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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

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Abstract *Delphinium barbeyi* is a common herbaceous wildflower in montane meadows at 2,900 m near the Rocky Mountain Biological Laboratory, and its flowers are important nectar resources for bumblebees and hummingbirds. During the period 1977–1999 flowering was highly variable in both timing (date of first flower ranged from 5 July to 6 August, mean=17 July) and abundance (maximum open flowers per 2×2-m plot ranged from 11.3 to 197.9, mean=82). Time and abundance of flowering are highly correlated with the previous winter's snowpack, as measured by the amount of snow remaining on the ground on 15 May (range 0–185 cm, mean=67.1). We used structural equation modeling to investigate relationships among snowpack, first date of bare ground, first date of flowering, number of inflorescences produced, and peak number of flowers, all of which are significantly correlated with each other. Snowpack depth on 15 May is a significant predictor of the first date of bare ground ($R^2=0.872$), which in turn is a significant predictor of the first date of flowering ($R^2=0.858$); snowpack depth is also significantly correlated with number of inflorescences produced ($R^2=0.713$). Both the number of inflorescences and mean date of first flowering are significant predictors of flowers produced (but with no residual effect of snowpack). Part of the effect of snowpack on flowering may be mediated through an increased probability of frost damage in years with lower snowpack – the frequency of early-season “frost events” explained a significant proportion of the variation in the number of flowers per stem. There is signifi-

cant reduction of flower production in La Niña episodes. The variation in number of flowers we have observed is likely to affect the pollination, mating system, and demography of the species. Through its effect on snowpack, frost events, and their interaction, climate change may influence all of these variables.

Keywords Climate change · *Delphinium barbeyi* · Flowering · Frost · Larkspur

Introduction

In addition to their role in plant sexual reproduction, flowers are important resources for pollinators and herbivores, usually providing nectar and/or pollen as nutritional rewards for pollinators, and floral tissue for herbivores. The fruits and seeds that result from their pollination also support frugivores and seed predators. Thus, patterns of seasonal availability (phenology) of floral resources, and variation in their abundance, can be of great ecological significance.

There is growing evidence that the global climate is changing (e.g., Easterling et al. 2000), and a matching concern for the consequences this will have for natural ecosystems. Although evidence is accumulating for biological responses to the changing climate (Hughes 2000), the response of many species to variation in climate remains largely unpredictable. One approach to considering the consequences of climate change for naturally occurring plant populations has been to manipulate temperature experimentally. This can be done in the field with electric heaters (e.g., Harte and Shaw 1995; Price and Waser 1998) or shelters (e.g., Henry and Molau 1997; Hollister and Webber 2000). Although these studies provide valuable insight into potential mechanisms driving plant response to climate change, treatment effects in these experiments may cause correlated changes in some environmental variables that would not be observed under natural conditions. The growing availability of long-term data sets for natural variation in plant phenology

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Table 1 Correlation matrix (values of r) for variables used in path analysis. Snowpack (cm) was measured on 15 May. *FDBG* first date of bare ground, *MDFF* mean date of first flower, *Inflorescences* total number of inflorescences with flowers in all plots, *Length* length of flowering (days), $n=22$. All correlations are significant at $P<0.05$

Variable	Snowpack	FDBG	MDFF	Inflorescences	Flower number	Length
Snowpack	1	–	–	–	–	–
FDBG	0.872	1	–	–	–	–
MDFF	0.805	0.858	1	–	–	–
Inflorescences	0.713	0.634	0.593	1	–	–
Flower number	0.715	0.63	0.636	0.982	1	–
Length	0.57	0.47	0.559	0.758	0.765	1
\bar{X}	66.046	144.228	77.3821	8.112	82.174	21.595
SD	56.705	13.784	8.626	4.958	58.09	4.99

and demography provides an alternate and complementary approach. In particular, it is becoming increasingly possible to correlate population-level response of organisms to annual variation in environmental variables, and then use these responses to gain insights into the potential consequences of predicted climate change.

Global warming may have a disproportionate effect on montane communities, because species in these habitats may not be able to respond to changes in temperature with a shift in latitudinal range, and because an upward shift in altitudinal range will be associated with a decrease in area (McDonald and Brown 1992). Furthermore, many montane species of the Rocky Mountains are influenced by snowpack, either directly or indirectly (e.g., Inouye and McGuire 1991), and if snowpack changes as some models (e.g., Giorgi et al. 1998) and evidence suggest it will, timing and abundance of flowering may change. For these species, predicted changes in precipitation associated with global climate change may have significant impacts in ways unrelated to global temperature. Changes in large-scale events such as the El Niño – Southern Oscillation (ENSO), which has been shown to have a variety of effects on terrestrial ecology (Holmgren et al. 2001), could also affect flowering of montane species of wildflowers.

Long-term data sets (>25 years) are available for many herbaceous plants found at the Rocky Mountain Biological Laboratory (RMBL, Gothic, Colo., USA) (e.g., Inouye and McGuire 1991; Inouye et al. 2000). Many of these species, especially those that flower in early spring, are important resources for hummingbirds and queen bumblebees, and may support pollinator populations for later flowering species. A previous study detected a link between variation in snowpack depth and the timing and abundance of flowering for the montane plant *Delphinium nuttallianum* Pritzell (previously *D. nelsonii* Greene) (Ranunculaceae) (Inouye and McGuire 1991). In this paper, we examine the flowering response of the sympatric congener *D. barbeyi* to annual variation in snowpack, and consider possible underlying mechanisms for its response.

Materials and methods

Delphinium barbeyi Huth (subalpine or tall larkspur; Ranunculaceae) is a long-lived herbaceous perennial species found in wet

meadows and bogs in the montane and subalpine zones of Colorado, Wyoming, and Utah (Nelson 1992). Plants produce multiple stems each year, about 1 m tall. Stems bearing inflorescences are about 1.5 m tall with dense racemes of dark purple flowers visited by bumblebees and hummingbirds (Inouye 1978; Wright 1988; Kotliar 1996). Mean date of flowering (first flower) is about 15 July in our study site, about 1 month after its congener *D. nuttallianum*.

A series of 2×2-m plots was established in 1973 (by D.W.I. and G.H. Pyke) near the RMBL (38°57.5'N, 106°59.3'W, 2,900 m elevation), for a study of flowering phenology. Twelve of these plots have had *D. barbeyi* flowering in them. Data were not collected in 1990 but otherwise analyses include data from 1977–1999. Approximately every other day, usually from late May until late August, the plots were examined and all flowers were counted. *Delphinium* flowers were counted per inflorescence, but a single plot may have contained one to several genets, each producing multiple inflorescences. Many of the genets in the plots appear to have persisted with little change throughout the length of the study.

Analyses presented in the current paper are based on averages across the 12 plots for peak floral abundance (maximum count per plot), inflorescence number (total flowering), and mean date of first flowering for each of 22 years. These measures of flowering phenology and abundance were examined with respect to seasonal and annual variation in snowpack depth, temperature, and date of first bare ground. Data on snowpack and date of first bare ground were collected by Billy Barr for a site located within 1 km and 50 m altitude of the study plots. Mean winter snowfall from 1977 to 1999 was 1,153 cm (SD=295, range=474–1,641 cm). Temperature and precipitation data were obtained from the Crested Butte weather station located 9.5 km from RMBL at elevation 2,704 m (published by the National Climatic Data Center).

After determining that snowpack, date of first bare ground, inflorescence number, flower number and flowering phenology are all significantly correlated (Table 1), we used structural equation modeling (SEM) StatSoft (1999), an extension of path analysis, to examine the joint effects of these variables. An in-depth discussion of the application of SEM to ecological datasets can be found in Mitchell (1992) and Shipley (1999). Briefly, both SEM and path analysis partition the correlations among a set of variables for a given causal model. The resulting path coefficients and their interpretation are analogous to those of partial regression coefficients from multiple regression. Structural equation modeling differs from path analysis in part by allowing for the simultaneous estimation of path coefficients and assessment of model fit. A non-significant χ^2 indicates that the data are not significantly different than predicted by the model, suggesting that the model adequately fits the data (Mitchell 1992). A useful property of path models is that they can be visualized in path diagrams by using one-directional arrows to represent the causal relationships among variables.

We used the standardized Multivariate ENSO Index (MEI) of Wolter and Timlin (1993, 1998) to identify medium to strong negative departures (La Niña conditions) as defined by index values of less than –0.5 from the MEI (1978, 1985, 1988, 1989, 1996, 1999). We also identified positive departures of index values

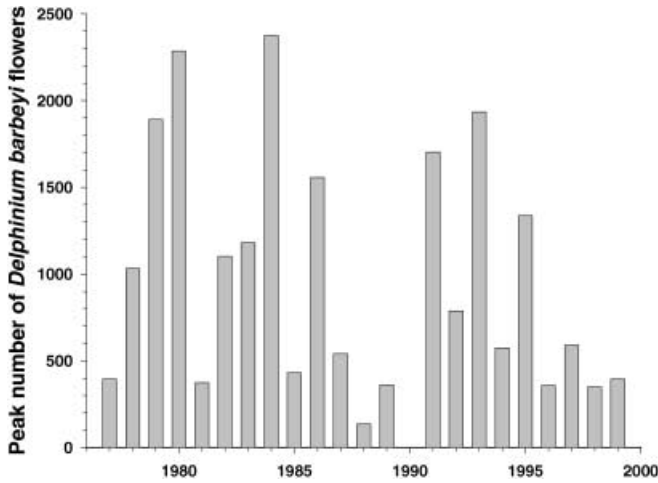


Fig. 1 The peak number of *Delphinium barbeyi* flowers in the 12 2×2-m plots for each year from 1973–1999 (no data were collected in 1990)

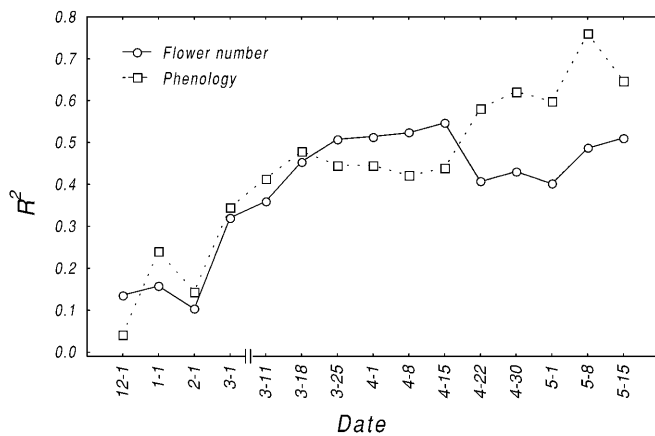
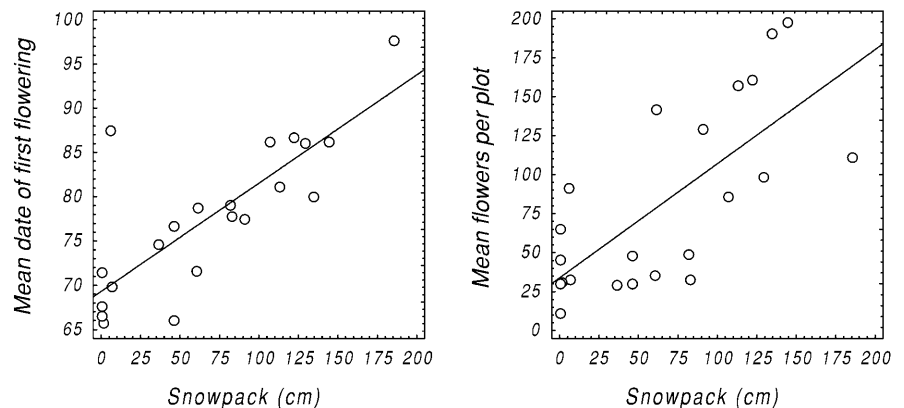


Fig. 2 Proportion of explained variance in flowering phenology and flower number for *D. barbeyi* as a function of snowpack depth between 1 December and 15 May (note the scale change after 1 March). Snowpack around 15 April and 8 May is the best predictor of flower number and flowering phenology respectively. Both flower number and flowering phenology are highly correlated with snowpack around 15 May, and this dataset was used in subsequent analyses

Fig. 3A, B Relationship between snowpack depth (cm) on 15 May (Snow) and mean date of first flowering (Julian date) or flower density. **A** Timing of flowering = $69.3 + 0.12 \times \text{Snow}$, Adj. $R^2 = 0.63$, $F_{1,20} = 36.7$, $P < 0.0001$. **B** Flower density = $33.82 + 0.73 \times \text{SP}$, Adj. $R^2 = 0.49$, $F_{1,20} = 20.87$, $P = 0.0002$



greater than 0.5 (El Niño conditions – years 1977, 1980, 1981, 1982, 1983, 1984, 1986, 1987, 1991, 1992, 1993, 1994, 1997, and 1998) We then used a Mann-Whitney U test to compare flower production in years with and without La Niña or El Niño conditions.

Results

Flowering in the 12 plots from 1977 to 1999 was highly variable, both in timing and abundance of flowering (Fig. 1). Date of first flowering (calculated as means for each year) ranged from 5 July (in 1981) to 6 August (in 1995; the mean for all plots and all years = 17 July). The mean maximum number of open flowers per plot (calculated from the totals for the date of peak flowering in each plot) ranged from 11.3 (in 1998) to 197.9 flowers (in 1984). The maximum range in number of open flowers for a single plot was 0–750. On average, flowers were present in a given plot in 16.8 of the 22 years (range 10–22; this does not count several cases in which flower buds were produced but were all killed by frost). Initial results indicated a significant positive relationship between total winter snowpack depth and both timing and abundance of flowering by *D. barbeyi*. However, snowpack depth varies throughout the winter, and there is no a priori expectation for when this relationship is strongest. To address this, we examined the linear fit between winter snowpack and subsequent summer flowering for snowpack measurements taken on the first day of each month between December and March, and then at approximately 1-week intervals until 15 May. Snowpack depths around 15 April and 8 May are the best predictors of flower number and the timing of flowering respectively. Because both flower number and flowering phenology are highly correlated with snowpack on 15 May (Figs. 2, 3) this dataset was used for subsequent analyses. Results were qualitatively similar (with no change in significance) when analyses were based on snowpack depth for either 15 April or 8 May. The mean snowpack remaining on 15 May was 66 cm (SD = 55.3, range = 0–185 cm).

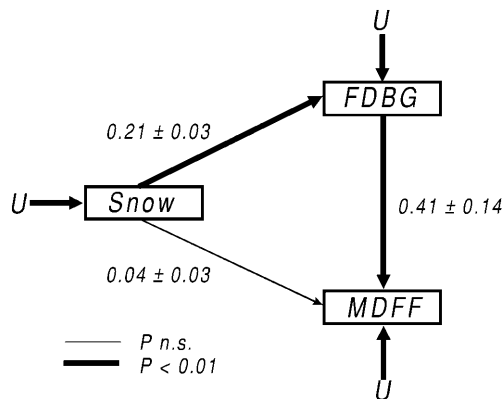


Fig. 4 Path diagram illustrating the joint relationship between snowpack (depth on 15 May), snowmelt (first date of bare ground), and timing of flowering (date of first flower) for *D. barbeyi*. *Snow* Snowpack, *FDBG* first date of bare ground (snowmelt), *MDFF* mean date of first flowering (timing of flowering). Unexplained variance is assigned to the latent variable specified by U. Path coefficients \pm SE are indicated adjacent to path arrows

Timing and length of flowering

Ramet stems in *D. barbeyi* genets are preformed by the fall before they appear above ground (Inouye, unpublished observations from excavating plants), and flower buds are probably also preformed the previous season, remain dormant all winter under the snow, and resume development again following snowmelt. Thus, snowpack depth may influence flowering phenology by determining the timing of snowmelt. After accounting for a significant positive effect of snowpack depth on the timing of snowmelt (i.e. first date of bare ground), and a significant positive effect of snowmelt date on timing of flowering (i.e. mean date of first flowering), snowpack had no additional effect on mean date of first flowering (Fig. 4).

Mean date of first flowering may also be determined by the duration of floral development during the year of flowering. We estimated length of floral development as the number of days from the first date of bare ground to mean date of first flowering. We found a significant negative relationship between the timing of snowmelt and length of floral development (Fig. 5); later snowmelt results in shorter development times. One explanation could be that length of floral development is determined in part by temperature. Because flowers that begin development sooner are exposed to colder temperatures, floral development in these colder years may take longer (i.e., more growing-degree days). A mutually non-exclusive hypothesis, not necessarily related to temperature, is that length of floral development is modulated by a developmental buffer, partly controlling for variation in the timing of flowering. If so, flowers that begin development later may show accelerated floral development, regardless of temperature, relative to flowers that begin development earlier.

To investigate these hypotheses, we used multiple regression analysis to consider the effects of mean median

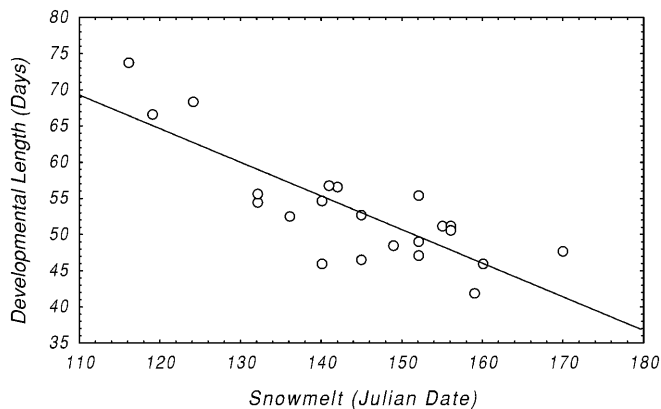


Fig. 5 Relationship between timing of snowmelt (Julian date, SM) and floral developmental period (number of days from snowmelt to mean date of first flowering, DAYS) for *D. barbeyi*. $\text{DAYS} = 120.4 - 0.46 \times \text{SM}$, Adj. $R^2 = 0.66$, $F_{1,20} = 41.73$, $P < 0.0001$

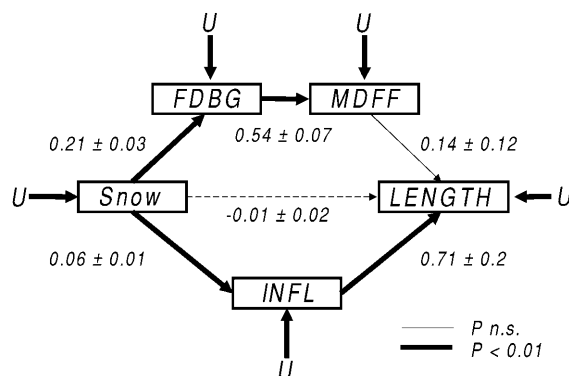


Fig. 6 Path diagram illustrating the joint relationship between snowpack (depth on 15 May), inflorescence number, and length of flowering for *D. barbeyi*. *Snow* Snowpack, *INFL* mean maximum inflorescence number, *LENGTH* length of flowering (days). Unexplained variance is assigned to the latent variable specified by U. Path coefficients \pm SE are indicated adjacent to path arrows. The data are not significantly different than predicted by this model ($\chi^2_{df=4} = 2.921$, $P = 0.57$)

daily temperature (calculated for the period of floral development) and timing of snowmelt on length of floral development. After including the effect of timing of snowmelt, there was no significant effect of mean median daily temperature on length of floral development ($t_{16} = -1.112$, $P = 0.283$).

Finally, we examined the effect of snowpack depth on the length of flowering. After including the direct and indirect effect of snowpack on the mean maximum number of inflorescences and mean date of first flowering, respectively, path analysis shows no direct effect of snowpack or mean date of first flowering on the length of flowering (Fig. 6). These results suggest that snowpack influences flowering phenology indirectly, through its effect on both the timing of snowmelt and subsequent floral development, and through its effect on inflorescence density.

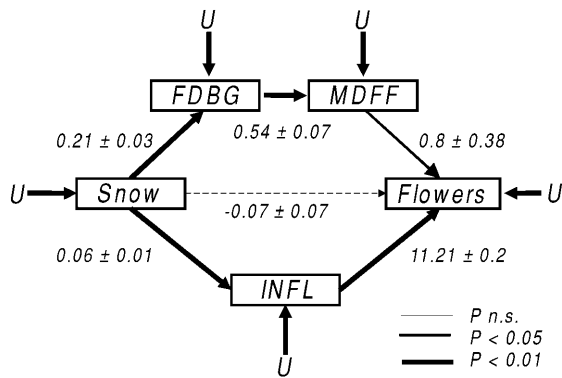


Fig. 7 Path diagram illustrating the joint relationship between snowpack, snowmelt (first date of bare ground), timing of flowering (date of first flower), inflorescence number, and flower abundance for *D. barbeyi*. Snow Snowpack, FDBG first date of bare ground (snowmelt), MDF mean date of first flowering (timing of flowering), INFL inflorescence number. Unexplained variance is assigned to the latent variable specified by U. Path coefficients \pm SE are indicated adjacent to path arrows. The data are not significantly different than predicted by this model ($\chi^2_{df=4}=3.69$, $P=0.45$)

Flower number

We investigated probable pathways for the effect of snowpack on variation in abundance of flowering, and found that snowpack has a direct positive effect on maximum inflorescence abundance (Fig. 7). First date of bare ground has a positive effect on mean date of first flowering, which itself has a somewhat weaker positive effect on flower abundance. Inflorescence number has a strong positive effect on flower number, whereas snowpack has no additional direct effect on flowering (Fig. 7). These results suggest that snowpack indirectly influences flowering by two mechanisms. In the first, snowpack has a positive effect on inflorescence number. In the second, snowpack influences flowering phenology, which itself influences flower abundance. Because floral development is delayed during years of high snowfall (see Timing of flowering), high snowfall may protect temperature-sensitive flower buds from the damaging effects of frost, which will be more common early in the spring.

Unfortunately, we do not have data on the frequency of frost-damaged flower buds, so we developed a metric of potential frost damage to explore this hypothesis. In part, potential frost damage was determined by the total number of days during which minimum temperature fell below some threshold (indicating frost damage) over the period from first date of bare ground summed through June. This temperature threshold was defined by the value that explained the greatest proportion of variation in the number of flowers per stem. Similarly, we included lag time in the model because there is a period of floral development during which buds are very small and may be largely immune to frost damage (D. Inouye, personal observation), perhaps protected in part by the leaves that are covering them (providing shelter from radiation frosts). Thus, the complete model was defined as: no.

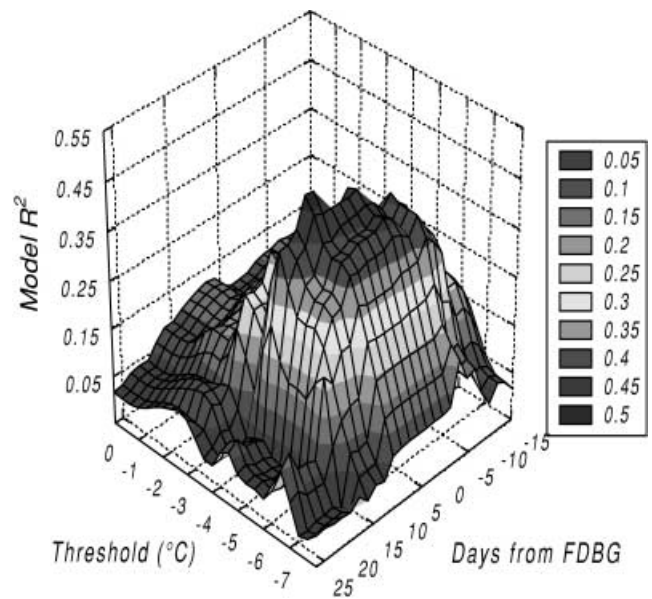


Fig. 8 Model fit (r^2) for the density of flowers per stem as a function of the sum total number of days where temperature falls below some threshold (t) and following some lag period from snowmelt (l , days from FDBG) through July. Critical values for temperature and lag period are defined as those that explain the greatest proportion of the variance in number of flowers per stem

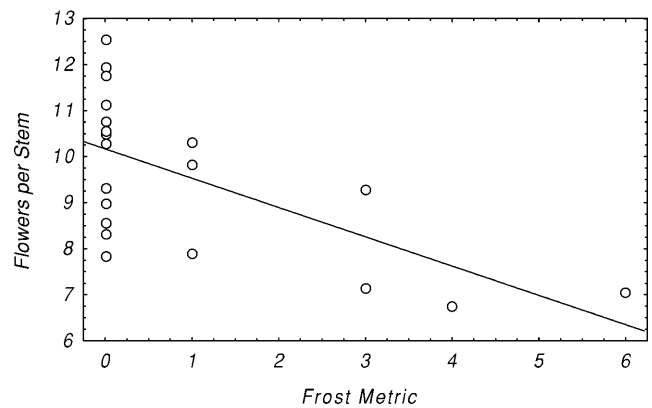


Fig. 9 Relationship between frost damage (M; see Fig. 8) and the number of flowers per stem (FPS). $\text{FPS} = 10.17 - 0.637 M$, Adj. $R^2 = 0.403$, $F_{1,19} = 12.834$, $P = 0.002$

flowers per stem \propto the sum of days during which temperature falls below some threshold, t , beginning at time of snowmelt + l , where t and l are determined by minimizing least squares. Least squares parameter estimates were obtained over the range -6.7 to -1.1°C (20 – 30°F in the NCDC data) for temperature (t) and -15 to 25 days from the first date of bare ground for the lag period (l) (Fig. 8). One thousand bootstrap replicates were performed (resampling the data set with replacement) to obtain mean values and confidence intervals for these estimates (the CI could not be obtained analytically). Results suggest that minimum temperatures below -5°C (95% CI = -6.4 to -4.2°C) as measured at the Crested

Butte weather station following a lag period of 2.4 days from snowmelt (95% CI=-12 to 16 days) as measured in Gothic significantly depress flowering (Fig. 9). How this translates to temperatures in the field at our sites is uncertain, but given that the weather station is about 200 m lower and measuring air temperature rather than the microclimate of exposed plants, the critical temperatures are probably somewhat lower than those shown in our model.

Effects of La Niña

We found that *D. barbeyi* plants produced significantly fewer stems and inflorescences in years characterized by medium to strong negative MEI departures in the spring and early summer ($P=0.006$ for stems and 0.007 for inflorescences; Mann-Whitney U). We found no differences in stem and inflorescence production in years characterized by positive departures in the same season (El Niño conditions) ($P=0.142$ for stems and 0.133 for inflorescences; Mann-Whitney U). Trends were not significant when we compared MEI data directly with flower production.

Discussion

Flowering in some environments can be triggered by environmental factors including photoperiod, onset of a rainy or dry season, or temperature. The high-mountain environment at our study site has a relatively short growing season; from 1975–1999 the time from snowmelt (first date of bare ground) until the first fall temperature of -3.9°C (measured in Crested Butte; a somewhat arbitrary temperature, but low enough to kill most of the above-ground parts of herbaceous perennials) has ranged from 73 to 145 days (mean=114.3). In such an environment the most reliable cue for initiation of the growing season is probably the disappearance of the previous winter's snow cover (which may correspond to a maximum in availability of soil water). Thus it is not surprising that there is a significant correlation between the first date of bare ground and the date of first flowering of *D. barbeyi*, and that none of the many species that have been investigated in related studies appear to use photoperiod as a cue for flowering (e.g., Inouye and McGuire 1991).

It is less obvious why there should be a significant correlation between how much snow falls the previous winter, which determines in large part the date of first bare ground, and the number of larkspur inflorescences. This correlation holds for both species of *Delphinium* that occur in the study area (Inouye and McGuire 1991; Saavedra 2000). The correlation is particularly puzzling as it seems likely that the number of inflorescences and flowers on them is determined sometime during the previous winter or even earlier, when the plant preforms its ramets. The insulating effect of snow is unlikely to differ

most years, as there is typically enough snow to prevent the ground from freezing, so that winter soil temperature is probably not a factor, and a watering experiment with *D. nuttallianum* did not affect the number of flowers or percent of flower abortion, although ramet density was not considered (D. Inouye, unpublished data). The causation behind these correlations remains enigmatic.

A similar correlation between winter precipitation and flowering has been reported for two orchid species (*Calopogon tuberosus* and *Platanthera blephariglottis*; Firmage and Cole 1988); this correlation was maintained for several years after the published study (Firmage, personal communication), with more inflorescences produced during years with higher precipitation. The authors suggested that the correlation found during their 8-year study was a consequence of damage to developing inflorescences during winters with low snow cover. At our study site, snowpack depth appears to be almost invariably deep enough to prevent the ground from freezing and causing damage to the plants.

Some models of climate change (e.g., Giorgi et al. 1998) predict that there will be increased winter precipitation in our part of the Rocky Mountains, and there already appears to be a trend in this direction for both the Sierra Nevada (Johnson 1998) and our area (Inouye et al. 2000). Snowpack has been shown, through both natural variation (e.g., Kudo 1993) and experimental manipulation of snowpack, using both shoveling snow (e.g., Galen and Stanton 1993, 1995; Dunne 2000) and drift fences (e.g., Weaver and Collins 1977; Sturges 1989; Scott and Rouse 1995), to have a variety of effects on vegetation and flowering. These include protection from frost (Bell and Bliss 1979), effects on subalpine meadow community pattern (Weaver 1974; Sturges 1989; Evans and Fonda 1990), change in developmental time (Holway and Ward 1963) and productivity (Billings and Bliss 1959; Weaver 1974), variation in percent cover and seed mass through changes in growing-season length (Galen and Stanton 1993, 1995), phenology (Weaver and Collins 1977; Kudo 1992; Morton 1994; Walker et al. 1995), seed set, and mating system (Kudo 1993). Leaf life-span, leaf mass per area (LMA), and leaf nitrogen concentration (Kudo et al. 1999) have also been demonstrated to respond to variation in snowpack. Thus, in addition to the changes we demonstrate for timing and abundance of flowering, increased winter precipitation may lead to a variety of other kinds of changes in montane plant communities.

Changes in the abundance of flowering could have consequences for the pollination and mating system of *D. barbeyi*, as predicted by host-visitor models of mutualism (Morales 2000) and as demonstrated for a variety of plant species. For example, the frequency of visitors (Jennersten and Nilsson 1993), behavior of visitors (Schmitt 1983; Kunin 1993), species of visitors (Conner and Neumeier 1995; Conner and Rush 1996), seed production (Krannitz and Maun 1991; Jennersten and Nilsson 1993; Kunin 1997; Bosch and Waser 1999), and rate of outcrossing (Van Treuren et al. 1993; Karron et al.

1995) have all been demonstrated to depend on flower abundance or density. Pollinators of *D. barbeyi* include species of *Bombus* (bumblebees), and in particular at our study site the long-tongued species *B. appositus* (Inouye 1978), and the hummingbird species *Selasphorus platycercus* (Broadtailed) and *S. rufus* (Rufous). Previous work at this site has demonstrated that flower abundance (an index that included *D. barbeyi*) has an influence on the number of hummingbirds banded (Inouye et al. 1991).

Frost, through its effects on flower abundance, can have consequences for plant demography, and plants' relationships with pollinators, herbivores, and seed predators (Inouye 2000). In the case of *D. barbeyi*, we have no data on plant demography but speculate that the effects of loss of potential seed production may extend to seedling production and hence to demography. Although cattle will sometimes eat (and are poisoned by) *D. barbeyi*, there do not appear to be other significant herbivores; sometimes dipteran larvae are found in the floral nectaries (Inouye, unpublished observation). All of these species, pollinators and herbivores, that interact with *D. barbeyi* are likely to be affected by changes in its abundance that may result from future changes in snowpack, either as a consequence of snowpack directly or its effects on frequency of frost.

Regional processes at the scale of the ENSO could also affect flowering on the local scale of our study. During La Niña years less moist air penetrates into the area during fall and spring, resulting in reduced tree growth (as indicated by smaller tree rings) and large fires (Veblen et al. 2000). Walker et al. (1995) found that a major ENSO event had effects on phenology and growth of two alpine forbs in their Front Range study site in Colorado. In our study area we found a significant correlation between La Niña conditions and reduced flower production, and a suggestive trend (no significant correlation) between stem production and precipitation or temperature; thus the nature of the effects of ENSO on flower production still remains uncertain and merits additional study. The frequency and magnitude of ENSO events may change with global warming (Timmerman et al. 1999; Easterling et al. 2000; Urban et al. 2000) and this change in frequency may have effects on *D. barbeyi* in the future.

Although the MEI and flower production were not significantly correlated, there are trends that seem to be developing that we will follow as our data set grows. In the nearby town of Crested Butte, where weather records have been kept since 1906, MEI significantly correlates to summer precipitation. Mean MEI values from mid-June to mid-August are negatively correlated with July precipitation and positively correlated with August precipitation in Crested Butte (1950–1999). This is apparent as less precipitation in July and more in August for El Niño conditions and the reverse for La Niña conditions. May and June also present trends of positive correlation (for June $P=0.1$ and for May $P=0.11$). This analysis suggests that changes in the frequency or magnitude of

ENSO events may also have subtle effects on flowering in the future.

The evidence seems to be accumulating that the climate is changing at our study site (Inouye et al. 2000), and that this change could have an effect on *D. barbeyi*, other plant species, and the animal species that interact with them. Many of the patterns we have found for *D. barbeyi* are also found for the earlier-flowering congener *D. nuttallianum* (Saavedra 2000), and the effect of climate change on pollinators could be significant because these two plant species are both very common in our study area and share some pollinators (bumblebee species and hummingbirds). We urge ecologists to look for or initiate other long-term studies to investigate similar phenomena. Although these kinds of data accumulate at the slow rate of one datum per year, data from our phenological studies suggest that it is possible to discern significant trends with as few as 7–8 years of data.

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