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EFFECTS OF CLIMATE CHANGE ON PHENOLOGY, FROST DAMAGE, AND FLORAL ABUNDANCE OF MONTANE WILDFLOWERS

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Abstract. The timing of life history traits is central to lifetime fitness and nowhere is this more evident or well studied as in the phenology of flowering in governing plant reproductive success. Recent changes in the timing of environmental events attributable to climate change, such as the date of snowmelt at high altitudes, which initiates the growing season, have had important repercussions for some common perennial herbaceous wildflower species. The phenology of flowering at the Rocky Mountain Biological Laboratory (Colorado, USA) is strongly influenced by date of snowmelt, which makes this site ideal for examining phenological responses to climate change. Flower buds of *Delphinium barbeyi*, *Erigeron speciosus*, and *Helianthella quinquenervis* are sensitive to frost, and the earlier beginning of the growing season in recent years has exposed them to more frequent mid-June frost kills. From 1992 to 1998, on average 36.1% of *Helianthella* buds were frosted, but for 1999–2006 the mean is 73.9%; in only one year since 1998 have plants escaped all frost damage. For all three of these perennial species, there is a significant relationship between the date of snowmelt and the abundance of flowering that summer. Greater snowpack results in later snowmelt, later beginning of the growing season, and less frost mortality of buds. Microhabitat differences in snow accumulation, snowmelt patterns, and cold air drainage during frost events can be significant; an elevation difference of only 12 m between two plots resulted in a temperature difference of almost 2°C in 2006 and a difference of 37% in frost damage to buds. The loss of flowers and therefore seeds can reduce recruitment in these plant populations, and affect pollinators, herbivores, and seed predators that previously relied on them. Other plant species in this environment are similarly susceptible to frost damage so the negative effects for recruitment and for consumers dependent on flowers and seeds could be widespread. These findings point out the paradox of increased frost damage in the face of global warming, provide important insights into the adaptive significance of phenology, and have general implications for flowering plants throughout the region and anywhere climate change is having similar impacts.

Key words: *climate change;* Delphinium barbeyi; Erigeron speciosus; *flowering; frost; growing season;* Helianthella quinquenervis; *phenology; Rocky Mountain Biological Laboratory; snowmelt, subalpine.*

Introduction

The phenology of reproduction is an important life history trait that influences fitness in a variety of ways. Reproducing at the wrong time, in advance of or after the appropriate season, may lead to failure in finding mates, failure to match demands of growing offspring with temporal peaks in food resources (e.g., Visser et al. 1998), or failure by a pollinator to find pollen and nectar, or failure of a flower to be pollinated. Given these potentially severe consequences, it is not surprising that in many cases the phenology of reproduction has evolved to rely on environmental cues that have proven to be reliable indicators of appropriate timing of reproductive effort. An ecological and evolutionary dilemma is posed to a variety of organisms now because of the environmental changes accompanying global climate change. Can they respond in appropriate ways to these ongoing changes so that their phenology remains synchronous with other species with which they interact? And can they adjust their responses to previously reliable environmental cues for timing of reproduction? These questions are difficult to answer without long-term observations and experiments.

The phenology of flowering by herbaceous wildflowers at high altitudes where there is significant snowfall is primarily a consequence of one environmental event, the disappearance of the snowpack (Inouye and Wielgolaski 2003). This event is in turn influenced by a variety of factors, including global, regional, and local climate. Global influences include ongoing changes in temperature and precipitation regimes, with high-altitude environments warming and receiving more precipitation as rain instead of snow (Beniston and Fox 1996, Johnson 1998). Regional influences on snowpack in the western United States include the El Niño/Southern Oscillation

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TABLE 1. Study species.

Species (family)	Common name	Average flowering dates	Units counted
Delphinium barbeyi (Ranunculaceae)	subalpine larkspur	mid-July	flowers and inflorescences
Helianthella quinquenervis (Asteraceae)	aspen sunflower	mid to late July	capitulae and inflorescences
Erigeron speciosus (Asteraceae)	aspen fleabane	late July	capitulae

(ENSO; Diaz et al. 2003) and the North Pacific Oscillation (Pacific Decadal Oscillation; Grissino-Mayer et al. 2004). Local influences include topographic variables such as slope and aspect, which affect the accumulation and melting of snowpack (Miller 1982, Kudo and Hirao 2006), and the occurrence of cold air drainage that creates thermal and phenological inversions (Lynov 1984). At present, the net result of these environmental changes seems to be a trend toward earlier snowmelt, and hence earlier arrival of spring in the western United States (Cayan et al. 2001) and other mountain areas (Dankers and Christensen 2005). The phenology of high latitudes may show many of the same characteristics that high altitudes do (Wielgolaski and Inouye 2003).

Earlier beginning of the growing season due to earlier snowmelt can have multiple consequences. It could increase the length of the photosynthetic period, if the end of the season remains fixed or changes to a later date. If drought is a problem at the end of the growing season, however, earlier snowmelt and longer snow-free periods may increase exposure of plants to this stress (Giménez-Benavides et al. 2007). Earlier snowmelt can significantly alter the dates on which species may come into bloom throughout the summer (Inouye and McGuire 1991, Inouye et al. 2002, 2003, Saavedra et al. 2003) because the ground and air will warm up when the snow disappears. For some species there may also be a correlation between timing of snowmelt and the abundance of flowering (e.g., *Delphinium* species [Inouye et al. 2002, Saavedra et al. 2003]).

One of the factors linking dates of snowmelt to flowering abundance is frost (Inouye 2000, Inouye et al. 2002). If the probability of spring frost on a particular calendar date remains fixed, but leaf or flower buds are being initiated at earlier dates and thus are more vulnerable when frosts occur, the frequency of frost damage to frost-sensitive species is expected to increase. Frost damage might also increase even if the date of last spring frost is becoming later, if the rate of change in frost dates is slower than that of change in snowmelt dates.

In this study, I report data for three species of high-altitude herbaceous wildflowers that have flower buds susceptible to frost damage (Table 1). All three of these long-lived perennials can experience total mortality of flower buds due to late spring frost events. The availability of a long-term data set on flowering phenology is used to look for evidence in the past few decades of changes suggested above in the timing of snowmelt relative to flowering, and possible influences on timing and abundance of flowering.

METHODS

Study site.—An ongoing long-term study of flowering phenology is being conducted at the Rocky Mountain Biological Laboratory (RMBL), in the Colorado Rocky Mountains (38°57′ N, 106°59′ W). RMBL is located at 2886 m elevation in the East River valley of the West Elk Mountains, approximately 9.5 km north of the town of Crested Butte, Colorado, USA. In 1973, several sets of 2 $\times$ 2 m plots were established by a group of researchers at RMBL for monitoring flowering phenology. For a separate study, two larger plots were established (1974 and 1975) to monitor abundance of flowering by *Helianthella quinquenervis*.

Focal species.—This study reports on data for *Delphinium barbeyi* and *Erigeron speciosus* (see Plate 1) from two subsets of the total of 30 phenology plots, one set in a mesic meadow on level ground (altitudes 2864–2870 m) adjacent to the junction of the East River and Copper Creek (originally established and monitored by Graham Pyke) and the other on dry rocky meadows at slightly higher elevations (2927–2970 m), along the Copper Creek trail and the portion of Forest Service trail #401 that crosses RMBL property. Data on flower abundance for *Helianthella quinquenervis* have been collected each year since 1974 from one plot (lower plot, 10 $\times$ 45 m; mean altitude about 2893 m) or 1975 for a second plot (upper plot, 10 $\times$ 36.5 m; mean altitude about 2905 m). GPS coordinates for the two plots, located above and below the Copper Creek trail in the Gothic town site, are available at the RMBL web site, and a map is presented in Fig. 1.

Empirical design.—Every other day for most or all of the growing season, all flowers in the 2 $\times$ 2 m phenology plots are counted, typically as number per inflorescence or ramet. A map, GPS coordinates for plot corners, and altitudes for the individual plots are available at the RMBL web site (*available online*).[4] For *Helianthella*, the number of flowers per stalk is counted on all inflorescences in each plot annually in July, and the number of inflorescences cut or broken off, and those with missing flowers (typically due to herbivory by deer or pocket gophers), is also counted. Since 1989, the annual mean number of flowers per stalk has been used to estimate the number of missing flowers (typically fewer than 1% of stalks were cut and/or missing flowers), to calculate a

[4] ⟨www.rmbl.org⟩

total number of flowers produced in each plot. Each year since 1994, counts have also been made of the number of frost-killed inflorescences. The inflorescences are typically developed enough to identify frost-killed ones easily (a stalk starts developing instead of just petioles on a vegetative rosette).

Environmental measurements.—Snowmelt data are from daily observations by billy barr of snowpack at a measurement station at the north edge of the RMBL, within 1 km of the plots. Temperature data are from the Crested Butte NOAA weather station.

Analytical methods.—Data for each phenology plot in each year are stored in individual spreadsheets. Statistical analyses were accomplished using SigmaPlot (Systat Software, San Jose, California, USA).

Results

The initiation of the flowering season at this study site is highly variable. Data from three additional species from the phenology plots that represent two of the earliest species and the latest to flower illustrate this, and help to set the context for variation and patterns shown by the three focal species. The first flowers each spring are typically *Claytonia lanceolata* (Portulacaceae), which bloom within a few days after snow melts; its first flowering dates have been as early as 14 April (2002) and as late as 9 June (1995) in the same 2×2 m plot (Rocky Meadow #7). The correlation between date of snowmelt and first flowering date is highly significant for species that flower early (e.g., for *Delphinium nuttallianum*, $r^2 = 0.734$, $P < 0.0001$; data for seven plots, 1975–2006, 1990 missing, mean flowering date 11 June, range 27 May–2 July) and late (e.g., for *Artemisia tridentata* [sagebrush], $r^2 = 0.600$, $P = 0.0001$; data only available from one plot, 1975–2006, 1989–1990 missing, mean flowering date 14 August, range 29 July–30 August).

Delphinium barbeyi

This species flowered in 3–12 plots/yr (mean 8.8; including frost-killed buds as years with flowering) between 1973 and 2006 (data were only collected on first flowering and not peak flowering for 1976, and no data were collected in 1990); non-flowering plants were present in most of the 12 plots in most years, but in some years most or all flower buds on plants that developed inflorescences were killed by frost, reducing the sample size for flowering dates. The average number of years (out of 32) that each plot had flowers was 25.2 (range 14–32). The earliest annual average for flowering (the first flower in all plots with flowers) was 1 July (day of year 182.7, in 2006; $n = 6$ plots) and the latest was 5 August (day of year 217.7, in 1995; $n = 10$ plots). The mean date of first flower (mean of annual means) was 14 July (day of year 195.7; median 15 July). For years with early snowmelt (before 19 May, day 139), there is no significant correlation between flowering date and snowmelt date (mean flowering date = day 189, 8 July), but for years with later snowmelt there is a significant correlation between these variables ($r^2 = 0.745$, $P < 0.0001$; Fig. 2). This split in the data set (made by visual inspection of the data) makes sense biologically as it indicates that there is a threshold effect between snowpack melt date and timing of flowering. This effect could be mediated by a requirement to accumulate a certain number of degree days before flowering occurs, with it taking longer to accumulate that heat sum in years with early snowmelt.

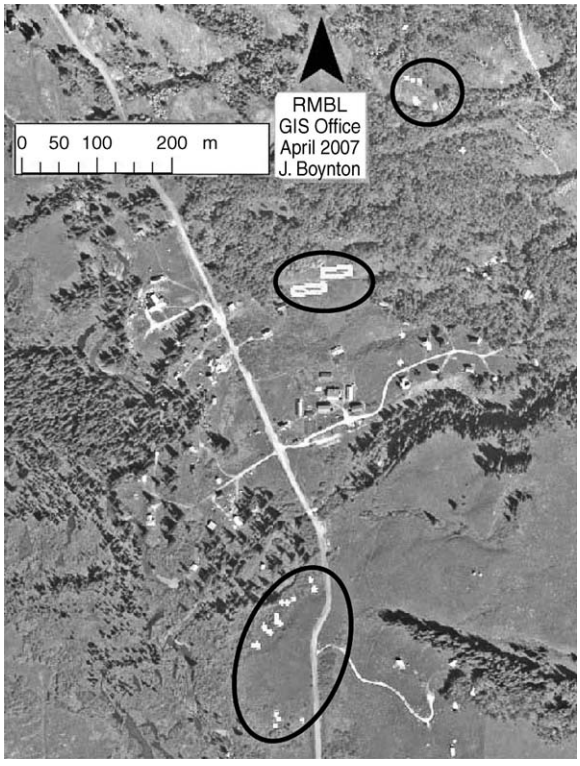


Fig. 1. Aerial view of the Rocky Mountain Biological Laboratory. The vertical road is Gunnison County Road 317, and north is indicated by the arrowhead. The plots used for *Delphinium barbeyi* and *Erigeron speciosus* are included in the upper and lower ellipses, and the *Helianthella quinquenervis* plots are the two larger plots in the middle ellipse.

As was reported in Inouye et al. (2002), there is a significant correlation between winter snowpack and the abundance of flowering for *Delphinium barbeyi*. Fig. 3 shows this relationship, using snowpack remaining on 30 April and including the seven additional years of data collected since that paper appeared; data for peak flowering were incomplete for 1973–1976. One plot (Veratrum Removal #1) had an unusually large number of flowers in 2004, causing that year to appear as an outlier.

Erigeron speciosus

This species is found in both dry, rocky meadow plots ($n = 7$ plots) and wet meadow plots ($n = 9$ plots), and because these tend to melt out at different times (rocky meadow plots are earlier) some correlations are shown

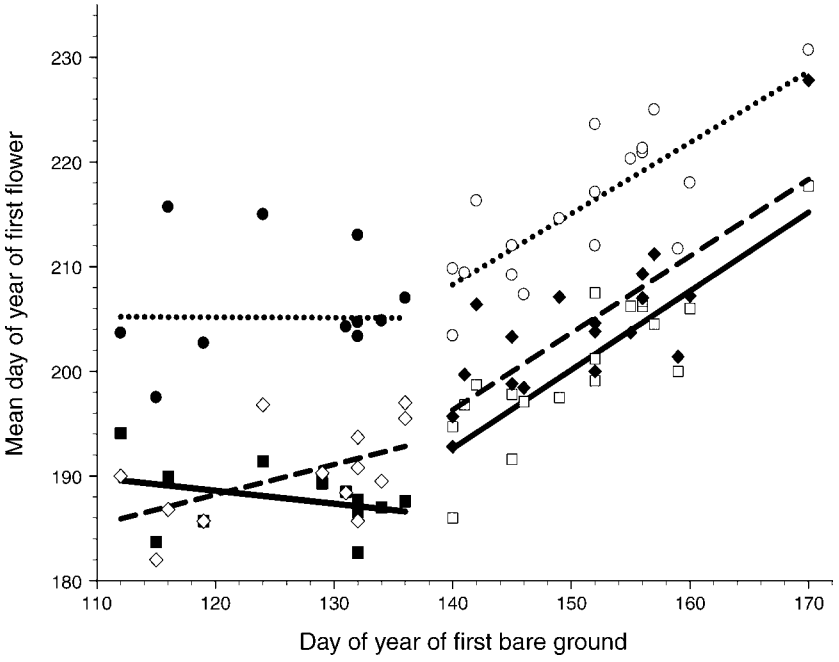


FIG. 2. The relationship between mean day of year of the first flowers of *Delphinium barbeyi* and *Erigeron speciosus* in the phenology plots and the day of year of first bare ground. The data were broken into two subsets by visual inspection; the early set (through day 139) has no significant slope or correlation for either species, and both are significant for the later set ($r^2 = 0.745$, $P < 0.0001$, $N = 18$ years). *Delphinium* data are shown with squares (solid for 12 early years, open for late years), and solid lines indicate the best fits. Data for *Erigeron* are shown separately for the seven dry, rocky, meadow plots (diamonds, open for 13 early years, solid for 18 late years) and nine wet meadow plots (circles; solid for early years and open for late years). For *Erigeron speciosus*, the equation for the later snowmelt dates for rocky meadow plots is $y = 0.734x + 93.506$ (dashed line, $r^2 = 0.629$, $P < 0.0001$); the equation for later snowmelt dates for wet meadow plots is $y = 0.679x + 113.223$ (dotted line, $r^2 = 0.620$, $P < 0.0001$).

separately for each habitat (Fig. 2). *Erigeron* flowered in 6–15 plots/yr (mean 11.0) between 1973 and 2006 (missing data for rocky meadow plots for 1976 and for both habitats in 1990); non-flowering plants were present in most of these plots in most years, but in some years most or all flower buds were killed by frost, reducing the sample size for flowering dates. The average number of years (out of 30) that these 15 plots

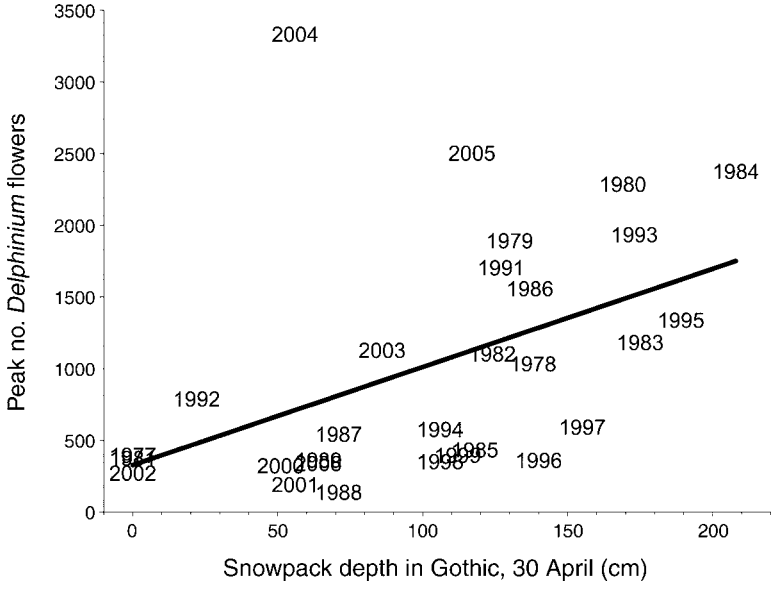


FIG. 3. The relationship between peak abundance of *Delphinium barbeyi* flowers and the amount of snow left on the ground on 30 April of that year ($y = 6.85x + 326.83$, $r^2 = 0.217$, $P = 0.011$, $N = 29$ years).

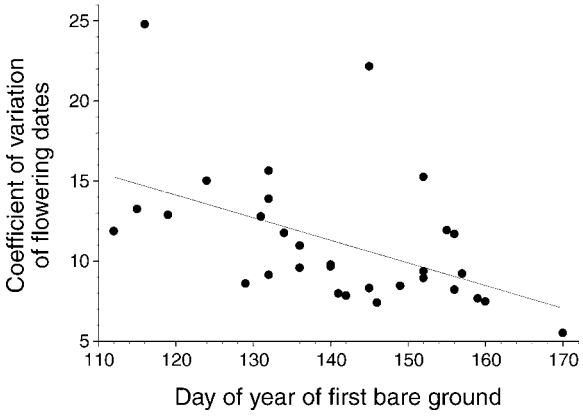


FIG. 4. The relationship between variability of flowering date of *Erigeron speciosus* and the date of snowmelt. Coefficient of variation is calculated using data from both habitats (dry and wet meadow.

had flowers was 22.3 (range 1–30). The earliest annual average for flowering (the first flower in all plots with flowers) was 9 July (day of year 190.2, in 2004; $n = 9$ plots) and the latest was 17 August (day of year 229.3, in 1995, $n = 12$ plots). The mean date of first flower (mean of annual means) was 30 July (day of year 210.5; median 25 July), and annual dates of first flower are dependent on snowmelt date. For wet meadow plots, in years with early snowmelt (before 19 May, day 139, $n = 12$ plots), there is no significant correlation between flowering date and snowmelt date (mean flowering date = 205, 24 July), but for years with later snowmelt there is a significant correlation between these variables ($r^2 = 0.620$, $P < 0.0001$, $n = 18$ plots; Fig. 2). For rocky meadow plots, in years with early snowmelt there is no significant correlation between flowering date and snowmelt date (mean flowering date = 190, 9 July, $n = 13$ plots), but for years with later snowmelt there is a significant correlation between these variables ($r^2 = 0.629$, $P < 0.0001$, $n =$ 18 plots; Fig. 2).

There is a significant correlation between the date of snowmelt and the coefficient of variation of flowering date ($r^2 = 0.247$, $P = 0.005$; Fig. 4), with earlier snowmelt correlating with increased variability in flowering date among plots. There is also a clear pattern between the first date of bare ground and the abundance of flowers the following summer. For years with early snowmelt (before 19 May, day 139), there is no significant correlation between number of flowers and snowmelt date (mean = 204 flowers), but for years with later snowmelt there is a trend between these variables ($r^2 =$ 0.131, $P = 0.14$; Fig. 5). This split in the data set makes sense biologically as it indicates that there may be a threshold effect between date of snowmelt and frost damage. It appears that if snow melts out before 19 May (or there is less than a meter of snow left on the ground on 30 April) there is a strong likelihood of frost damage the following summer.

Helianthella quinquenervis

The number of flower heads of the aspen sunflower in the two plots combined has varied over four orders of magnitude from 1975 to 2006, ranging from 1 (2004) to 4448 (1982) (Fig. 6). Since 1992, when I first began quantifying frost damage, the percentage of flower buds

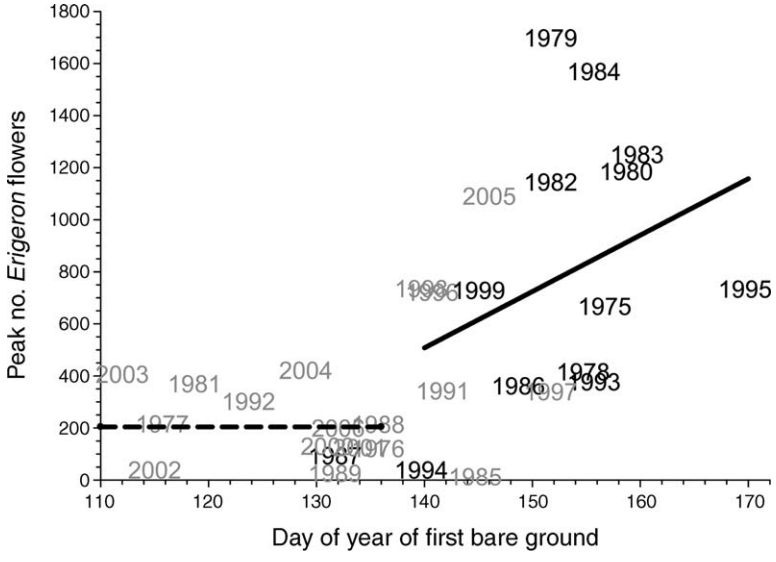


FIG. 5. The relationship between peak abundance of *Erigeron speciosus* flowers and the first date of bare ground of that year. The data were broken into two subsets by visual inspection; the early set (through day 139) has no significant slope or correlation. The dashed line indicates the mean number of flowers for years with snowmelt dates earlier than 19 May (day 139). The equation for the later snowmelt dates (solid line) is $y = 21.65x - 2523.30$, $r^2 = 0.131$, $P = 0.14$). The driest summer from 1925 to 2006 was 1994, and most flower buds dried up before opening. Years in gray are those in which I recorded evidence of frost damage in my field notes.

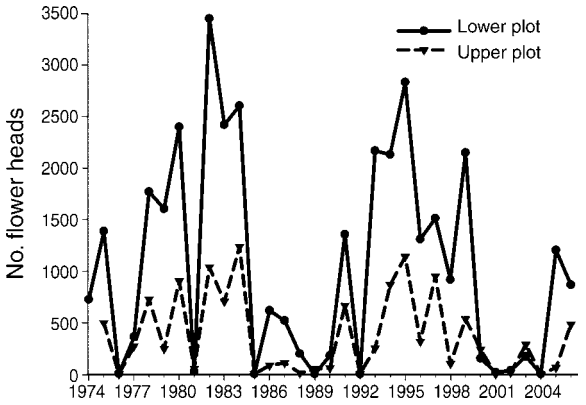


FIG. 6. The number of unfrosted *Helianthella quinquenervis* flower heads in two plots (lower plot, 450 m^2; upper plot, 365 m^2) at the Rocky Mountain Biological Laboratory, Colorado, USA. Years with very few flowers are typically years in which frost killed most flower buds.

killed by frost has ranged from 0% to 100% (Fig. 7). Over the past eight years, bud mortality has been zero in one year; in the other seven years it has ranged from 65% to 100%. The probability and degree of frost damage appears to be correlated with the previous winter's snowpack. For years with early snowmelt (before 19 May, day 139), there is no significant correlation between the number of unfrosted flower heads and snowmelt date, but for years with later snowmelt there is a significant correlation between these variables ($r^2 = 0.363$, $P = 0.008$; Fig. 8).

DISCUSSION

Collectively, these results provide evidence for significant and detrimental impacts of current climate trends on some subalpine flowers, mediated by their phenological responses to snowmelt. The impacts are variable among species, but are clearly related to life history, and have the potential to result in demographic changes in the populations due to lack of seed production. All three of the three focal wildflower species are long-lived perennials, with life spans that can probably reach multiple decades (estimates based on excavation of roots and tagging of individual *Helianthella* plants). This confers an element of stability to their presence in these plots, although there is evidence of turnover. For example, in one phenology plot (Willow-Meadow Interface #2) *Delphinium barbeyi* has only flowered in one year since 1988, and in another (Willow-Meadow Interface #5) it has not flowered since 1993 (although there were aborted flower stalks in 1994). It first appeared in *Veratrum* Removal Plot #1 in 1979 (possibly a consequence of the removal of *Veratrum tenuipetalum* (Melanthiaceae (Liliaceae)) beginning in 1974).

During this study, there has been an increase in the frequency of frost damage. For example, during the first 11 years of the *Helianthella* study (1974–1984) there were two years with significant frost damage (inferred as years with almost no flowers), while there have only been two years without significant frost damage in the past 11 years (Figs. 6 and 7). Biologically, it makes sense that there might be a threshold level of snow that will delay flower bud development beyond the time when frost is still likely to occur. The data reported in this paper are consistent with the interpretation that the likelihood and degree of frost damage to flower buds are strongly affected by snowmelt date.

Radiation frost (exposure to the cold night sky) alone does not seem to cause significant damage to flowers at

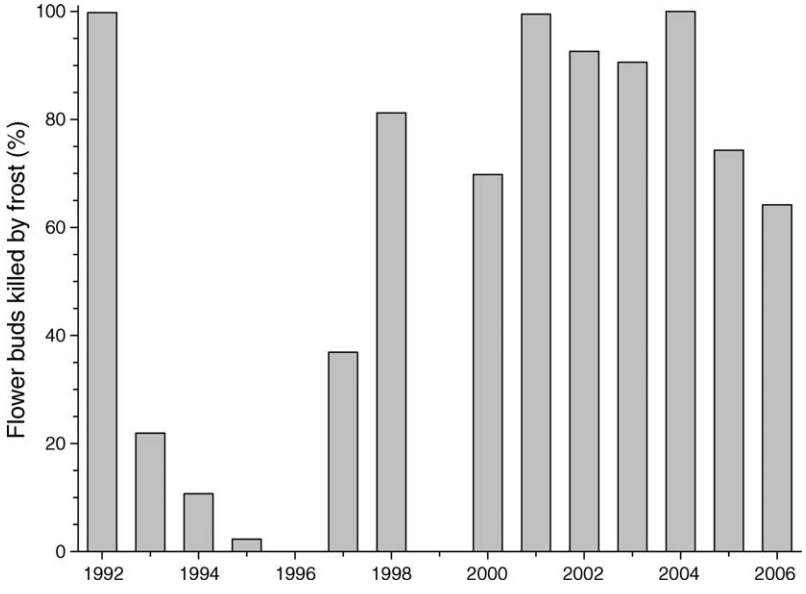


FIG. 7. The percentage of *Helianthella quinquenervis* flower buds that were killed by frost, 1992–2006. Data are from both plots (upper and lower) combined.

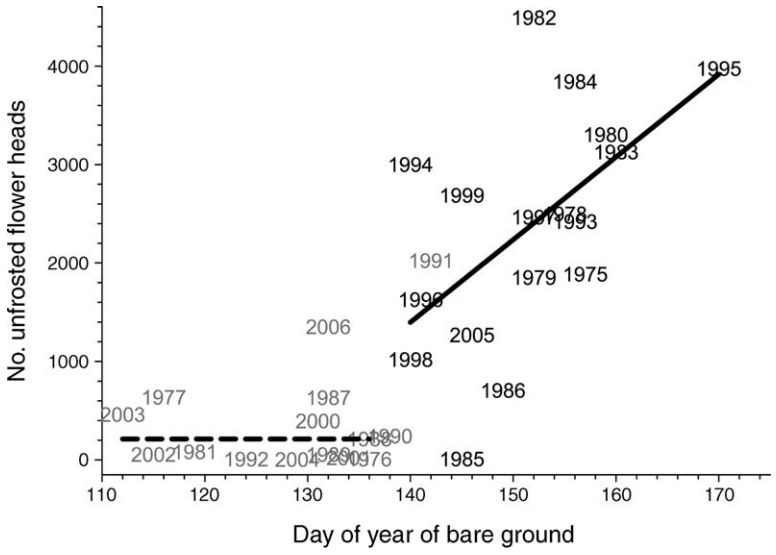


FIG. 8. The relationship between production of *Helianthella quinquenervis* flower heads that were not killed by frost in two plots and the first date of bare ground. The data were broken into two subsets by visual inspection; the early set (through day 139, in gray) has no significant slope or correlation, and both are significant for the later set ($r^2 = 0.313$, $P = 0.02$). The five partially overlapping early snowmelt data points are (counterclockwise from 2004) 1989, 2001, 1976, 1990, and 1988.

the study site; it is primarily convective frost (cold air masses) that affects them. The minimum temperature in June, when the frost damage occurs, has been trending ($r^2 = 0.077$, $P = 0.06$; data for the Crested Butte NOAA weather station, 1960–2005) toward lower temperatures; during the time of this study (1973–2005) the June minimum has averaged −4.3°C (range −1.7°C to −8.3°C). Unless this trend is reversed, potentially through global warming, frost damage is likely to continue to be a common event.

Several other species in my study site at RMBL are affected by spring frost that kills leaf buds, inflorescences, and developing fruits. For example, frost can damage new growth on Engelmann spruce (*Picea engelmannii*; Pinaceae) and subalpine fir (*Abies lasiocarpa*; Pinaceae), leaves of *Heracleum lanatum* (Apiaceae), fruits of *Erythronium grandiflorum* (Liliaceae), and inflorescences of *Ligusticum porteri* (Apiaceae), *Heuchera parviflora* (Saxifragaceae), *Veratrum tenuipetalum, Thalictrum fendleri* (Thalictraceae), and *Lupinus argenteus* (Fabaceae). There can be differences within a genus; for example *Delphinium nuttallianum*, which flowers much earlier than *D. barbeyi*, is not sensitive to frost, and *Erigeron flagellaris*, *E. elatior,* and *E. coulteri* do not seem to suffer frost damage.

In some cases, when most but not all flower buds are killed by frost, it appears that it may be the later-developing buds that survive, as flowering may be delayed beyond what would otherwise be predicted from the time of snowmelt. This could be responsible for the observed correlation between the coefficient of variation of flowering date by *Erigeron* and snowmelt date (Fig. 4). In this species some buds may survive frost, particularly in the rocky meadow plots, which are at a higher altitude and may escape effects of cold air drainage, and the combination of these flowers that may open at a "normal" date and those late-developing buds on plants on which most buds were killed by frost would generate a larger range of flowering dates. Kudo et al. (2008) found that flowering dates of early spring plants were more variable than those of later-flowering species, and attributed this to their dependence on timing of snowmelt.

The effects of frost on wildflowers at this study site are highly variable on a small geographic scale. Cold air drainage appears to play an important role in affecting low-lying areas, and the few degrees difference that this can make over a small scale of altitude was evident in the 2006 frost. In four of the five years in which there was more than a 10% difference between the upper and lower plots in frost kill of flower buds of *Helianthella* plants, the lower plot had the greater level of damage. In 2006, for example, the lower plot had 70% frost kill, and the upper plot 47%. There is 12.3-m difference in altitude between these plots (difference between the mean altitudes of upper and lower edges of each plot), but the minimum June temperatures was −3.37°C in the lower plot and −1.51°C in the upper plot (on 23 June 2006 for both plots; data recorded every 15 minutes with Hobo Pro Series data loggers [Onset, Pocasset, Massachusetts, USA]). The temperature in one of the phenology plots (Wet Meadow 1), which is at 2870 m, was −3.37°C on the same night (but −4.3°C on 16 June), and in this area all of the *Helianthella* flower buds were killed in 2006. In contrast to the high mortality in these plots, there was almost no frost damage in 2006 to



PLATE 1. (Above) *Erigeron speciosus* (Asteraceae) is an important nectar resource for the butterfly *Speyeria mormonia* (Mormon fritillary); (below) a frostkilled bud of *E. speciosus*. Photo credits: D. W. Inouye. A color photograph of *Helianthella quinquenervis* (Asteraceae) is available in the *Bulletin* of the Ecological Society of America 88(4).

Helianthella plants along trail 401, a few hundred meters away from the *Helianthella* plots and about 89 m higher, no frost damage to plants along County Road 317 in Mount Crested Butte (altitude about 2895 m, 5.8 km from RMBL), but 100% mortality at Horse Ranch Park (altitude 2706 m, 18.5 km from RMBL). This variation, even within very similar altitudes, indicates the importance of microclimate in determining both patterns of snowmelt and later air temperature.

Because these plant species are long-lived perennials, it is possible that the loss of reproductive potential due to frost damage to flower buds may not play a significant role in the long-term demography of their populations, if they are not limited by seed input. However, preliminary analysis of data for *Helianthella* from a demographic study at RMBL (D. Inouye, *unpublished data*) shows that the number of plants in a set of six 1.5×5 m plots has decreased significantly over the past nine years. During this period there has been significant recruitment of seedlings in only two years (1998, 2000); no seedlings have been found since 2000, following the last year without significant frost damage

to flower heads (1999, see Fig. 6). If this trend of significant frost damage were to continue for many years, the population decline would probably continue. Even without recruitment, local extinction would take many years given the longevity of the plants.

Although it may seem paradoxical that a consequence of global warming is an increase in the frequency of frost damage, for the species described in this paper, and for those others mentioned that also suffer frost damage, there has been an increase in the past several years in the frequency of frost that damages vegetative or reproductive parts. The observed trend toward lower June minimum temperatures over the past few decades is not predicted by models of global warming, which in fact predict that night-time temperatures may be warming faster than daytime temperatures (Easterling et al. 2000). The phenomenon of earlier snowmelt and greater frost exposure may be a general phenomenon at high altitudes and high latitudes, as it has also been documented in a subarctic tundra community (Wipf et al. 2006). Bannister et al. (2005) suggested that the dependence on day length and temperature for development of frost tolerance of the alpine New Zealand species they examined was likely to confer protection even in the face of global warming, but assumed that incidence of frosts would be reduced. Scheifinger et al. (2003) found that frost events (last occurrence of daily minimum temperatures below a certain threshold) in Europe have been moving faster to earlier occurrence dates than have phenological phases during the preceding decade, and suggested that the risk of late spring frost damage should have been lower as a consequence.

Some animal species may be similarly reliant upon melting of the snowpack to set phenological clocks. For example, laying date and clutch size of American Pipets in alpine Wyoming are correlated with snowmelt date (Hendricks 2003). At my study site, the phenology of bumble bee queen emergence (from spending the winter underground) is probably tied to snowmelt in a fashion similar to that of plant development and flowering (D. Inouye, *personal observation*). Species of seed predators such as the tephritid flies that use *Helianthella* flowers as a host, and overwinter as adults, are probably also linked to snowmelt in their emergence. The abundance of these seed predators seems to have declined significantly in recent years (compared to levels reported in Inouye and Taylor [1979]; D. Inouye, *personal observation*), probably due to loss of opportunities for oviposition in flower heads. It is likely that other species of pollinators and herbivores are also tied phenologically to snowmelt dates.

One recent event that seems to have a significant effect on winter snowfall at my study site, and therefore plays a role in frost damage, is the change of phase of the North Pacific Oscillation (Pacific Decadal Oscillation), which has also been shown to influence precipitation and fire regimes in the Rocky Mountains (Schoennagel et al. 2005). The state of this 50–75 year sea surface temperature cycle has influenced winter precipitation at RMBL (data from 1935 to 2004, $P < 0.05$), and may be responsible in part for the trend toward more precipitation falling as rain instead of snow (Knowles et al. 2006). The phase change in 1998 falls about half-way through the data set for percentage of *Helianthella* flower buds killed by frost. The mean from 1992 to 1998 is 36.1% of buds killed by frost, and for 1999–2006 the mean is 73.9% (t test, $P = 0.06$). This appears to be an example of a regional climate change that is having an effect on phenology and, mediated by the effects of frost, on flowering and potentially plant demography and other species (pollinators, seed predators, parasitoids) involved in the trophic cascade starting with these wildflowers. Climate change at local and global scales may also be having an effect, but is more difficult to discern in this study, although the trend toward lower June minimum temperatures may be an effect at the local scale.

Conclusions

Both the timing and abundance of flowering by the species described in this paper are highly variable, and this variation is strongly influenced by differences among years in the amount of winter snowfall and subsequent snowmelt. Winter precipitation is likely to continue to be relatively light for the next couple of decades, until the next phase change of the North Pacific Oscillation. This supports the conclusion that frost is likely to be an important factor affecting the abundance of flowering in sensitive species, and that a continued reduction in seed production is likely to have demographic consequences.

This and other studies provide strong evidence for ecological constraints on phenological responses to rates of environmental change. Of course not all ecosystems experience frost, and in some cases frost may not be an important factor even if it does occur (e.g., Kudo et al. 2008), but a general message from this study and all the others in this Special Feature is that long-term records may be required to tease out the environmental variables that affect phenology. Non-scientists can contribute to these efforts (Miller-Rushing and Primack 2008), and participation by this audience is a goal of the National Phenology Network. Although I have focused on herbaceous species, it may be important to consider how phenology of woody species may differ (e.g., Rich et al. 2008), and while I focused on a small spatial scale (2×2 m plots), satellite remote sensing can also be a valuable tool for phenological studies (Rich et al. 2008). I focused on flowering phenology, but as Post et al. (2008) point out, not all life history events respond similarly to environmental variation. No matter the scale at which it is measured, or who is collecting the data, it is likely that phenology will become a more common element of scientific studies of the effects of future climate change.

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