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Changes in flowering and abundance of *Delphinium nuttallianum* (Ranunculaceae) in response to a subalpine climate warming experiment

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Abstract

High-altitude and high-latitude sites are expected to be very sensitive to global warming, because the biological activity of most plants is restricted by the length of the short snow-free season, which is determined by climate. Long-term observational studies in subalpine meadows of the Colorado Rocky Mountains have shown a strong positive correlation between snowpack and flower production by the forb *Delphinium nuttallianum*. If a warmer climate reduces annual snowfall in this region then global warming might reduce fitness in *D. nuttallianum*. In this article we report effects of experimental warming on the abundance and flower production of *D. nuttallianum*. Plant abundance (both flowering and vegetative plants) was slightly greater on warmed than control plots prior to initiation of the warming treatment in 1991. Since 1994 experimental warming has had a negative effect on *D. nuttallianum* flower production, reducing both the abundance of flowering plants and the total number of flowers per plant. Flower bud abortion was higher in the heated plots than the controls only in 1994 and 1999. Results from both the warming experiment and analyses of unmanipulated long-term plots suggest that global warming may affect the fecundity of *D. nuttallianum*, which may have cascading effects on the pollinators that depend on it and on the fecundity of plants that share similar pollinators.

Keywords: alpine, climate change, Delphinium, fitness, flower abortion, flower production, Ranunculaceae, Rocky Mountain Biological Laboratory, snowpack

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Introduction

There is increasing evidence that humans have modified the global climate by increasing the level of greenhouse gases in the atmosphere. A doubling of atmospheric CO_2 concentration and increase in concentration of other greenhouse gases is predicted to trigger an average temperature increase of 1–6 °C in the next century, and is also predicted to affect precipitation patterns, soil moisture, and snow and ice cover (IPCC, 2001a). Ecosystems may be affected by global warming via species-specific changes in rates and timing of plant growth that can alter the relative abundances of species (Bazzaz, 1990; Chapin *et al*., 1995; Harte & Shaw, 1995; Shaver *et al*., 1998; IPCC, 2001b). Temperature increases due to global warming are predicted to have a particularly strong effect on high-altitude and latitude environments (Schneider, 1975, 1993; Schneider & Thompson, 1981; IPCC, 2001b). Climate change would most likely affect the length of the snow-free growing season in both arctic and alpine environments, affecting as a consequence these ecosystems that are characterized by a short snow-free growing season. Experimental and observational studies in these environments have been used to test climate change predictions (Galen & Stanton, 1991, 1993; Walker *et al*., 1993, 1995; Grabherr *et al*., 1994; Chapin *et al*., 1995; Harte & Shaw, 1995; Mølgaard & Christensen, 1997; Price & Waser, 1998; Saavedra, 2000, 2002; Dunne *et al*., 2003).

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Many of these studies suggest that responses to climate change will be species-specific (Chapin *et al*., 1995; Harte & Shaw, 1995; Henry & Molau, 1997; Price & Waser, 1998; Shaver *et al*., 1998; de Valpine & Harte, 2001), variable between sites (Havström *et al*., 1993; Stenström & Jónsdóttir, 1997; Arft *et al*., 1999; Hollister, 1999) and variable across time (Chapin *et al*., 1995; Chapin & Shaver, 1996; Arft *et al*., 1999; Hollister, 1999).

Recent reviews of long-term data (Hughes, 2000; IPCC, 2001b; Root & Schneider, 2002; Parmesan & Yohe, 2003; Root *et al*., 2003) also showed that species in different habitats are responding differently to climate change and that the differential changes of various species to climate change might lead, among other things, to a progressive decoupling of species interactions (e.g. plants and pollinators) and to an increased presence of opportunistic, weedy or highly mobile species in sites where local populations are going extinct. Changes in the dynamics of individual species (e.g. abundance, phenology) could have a great impact on communities and ecosystem processes by altering species interactions (Carpenter *et al*., 1993; Sanford, 1999) and knowledge of the fitness consequences of climate change on key species could offer insights into how communities and ecosystems might change with climate change. For example, warming has the potential to increase the predatory rates of *Pisaster* in the Oregon coast. This might lead to a shift in species abundance by reducing the extent of mussel beds, and therefore reducing the abundance of the species that use this habitat (Sanford, 2002). The plant *Delphinium nuttallianum* (Nelson's larkspur) is a species that can serve as a model for other species globally to understand the potential fitness effects of climate change on species and communities. *Delphinium nuttallianum* is an important plant species in the Rocky Mountains as an early source of nectar for both hummingbirds (Waser, 1976; Inouye *et al*., 1991) and queen bumblebees (Inouye & McGuire, 1991). At our study site, near the Rocky Mountain Biological Laboratory (RMBL), broad-tailed hummingbirds (*Selasphorus platycercus*) rely heavily on the sequential flowering of three flowering plants for nectar: *D. nuttallianum*, *Ipomopsis aggregata* and *Delphinium barbeyi* (Waser, 1978). If the distribution and abundance of *D. nuttallianum* were to be affected by climate change we could also expect changes in the abundance of pollinators that depend on this plant, and in the fecundity of plants that share its pollinators. In an earlier observational study of subalpine meadows in the Colorado Rocky Mountains, Inouye & McGuire (1991) reported a positive and strong correlation between flower production of *D. nuttallianum* and total snow accumulation during the previous winter. They suggested that if a warmer climate reduces mean annual snowfall, then climate warming has the potential to lower flower production of *D. nuttallianum* and other early flowering herbaceous species, and consequently to reduce the number and relative proportion of such species in this habitat over the long-term.

To explore further the possible effects of global warming on flower production of *D. nuttallianum,* we tested Inouye & McGuire's (1991) prediction that global warming might trigger a decrease in flower production by analysing a much longer time series of data on snowmelt date and flower abundance (1975–2000). We also tested their prediction with a 10-year experimental study of the effects of infrared heaters used to simulate expected global warming on flower abundance of *D. nuttallianum*. Since the heaters advanced snowmelt and dried the soil in heated vs. unheated control plots (Harte & Shaw, 1995; Harte *et al*., 1995; Price & Waser, 1998), this experiment simulated the effects of low-snowfall years.

Materials and methods

Study site and system

Delphinium nuttallianum Pritzel (formerly *Delphinium nelsonii* Greene; Weber & Wittmann, 1996) (Ranunculaceae) is a perennial herb (forb) and is one of the first species to flower after snowmelt (generally between late May and late June) in the meadows near the RMBL, Colorado. *Delphinium nuttallianum* is found in dry meadows of the Rockies throughout the western USA from South Dakota and Idaho to Colorado, Utah and northern Arizona (Harrington, 1964; Waser & Price, 1990). *Delphinium nuttallianum* plants overwinter as small tuber-like roots, sprout after snowmelt, and are vegetatively active only for 3–5 weeks (typically from early June until late June–early July) after which above-ground structures senesce and the plants become dormant again until the next summer (Waser & Price, 1994). *Delphinium nuttallianum* preforms flower buds and it flowers not long after snow melts; in our site the first flower has been observed between 14 May and 12 July between the years 1975 and 2000. It takes 3–7 years for *D. nuttallianum* to flower for the first time and longer to reach full flower production (Waser & Price, 1991). Each plant produces only one inflorescence, which has 1–15 flower buds (Waser & Price, 1981). At the RMBL, *D. nuttallianum* is pollinated primarily by hummingbirds and bumblebees (Waser, 1978).

The study was in a subalpine meadow in the Colorado Rocky Mountains, near the RMBL (38°57′N, 106°59′W, 2900 m elevation), in southwestern Colorado, USA. The experiment was located on a glacial moraine with a natural gradient of snowmelt from north to south, and a moisture gradient from a dry ridge to moist swale (figures of the experimental treatments are in Harte & Shaw, 1995 and Price & Waser, 1998).

We also present data on *D. nuttallianum* flower production in plots located in a nearby rocky meadow habitat. These plots were used to test for a relationship between *D. nuttallianum* flower number and snowmelt date, as reported by Inouye & McGuire (1991) and to compare the temporal pattern of control plants from the warming experiment to unmanipulated plots arranged in this nearby habitat. Snowfall and snowpack data were recorded at a permanent measurement site in Gothic within 0.6–1.0 km of the two areas where plots were located. Table 1 shows snowfall for the years in which we present data for the warming meadow experiment.

Experimental design

The warming experiment consisted of ten $3 \times 10\,m^2$ plots arranged along the moraine, with plot number 10 located on the northern most location and plot 1 in the most southern, separated by at least 2 m. (Note that Price & Waser (1998, 2000) numbered plots in the opposite direction from Harte *et al*., 1995 and Harte & Shaw, 1995; we have followed the numbering from Harte's papers). Even-numbered plots were assigned to the warming treatment while odd-numbered plots were controls (no warming). Temperature was increased in the warmed plots with electrical heaters suspended 2 m aboveground. The experimental plots were established in 1990 and heaters were turned on in January of 1991. Initially (1991–1993) only two heaters were suspended above warmed plots producing a flux of $15\,W\,m^{-2}$ in the central area; in May 1993 an additional heater was added, which increased the infrared radiation (IR) flux to about $22\,W\,m^{-2}$ in the central area of the plots (75% of the total area; for more detail of the layout see Harte & Shaw, 1995; Harte *et al*., 1995; or Price & Waser, 1998). The $22\,W\,m^{-2}$ increase in IR flux was selected because its effect on soil temperature was expected to be comparable to the effect of doubling CO_2 (Ramanathan, 1981; Harte *et al*., 1995). The warming treatment advanced snowmelt, increased soil temperature and decreased soil moisture (Harte *et al*., 1995; Harte & Shaw, 1995; Price & Waser, 1998). The warming treatment also increased gross nitrogen mineralisation rates in some years (xeric zone, 1991, 1992; Shaw & Harte, 2001). The experimental increase in downward infrared radiation altered three environmental variables likely to change with global warming: temperature (plant and soil), soil moisture, and snowmelt date. Although the warming experiment was a reasonable simulation of global warming, it had limitations. It did not warm the air over the plots, since the heating occurred only by downward IR flux, and it did not simulate potential covarying changes in precipitation, or in CO_2.

Table 1 Winter snowfall totals in Gothic Colorado

Year	Snowfall (cm)
1990	964
1991	1076
1992	692
1993	1469
1994	954
1995	1641
1996	1200
1997	1496
1998	1171
1999	1144

Data courtesy of Billy Barr (RMBL).

Data collection

From 1994 to 1999, we collected data on *D. nuttallianum* flowering in the warming experiment in early summer (10 June−21 July) when most *D. nuttallianum* plants were in flower. We counted the number of flowering plants, the numbers of buds, open flowers or fruits per plant (hereafter referred to as the total number of flowers per plant), and the number of aborted buds in each plot, and we calculated the percentage of these aborted flowers. These counts were made after the peak of flowering, so that in some cases we were counting the presence of fruits rather than flowers. At this time there is little ambiguity about whether or not the remaining buds will produce normal flowers. Aborted buds are normally found only at the top of the inflorescence, and are typically under 1 mm in size, and brown.

We also collected data on flowering from a set of eight $2 \times 2\,m^2$ unmanipulated plots every other day during the growing season (1975–2000 except for 1990) to determine the annual peak number of inflorescences and flowers. Open flowers were counted on all inflorescences in each plot, and the maximum counts for all plots were summed for each year to calculate a total.

In order to determine whether there was an initial difference in plant abundance before the experiment started between control and warming plots we also analysed data on *D. nuttallianum* abundance from 1990 to 1994 on a belt transect (0.25 m wide × 8 m long) established inside each of the experimental study plots. Each belt transect was centred 87.5 cm south of the midline of its plot, and correspondingly 62.5 cm from the south boundary of the plot; the 67.5 figure reported in Price & Waser (2000) is a typographic error. Each transect was divided into 32 contiguous quadrats ($0.25 \times 0.25\,m^2$). In each quadrat we determined *D. nuttallianum* abundance by counting the number of quadrats in which the species

was present (flowering or not) (for more details in the methodology see Price & Waser, 2000).

Analysis

We used the MIXED procedure in SAS (Version 6; Littell *et al*., 1996; SAS, 1997) for all analyses to test for the effect of the warming treatment on the reproduction and abundance of *D. nuttallianum* plants. The response variables analysed were: (a) abundance of plants (measured as frequency of occurrence per plot), (b) abundance of flowering plants (number per plot), (c) flower number per plant (including normal buds if the census was conducted before they opened), and (d) mean proportion of flower buds aborted per plant and plot.

We used ANCOVA with year as the repeated measure and plot number as the covariate. We used plot number as a covariate in all models since it has been shown that plot number

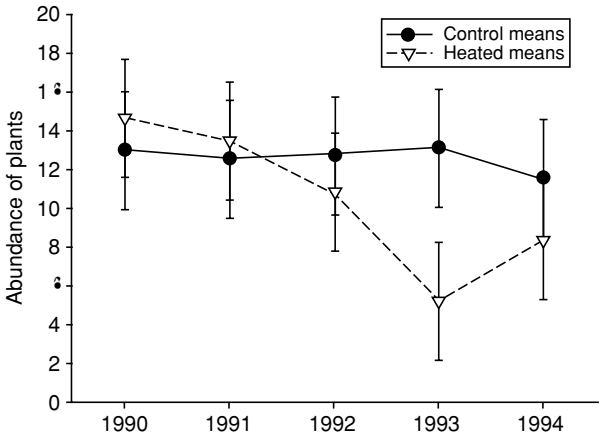


Fig. 1 Abundance of *D. nuttallianum* plants in control and treatment plots, 1990–1994. Values are number of quadrats (out of 32) in which *D. nuttallianum* was present, out of 32 quadrats per plot. This includes seedlings, vegetative juveniles, and flowering individuals. The species was counted as present if any plant part occurred in the quadrat. Error bars represent 95% comparison limits.

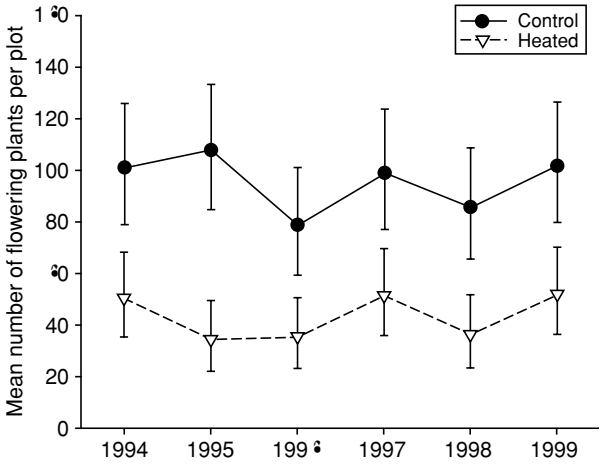


Fig. 2 Mean number of flowering *D. nuttallianum* plants (back-transformed data) in control and treatment plots from 1994 to 1999. Error bars represent 95% comparison limits.

ANCOVA indicated that the abundance of flowering plants was significantly higher in the control plots than in the warmed plots for all years (Fig. 2) ($P = 0.0047$) and that there was a year effect as well (Table 2). Plot number and plot number by year affected flowering plant abundance significantly (Table 2).

Effect of experimental warming on total number of flowers per plant

Experimental warming decreased the average number of flowers per plant (control mean = 4.52 flowers/plant; SE = 0.18 vs. treatment mean = 3.95 flowers/plant; SE = 0.18). ANCOVA indicated that treatment had a non-significant ($P = 0.06$) and year a strongly significant effect on the average number of flowers per plant. Plot number did not affect flower number significantly (Table 3). Every year plants from the control plots had more flowers than the plants from the heated plots (Fig. 3).

Effect of experimental warming on mean proportion of flower buds aborted per plant and plot

The abortion of flower buds was similar in warming and control plots in all years except 1994 and 1999, when flower abortion was significantly higher in the treatment plots than the controls (Fig. 4). The ANCOVA showed that after adjusting for plot number and year, the interaction treatment-by-year had a statistically significant effect on flower bud abortion. Treatment alone had no effect on flower bud abortion (Table 4). Plot number and the interaction of plot number by year significantly affected flower bud abortion (Table 4).

Table 2 Results from ANCOVA of the effect of warming on the abundance of flowering *Delphinium nuttallianum* plants, 1994–1999 ($n = 60$ observations)

Source	Effect	LSdf	Ddf	*F*	*P*
Treatment	**Fixed**	**1**	**7.33**	**16.0**	**0.0047**
Year	**Fixed**	**5**	**12.8**	**18.51**	**0.0001**
Year*treatment	Fixed	5	12.8	0.60	0.7007
Plot number	**Fixed**	**1**	**7.33**	**17.3**	**0.0038**
Plot number*year	**Fixed**	**5**	**12.8**	**22.72**	**0.0001**
Residual	Random	42			

Plot number used as the covariate. Repeated = year; Used ddfm = Satterthwaite to estimate df; LSdf = least squares degrees freedom; Ddf = denominator degree of freedom. Significant effects are shown in boldface type.

Table 3 Results from ANCOVA of the average number of flowers per *Delphinium nuttallianum* plant, 1994–1999 ($n = 60$ observations)

Source	Effect	LSdf	Ddf	*F*	*P*
Treatment	Fixed	1	7.35	4.87	0.0614
Year	**Fixed**	**5**	**15.1**	**11.78**	**0.0001**
Year*treatment	Fixed	5	15.1	0.32	0.8944
Plot number	Fixed	1	7	1.05	0.3389
Residual	Random	47			

Plot number used as the covariate. Repeated = year; Used ddfm = Satterthwaite to estimate df; LSdf = least squares degrees freedom; Ddf = denominator degree of freedom. Significant and marginally significant effects are shown in boldface type.

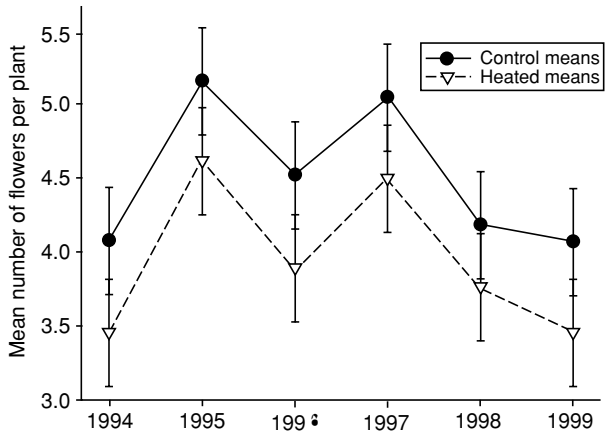


Fig. 3 Mean number of flowers per plant in control and treatment plots from 1994 to 1999. Error bars represent 95% comparison limits.

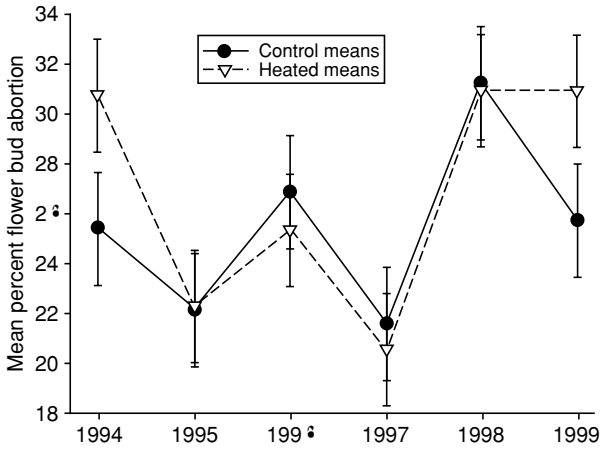


Fig. 4 Mean percentage of flower bud abortion per plant (back-transformed) in control and treatment plots from 1994 to 1999. Error bars represent 95% comparison limits.

Table 4 Results from ANCOVA of the average proportion of flower bud abortion per *Delphinium nuttallianum* plant, 1994–1999 ($n = 60$ observations)

Source	Effect	LSdf	Ddf	*F*	*P*
Treatment	Fixed	1	7	1.20	0.3089
Year	**Fixed**	**5**	**35**	**3.18**	**0.0180**
Year*treatment	**Fixed**	**5**	**35**	**2.59**	**0.0425**
Plot number	**Fixed**	**1**	**7**	**5.65**	**0.0492**
Plot number*year	**Fixed**	**5**	**35**	**2.72**	**0.0351**
Residual	Random	42			

Plot number used as the covariate. Repeated = year; Used ddfm = Satterthwaite to estimate df; LSdf = least squares degrees freedom; Ddf = denominator degree of freedom. Significant effects are shown in boldface type.

Correlational analysis from long-term data (unmanipulated plots) and from the warming meadow plots

We replicated the analysis from Inouye & McGuire (1991), and corroborated their result that maximum number of open flowers per plot decreases with a decrease of total winter snowfall ($r = 0.663$, $P = 0.0003$) (Fig. 5). The nature of this response is explained better by the correlation between total number of individuals flowering and snowpack ($r = 0.688$, $P = 0.0001$) (Fig. 5) than by the maximum number of open flower per plant ($r = 0.26$, $P = 0.21$), suggesting that number of flowering plants rather than maximum number of open flower per plant is more sensitive to winter snowfall.

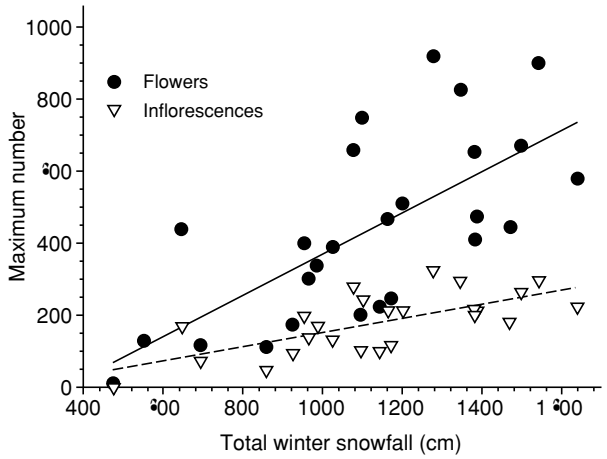


Fig. 5 Relationship of peak flower abundance (●) and peak number of flowering individuals (▽) on any one date each year to total snowfall in the previous winter. Data from eight $2 \times 2\,m^2$ Rocky Meadow plots at RMBL, 1975–2000.

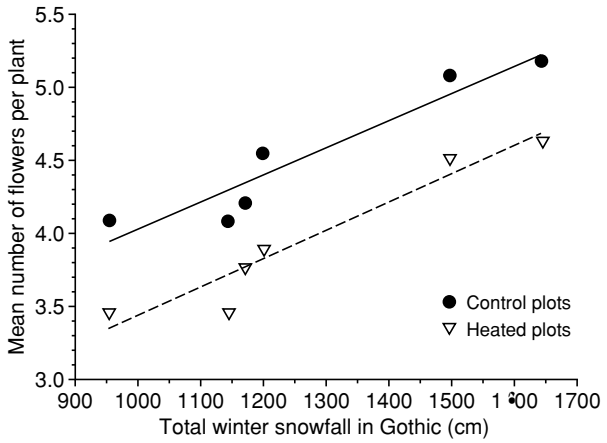


Fig. 6 Relationship between the mean number of flowers per plant and total snowfall in the previous winter. Data from the heated and control plots at RMBL, 1994–1999.

In contrast to data from the unmanipulated plots, the six years of data from the experimental plots (1994–1999) indicated that there was a highly significant correlation between total winter snowfall and mean number of flowers per plant: heated plots $r = 0.962$, $P = 0.002$; control plots $r = 0.948$, $P = 0.004$ (Fig. 6).

Discussion

The results of this experiment show the value of combining long-term observation of natural populations with experimental work to understand the mechanisms by which plants may respond to changes in climate. Inouye & McGuire (1991) predicted that a decline in snowfall, a potential consequence of climate warming, might lower flower production of *D. nuttallianum*. The warming experiment made it possible to test this hypothesis indirectly, since warming mimicked low-snowfall years by advancing date of snowmelt and significantly reducing soil moisture (Harte & Shaw, 1995; Harte *et al*., 1995; Price & Waser, 1998; Saavedra, 2000). In this light, predictions by Inouye & McGuire (1991) were supported by this warming experiment. First, *D. nuttallianum* plants responded to the warming treatment both by having fewer flowering plants and fewer flowers per plant in the heated plots than in the controls. Second, flower bud abortion was significantly higher in the heated plots than in the controls in 1994 and since winter snow accumulation was low in 1994 (954 cm snowpack, vs a range of 1171–1641 cm for other years in the study), this further suggests that a change in snowfall might trigger a change in flower production for *D. nuttallianum* (more aborted flowers leads to fewer flowers per plant). Nevertheless, comparing long-term flower production against flower production in the warming experiment might have its limitations. A comparison of slopes of the long-term data suggests that the abundance of flowering plants and therefore total number of flowers responded strongly to snow cover and that average flower number per flowering plant did not, whereas the experimental plots indicate that there is a highly significant correlation between total winter snowfall and mean number of flowers per plant. These patterns can not be compared directly, as in one case the data are for total number of flowers produced on each plant (the experimental study) and in the other for maximum number of flowers open (the Rocky Meadow plots). In addition, plants in drier, rockier soil (the unmanipulated Rocky Meadow plots) tended to produce smaller inflorescences with fewer flowers than plants in deeper, moister soil (the heating experiment).

Both experimental warming and the long-term data suggest that the number of individuals flowering is more sensitive to environmental conditions than the number of flowers per plant. In *D. nuttallianum*, a substantial fraction of individual plants often forego flowering altogether (approximately 30% in 1996 and 1997; F. Saavedra, personal observation). Higher soil temperatures and lower soil moisture (Harte *et al*., 1995) in heated plots appear to be key factors that induce plants to abandon flowering. Many plant species flower only after having accumulated sufficient resources, and the reduction of soil moisture caused by natural or experimental variation in water input early in the summer might limit *D. nuttallianum* growth and resource accumulation by limiting the length of its growing season. In addition, we have seen plants that have succumbed to water stress before the time of flowering. There is an alternative, mechanistic, hypothesis for the tendency of plants to respond to stress by ceasing to flower altogether. Like many other subalpine plants, *D. nuttallianum* preforms buds for flowering one year in advance. It may therefore be difficult for plants to alter flower number after this point, leaving only the option to flower or not to flower.

An initial decline in overall flower abundance of *D. nuttallianum* populations due to environmental conditions might affect the population dynamics of the species. For example, Bosch & Waser (1999) found that sparse populations of *D. nuttallianum* at the RMBL had significantly lower seed set relative to dense populations, presumably as a result of reduced pollinator visitation. We have no data for seedling establishment or growth for *D. nuttallianum* in the warming experiment and therefore cannot speculate on the effect of global warming on this part of the plant reproductive cycle. Climate effects on *D. nutallianum* might indirectly affect the balance of other plant species. Evidence from the field suggests that *D. nuttallianum* might act as a mutualistic partner with later-flowering species by sustaining migratory populations of broad-tailed hummingbirds. Specifically, years with lower flowering abundance for *D. nuttallianum* show both reduced numbers of broad-tailed hummingbirds (Inouye *et al*., 1991) and lower fecundity of the sympatric plant *I. aggregata* (Waser, 1976; Waser & Real, 1979). Climate change could have a direct effect on the reproduction of plant species and could potentially disrupt plant–pollinator interactions (Bond, 1995). If global warming reduces the flower abundance of *D. nuttallianum* we might see a cascading effect on the pollinators that depend on this species and on the fecundity of the plant species that share those pollinators.

Warming may also directly affect flower abundance of other herbaceous species in high altitude sites whose flowering is linked to snowpack (Inouye *et al*., 2002). *Delphinium nuttallianum* is one of four species (out of 11) that showed reduced biomass after experimental warming in a field study by de Valpine & Harte (2001). Since warming decreases soil moisture but increases nitrogen

mineralisation (Harte *et al*., 1995; Shaw & Harte, 2001), the authors speculated that *D. nuttallianum* and three other species might be more limited by water availability than by nutrients, an inference that fits well with our experimental and survey data. We think that *D. nuttallianum* represents a group of 'spring ephemeral' forbs that flower early after snowmelt, relying primarily on moisture from snowmelt, and then cease vegetative growth and reproduction for the rest of the growing season. This whole group is likely to change in similar ways if there is a change in water input from winter precipitation, either because of a change in total snowpack, or a change in the rate of evaporation because soil temperatures are higher early in the season. In support of this, initial observations (1999–2001) of an even earlier-flowering species, *Erythronium grandiflorum* (glacier lily; Liliaceae), indicate that a similar decline in number of flowering plants has occurred in the heated plots (Inouye, unpublished data). Thus drought-sensitive forb species and the animal species that depend on them (e.g. pollinators), may decline in subalpine habitats and that more drought-tolerant species (e.g. sagebrush) may eventually increase.

As with any climate change experiment, the warming experiment has limitations. The experiment fails to warm the air over the unenclosed plots, it does not increase CO_2, and it does not address potential and poorly understood changes in precipitation. Although most models of climate change predict earlier snowmelt and/or later initial snow accumulation (Boer *et al*., 1992; Brown *et al*., 1994; CSIRO, 1994; Whetton *et al*., 1996), other models of the potential consequences of climate change for winter precipitation in our study area suggest increases in snowpack (Giorgi *et al*., 1998). There is evidence that this is indeed occurring. First, a plot of winter snowfall at the study site (2920 m) since 1974 suggests that a slight but nonsignificant increase ($r = 0.211$, $P = 0.311$) of total winter snowfall has already occurred at the RMBL since 1975 (Inouye *et al*., 2000; date of snowmelt has not changed significantly in the same period of time, B. Barr, unpublished data). The second source of evidence for an increase in winter snowfall comes from the Sierra Nevada. Data on snow accumulation from 1937 to 1997 show that in sites under 2400 m snow is both accumulating less and melting earlier, whereas in sites above that elevation snow accumulation is higher yet still melts earlier (Johnson, 1998). If predictions of greater winter precipitation are upheld, then increased snowpack in the future could help mitigate predicted effects of climate change on soil temperature and soil moisture. Further experimental manipulations of snow levels, snowmelt date, and soil moisture levels are ongoing to determine how these factors interact with respect to the reproductive traits of subalpine plants. Results from these experiments can be combined with explicit models to predict possible outcomes of continued climate change.

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