes in each garden ($F_{altitude} = 3.26, P = 0.04, F_{garden} = 2.61, P = 0.08, F_{altitude \times garden} = 0.24, P = 0.24$), indicating that the observed in situ size differences were due to ecotypic variation among altitudes. Plants from all altitudes expressed similar prefloration intervals, dates of reproduction, and number of fruits within each garden, demonstrating no ecotypic differentiation for phenology or fecundity at the experimental altitude. Altitude × garden interactions on number of fruits and fruiting date were nonsignificant at the $P < 0.05$ level, further indicating no differences among populations in the level of plasticity expressed for these traits. The only trait expressing plasticity among gardens was the prefloration interval (Fig. 3). Plants in the earliest melting gardens demonstrated longer prefloration intervals than those in later melting gardens, regardless of native altitude ($F_{garden} = 11.79, P < 0.001$; $F_{altitude \times garden} = 0.15, df = 2, P = 0.96$). Thus, plants from all altitudes expressed similar plastic changes in the prefloration interval, in response to early, intermediate, and late snowmelt among experimental gardens.

Comparisons of directional selection coefficients in the common garden experiment revealed similar responses among plants from each altitude (Table 3b). Overall and separate directional selection coefficients and differentials were negative for the prefloration interval and positive for leaf area in all cases. Heterogeneity of slopes tests on the regression equations for each altitude and for each garden were not significant, in-

TABLE 3. Selection gradients measuring the magnitude of direct selection (β) and selection differentials measuring the magnitude of total selection (S) on the prefloration interval and leaf area of *Potentilla pulcherrima*: (a) at different altitudes in Gunnison National Forest, Colorado, USA, and (b) in common garden experiment at Rocky Mountain Biological Laboratory, Gothic, Colorado, USA. * $P < 0.05$, ** $P < 0.01$.

Native altitude	Prefloration interval (d)		Leaf area (cm ²)	
	(β)	(S)	(β)	(S)
(a) Field observations				
Low	-0.14**	-0.14**	-0.03	+0.21**
Intermediate	-0.08	-0.06	+0.31**	+0.31**
High	-0.25**	-0.22**	+0.48**	+0.12**
All	+0.25**	+0.24**	+0.01	+0.30**
(b) Common garden experiment				
Low	-0.27**	-0.26*	+0.13**	+0.13
Intermediate	-0.22	-0.40**	+0.56*	+0.66**
High	-0.32**	-0.44**	+0.22**	+0.38**
All	-0.28**	-0.38**	+0.34**	+0.42**

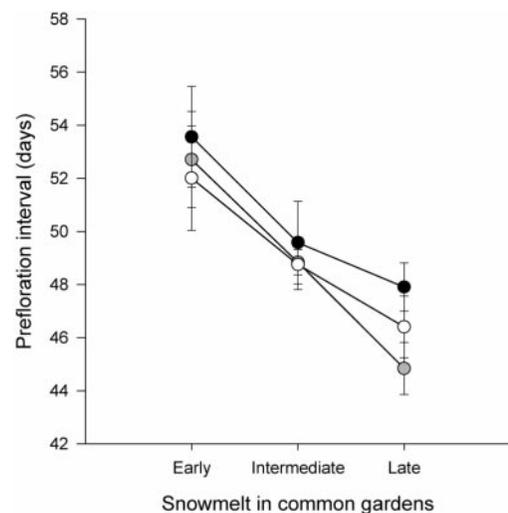


Fig. 3. Prefloration interval for *Potentilla pulcherrima* in the common garden experiment. Mean (± 1 SE) number of days from emergence to reproduction in early-, intermediate-, and late-melting common gardens. Each line connects the mean values for populations from low (closed symbols), intermediate (gray symbols), and high (open symbols) altitude.

dicating no effects of native altitude or garden on the selection regression results. Natural selection on phenological plasticity therefore did not differ among altitudes, but rather favored shorter prefloration intervals irrespective of native or local snowmelt conditions. Compression of the prefloration interval by plants from lower altitudes at the experimental altitude may therefore be considered adaptive, while the lengthening of this interval by plants from higher altitudes appears to be a non-adaptive response.

DISCUSSION

Although average size, prefloration interval, and fecundity were all reduced in progressively later melting sites, direct selection (\hat{s}) and indirect selection (β) favored shorter prefloration intervals at both ends of the altitudinal gradient. Thus, there were significant fitness advantages to shorter prefloration intervals in both early and late melting sites, even after accounting for strongly positive selection on size. Because higher altitude sites are characterized by progressively later snowmelt, this negative trend between fecundity and prefloration interval length at high altitudes supports the hypothesis that rapid reproduction evolves in response to shorter growing seasons (Molau, 1993; Theurillat and Schlüssel, 2000). The common garden experiment demonstrated that accelerated reproduction in later melting sites can be attributed to phenotypic plasticity, rather than genetically determined periodicity. Negative selection on the prefloration interval in the experimental plants confirmed that this plasticity is in an adaptive direction. Previous work suggests that high-altitude populations of other alpine and subalpine species can compensate for short growing seasons by accelerating seasonal carbohydrate cycles (Mooney and Billings, 1961; Bliss, 1985; Starr et al., 2000) and by reproducing more rapidly than their lower altitude counterparts. While many studies have documented altitudinal variation in fecundity and reproductive dates (Galen and Stanton, 1991; Kudo, 1991, 1992, 1993; Galen and Stanton, 1995; Pickering, 1995; Levesque et al., 1997), whether and how plasticity in maturation rates affect the chronological sequence of development is virtually unknown in these systems (Diggle, 1999). The duration of growth and the reproductive interval have been experimentally altered in some species (Molau and Shaver, 1997; Welker et al., 1997; Price and Waser, 1998; Totland, 1999; Sandvik and Totland, 2000), whereas others express notable homeostasis regardless of habitat (Holway and Ward, 1965a) or experimental treatment (Starr et al., 2000). This study is the first to provide direct measures of both natural selection and plasticity on the prefloration interval and therefore provides an adaptive mechanism for accelerated reproductive phenology in late melting populations of a single species.

It has been suggested that rapid reproduction at higher altitudes, compared to slower reproduction at lower altitudes, represents a fitness trade-off between size at reproduction and the ability to reach maturity quickly (Clausen et al., 1948; Holway and Ward, 1965a; Kudo, 1992; Stenstrom and Molau, 1992; Molau, 1993; Levesque et al., 1997; Theurillat and Schlüssel, 2000). However, there was no evidence for divergent allocation strategies in early vs. late melting sites (Theurillat and Schlüssel, 2000). This study accounted for correlations between size and phenology by including total leaf area in the measurement of directional selection coefficients (β). Whereas a directional change in β would indicate evolutionary

trade-offs between habitats (Mitchell-Olds and Shaw, 1987), the negative coefficients at all altitudes indicate that selection on the prefloration interval is not constrained by positive selection on size. The fact that selection differentials and coefficients were negative in the experimental gardens, regardless of positive correlations between fecundity and size, also indicates size and prefloration interval are not genetically correlated. This contrasts with theoretical predictions that cumulative allocation to growth should determine the time of reproductive maturity (Bazzaz and Ackerly, 1992; Kozłowski, 1992; Prock and Körner, 1996) and suggests instead that size-dependent fecundity does not dictate selection on the timing of reproduction in all environments (Schmid and Weiner, 1993; Callahan and Pigliucci, 2002).

Given that longer growing seasons result in higher fecundity and longer prefloration intervals in *P. pulcherrima* across its range, negative selection on the prefloration interval at the low altitude was perhaps more surprising. Even more striking was the fact that the plastic response of lengthening the prefloration interval at the experimental altitude did not appear to be adaptive, because of the consistently strong negative selection on this trait. The most likely explanation for selection on rapid reproduction in earlier melting sites is the late-season declines in soil moisture at lower altitudes. Earlier melting sites are often drier than later melting sites due to steeper soil moisture declines as the season progresses (Billings and Bliss, 1959; Holway and Ward, 1965b; Ehleringer and Miller, 1975; Isard, 1986; Friend and Woodward, 1990), and some high altitude species have been shown to reproduce earlier in drier years (Holway and Ward, 1965a). For *P. pulcherrima*, the regression of plant traits on environmental factors demonstrates that leaf area and prefloration intervals were negatively related to snowmelt date, but positively related to soil moisture. Although warmer conditions during early growth may also accelerate developmental rates (Molau, 1997; Sandvik and Totland, 2000), there was no evidence that temperature affected the prefloration interval in this system. Moreover, comparisons of phenotypic selection coefficients showed no evidence that natural selection on the prefloration interval differed between the high and low altitudes. It is therefore possible to conclude that opposing temporal constraints at the lower and upper ends of the altitudinal gradient exert similar selective pressures on this trait (Lande and Arnold, 1983; Bennington and McGraw, 1995). Long, dry seasons at lower altitudes and short, wet seasons at higher altitudes both favor the most rapidly reproducing individuals. While it is well established that annual schedules for release from snowpack can have dramatic effects on the amount of time available for growth and reproduction (Inouye and McGuire, 1991; Inouye et al., 2002; Kudo, 1991; Galen and Stanton, 1991; Walker et al., 1993), the current results underscore the importance of other factors, such as seasonal soil moisture declines, which can limit growth (Holway and Ward, 1965b; Walker et al., 1993; Price and Waser, 1998), and thereby determine the functional endpoint of the growing season. These results agree with the cautionary prediction that high altitude plant responses to climatic changes will depend upon multiple factors (Henry and Molau, 1997; Welker et al., 1997; Price and Waser, 1998; Sandvik and Totland, 2000; Starr et al., 2000). Moreover, the results demonstrate that accurately predicting the effects of altered growing season lengths will require more careful consideration of late season conditions in the subalpine zone.

Contraction of the prefloration interval in later melting gar-

dens further demonstrates that plastic changes in phenology are elicited by only a few days' difference in snowmelt timing within the subalpine zone, where both local and altitudinal heterogeneity can be quite large. This is notable, since the few studies concerned with small-spatial-scale, adaptive responses to snowmelt have focused on alpine tundra species (e.g., Galen and Stanton, 1993). Elongation of the prefloration interval in the earlier melting gardens may also be explained by small-scale and/or interannual heterogeneity in the environment. One possibility is simply that development is slowed by drought or other physiological stresses in earlier melting sites, such as fine-scale variation in temperature that were not detected here (Molau, 1997; Sandvik and Totland, 2000). Alternatively, slowing reproduction in response to early snowmelt may be favorable over the lifetime of these long-lived perennials due to unpredictable interactions between spatial and interannual variation in snowmelt (Sørensen, 1941), even though it was not adaptive in the year of the study. A major limitation in the interpretation of phenotypic selection analyses is that they assume no variation in selection from year to year. Interannual effects on selection can be as large as or larger than spatial variation in fitness (Stratton and Bennington, 1998), and altered annual precipitation patterns can have inconsistent effects on flowering times and other life history characters of high altitude plants (Inouye and McGuire, 1991; Walker et al., 1995). In this study, interannual effects on selection were marginally detectable within three years of observation and may vary considerably over the decade or longer lifespan of *Potentilla*, as well as many other subalpine perennials.

Information on genetic structure and outcrossing rates could provide additional insight into selection on prefloration intervals in *P. pulcherrima*. Because the common garden study did not test for genotype-by-environment interactions as measured by reaction norms (Bradshaw, 1965), the role of narrow sense genetic variation within and among altitudes is unclear. Genotypes may differ in size, prefloration interval, and the strength of correlation between these traits (Geber, 1990; Bennington and McGraw, 1995) and in the degree of plasticity expressed in a given environment (Sultan, 1995). Weaker selection in intermediate sites may be due to contrasting selection in microsites (Kalisz, 1986; Bennington and McGraw, 1995) or to equal fitness advantages from outcrossing with either high or low altitude populations. While many *Potentilla* species are capable of selfing, pollinator visitation and outcrossing have been shown to enhance seed set in the subarctic-subalpine species *P. nivea* and *P. crantzii* (Eriksen, 1996; Eriksen and Popp, 2000). Hence, variation in the prefloration interval of *P. pulcherrima* may also involve selection for reproductive synchrony both within and between altitudes (Galen and Stanton, 1995; Pickering, 1995; Brody, 1997).

In summary, environmental cues at relatively small spatial scales, rather than cumulative allocation to growth or genetically determined periodicity among populations, appear to control the amount of time allocated to growth prior to reproduction in *P. pulcherrima*. The adaptive nature of these responses may vary considerably within this species depending upon microsite, altitude, and year. In particular, high altitude populations may experience negative fitness consequences if lengthening of the prefloration interval accompanies predicted patterns of earlier snowmelt and drier conditions, despite a longer snow-free season in their native habitats. Predicted phenological responses to single factors, and generalizations even for a single species, should therefore be made with extreme

caution. A better understanding of environmental and genetic control over reproductive timing will be valuable for predicting longer term evolutionary responses of subalpine plants to altered and increasingly variable snowmelt patterns in this region.

LITERATURE CITED

- ALATALO, J. M., AND O. TOTLAND. 1997. Response to simulated climatic change in an alpine and subarctic pollen-risk strategist, *Silene acaulis*. *Global Change Biology* 3, Suppl. 1: 74–79.
- AYDELOTTE, A. R., AND P. K. DIGGLE. 1997. Analysis of developmental preformation in the alpine herb *Caltha leptosepala* (Ranunculaceae). *American Journal of Botany* 84: 1646–1657.
- BAZZAZ, F. A., AND D. D. ACKERLY. 1992. Reproductive allocation and reproductive effort in plants. In M. Fenner [ed.], *Seeds: the ecology of regeneration in plant communities*. Oxon, New York, New York, USA.
- BELL, K. L., AND L. C. BLISS. 1979. Autecology of *Kobresia bellardii*: why winter snow accumulation limits local distribution. *Ecological Monographs* 49: 377–402.
- BENEDICT, J. B. 1990. Lichen mortality due to late-lying snow: results of a transplant study. *Arctic and Alpine Research* 72: 81–89.
- BENNINGTON, C. C., AND J. B. MCGRAW. 1995. Natural selection and ecotypic differentiation in *Impatiens pallida*. *Ecological Monographs* 65: 303–323.
- BILLINGS, W. D., AND L. C. BLISS. 1959. An alpine snowbank environment and its effects on vegetation, plant development and productivity. *Ecology* 40: 389–397.
- BLISS, L. C. 1956. A comparison of plant development in microenvironments of arctic and alpine tundras. *Ecological Monographs* 26: 303–337.
- BLISS, L. C. 1962. Adaptations of arctic and alpine plants to environmental conditions. *Arctic* 15: 117–144.
- BLISS, L. C. 1985. Alpine. In B. F. Chabot and H. A. Mooney [eds.], *Physiological ecology of North American plant communities*, 41–65. Chapman and Hall, New York, New York, USA.
- BRADSHAW, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* 13: 115–155.
- BRODY, A. K. 1997. Effects of pollinators, herbivores, and seed predators on flowering phenology. *Ecology* 78: 1624–1631.
- CALLAHAN, H. S., AND M. PIGLIUCCI. 2002. Shade-induced plasticity and its ecological significance in wild populations of *Arabidopsis thaliana*. *Ecology* 83: 1965–1980.
- CARUSO, C. M. 2001. Differential selection on floral traits of *Ipomopsis aggregata* growing in contrasting environments. *Oikos* 94: 295–302.
- CLAUSEN, J., D. KECK, AND W. HIESEY. 1948. Experimental studies on the nature of species. III. Environmental responses of climatic races of *Achillea*. Carnegie Institute of Washington Publication Number 581, Washington, D.C., USA.
- DEL POZO, A., C. OVALLE, J. ARONSON, AND J. AVENDANO. 2002. Ecotypic differentiation in *Medicago polymorpha* L. along an environmental gradient in central Chile. I. Phenology, biomass production and reproductive patterns. *Plant Ecology* 159: 119–130.
- DE VALPINE, P., AND J. HARTE. 2001. Plant responses to experimental warming in a montane meadow. *Ecology* 82: 637–648.
- DIGGLE, P. K. 1997. Extreme preformation in alpine *Polygonum viviparum*: an architectural and developmental analysis. *American Journal of Botany* 84: 154–169.
- DIGGLE, P. K. 1999. Heteroblasty and the evolution of flowering phenologies. *International Journal of Plant Sciences* 160: S123–S134.
- DIGGLE, P. K. 2002. A developmental morphologist's perspective on plasticity. *Evolutionary Ecology* 16: 267–283.
- EHLERINGER, J., AND P. C. MILLER. 1975. Water relations of selected plant species in the alpine tundra, Colorado. *Ecology* 56: 370–380.
- EMERY, R. J. N., C. C. CHINNAPPA, AND J. G. CHMIELEWSKI. 1994. Specialization, plant strategies, and phenotypic plasticity in populations of *Stellaria longipes* along an elevational gradient. *International Journal of Plant Sciences* 155: 203–219.
- ERIKSEN, B. 1996. Mating systems in two species of *Potentilla* from Alaska. *Folia Geobotanica and Phytotaxonomica* 31: 333–344.
- ERIKSEN, B., AND M. POPP. 2000. Pollen tube growth and seed set in naturally and artificially pollinated plants of *Potentilla nivea* and *P. crantzii* (Ro-

- saceae). *Scandinavian Association for Pollination Ecology honours Knut Fægri* 39: 55–65.
- FITTER, A. H., AND R. S. R. FITTER. 2002. Rapid changes in flowering time in British plants. *Science* 296: 1689–1691.
- FRIEND, A. D. 1995. Responses of snowbed plant-species to changes in growing-season length. *Ecology* 76: 1546–1557.
- FRIEND, A. D., AND F. I. WOODWARD. 1990. Evolutionary and ecophysiological responses of mountain plants to the growing season environment. *Advances in Ecological Research* 20: 59–124.
- GALEN, C., AND M. L. STANTON. 1991. Consequences of emergence phenology for reproductive success in *Ranunculus adoneus* (Ranunculaceae). *American Journal of Botany* 78: 978–988.
- GALEN, C., AND M. L. STANTON. 1993. Short-term responses of alpine buttercup to experimental manipulations of growing season length. *Ecology* 74: 1052–1058.
- GALEN, C., AND M. L. STANTON. 1995. Responses of snowbed plant species to changes in growing season length. *Ecology* 76: 1546–1557.
- GEBER, M. 1990. The cost of meristem limitation in *Polygonum arenastrum*: negative genetic correlations between fecundity and growth. *Evolution* 44: 799–819.
- GEBER, M., AND T. DAWSON. 1993. Evolutionary responses of plants to global change. In P. Kareiva, J. Kingsolver, and R. Huey [eds.], *Biotic interactions and global change*, 179–197. Sinauer, Sunderland, Massachusetts, USA.
- GROSS, R. S., AND P. A. WERNER. 1983. Relationships among flowering phenology, insect visitors, and seed-set of individuals: experimental studies on four co-occurring species of goldenrod (*Solidago*: Compositae). *Ecological Monographs* 53: 95–117.
- GUGERLI, F. 1998. Effect of elevation on sexual reproduction in alpine populations of *Saxifraga oppositifolia* (Saxifragaceae). *Oecologia* 114: 60–66.
- HENRY, G. H. R., AND U. MOLAU. 1997. Tundra plants and climate change: the International Tundra Experiment (ITEX). *Global Change Biology* 3, Suppl. 1:1–9.
- HOLWAY, J. G., AND R. T. WARD. 1965a. Phenology of alpine plants in Northern Colorado. *Ecology* 46: 73–83.
- HOLWAY, J. G., AND R. T. WARD. 1965b. Snow and melt-water effects in an alpine area of Colorado. *American Midland Naturalist* 60: 189–197.
- HOUGHTON, J., L. FILHO, B. CALLANDER, N. HARRIS, A. KATTENBURG, AND K. MASKELL. 1996. Climate change 1995—the science of climate change. Working group I, Second assessment report of The Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, New York, New York, USA.
- INOUE, D. W., AND A. D. MCGUIRE. 1991. Effects of snow-pack on timing and abundance of flowering in *Delphinium nelsonii* (Ranunculaceae). *American Journal of Botany* 78: 997–1001.
- INOUE, D. W., M. A. MORALES, AND G. J. DODGE. 2002. Variation in timing and abundance of flowering by *Delphinium barbeyi* Huth (Ranunculaceae): the roles of snowpack, frost, and La Niña, in the context of climate change. *Oecologia* 130: 543–550.
- ISARD, S. A. 1986. Factors influencing soil moisture and plant community distribution on Niwot Ridge, Front Range, Colorado, USA. *Arctic and Alpine Research* 18: 83–96.
- KALISZ, S. 1986. Variable selection on the timing of germination in *Collinsia verna* (Scrophulariaceae). *Evolution* 40: 479–491.
- KOZLOWSKI, J. 1992. Optimal allocation of resources to growth and reproduction: implications for age and size at maturity. *Trends in Ecology and Evolution* 7: 15–18.
- KUDO, G. 1991. Effects of snow-free period on the phenology of alpine plants inhabiting snow patches. *Arctic and Alpine Research* 23: 436–443.
- KUDO, G. 1992. Performance and phenology of alpine herbs along a snow-melting gradient. *Ecological Research* 7: 297–304.
- KUDO, G. 1993. Relationship between flowering time and fruit-set of the entomophilous alpine shrub, *Rhododendron aureum* (Ericaceae), inhabiting snow patches. *American Journal of Botany* 80: 1300–1304.
- LACEY, E. P., AND R. PACE. 1983. Effect of parental flowering and dispersal times on offspring fate in *Daucus carota* (Apiaceae). *Oecologia* 60: 274–278.
- LANDE, R., AND S. ARNOLD. 1983. The measurement of selection on correlated characters. *Evolution* 37: 1210–1226.
- LEVESQUE, E., G. H. R. HENRY, AND J. SVOBODA. 1997. Phenological and growth responses of *Papaver radicum* along altitudinal gradients in the Canadian high arctic. *Global Change Biology* 3: 125–145.
- LUZAR, N. 2001. Flower heliotropism and floral heating of five alpine plant species and the effect on flower visiting in *Ranunculus montanus* in the Austrian Alps. *Arctic Antarctic and Alpine Research* 33: 93–99.
- MCGRAW, J. B. 1987. Experimental ecology of *Dryas octopetala* ecotypes: IV. Fitness response to reciprocal transplanting in ecotypes with differing plasticity. *Oecologia* 73: 465–468.
- MITCHELL-OLDS, T., AND R. SHAW. 1987. Regression analysis of natural selection: statistical inference and biological interpretations. *Evolution* 41: 1149–1161.
- MOLAU, U. 1993. Relationships between flowering phenology and life-history strategies in tundra plants. *Arctic and Alpine Research* 25: 391–402.
- MOLAU, U. 1997. Responses to natural climatic variation and experimental warming in two tundra plant species with contrasting life forms: *Cassiope tetragona* and *Ranunculus nivalis*. *Global Change Biology* 3: 97–107.
- MOLAU, U., AND G. R. SHAVER. 1997. Controls on seed production and seed germinability in *Eriophorum vaginatum*. *Global Change Biology* 3: 80–88.
- MOONEY, H., AND W. BILLINGS. 1961. Comparative physiological ecology of arctic and alpine populations. *Ecological Monographs* 31: 1–29.
- PICKERING, C. M. 1995. Variation in flowering parameters within and among five species of Australian alpine *Ranunculus*. *Australian Journal of Botany* 43: 103–112.
- PRICE, M. V., AND N. M. WASER. 1998. Effects of experimental warming on plant reproductive phenology in a subalpine meadow. *Ecology* 79: 1261–1271.
- PROCK, S., AND C. KÖRNER. 1996. A cross-continental comparison of phenology, leaf dynamics and dry matter allocation in arctic and temperate zone herbaceous plants from contrasting altitudes. *Ecology Bulletin* 45: 93–103.
- REEKIE, E. G., AND F. A. BAZZAZ. 1987. Reproductive effort in plants. *American Naturalist* 129: 876–919.
- ROBERTSON, C. 1895. The philosophy of flower seasons, and the phenological relations of the entomophilous flora and the anthophilous insect fauna. *American Naturalist* 29: 97–117.
- SANDVIK, S. M., AND O. TOTLAND. 2000. Short-term effects of simulated environmental changes on phenology, reproduction, and growth in the late-flowering snowbed herb *Saxifraga stellaris* L. *Ecoscience* 7: 201–213.
- SCHMID, B., AND J. WEINER. 1993. Plastic relationships between reproductive and vegetative mass in *Solidago altissima*. *Evolution* 47: 61–74.
- SIMPSON, G. G., AND C. DEAN. 2002. Flowering—*Arabidopsis*, the Rosetta Stone of flowering time? *Science* 296: 285–289.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry—the principles and practice of statistics in biological research*, 3rd ed. Freeman and Company, New York, New York, USA.
- SØRENSEN, T. 1941. Temperature relations and phenology of the northeast Greenland flowering plants. *Meddelelser om Grønland* 125: 1–305.
- STANTON, M. L., C. GALEN, AND J. SHORE. 1997. Population structure along a steep ecological gradient: consequences of flowering time and habitat variation in the snow buttercup, *Ranunculus adoneus*. *Evolution* 51: 79–94.
- STARR, G., S. F. OBERBAUER, AND E. W. POP. 2000. Effects of lengthened growing season and soil warming on the phenology and physiology of *Polygonum bistorta*. *Global Change Biology* 6: 357–369.
- STENSTROM, M., AND U. MOLAU. 1992. Reproductive ecology of *Saxifraga oppositifolia*—phenology, mating system, and reproductive success. *Arctic and Alpine Research* 24: 337–343.
- STINSON, K. A. 1998. Effects of snowmelt timing on three high altitude *Potentilla* species: growth, reproduction, and distribution. Ph.D. dissertation, Princeton University, Princeton, New Jersey, USA.
- STRATTON, D. A. 1998. Reaction norm functions and QTL—environment interactions for flowering time in *Arabidopsis thaliana*. *Heredity* 81: 144–155.
- STRATTON, D. A., AND C. C. BENNINGTON. 1998. Fine-grained spatial and temporal variation in selection does not maintain genetic variation in *Eriogonum annuus*. *Evolution* 52: 678–691.
- SULTAN, S. E. 1995. Phenotypic plasticity and plant adaptation. *Acta Botanica Neerlandica* 44: 363–383.
- THEURILLAT, J. P., AND A. GUIGAN. 2001. Potential impact of climate change on vegetation in the European Alps: a review. *Climatic Change* 50: 77–109.
- THEURILLAT, J. P., AND A. SCHLÜSSEL. 2000. Phenology and distribution

- strategy of key plant species within the subalpine-alpine ecocline in the Valaisan Alps (Switzerland). *Phytocoenologia* 30: 439–456.
- TOTLAND, O. 1997. Limitations on reproduction in alpine *Ranunculus acris*. *Canadian Journal of Botany—Revue Canadienne De Botanique* 75: 137–144.
- TOTLAND, O. 1999. Effects of temperature on performance and phenotypic selection on plant traits in alpine *Ranunculus acris*. *Oecologia* 120: 242–251.
- TOTLAND, O., AND W. EIDE. 1999. Environmentally-dependent pollen limitation on seed production in alpine *Ranunculus acris*. *Ecoscience* 6: 173–179.
- TURESSON, G. 1922. The genotypical response of the plant species to the habitat. *Hereditas* 3: 147–236.
- WAGNER, J., AND E. MITTERHOFER. 1998. Phenology, seed development, and reproductive success of an alpine population of *Gentianella germanica* in climatically varying years. *Botanica Acta* 111: 159–166.
- WALKER, D. A., J. C. HALFPENNY, M. D. WALKER, AND C. A. WESSMAN. 1993. Long term studies of snow-vegetation interactions. *BioScience* 43: 287–301.
- WALKER, M. D., R. C. INGERSOLL, AND P. J. WEBBER. 1995. Effects of interannual climate variation on phenology and growth of two alpine forbs. *Ecology* 76: 1067–1083.
- WASER, N. M. 1978. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology* 59: 934–944.
- WASER, N. M., AND M. V. PRICE. 1985. Reciprocal transplant experiments with *Delphinium nelsonii* (Ranunculaceae). Evidence for local adaptation. *American Journal of Botany* 72: 1726–1732.
- WEBER, W., AND R. WITTMANN. 1996. Colorado flora: Western slope, revised ed. University Press of Colorado, Niwot, Colorado, USA.
- WELKER, J. M., U. MOLAU, A. N. PARSONS, C. H. ROBINSON, AND P. A. WOOKEY. 1997. Responses of *Dryas octopetala* to ITEX environmental manipulations: a synthesis with circumpolar comparisons. *Global Change Biology* 3, Suppl. 1:61–73.
- YANOVSKY, M. J., AND S. A. KAY. 2002. Molecular basis of seasonal time measurement in *Arabidopsis*. *Nature* 419: 308–312.