

SUBALPINE MEADOW FLOWERING PHENOLOGY RESPONSES TO CLIMATE CHANGE: INTEGRATING EXPERIMENTAL AND GRADIENT METHODS

JENNIFER A. DUNNE,^{1,2,4} JOHN HARTE,^{1,2,3} AND KEVIN J. TAYLOR²

¹Energy and Resources Group, University of California, Berkeley, California 94720 USA

²Rocky Mountain Biological Laboratory, P.O. Box 519, Crested Butte, Colorado 81224 USA

³Department of Environmental Science, Policy and Management, University of California, Berkeley, California 94720 USA

Abstract. We integrated experimental and natural gradient field methods to investigate effects of climate change and variability on flowering phenology of 11 subalpine meadow shrub, forb, and graminoid species in Gunnison County, Colorado (USA). At a subalpine meadow site, overhead electric radiant heaters advanced snowmelt date by 16 d and warmed and dried soil during the growing season. At three additional sites, a snow removal manipulation advanced snowmelt date by 7 d without altering growing season soil microclimate. We compared phenological responses to experimental climate change with responses to natural microclimate variability across spatial gradients at small and landscape scales, as well as across a temporal gradient from a separate study.

Both manipulations significantly advanced timing of flowering for the group of species and for most species individually, closely paralleling responses of timing to natural spatial and temporal variability in snowmelt date. Snowmelt date singularly explained observed shifts in timing only in the earliest flowering species, *Claytonia lanceolata*. Among all other species except *Artemisia tridentata* var. *vaseyana*, the latest flowering species, a consistent combination of temperature-related microclimate factors (earlier snowmelt date, warmer soil temperatures, and decreased soil degree-days) substantially explained earlier timing. Both manipulations also extended flowering duration for the group of species, similar to species' responses to natural snowmelt variability at small spatial scales. However, only early flowering species displayed consistent, significant changes in duration, with extended duration related to earlier snowmelt or warmer spring soil temperatures. Soil moisture was generally not a significant explanatory factor for either timing or duration of flowering. Best-fit microclimate models explained an average of 82% of variation in timing but only 38% of variation in duration across species.

Our research demonstrates the value of comparing and synthesizing results of multiple field methods within a single study. This integrated approach makes it easier to identify robust community-wide trends, as well as species-specific responses of phenology to climate change. The predicted short-term flowering phenology responses to temperature-related aspects of climate change may lead to longer term asynchronies in interspecific interactions, potentially altering population and evolutionary dynamics, community structure, and ecosystem functioning.

Key words: climate change; flowering phenology; gradient analysis; Gunnison Basin, Colorado (USA); montane, Rocky Mountains; snowmelt date; soil microclimate; subalpine meadow; temperature changes; warming experiment.

INTRODUCTION

At high elevations and latitudes, temperature increases associated with anthropogenic climate change may have strong impacts on terrestrial vegetation. Warming is predicted to be greater in these regions, and snowpack, which affects soil moisture and timing of the growing season, is sensitive to changes in temperature (Karl et al. 1993). For most regions with snow-

pack, scientists predict that global warming will significantly reduce the duration and extent of snow cover during the year (Boer et al. 1992, Brown et al. 1994, CSIRO 1994, Whetton et al. 1996), with some changes already occurring (Baumgartner and Apfl 1994, Groisman et al. 1994, IPCC 2001). In northern montane regions, climate change may lead to more winter precipitation, resulting in initial increases in snowpack at high elevations (Johnson 1998, Inouye et al. 2000). However, increasingly warm winter temperatures are likely to augment winter rain and run-off at the expense of snowpack (Beniston and Fox 1996, Fitzharris 1996, Kattenberg et al. 1996).

The current study focuses on reproductive phenology responses of subalpine meadow plants to climate

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⁴ Present address: Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, New Mexico 87501 USA.
E-mail: jdunne@santafe.edu

change and variability. During >100 yr of modern academic investigations on plant phenology (Clarke 1893, Robertson 1895; see Rathcke and Lacey 1985 for review), two main lines of research have developed. One line of environmental research addresses the relationship of the timing of plant developmental stages to abiotic factors such as photoperiod (Hamner and Bonner 1938, Panje and Srinivasan 1959, Heide 1992, White 1995, Guo et al. 1998) and climatic constraints including temperature averages (Sørensen 1941, Lindsey and Newman 1956, Holway and Ward 1965, Vasek and Sauer 1971, Fitter et al. 1995), temperature accumulations (Jackson 1966, Sparks and Carey 1995, White 1995, Thórhallsdóttir 1998), moisture (Holway and Ward 1963, Vasek and Sauer 1971), and snowpack or snowmelt characteristics (Holway and Ward 1965, Galen and Stanton 1991, Inouye and McGuire 1991, Walker et al. 1995). A second line of evolutionary research addresses the genetic basis and natural selection of plant phenology. This research agenda encompasses ongoing debates (Rabinowitz et al. 1981, Ollerton and Lack 1992) about the importance of phylogenetic (Kochmer and Handel 1986, Johnson 1992) and life form constraints (Graninger 1939, Whitehead 1969, Zimmerman et al. 1989, Díaz et al. 1994) vs. biotic interactions, particularly with pollinators (Mosquin 1971, Waser 1978, Stiles 1979, Cole 1981, Gross and Werner 1983, Brody 1997, O'Neil 1999). Our study is environmental by design, and focuses on phenotypic rather than evolutionary (Geber and Dawson 1993) responses of plant flowering phenology to climate change.

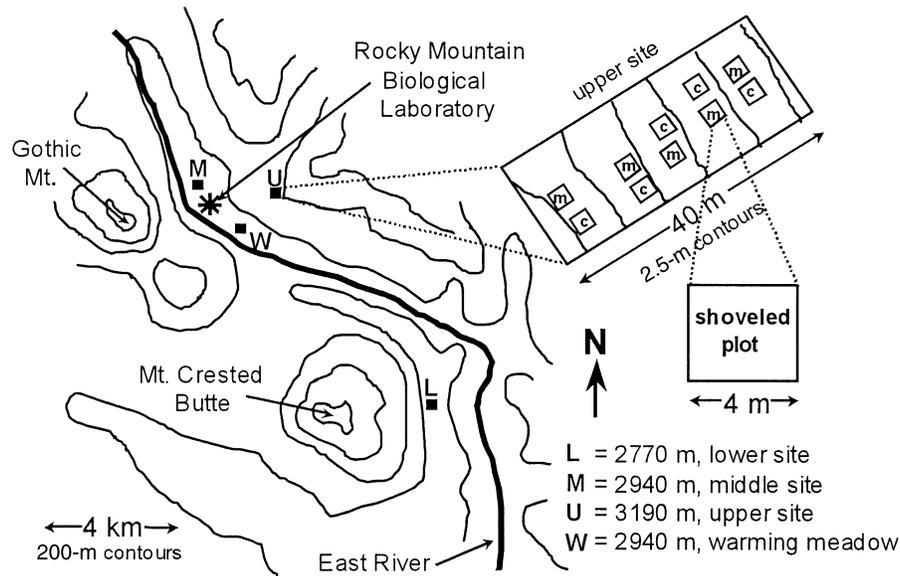
We address three basic questions. First, is snowmelt date the primary microclimate factor influencing flowering phenology in subalpine meadow plants, as widely reported for many subalpine and alpine species (e.g., Billings and Bliss 1959, Holway and Ward 1965, Billings and Mooney 1968, Galen and Stanton 1991, Inouye and McGuire 1991, Shaver and Kummerow 1992, Walker et al. 1995, Price and Waser 1998)? In particular, we were interested in whether factors other than snowmelt date, including soil moisture, soil temperature, and cumulative energy inputs, substantively explain variability in flowering phenology. Second, are there community-wide trends in flowering phenology responses to climate change and variability (e.g., Holway and Ward 1965, Thórhallsdóttir 1998) as opposed to more species-specific responses (e.g., Galen and Stanton 1995)? Third, are two different aspects of flowering phenology, the timing and duration of flowering, constrained (1) by the same microclimate factors and (2) to the same degree by microclimate? Previous studies have tended to focus on explanatory models for only one aspect of phenology, typically timing of flowering, for particular species (Sparks and Carey 1995, White 1995) or have not developed models useful for making comparisons (Price and Waser 1998).

Identifying these types of patterns and mechanisms of plant phenotypic responses to environmental variability is a necessary step for predicting impacts of anthropogenic climate change on plants, the species that interact with them, and their ecosystems. In subalpine and alpine regions with seasonal snow cover, a few studies have explicitly predicted effects of climate change on vegetation (plant phenology, abundance, biomass, establishment) based on plant responses to interannual variation in the snowpack (e.g., Inouye and McGuire 1991), spatial variation of snowpack at multiple scales (e.g., Walker et al. 1993), and snowpack manipulations (e.g., Galen and Stanton 1993). The various natural gradient and manipulation methods of these and related studies capture an important aspect of climate change in northern montane ecosystems: changes to snowpack and the timing of the growing season. However, the reliability of their predictions is limited to the degree that snowpack studies fail to encompass accurately other aspects of anthropogenic climate warming including changes to air and soil temperature, soil moisture, solar insolation, and nutrient cycling.

Some researchers have turned to experiments that explicitly simulate climate change, such as warming of subalpine meadow plots using overhead electric radiant heaters (Harte and Shaw 1995) and open top chamber experiments at a variety of International Tundra Experiment (ITEX) arctic and alpine sites (Henry and Molau 1997, Arft et al. 1999). In these studies, snowpack changes occur as a result of warming rather than direct manipulation or natural variability, and snowpack varies in conjunction with other microclimate changes (Harte et al. 1995, Marion et al. 1997). However, all warming studies also fail to simulate some aspects of climate change (e.g., CO₂ levels, disturbance), as well as altering other factors in unexpected or unwanted ways (Kennedy 1995, Shen and Harte 2000). Although experiments allow clearer inference of mechanisms, they typically occur at small spatio-temporal scales, potentially limiting generality. Gradient research can occur over broader scales but mechanisms are more difficult to identify.

To overcome the limitations of any single gradient or experimental method, a few studies of subalpine and alpine vegetation have combined snowpack (Galen and Stanton 1995) or warming (Price and Waser 1998) experiments with small-scale spatial gradient analysis. Our study employs and extends this multi-method approach by integrating, for the first time, all five methods mentioned: snowpack manipulation, experimental warming, and gradient analyses of variability across small spatial scales, landscape spatial scales, and years. We expanded an ongoing, year-round ecosystem-warming experiment at a subalpine meadow in the Colorado Rockies (e.g., Harte et al. 1995, Harte and Shaw 1995, Saleska et al. 1999, de Valpine and Harte 2001) by adding three meadow sites along an elevational gra-

a) Upper Gunnison Valley, Colorado



b) Warming Meadow

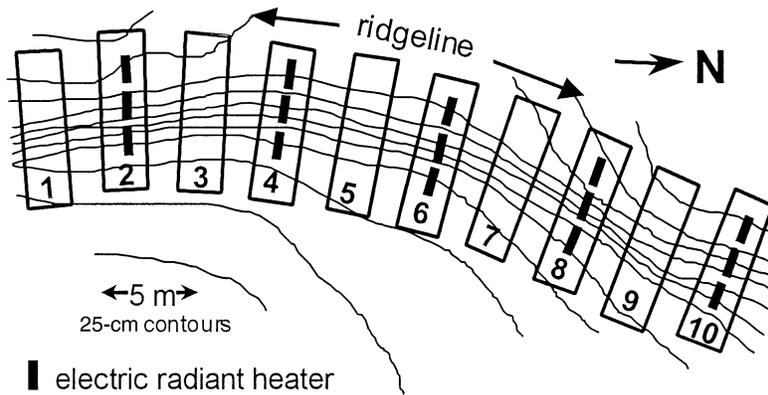


FIG. 1. (a) The location of three elevational sites and the warming meadow at and near the Rocky Mountain Biological Laboratory. The insets display the plot layout of a representative elevational site (c, control; m, manipulated). (b) The layout of 10 study plots at the warming meadow.

dient. We conducted a spring snow removal manipulation at the new sites over multiple years. At all four sites we collected phenological data to determine trends in the mean timing and duration of flowering for 11 perennial angiosperm species. We recorded microclimate data to explore relationships of observed flowering phenology variability to experimental and natural variation in several microclimatic factors including snowmelt date, soil temperature, soil moisture, and soil degree-days.

METHODS
Study sites

We established four study sites at and near the Rocky Mountain Biological Laboratory (RMBL), Gunnison

County, Colorado (latitude 38°53' N, longitude 107°02' W, elevation 2920 m) (Fig. 1a). At moderately high elevations, the regional vegetation consists of a mosaic of four primary ecosystem types: Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)–subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forest, quaking aspen forest (*Populus tremuloides* Michx.), open meadow that ranges from moist to dry, and wetland willow (*Salix* spp.) carrs. Our research focused on dry, rocky subalpine meadows where *Artemisia tridentata* var. *vaseyana* is the dominant shrub (see Table 1 for taxonomic authorities of study species). These meadows comprise part of an extensive ecotone connecting Great Basin shrub habitat to Rocky Mountain subalpine meadow habitat. The highest elevation site (3170 m)

TABLE 1. Eleven subalpine meadow plant species studied for flowering phenology at the Rocky Mountain Biological Laboratory, Gothic, Colorado.

Species	Common name	Family	Type	Sites
<i>Artemisia tridentata</i> Nutt. var. <i>vaseyana</i> (Rydb.) Boivin†	mountain big sagebrush	Asteraceae	shrub	L, M, U, W
<i>Claytonia lanceolata</i> Pursh†	spring beauty	Portulacaceae	forb	M, U
<i>Delphinium nuttallianum</i> Pritz. ex Walp.†	Nelson's larkspur	Ranunculaceae	forb	L, M, U, W
<i>Erigeron speciosus</i> (Lindl.) DC.	fleabane	Asteraceae	forb	L, M, U, W
<i>Eriogonum subalpinum</i> Greene†	wild buckwheat	Polygonaceae	forb	M, U, W
<i>Eriogonum umbellatum</i> Torr.	wild buckwheat	Polygonaceae	forb	L
<i>Festuca thurberi</i> Vasey	fescue	Poaceae	grass	L, M, U, W
<i>Helianthella quinquenervis</i> (Hook.) Gray	little sunflower	Asteraceae	forb	U, W
<i>Lathyrus lanszwertii</i> Kellogg var. <i>leucanthus</i> (Rydb.) Dorn†	white peavine	Fabaceae	forb	L, M, U, W
<i>Mertensia fusiformis</i> Greene†	bluebell	Boraginaceae	forb	L, M, U, W
<i>Potentilla hippiana</i> Lehm.	cinquefoil	Rosaceae	forb	U, W

Note: Abbreviations are: L, lower site; M, middle site; U, upper site; W, warming meadow.

† Species studied by Price and Waser (1998) at the warming meadow from 1991 to 1994. Price and Waser refer to *Artemisia tridentata* var. *vaseyana* as *Seriphidium vaseyanum* and to *Lathyrus lanszwertii* var. *leucanthus* as *Lathyrus leucanthus*, and they identify *Mertensia fusiformis* as *Mertensia brevistyla*.

is close to an elevational limit for successful establishment and growth of *Artemisia*. We identified 99 angiosperm species in the study plots, including 9 shrubs, 68 forbs, and 22 graminoids, ~90% of which are perennial (Dunne 2000).

At RMBL, snowfall generally begins in September, snowpack starts to accumulate in October, and snowmelt typically concludes in May. From 1989–1999, winter snowfall at RMBL averaged 1180 cm per year (equivalent to 79 cm of water), comprising ~80% of total annual precipitation, and maximum snowpack averaged 197 cm depth (b. barr, unpublished data). Mean daily average air temperature was ~2°C.

Experimental design

In 1990, 10 experimental plots (3 × 10 m) were established in a subalpine meadow site at RMBL referred to as the “warming meadow” (Harte et al. 1995). The plots were laid out in an arc, from 88° E at plot 1 to 126° SE at plot 10, with control and treatment plots alternating to facilitate separation of treatment effects from north to south plot position effects (Fig. 1b). The current 1995–1998 study focused on the upper third of the plots, located along a dry, rocky moraine ridgeline where *Artemisia* occurs. In January 1991, two electric radiant heaters were suspended 2.5 m above the ground parallel to the 10-m midline for each treatment plot. These heaters produced a nearly uniform 15 W/m² year-round additional heat flux over 80% of the plot soil surface (Harte et al. 1995). In May 1993, Harte and colleagues added a third heater to each plot and increased the heat flux to 22 W/m² for more accurate simulation of warming predicted due to doubling of atmospheric CO₂ (Harte and Shaw 1995).

In the summer of 1995, we established three sites along an elevational gradient in the same watershed as the warming meadow to examine changes in climate and subalpine meadow ecosystem properties at a landscape level (Fig. 1a). We placed a “lower site” at the

southeast base of Mt. Crested Butte, a “middle site” at RMBL at the same elevation and ~500 m north of the warming meadow, and an “upper site” on Red Rock Mountain above RMBL. These three “elevational sites” span an elevational change of 420 m and maximum intersite distance of 12.8 km. We selected the elevational sites based on their similarity to the dry zone of the warming meadow, with *Artemisia* the dominant shrub and *Festuca thurberi* the dominant graminoid. Of 99 species, at least 22 species (2 shrubs, 15 forbs, and 5 graminoids) were common to all four sites. The sites have similar slopes (6°–10°) and rocky loam soils, and have been protected from cattle grazing for several decades. Average annual air temperatures for 1997–1998 were 2.4°, 1.7°, and 1.4°C at the lower, middle, and upper sites, with 1998 warmer than 1997 (Fig. 2).

At each elevational site, five pairs of 4 × 4 m plots were laid out with spacing of at least 2 m (Fig. 1a). We randomly assigned a treatment and control plot in each pair. We conducted a snow removal manipulation

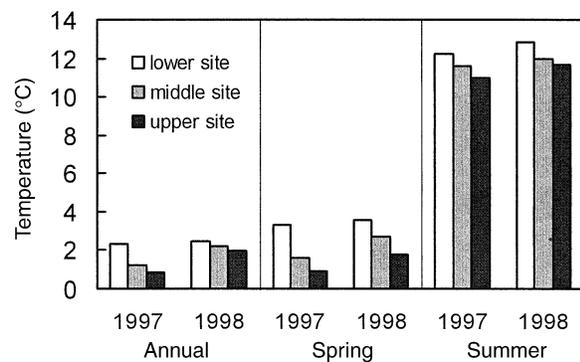


FIG. 2. Average air temperatures at three subalpine meadows along an elevational gradient near the Rocky Mountain Biological Laboratory, Gothic, Colorado. Designations are: annual, 1 January to 31 December; spring, 1 April to 31 May; summer, 1 June to 31 August.

to induce earlier snowmelt, one of the strongest microclimate effects of the warming meadow treatment (Harte et al. 1995). Our goal was to alter snowmelt date without inducing changes in other microclimate factors associated with the warming treatment, particularly warmer and drier growing season soil. Prior to snowmelt in 1996–1998, when spring snowpack levels decreased to ~1 m depth, we shoveled snow over the course of several weeks from 5 × 5 m squares centered on each treatment plot. We reduced snow depth by less than one-half on any given day, and placed shoveled snow to the outside edge of the plots to avoid augmenting soil moisture in downhill plots. Although snow removal decreased snowpack, this simulated reduced winter snowpack likely to occur with climate warming in this region. Once shoveling exposed the tops of *Artemisia* the manipulation ceased, both to avoid plant damage and because the lower albedo of the shrubs, which retain leaves under the snowpack, accelerated remaining snowmelt.

Monitoring and basic variables

Microclimate.—We monitored soil moisture and temperature every 2 h year-round at 12 and 25 cm depths in all 40 plots using gypsum blocks and thermocouples connected to multiplexers and dataloggers (CR10x, Campbell Scientific, Logan, Utah). We logged two-hourly air temperature data from elevational site weather stations from 1997–1998. We defined snowmelt date (Melt) for each plot as the day when 12-cm soil temperature reached and remained above 1°C. In 1996 at the elevational sites, before the dataloggers were operational, we defined Melt as the day when a plot displayed 90% bare ground. For each plot, we calculated daily soil moisture and temperature averages over 12 depth-averaged readings per diurnal cycle. We used the daily averages to calculate spring soil temperature (T_{spr}), summer soil temperature (T_{sum}), and summer soil moisture (M_{sum}). We defined spring as 1 April to 31 May, which encompassed most of the snowmelt period, and summer as 1 June to 31 August, the period of most plant growth and activity. Because of large data gaps due to equipment failure, we excluded warming meadow T_{spr} from statistical analysis.

Phenology.—From 1995–1998 at the warming meadow and 1996–1998 at the elevational sites, we monitored reproductive phenology for 11 perennial plant species common enough to have at least five flowering individuals in most of the plots at one or more sites (Table 1). Price and Waser (1998) studied six of the same species for phenology trends at the warming meadow from 1991–1994. We monitored additional species including *Festuca* and the two forbs with the largest forb aboveground biomass in the dry zone of the warming meadow, *Helianthella quinquenervis* and *Erigeron speciosus* (de Valpine and Harte 2001). The species studied constitute 11% of vascular plant species identified at the four sites, comprise over two-thirds of

the total aboveground plant biomass in the plots, and represent a variety of growth forms, phylogenies, abundances, flowering times, and reproductive strategies.

We began phenological monitoring after snowmelt and censused plants once per week during the growing season, usually ending in September. Once multiple individuals of a species in a plot started to form buds, we flagged five individuals. We flagged replacement plants, using the nearest viable candidate, if buds aborted or failed to develop or if there was substantial herbivory. Such problems rendered some data sets unusable. For example, *Lathyrus lanszwertii* var. *leucanthus*, one of the few nitrogen fixers in our plots, experienced ~90% floral herbivory. We monitored individuals for the presence of seven phenological stages generally following Price and Waser (1998): we recorded “0” for a plant not yet flowering, “1” for unopened buds, “2” for open flowers, “3” for old flowers, “4” for initiated fruit, “5” for enlarged fruit, and “6” for dehisced fruit. For *Festuca* we used five phenological stages: “0” for a plant with flower stalks, “1” for presence of spikelets, “2” for exerted anthers and styles from the spikelet florets, “3” for dried and broken-off anthers and styles, indicating a developing seed, and “4” for disarticulated seeds.

For each plant on each observation day we calculated a single unweighted phenological score by averaging the stages present on the individual. Thus, a plant with two buds (stage 1), two flowers (stage 2), one old flower (stage 3), and one initiated fruit (stage 4) was assigned a phenological score of $(1 + 2 + 3 + 4)/4 = 2.5$. We tracked presence/absence rather than number of stages and used unweighted scores for direct comparability to Price and Waser (1998), to make more meaningful comparisons among species with widely varying flowering morphology, and because it saved the time necessary to track a broad set of species across multiple sites. We fit linear regressions to the sequence of phenological scores for each plant as a function of day of year, using data from the last observation day that only buds were present (score of 1) through the first observation day that all fruits were dehisced (score of 4 for *Festuca*, 6 for other species). We calculated regressions for individuals with at least four stages observed throughout the flowering cycle (three stages for *Festuca*). The 3698 individual regressions displayed highly significant fits (average $r^2 = 0.91 \pm 0.07$ [1 SD]; maximum $r^2 = 1.00$, minimum $r^2 = 0.52$; all P values < 0.001).

Using the regression equations, we calculated two phenology variables for each plant: timing (Timing) and duration (Duration) of flowering. Timing refers to the estimated day of year when the plant reached a phenological stage of 3.5, midway between stage 1 (buds only) and 6 (fruits dehisced). Duration refers to the number of days for a plant to progress from stage 1 (buds only) to stage 5 (enlarged fruits). Although Timing and Duration could be calculated for any stages, we used the same definitions as Price and Waser (1998).

For *Festuca*, we calculated Timing for stage 2.5 and Duration from stage 1 to 3. We used plot averages of Timing and Duration over replicate individuals within a species as basic units of analysis.

Analysis

We conducted all statistics with SYSTAT 7.0 (SYSTAT 1997). We used pairwise Pearson correlation matrices with a Bonferroni procedure to correct P values for multiple comparisons to look at associations among the four microclimate variables (T_{spr} , T_{sum} , M_{sum} , Melt). We used ANOVA and ANCOVA to investigate treatment, site, year, and plot position effects on the four microclimate and two phenological variables. We used univariate and multivariate linear regression analysis to investigate phenology–microclimate relationships. Analyses were conducted separately for the warming meadow and the elevational sites because of experimental design differences.

Treatment, plot position, and site effects.—At the warming meadow, we conducted repeated-measures ANCOVAs (RMANCOVA) with treatment as a fixed factor, year as the repeated measure, and plot position as a covariate. Plot position, represented by plot number, often covaries with microclimate and phenological variables (Harte et al. 1995, Price and Waser 1998). We decided to use plot position as a covariate after assessing that the homogeneity of slopes assumption (treatment \times plot, $P > 0.05$) was met in 11 of 12 microclimate–year combinations and in 55 of 58 species–year combinations for Timing and Duration. For a more direct comparison to Price and Waser (1998) results and to examine statistical robustness of some effects, we conducted a second analysis of treatment and plot position effects. We removed effects of year and plot position from the microclimate and phenology variables and conducted randomized-blocks ANOVAs (RBANOVA) on the residuals, determining the treatment effect over the treatment \times block interaction, which specifies the warming treatment as a fixed effect and block (pair of adjacent treatment and control plots) as a random effect. To examine plot position effects, we removed the effects of year from the variables and regressed the residuals against plot position.

At the elevational sites, we also conducted two types of ANOVAs. We ran two-factor repeated-measures ANOVAs (RMANOVA) with treatment and site as fixed factors and year as the repeated measure, and used a Bonferroni procedure to make post hoc comparisons of site differences. We then examined treatment effects by removing year and site effects from the variables and running randomized-blocks ANOVAs (RBANOVA) on the residuals, with fixed effects, random effects, and blocks defined as at the warming meadow.

Phenology as a function of microclimate.—We used linear regressions to investigate the relationship between phenology variables and snowmelt date across all plots and years at the warming meadow and across

the elevational sites. At the warming meadow, this snowmelt effect represented phenological responses to a small-scale spatial snowmelt gradient, and across the elevation sites it represented responses to a landscape-scale spatial snowmelt gradient. A separate long-term study provided snowmelt effects on timing of flowering across an interannual temporal gradient.

The previously described analysis of plot position effects provided a way to indirectly infer phenology responses to small-scale spatial microclimate variability along an exposure gradient at the warming meadow. In an additional indirect analysis of microclimate effects, we ran RBANOVAs on the residuals from regressions of Timing and Duration against snowmelt date at the warming meadow to examine statistically for any residual effects of warming beyond effects of early snowmelt.

To directly investigate the relationships of phenology to nonsnowmelt date aspects of microclimate, we developed three phenological soil microclimate variables using the more complete 1997–1998 elevational site data: (1) average soil temperature (T_{f1}) during the months in which most of the flowering cycle occurred for each species, (2) average soil moisture (M_{f1}) during the same time periods, and (3) soil degree-days (DD_{soil}) leading up to Timing for each species, defined as (Timing – Melt) \times (average soil temperature during the days from Melt to Timing). The flowering periods used to calculate T_{f1} and M_{f1} were May/June for *Claytonia lanceolata*, *Mertensia fusiformis*, and *Delphinium*; July/August for *Festuca*, *Eriogonum u.*, *Eriogonum s.*, and *Erigeron*; and August/September for *Artemisia*. We generated univariate linear regressions for Timing and Duration as a function of those three variables plus spring soil temperature (T_{spr}) for each species across all plots and years. We then investigated multiple linear regression models through interactive backward stepping starting with four microclimate variables: Melt, T_{f1} , M_{f1} , and DD_{soil} . We excluded spring soil temperature (T_{spr}) from multiple regression analysis due to high correlation with T_{f1} of early flowering species and with Melt. Because these analyses were limited to elevational site data, they reflect phenology–microclimate relationship across a landscape-scale spatial gradient only.

RESULTS

Microclimate

Warming meadow trends.—Snowmelt proceeded from north to south at the warming meadow due to decreasing southern exposure of lower numbered plots (RMANCOVA plot $F_{1,7} = 45.66$, $P < 0.001$) (Figs. 1b and 3). From 1995–1998, snowmelt date was ~ 14 d earlier in the most northern vs. southern control plots. Average control plot snowmelt date was earlier with lower total snowpack in the preceding winter (1991–1999, linear regression: $r^2 = 0.777$, $df = 7$, $P = 0.002$)

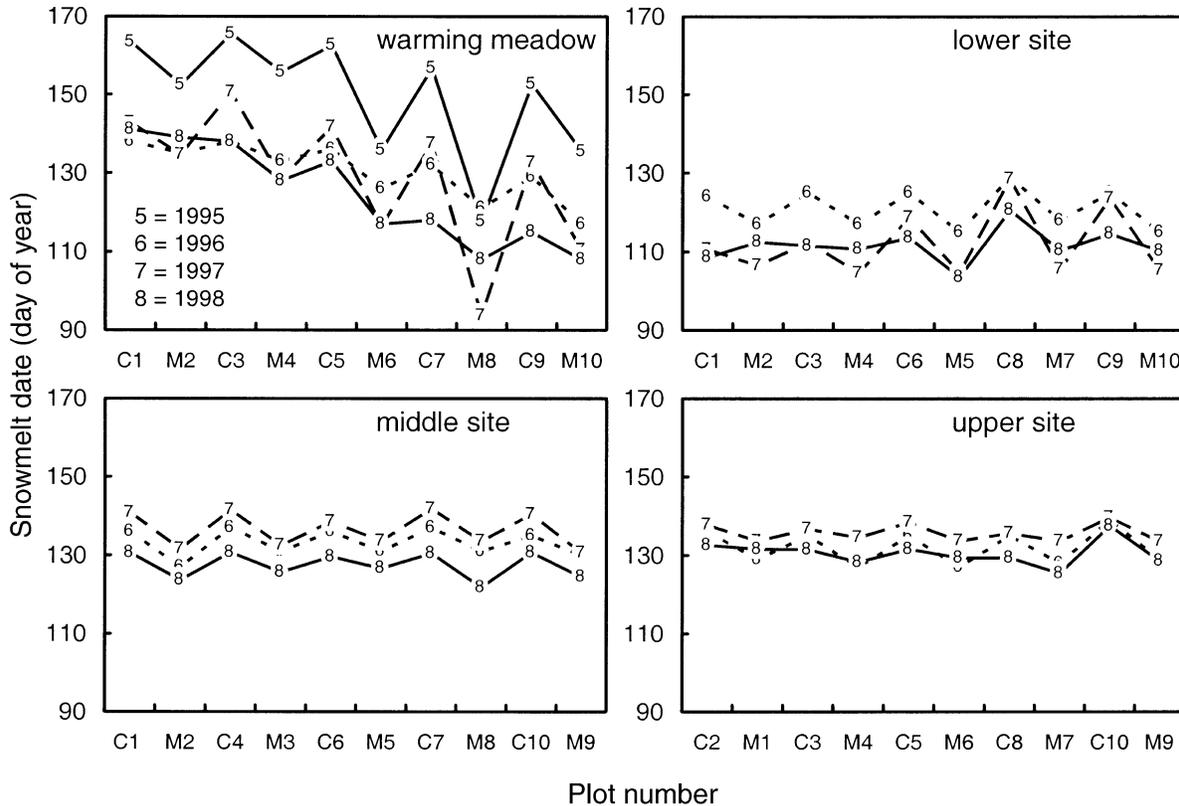


FIG. 3. Snowmelt date in the upper zone of each plot at the warming meadow from 1995–1998 and in the three elevational sites (lower, middle, upper) from 1996–1998 (C, control; M, manipulated plots). Overhead electric radiant heaters warmed the manipulated plots at the warming meadow, and manipulated plots at the elevational sites had spring snow partially removed. Control plots alternate with neighboring manipulated plots to clearly show the treatment effect at each site. The warming meadow plots show the increasing southern exposure effect of advancing snowmelt date in higher numbered plots.

(b. barr, unpublished data). Warming advanced Melt by ~ 16 d from 1995–1998 (RMANCOVA tr [treatment] $F_{1,7} = 13.89$, $P = 0.007$; RBANOVA tr $F_{1,4} = 13.34$, $P = 0.022$).

The warming treatment increased spring soil temperatures by 1.9°C and summer soil temperatures by 1.2°C (T_{sum} : RMANCOVA tr $F_{1,7} = 8.316$, $P = 0.024$; RBANOVA tr $F_{1,4} = 4.905$, $P = 0.091$) (Table 2). Unlike Melt, plot position did not affect T_{sum} (RMANCOVA plot $F_{1,7} = 0.068$, $P = 0.847$). The warming treatment decreased summer soil moisture by 14% (RMANCOVA tr $F_{1,6} = 5.457$, $P = 0.058$; RBANOVA tr $F_{1,3} = 26.99$, $P = 0.014$) (Table 2). Soil tended to be drier in more south-facing plots (RMANCOVA plot $F_{1,6} = 3.862$, $P = 0.097$). Earlier Melt correlated highly with drier M_{sum} ($r = 0.898$, $P < 0.001$) and marginally with warmer T_{sum} ($r = -0.494$, $P = 0.081$), which also correlated marginally with drier M_{sum} ($r = -0.557$, $P = 0.075$).

Elevational site trends.—At the elevational sites from 1996–1998, snow removal advanced date of snowmelt an average of 9, 7, and 5 d at the lower, middle, and upper sites (RMANOVA tr $F_{1,24} = 74.18$, $P < 0.001$; RBANOVA tr $F_{1,14} = 66.59$, $P < 0.001$)

(Table 2, Fig. 3). Treatment effects did not vary significantly by site (RBANOVA tr \times site $F_{2,24} = 1.790$, $P = 0.189$). The earliest Melt occurred at the lower site, with no difference between the middle and upper sites (RBANOVA, lower $<$ middle, upper, $P < 0.001$; middle = upper, $P = 1.000$).

Snow removal increased spring soil temperatures (RMANOVA tr $F_{1,22} = 43.54$, $P < 0.001$, RBANOVA tr $F_{1,13} = 2.544$, $P = 0.135$) (Table 2). T_{spr} decreased with increasing elevation (RBANOVA, lower $>$ middle, $P < 0.001$; middle $>$ upper, $P = 0.026$), similar to air temperature trends (Fig. 2). Snow removal had no effect on summer soil temperature (RMANOVA tr $F_{1,22} = 0.169$, $P = 0.685$; RBANOVA tr $F_{1,14} = 0.188$, $P = 0.671$) or moisture (RMANOVA tr $F_{1,17} = 0.064$, $P = 0.803$; RBANOVA tr $F_{1,13} = 0.250$, $P = 0.625$) (Table 2). The lower site had the driest soil (RBANOVA, lower $<$ middle, upper, $P < 0.015$). The middle site had the warmest T_{sum} (RBANOVA, lower $<$ middle, $P = 0.002$; lower $>$ upper, $P = 0.002$), which differed from Melt, air temperature, T_{spr} , and M_{sum} trends, probably due to differences in vegetative cover (Dunne 2000). Warmer T_{spr} , drier M_{sum} , and earlier Melt all correlated (Melt vs. T_{spr} , $r = -0.934$, $P < 0.001$; Melt vs.

TABLE 2. Average soil microclimate at four subalpine meadows near Gothic, Colorado.

Site	Year	Melt (day of year)		T_{spr} ($^{\circ}\text{C}$)	
		Control	Treatment	Control	Treatment
Warming meadow	1995	160.2 (6.8)	139.4 (2.4)	0.02 (0.10)	1.29 (0.39)
	1996	134.6 (1.8)	126.4 (3.4)
	1997	141.0 (3.0)	116.7 (7.2)	1.14 (0.50)/3	4.09 (0.45)/3
	1998	129.0 (5.3)	120.0 (6.0)	2.08 (0.09)/3	3.63 (1.07)/3
Lower	1996	125.8 (0.8)	116.4 (0.6)
	1997	118.8 (3.4)	105.3 (0.3)	4.16 (0.14)	5.72 (0.34)
	1998	113.8 (2.0)	109.5 (1.5)	4.86 (0.20)	5.21 (0.11)
Middle	1996	136.2 (0.4)	130.6 (0.2)
	1997	140.6 (0.6)	132.4 (0.6)	1.29 (0.12)	2.53 (0.03)/4
	1998	130.4 (0.2)	124.5 (0.8)	3.35 (0.15)	4.19 (0.10)/4
Upper	1996	136.0 (0.8)	128.0 (0.4)
	1997	137.6 (0.7)	133.8 (0.2)	1.39 (0.08)	1.68 (0.06)/4
	1998	132.5 (1.4)	128.7 (1.0)	2.38 (0.09)	2.64 (0.09)

Notes: Date reported are: Melt, snowmelt date; T_{spr} , average spring soil temperature (1 April to 31 May); T_{sum} , average summer soil temperature (1 June to 31 August); M_{sum} , average summer soil moisture (1 June to 31 August). Standard errors are shown in parentheses; $N = 5$ except where noted after slash.

M_{sum} , $r = 0.679$, $P = 0.001$; T_{spr} vs. M_{sum} , $r = -0.628$, $P = 0.004$).

Phenology

Effects of warming treatment and plot position.—Experimental warming significantly advanced timing of flowering for the group of species examined (negative effects for eight of eight species, binomial test, $P = 0.008$) (Table 3) as well as most individual species (Tables 3 and 4). Later flowering species responded more weakly to the warming treatment (linear regression of warming effect vs. Timing, $r^2 = 0.56$, $df = 7$, $P = 0.033$). Species flowered earlier in more south-facing, earlier melting plots, both as a group (negative effects for eight of eight species, binomial test, $P = 0.008$) and individually. The plot position effect decreased with later flowering time (linear regression of slope vs. Timing, $r^2 = 0.72$, $df = 7$, $P = 0.008$).

Experimental warming extended duration of flowering for the group of species (positive effects for eight of eight species, binomial test, $P = 0.008$) (Table 3), but almost no species displayed significant treatment effects (Tables 3 and 4). Although species flowered longer in more south-facing, earlier melting plots (positive effects for eight of eight species, binomial test, $P = 0.008$), only the two earliest flowering species, *Mertensia* and *Delphinium*, displayed significant plot position effects.

Effects of snow removal treatment and site.—Snow removal at the elevational sites advanced timing of flowering for the group of species (negative effects for eight of eight species, binomial test, $P = 0.008$) (Table 5) and for most individual species, although significance varied somewhat with different statistical methods (Tables 5 and 6). Later flowering species responded more weakly to the snow removal treatment (linear regression of snow removal effect vs. Timing, $r^2 = 0.81$, $df = 7$, $P = 0.002$). The treatment effect did not tend to vary by site or year (results not shown). Across

species, Timing varied significantly by site and was 4–10 d earlier at the lower than the middle site and 1–4 d earlier at the middle than the upper site (Table 6).

Snow removal extended Duration for the group of species except *Artemisia* (positive effects for seven of eight species, binomial test, $P = 0.07$) (Table 5), with many species displaying significant treatment effects (Tables 5 and 6). Treatment effects on Duration did not tend to vary significantly by site or year (results not shown). Duration did not vary consistently or significantly by site for any species (Table 6).

Phenology as a function of snowmelt date.—All warming meadow species displayed earlier Timing as a function of earlier snowmelt date (positive effects for eight of eight species, binomial test, $P = 0.008$), with highly significant Melt effects for all species but *Festuca* (for seven of eight species, $r^2 = 0.53$ – 0.76 , P values < 0.001) (Table 3). Across species, Timing ranged from 0.3 to 0.7 d earlier with every day of earlier Melt. Although Timing in earlier flowering species tended to respond more strongly to changes in Melt, the relationship was not significant (correlation of slope of snowmelt date effect vs. Timing, $r = 0.47$, $P = 0.24$). Most species experienced longer Duration with earlier Melt (negative effects for seven of eight species, binomial test, $P = 0.07$), but only three species, including *Mertensia* and *Delphinium*, displayed significant relationships (Table 3).

At the elevational sites, the group of species displayed earlier Timing with earlier Melt (positive effects for eight of eight species, binomial test, $P = 0.008$), with significant Melt effects for all species but *Eriogonum u.* (range of $r^2 = 0.14$ – 0.74 , P values < 0.01) (Table 5). Timing generally ranged from 0.2 to 0.8 d earlier for each day of earlier Melt. Early flowering species were more sensitive to snowmelt date than later flowering species (correlation of slope of snowmelt date effect vs. Timing, $r = 0.90$, $P = 0.005$). The three

TABLE 2. Extended.

T_{sum} (°C)		M_{sum} (%)	
Control	Treatment	Control	Treatment
13.24 (0.25)	14.41 (0.29)	27.6 (0.4)/4	24.3 (0.8)
13.88 (0.29)	15.10 (0.25)	22.1 (0.4)/4	18.2 (1.4)
14.00 (0.35)	14.78 (0.29)	21.9 (0.8)/4	21.0 (0.5)
14.02 (0.41)	15.60 (0.14)	20.9 (1.8)/4	16.7 (2.1)
...
13.80 (0.24)	13.57 (0.28)	17.5 (1.3)/4	19.3 (0.9)
14.23 (0.24)	13.94 (0.31)	9.6 (1.0)/4	13.2 (0.5)
...
14.88 (0.36)	14.63 (0.37)/4	20.2 (1.9)	16.0 (1.2)
14.79 (0.32)	14.60 (0.31)/4	21.3 (2.3)/4	19.3 (4.4)/2
...
12.78 (0.49)	12.75 (0.24)/4	21.8 (1.3)	21.5 (0.9)
13.13 (0.49)	13.42 (0.37)/4	17.1 (1.1)/4	16.7 (1.3)/4

earliest flowering species had significantly longer Duration with earlier Melt, but other species lacked a consistent or significant relationship (Table 5).

Phenology as a function of soil microclimate.—Two indirect analyses provided insight into whether snowmelt date was the primary factor influencing flowering phenology. First, if the warming treatment altered Timing via changes to Melt rather than soil microclimate or other factors, species' responses to the warming treatment should be approximately double their responses to snow removal, since the average difference in control/treatment snowmelt date was 2.3-fold greater

in the heated vs. snow removal plots (Table 2). For six species that overlapped between the two manipulations, *Festuca* displayed a 4.1-fold greater response to the warming treatment, the four forbs displayed a 1.5- to 2.1-fold increase, and *Artemisia* had a 1.2-fold increase (Tables 3 and 5), suggesting that *Festuca* had stronger, the forbs had slightly weaker, and *Artemisia* had much weaker than expected responses of Timing to the warming treatment. Since many treatment effects on Duration were not individually significant, we did not do a similar comparison. Second, statistically calculated residual warming effects beyond snowmelt date delayed

TABLE 3. Responses of plant flowering phenology to variable effects at a subalpine meadow.

A) Timing		Plot position		Warming		Snowmelt date			Residual warming	
Species	Day of year	Slope	<i>P</i>	Effect	<i>P</i>	Slope	<i>P</i>	<i>r</i> ²	Effect	<i>P</i>
<i>Mertensia</i>	173	-1.82	<0.001	-6.53	0.016	0.68	<0.001	0.76	2.14	0.148
<i>Delphinium</i>	185	-1.63	<0.001	-5.52	0.009	0.58	<0.001	0.79	1.86	0.132
<i>Festuca</i>	219	-0.68	0.426	-4.16	...	0.36	0.054	0.28	-1.08	...
<i>Eriogonum s.</i>	220	-1.18	<0.001	-3.19	0.067	0.29	<0.001	0.66	-0.22	0.781
<i>Helianthella</i>	222	-1.34	0.015	-6.65	0.038	0.72	<0.001	0.72	1.97	0.707
<i>Potentilla</i>	224	-0.93	0.078	-3.68	0.339	0.57	<0.001	0.64	4.86	0.062
<i>Erigeron</i>	227	-1.28	0.011	-4.38	0.022	0.60	<0.001	0.61	3.63	0.112
<i>Artemisia</i>	251	-0.59	0.108	-1.41	0.325	0.37	<0.001	0.53	3.51	0.001

B) Duration		No. days	Slope	<i>P</i>	Effect	<i>P</i>	Slope	<i>P</i>	<i>r</i> ²	Effect	<i>P</i>
<i>Mertensia</i>	33	0.83	<0.001	0.83	0.628	-0.15	<0.001	0.30	-0.64	0.712	
<i>Delphinium</i>	31	0.52	0.011	2.12	0.112	-0.12	0.001	0.26	0.80	0.394	
<i>Festuca</i>	50	0.18	0.089	0.62	...	-0.33	0.376	0.07	-2.20	...	
<i>Eriogonum s.</i>	56	0.70	0.146	3.26	0.076	-0.18	0.123	0.09	0.97	0.616	
<i>Helianthella</i>	44	0.61	0.185	1.38	0.959	-0.32	0.758	0.00	1.35	0.888	
<i>Potentilla</i>	46	0.81	0.156	4.64	0.022	-0.04	0.689	0.01	5.28	0.024	
<i>Erigeron</i>	41	0.61	0.051	1.81	0.238	-0.14	0.008	0.18	0.24	0.818	
<i>Artemisia</i>	36	0.11	0.689	2.21	0.286	0.06	0.411	0.02	1.59	0.252	

Notes: Mean Timing ("Day of year") and Duration ("No. days") are calculated over all years for control plots. (For Day of year, day 173 = 22 June; day 251 = 8 September.) Plot position: linear regression of phenology variable with effects of year removed as a function of plot number. Warming: randomized-blocks ANOVA of phenology variable with effects of year and plot position removed, category = treatment. Snowmelt date: linear regression of phenology variable as a function of snowmelt date. Residual warming: randomized-blocks ANOVA of phenology variable with effects of snowmelt date removed, category = treatment. Each "Effect" column reports the mean residual for heated plots minus the mean residual for control plots. ANOVAs were not performed on *Festuca* due to incomplete data. Because of opposite plot numbering and definition of "effect," our plot position slopes and warming effects have opposite signs from Price and Waser (1998). Significant slopes and effects are shown in bold.

TABLE 4. Effects of experimental warming, year, and plot position on plant flowering phenology at a subalpine meadow.

Species	Warming			Year			Warming × Year			Plot position		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Timing												
<i>Mertensia</i>	1, 7	22.46	<0.001	3, 21	84.05	<0.001	3, 21	4.39	0.015	1, 7	42.61	<0.001
<i>Delphinium</i>	1, 7	23.79	0.002	3, 21	69.01	<0.001	3, 21	1.71	0.195	1, 7	51.33	<0.001
<i>Eriogonum s.</i>	1, 5	39.04	0.002	2, 10	3.62	0.066	2, 10	8.02	0.008	1, 5	74.09	<0.001
<i>Helianthella</i>	1, 3	31.79	0.011	2, 6	10.50	0.011	2, 6	1.78	0.247	1, 3	20.88	0.020
<i>Potentilla</i>	1, 4	10.59	0.031	3, 12	22.51	<0.001	3, 12	0.17	0.913	1, 4	7.03	0.057
<i>Erigeron</i>	1, 5	7.89	0.038	3, 15	64.31	<0.001	3, 15	0.36	0.782	1, 5	12.69	0.016
<i>Artemisia</i>	1, 6	1.47	0.271	3, 18	33.67	<0.001	3, 18	0.46	0.717	1, 6	6.30	0.046
Duration												
<i>Mertensia</i>	1, 7	0.46	0.521	3, 21	4.38	0.011	3, 21	2.16	0.124	1, 7	13.04	0.009
<i>Delphinium</i>	1, 7	6.60	0.037	3, 21	1.40	0.271	3, 21	4.75	0.014	1, 7	9.42	0.018
<i>Eriogonum s.</i>	1, 5	2.57	0.170	2, 10	3.79	0.010	2, 10	0.05	0.949	1, 5	3.00	0.114
<i>Helianthella</i>	1, 3	6.95	0.078	2, 6	0.44	0.662	2, 6	0.06	0.944	1, 3	6.66	0.083
<i>Potentilla</i>	1, 4	7.56	0.051	3, 12	11.58	0.001	3, 12	2.79	0.086	1, 4	3.88	0.120
<i>Erigeron</i>	1, 5	0.47	0.524	3, 15	0.96	0.435	3, 15	2.47	0.102	1, 5	4.27	0.094
<i>Artemisia</i>	1, 6	1.10	0.335	3, 18	6.67	0.004	3, 18	1.34	0.295	1, 6	0.00	0.952

Notes: The table presents results of RMANCOVA of the phenology variable, with category = warming treatment, year as the repeated measure, and plot as a covariate. Significant *F* values are shown in bold.

Timing for six of eight species, but effects were significant or nearly so only in two later flowering species, *Potentilla* and *Artemisia* (Table 3). Residual warming effects increased Duration in six of eight species, but effects were significant only for *Potentilla*.

Direct analyses of soil microclimate factors at the elevational sites suggest that warmer spring soil temperatures (T_{sp}) advanced Timing for the group of spe-

cies (negative effects for eight of eight species, binomial test, $P = 0.008$), significantly so for all but *Eriogonum u.* (Table 7). T_{sp} explained more variability in Timing than did Melt, with an average difference in r^2 of 0.19 (Tables 5 and 7). As with Melt and plot position, changes in T_{sp} were associated with greater Timing shifts in early vs. later flowering species. For six of eight species, warmer soils during the flowering period

TABLE 5. Responses of plant flowering phenology to experimental snow removal and snowmelt date in subalpine meadows along an elevational gradient.

A) Timing		Day of year	Snow removal		Snowmelt date		
Species	Sites		Effect	<i>P</i>	Slope	<i>P</i>	r^2
<i>Claytonia</i>	M, U	158	-3.77	0.001	0.80	<0.001	0.56
<i>Mertensia</i>	L	157	-3.83	0.103	0.63	<0.001	0.73
<i>Delphinium</i>	M, U	182	-3.23	0.002	0.64	<0.001	0.74
<i>Festuca</i>	L, M, U	217	-1.02	0.163	0.56	<0.001	0.62
<i>Eriogonum u.</i>	L	220	-0.90	0.588	0.08	0.355	0.03
<i>Eriogonum s.</i>	M, U	222	-2.06	0.045	0.28	0.003	0.14
<i>Erigeron</i>	L, M, U	223	-2.12	0.593	0.39	<0.001	0.37
<i>Artemisia</i>	L, M, U	249	-1.19	0.005	0.16	<0.001	0.17
B) Duration		No. days	Effect	<i>P</i>	Slope	<i>P</i>	r^2
Species	Sites						
<i>Claytonia</i>	M, U	27	2.65	0.038	-0.31	0.016	0.10
<i>Mertensia</i>	L	37	3.20	0.022	-0.29	<0.001	0.34
<i>Delphinium</i>	M, U	30	3.10	0.004	-0.16	0.002	0.11
<i>Festuca</i>	L, M, U	51	0.47	0.869	-0.11	0.387	0.01
<i>Eriogonum u.</i>	L	59	3.49	0.067	-0.03	0.883	0.00
<i>Eriogonum s.</i>	M, U	55	4.66	0.005	0.28	0.140	0.04
<i>Erigeron</i>	L, M, U	43	0.52	0.772	0.09	0.189	0.02
<i>Artemisia</i>	L, M, U	34	-0.02	0.950	0.01	0.874	0.00

Notes: Mean Timing ("Day of year") and Duration ("No. days") are calculated over all years and sites for control plots. (For Day of year, day 158 = 7 June; day 249 = 6 September.) Snow removal: randomized-blocks ANOVA of phenology variable (with year and site effects removed for multi-site species and year effects removed for single-site species), category = treatment. Snowmelt date: linear regression of phenology variable as a function of snowmelt date. Each "Effect" column reports the mean residual for shoveled plots minus the mean residual for control plots. Significant effects and slopes are shown in bold. Site abbreviations as in Table 1.

(T_{f1}) advanced Timing, significantly so for all six (Table 7). Drier flowering period soil (M_{f1}) advanced Timing for six of eight species, a significant effect only for *Festuca* and *Erigeron*. Timing did not display a significant relationship to soil degree-days (DD_{soil}). Multivariate models provided a slightly different perspective (Table 8). Seven of eight species had highly significant microclimate multivariate models for Timing with better fits than any univariate model, with five species' models displaying $r^2 \geq 0.92$. Soil moisture was never a significant variable. Earlier Timing was associated with earlier Melt, warmer soil temperatures, and lower DD_{soil} for most species, generally in that order of importance. The exceptions were earlier Timing associated with cooler T_{f1} in *Eriogonum u.* and with earlier Melt and cooler T_{f1} in *Artemisia*.

Warmer T_{spr} and T_{f1} significantly extended DURATION for *Mertensia* and *Delphinium*, but otherwise, there were few significant or consistent relationships within and among species to single microclimate factors (Table 7). Single factor models provided the best fit for the three earliest flowering species, with longer Duration associated with earlier Melt or warmer T_{spr} (Table 8). Four later flowering species displayed significant multivariate models for Duration with better fits than any univariate model. For those species, T_{f1} and DD_{soil} were the most important variables, with longer Duration in later forb species related to cooler T_{f1} and increased DD_{soil} , and in *Festuca* to warmer T_{f1} and decreased DD_{soil} . Earlier Melt, the least important variable, generally decreased Duration of those species. *Artemisia* lacked a significant model. As with Timing, soil moisture was never a significant variable. Across species, microclimate models explained on average 82% of the variation in Timing but only 38% of the variation in Duration (Table 8).

DISCUSSION

Implications for anthropogenic climate change

If anthropogenic climate change results in earlier snowmelt and warmer temperatures in the Rocky Mountain region, subalpine meadow species, including graminoids, forbs, and shrubs, are likely to flower much earlier and for slightly longer periods, with particularly strong effects seen in early flowering species. Univariate linear regressions suggest that flowering time will advance by up to 11 d for every two weeks of earlier snowmelt or for every 2°C increase in average spring or growing season soil temperatures. Substantial shifts in flowering phenology have the potential to disrupt relationships that plants have with animal, fungal, and bacterial species that act as pollinators, seed dispersers, herbivores, seed predators, and pathogens (e.g., Rathcke and Lacey 1985, Brody 1997). Such disruptions should be strongest when (1) the phenology of interacting species is influenced by different abiotic or biotic factors, or in different ways by the same factors,

than those triggering plant development and phenology, and (2) the relationship between a plant species and its interactor is specialized or particularly important for either species.

Differences in phenological responses to climate change among plant species with varying growth forms and life-history traits can also introduce asynchronies into plant-plant relationships. Changes in timing and duration of flowering, affecting overlap of temporally neighboring plants (Price and Waser 1998), can alter both direct (e.g., competition for resources) and indirect (e.g., those mediated by shared pollinators or herbivores) plant interactions. For example, multiple plant species often share the same interacting species (e.g., at RMBL: Waser 1978, Waser and Real 1979, Brody 1997). If an early flowering species such as *Delphinium nuttallianum* undergoes dramatic phenological changes due to warming that impair the ability of queen bumblebees and hummingbirds to gain early season nutrition, later flowering species such as *Ipomopsis aggregata* (Pursh) Grant. that depend on those pollinators may in turn be negatively impacted (Waser and Real 1979, Inouye and McGuire 1991). Thus, climate change impacts on flowering phenology will not only directly affect particular plant species but can alter broader community structure and ecosystem functioning.

Climate warming can also instigate evolutionary responses. Climate change may directly alter plant fitness (e.g., Galen and Stanton 1991, 1993, Wookey et al. 1993), as well as indirectly alter reproductive success of plants and their interactors via impacts on flowering phenology (e.g., Beattie et al. 1973, Schemske 1977, Gross and Werner 1983, Lacey and Pace 1983, Schmitt 1983, English-Loeb and Karban 1992, Peterson 1997, Bishop and Schemske 1998). Prior studies at RMBL provide insights on potential fitness responses for several of our study species. Although Price and Waser (1998) reported that fruit set increased slightly for eight of nine species as a result of the warming treatment, the effect was not significant for individual species. However, there is strong evidence for two early flowering forbs, *Delphinium* and *Erythronium grandiflorum* Pursh., that plant abundance and/or flower production decreases with lower winter snow accumulation, earlier snowmelt date, and as a result of the warming treatment (Inouye and McGuire 1991, Saavedra 2000; D. W. Inouye, unpublished data). Another study found that the warming treatment negatively affected early flowering *Delphinium*, *Mertensia*, and *Lathyrus* as well as later flowering *Erigeron*, and positively affected later flowering *Helianthella* and *Eriogonum s.*, in terms of abundance, size, or number of flowers (de Valpine and Harte 2001). These studies suggest that global warming may have more negative than positive fitness effects on subalpine meadow plant species at our sites, particularly for early flowering species.

Below, we discuss more detailed results about experimental climate change impacts and microclimate

TABLE 6. Effects of experimental snow removal, site, and year on plant flowering phenology in subalpine meadows along an elevational gradient.

Species	Sites	Snow removal			Site		
		df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Timing							
<i>Claytonia</i>	M, U	1, 16	35.45	<0.001	1, 16	33.35	<0.001
<i>Mertensia</i>	L	1, 8	7.80	0.023
<i>Delphinium</i>	M, U	1, 18	16.83	0.001	2, 18	145.00	<0.001
<i>Festuca</i>	L, M, U	1, 15	9.18	0.007	2, 15	146.71	<0.001
<i>Eriogonum u.</i>	L	1, 7	1.37	0.281
<i>Eriogonum s.</i>	M, U	1, 16	8.72	0.009	1, 16	23.93	<0.001
<i>Erigeron</i>	L, M, U	1, 19	6.81	0.017	2, 19	27.73	<0.001
<i>Artemisia</i>	L, M, U	1, 17	1.94	0.182	2, 17	4.22	0.033
Duration							
<i>Claytonia</i>	M, U	1, 16	8.24	0.011	1, 16	2.76	0.116
<i>Mertensia</i>	L	1, 8	8.39	0.020
<i>Delphinium</i>	M, U	1, 18	15.82	<0.001	2, 18	1.72	0.208
<i>Festuca</i>	L, M, U	1, 15	2.16	0.162	2, 15	2.65	0.103
<i>Eriogonum u.</i>	L	1, 7	9.79	0.017
<i>Eriogonum s.</i>	M, U	1, 16	17.06	<0.001	1, 16	1.45	0.247
<i>Erigeron</i>	L, M, U	1, 19	0.06	0.808	2, 19	1.56	0.235
<i>Artemisia</i>	L, M, U	1, 17	6.47	0.021	2, 17	3.29	0.062

Notes: The table presents results of RMANOVA of the phenology variable, with categories = snow removal treatment and site (where more than one site is represented) and with year as the repeated measure. Site differences = mean Timing or Duration at a lower minus a higher elevation site. Significant *F* values and site differences are shown in bold. Site abbreviations are as in Table 1.

constraints on subalpine meadow flowering phenology. We integrate results from two climate manipulations (warming and snow removal) and three natural climate gradients (small-scale spatial, landscape-scale spatial, and interannual temporal). The use of multiple methods underscores the robustness of observed strong temperature-related constraints on timing of flowering across species compared to the much weaker and more variable role of climatic factors for duration of flowering. Our multi-method approach also allows comparison of indirect and direct inferences of the importance of snowmelt date vs. other microclimate factors for phenology.

Phenological responses to experimental climate change

Both the warming and snow removal treatments advanced timing of flowering, in most cases significantly, for all species monitored. Price and Waser (1998) reported similar results for an overlapping set of species at the warming meadow from 1991–1994. However, they observed smaller and less significant phenological changes than those we observed from 1995–1998. This is due to smaller treatment effects on microclimate during the first study as a result of lower infrared radiator flux. For example, snowmelt date was ~6 d earlier in treatment plots from 1991–1994 compared to ~16 d from 1995–1998. Similarly, treatment effects on timing of flowering were weaker at the elevational sites, where snow removal advanced snowmelt by ~7 d and did not alter growing season soil microclimate, compared to the warmer, drier soils and more pronounced shifts in snowmelt date in the warming meadow heated plots.

Both treatments also increased duration of flowering for most species. However, unlike timing of flowering, duration responded more strongly and significantly to snow removal than warming, particularly for early flowering species. This suggests that additional effects of warmer and drier soil in the heated plots may stress the plants, resulting in a tendency toward shorter duration that offsets some of the increases in duration seen as a result of earlier snowmelt.

Phenological responses to microclimate variability

Snowmelt date.—The timing of flowering in most species consistently and strongly related to date of snowmelt. For all species at both small (within the warming meadow) and landscape (across the elevational sites) spatial scales, earlier snowmelt date advanced flowering. This general snowmelt–timing relationship holds whether examined directly or inferred indirectly from the effects of the warming treatment, the snow removal treatment, or the snowmelt gradient represented by plot position. Price and Waser (1998) reported similar relationships between timing of flowering and snowmelt date at the warming meadow. Interannual data from a long-term RMBL subalpine meadow study also suggested that first flowering date for all herbaceous and shrubby plants advances with lower snowpack depth (total or on 30 April) or earlier snowmelt date (D. W. Inouye, unpublished data, as referred to in Inouye et al. 2000). Advanced flowering time associated with earlier snowmelt date, shallower snowpack, or lower total snowfall, three highly correlated variables, appears to be a general property of subalpine, alpine, and arctic species (Billings and Bliss

TABLE 6. Extended.

Site differences (no. days)			Year		
L-M	M-U	L-U	df	F	P
...	-3.7	...	2, 32	79.99	<0.001
...	2, 16	13.47	<0.001
...	-4.1	...	2, 36	89.71	<0.001
-10.0	-2.1	-12.1	2, 30	69.16	<0.001
...	2, 14	26.45	<0.001
...	-3.4	...	2, 32	36.77	<0.001
-5.1	-1.6	-6.6	2, 38	102.91	<0.001
-3.8	-0.6	-4.4	2, 34	51.48	<0.001
...	-1.5	...	2, 32	5.72	0.008
...	2, 16	24.65	<0.001
...	1.4	...	2, 36	0.32	0.728
-1.5	-1.4	-2.8	2, 30	94.41	<0.001
...	2, 14	72.55	<0.001
...	1.4	...	2, 32	52.13	<0.001
-1.9	1.7	-0.2	2, 38	103.75	<0.001
-0.2	-2.1	-2.3	2, 34	4.54	0.018

1959, Holway and Ward 1963, 1965, Fareed and Caldwell 1975, Bock 1976, Owen 1976, Ostler et al. 1982, Ram et al. 1988, Ratcliffe and Turkington 1989, Galen and Stanton 1991, 1995, Inouye and McGuire 1991, Kudo 1991, 1992, Walker et al. 1995, Price and Waser 1998, Arft et al. 1999; but see Þórhallsdóttir 1998). Our results further corroborate this finding at a community level and extend it to several previously unexamined species.

The exception to the snowmelt–timing relationship in our study was *Eriogonum umbellatum*, the only study

species restricted to the lower site. Two hypotheses may explain our failure to observe a significant role of snowmelt date in *Eriogonum u.* flowering time. First, it may be an artifact of the lack of variability in snowmelt date at the lower site. Second, as a lower elevation species than other species monitored, *Eriogonum u.* grows in environments less constrained by extremely short growing seasons. As a result, *Eriogonum u.* may respond more weakly to snowmelt cues in favor of other cues. We hypothesize that plant phenology should increasingly decouple from snowmelt in lower elevation species and with decreasing elevation.

Along the elevational gradient, both the sensitivity to and the variance explained by snowmelt date generally decreased in later flowering species. Surprisingly, this pattern did not hold at the smaller spatial scale of the warming meadow, where the variance explained by snowmelt date tended to be uniformly high and later flowering species were more sensitive to changes in snowmelt date than along the elevational gradient. However, two early flowering species, *Mertensia* and *Delphinium*, displayed similar relationships to changes in snowmelt date at both spatial scales. A long-term study at RMBL of interannual variation from 1975–1999 (Inouye et al. 2000; D. W. Inouye, unpublished data) related first date of flowering in *Mertensia*, *Delphinium*, and *Erigeron* to first date of snow-free ground. Inouye’s data reveal comparable snowmelt–timing relationships across this temporal gradient, particularly for the early flowering species, to what we found for both small- and landscape-scale spatial variation in snowmelt date (Table 9). The consistency of responses to temporal and spatial variation was also

TABLE 7. Flowering phenology as a univariate function of four microclimate variables in subalpine meadows along an elevational gradient.

Species	T_{spr}			T_{fl}			M_{fl}			DD _{soil}		
	Slope	r^2	P	Slope	r^2	P	Slope	r^2	P	Slope	r^2	P
Timing												
<i>Claytonia</i>	-4.59	0.82	<0.001	-2.95	0.53	<0.001	17.09	0.05	0.200	0.00	0.00	0.996
<i>Mertensia</i>	-5.49	0.87	<0.001	-5.26	0.71	<0.001	53.88	0.10	0.063	-0.01	0.00	0.870
<i>Delphinium</i>	-4.74	0.89	<0.001	-4.41	0.70	<0.001	28.19	0.05	0.123	0.03	0.05	0.107
<i>Festuca</i>	-4.98	0.78	<0.001	-3.18	0.19	0.002	76.99	0.16	0.006	0.02	0.05	0.133
<i>Eriogonum u.</i>	-0.92	0.04	0.426	2.27	0.30	0.013	-3.62	0.00	0.908	0.02	0.09	0.210
<i>Eriogonum s.</i>	-1.90	0.38	<0.001	-1.36	0.28	0.001	11.21	0.02	0.403	-0.01	0.16	0.016
<i>Erigeron</i>	-3.53	0.58	<0.001	-3.44	0.27	<0.001	65.70	0.15	0.007	0.01	0.01	0.404
<i>Artemisia</i>	-1.08	0.31	<0.001	0.49	0.04	0.201	-0.10	0.00	0.993	-0.00	0.01	0.616
Duration												
<i>Claytonia</i>	0.67	0.02	0.375	-0.42	0.01	0.484	15.17	0.06	0.165	0.01	0.01	0.573
<i>Mertensia</i>	2.47	0.48	<0.001	2.15	0.32	<0.001	-5.70	0.00	0.754	0.03	0.06	0.161
<i>Delphinium</i>	1.52	0.34	<0.001	1.44	0.28	<0.001	2.69	0.00	0.816	0.00	0.00	0.714
<i>Festuca</i>	0.13	0.00	0.906	1.97	0.04	0.153	-12.40	0.00	0.765	-0.02	0.04	0.172
<i>Eriogonum u.</i>	0.83	0.01	0.768	-7.76	0.59	<0.001	84.51	0.09	0.231	-0.03	0.05	0.325
<i>Eriogonum s.</i>	-3.39	0.20	0.007	-1.75	0.07	0.111	26.90	0.02	0.429	-0.01	0.02	0.450
<i>Erigeron</i>	-1.43	0.10	0.027	-1.70	0.07	0.069	58.19	0.13	0.014	0.03	0.23	<0.001
<i>Artemisia</i>	0.56	0.03	0.210	1.24	0.09	0.038	-13.34	0.01	0.635	0.01	0.08	0.043

Notes: The table presents results from regression analysis of phenology variables as simple linear functions of average spring soil temperature (T_{spr}), average flowering period soil temperature (T_{fl}), average flowering period soil moisture (M_{fl}), and soil degree-days from snowmelt to flowering (DD_{soil}). Significance is determined using a Bonferroni corrected level of $P \leq 0.0125$. Significant regression slopes are shown in bold.

TABLE 8. Best-fit linear regression model terms for flowering phenology as a function of microclimate in subalpine meadows along an elevational gradient.

Species	Timing		Duration	
	Terms	r^2	Terms	r^2
<i>Claytonia</i>	Melt(+), T_{f1} (-), DD_{soil} (+)	0.89	Melt(-)	0.10
<i>Mertensia</i>	Melt(+), T_{f1} (-), DD_{soil} (+)	0.98	T_{spr} (+)	0.48
<i>Delphinium</i>	T_{f1} (-), Melt(+), DD_{soil} (+)	0.98	T_{spr} (+)	0.34
<i>Festuca</i>	Melt(+), T_{f1} (-), DD_{soil} (+)	0.93	T_{f1} (+), DD_{soil} (-), Melt(+)	0.29
<i>Eriogonum u.</i>	T_{f1} (+)	0.30	T_{f1} (-), DD_{soil} (+)	0.78
<i>Eriogonum s.</i>	T_{f1} (-), DD_{soil} (+), Melt(+)	0.55	T_{f1} (-), DD_{soil} (+), Melt(+)	0.40
<i>Erigeron</i>	Melt(+), T_{f1} (-), DD_{soil} (+)	0.92	DD_{soil} (+), T_{f1} (-), Melt(+)	0.64
<i>Artemisia</i>	Melt(+), T_{f1} (+)	0.44	no significant model	...

Notes: Multivariate models were generated through interactive backward stepping using the starting variables of snowmelt date (Melt), average soil temperature, moisture, and degree-days during the flowering period (T_{f1} , M_{f1} , DD_{soil}), and T_{spr} = spring soil temperature. Model terms for multiple linear regressions are given in order of importance, based on the absolute magnitude of standardized coefficients. Univariate models were generated with simple linear regressions. The sign of the estimated coefficients is shown in parentheses next to the model term.

evident for *Delphinium* and *Mertensia* from initial trends in the short temporal sequences (3–4 yr) of the current study (Dunne 2000).

The tendency of later flowering species to respond more strongly to changes in snowmelt date within the warming meadow may reflect strong adjustment of populations, regardless of flowering time, to local, long-term cues of the start of the growing season. Increased variance and decreased sensitivity of flowering time in later flowering species across the elevational sites may reflect differential responses among populations to the effects of other abiotic and biotic factors that vary among sites. The similar response of early flowering species to snowmelt date regardless of spatial or temporal scale likely reflects the lack of time between snowmelt and flowering for other factors to introduce additional variation to timing of flowering.

Species generally displayed longer duration of flowering with earlier snowmelt. However, only the earliest flowering species displayed individually significant responses to snowmelt date, regardless of scale or as inferred from the manipulations or plot position effects. Unlike timing of flowering, there were no other obvious commonalities in snowmelt–duration relationships across species, scales, or methods. The timing of the

growing season thus appears to be a very weak constraint on duration of flowering in all but the earliest flowering species we studied.

We used two indirect analyses, statistical assessment of residual warming treatment effects and comparison of snow removal vs. warming treatment effects, to examine impacts of climate warming on timing of flowering apart from changes to snowmelt date. Together, the analyses suggest that nonsnowmelt date affects (1) advanced flowering of *Festuca* augmenting snowmelt date effects, (2) slightly delayed flowering of forbs reducing snowmelt date effects, and (3) significantly delayed flowering of *Artemisia* largely counteracting snowmelt date effects (as also reported by Price and Waser 1998). Although these results imply that aspects of climate warming apart from earlier snowmelt date influence timing of flowering, direct microclimate analysis is a more robust way to assess and predict the relative importance of multiple climate change factors for inducing phenotypic responses.

Soil moisture.—In our study plots, earlier snowmelt date was a function of lower preceding winter snowpack (see also Inouye and McGuire 1991), and it correlated with drier growing season soil, suggesting that variation in soil moisture might also impact phenology.

TABLE 9. Response of timing of flowering to snowmelt date across three natural climate gradients in subalpine meadows near the Rocky Mountain Biological Laboratory (RMBL), Gothic, Colorado.

Species	Interannual (meadows near RMBL)			Small-scale spatial (warming meadow)			Landscape-scale spatial (elevational site)		
	Slope	P	r^2	Slope	P	r^2	Slope	P	r^2
<i>Mertensia</i>	0.79	<0.001	0.85	0.68	<0.001	0.76	0.63	<0.001	0.73
<i>Delphinium</i>	0.63	<0.001	0.76	0.58	<0.001	0.79	0.64	<0.001	0.74
<i>Erigeron</i>	0.33	<0.001	0.41	0.60	<0.001	0.61	0.39	<0.001	0.37

Notes: Interannual trends describe linear regression of first flowering date as a function of first date of snow-free ground from 1975 to 1999 at a single site for each species (Inouye et al. 2000; D. W. Inouye, unpublished data). Small-scale spatial trends describe linear regression of Timing as a function of snowmelt date among plots at the warming meadow. Landscape-scale spatial trends describe linear regression of Timing as a function of snowmelt date among plots at the elevational sites. Significant slopes are shown in bold.

Other studies have suggested that soil moisture may play a role in limiting, extending, or shifting timing of flowering (e.g., Holway and Ward 1965, Vasek and Sauer 1971, Zimmerman et al. 1989), although only a few studies have explicitly investigated it (Johnson 1992, Sparks and Carey 1995, Walker et al. 1995, Thórhallsdóttir 1998). Soil moisture played surprisingly little role in either the timing or duration of flowering for most species we monitored. It is possible that because the two growing seasons that we have detailed microclimate data for were not remarkably dry or wet, we did not observe soil moisture conditions that would make a difference to flowering phenology. However, *Erigeron*, one of the dominant forbs, as well as the only grass we monitored, *Festuca*, did display significantly earlier timing of flowering with drier soil, assessed as a univariate factor. This sensitivity of *Erigeron* flowering phenology to soil moisture is consistent with results from a concurrent RMBL study. *Erigeron* displayed significant increases in aboveground biomass and flower production with water additions, suggesting that observed declines of *Erigeron* in the warming treatment plots may be attributable to water limitation (de Valpine and Harte 2001).

Soil temperature.—Several researchers have reported that temperature, either preceding averages (e.g., Fitter et al. 1995, Sparks and Carey 1995) or degree-days (e.g., Jackson 1966, White 1995, Thórhallsdóttir 1998) explains significant variability in temperate ecosystem flowering phenology. The correlation of earlier snowmelt date with warmer soil temperatures in our plots suggests that temperature may play a significant role in driving subalpine meadow phenology. Also, the presence of significantly later flowering of some species at the upper vs. middle site, which have similar snowmelt dates, suggests that significantly cooler conditions at the upper site may play an important role in timing of flowering.

While those lines of evidence suggest that warmer soil temperatures might be associated with earlier flowering, another line of evidence suggests the opposite. The indirect statistical analyses discussed previously suggest that residual effects of the warming treatment beyond snowmelt date tend to slightly delay flowering for all species but *Festuca*. What do we know about those residual effects? Since the warming treatment significantly increased soil temperature and decreased soil moisture, and because timing of flowering does not appear related to soil moisture, we can infer that warmer soil temperature comprises the “residual” effect that tends to delay flowering in most species. However, direct microclimate analyses show that warmer soil temperatures significantly advanced flowering in most species, with the exception of *Artemisia*, the only species that displayed individually significant residual warming effects. Thus, although flowering time of *Festuca* and *Artemisia* displayed consistent, and opposite, relationships to soil temperature both as inferred indi-

rectly from the warming experiment and as directly assessed along a natural climate gradient, the relationship of forb flowering time to indirectly vs. directly analyzed soil temperature effects was inconsistent. This may suggest that (1) there is a transient, weak, positive response of forb flowering time to soil warming that will reverse over time and at broader spatial scales, or (2) some other residual aspect of experimental warming besides soil warming is responsible for slight forb flowering delays. Cumulative energy inputs, measured as soil degree-days, did not emerge as a consistent or significant univariate factor in timing of flowering.

Flowering duration for two early flowering forbs, *Mertensia* and *Delphinium*, increased significantly with warmer soil temperatures. Since soil temperature tends to correlate negatively with snowmelt date, this result corroborates patterns of extended duration observed in those species in response to experimental climate warming, more southern plot exposure, and earlier snowmelt due to manipulation or natural variability. However, all other species generally displayed inconsistent and insignificant univariate temperature–duration relationships.

Multivariate models.—Spring soil temperatures predicted a greater amount of variability in flowering time than snowmelt date, perhaps because spring soil temperature integrates timing of snowmelt with early growing season air and soil temperature parameters important for ramping up metabolic activity in perennial plants. The high degree of fit of simple spring soil temperature models for most species is empirically compelling but conceptually unsatisfying. Models that individuate different aspects of temperature effects, including changes to snowpack, average temperature conditions, and cumulative energy inputs, may prove more useful for understanding potential climate warming impacts on phenology. We found that best-fit models for timing of flowering in most species incorporated some combination of earlier snowmelt date, warmer flowering period soil temperature, and decreased soil degree-days to explain earlier flowering, generally in that order of importance. Multivariate microclimate models for timing of flowering explained ~30–50% more variance over univariate snowmelt date models for all species but *Claytonia*, the earliest flowering species, which displayed an increase of only 8%. This suggests that *Claytonia* is the only species whose flowering time is singularly controlled by snowmelt date. For all other species that do not flower immediately following snowmelt, other temperature-related constraints appear to play additional significant, if secondary, roles.

Our results suggest that a prior warming meadow study (Price and Waser 1998), which concluded that earlier timing of flowering due to experimental warming “was entirely explained by earlier snowmelt in the case of six plant species,” overstated the importance of snowmelt date. They based this conclusion on an

indirect statistical analysis, which found insignificant residual warming effects beyond snowmelt date for six species, something we also found for six species. However, our direct analysis of microclimate–timing relationships across several sites suggests that this lack of significance may be an artifact of small sample size at the warming meadow.

While earlier snowmelt date or warmer soil temperatures best explained extended duration in early flowering species, multivariate models provided stronger fits for later flowering species. In later flowering forb species cooler soil, increased soil degree-days, and later snowmelt date tended to extend duration, while in *Festuca*, warmer soil, decreased soil degree-days, and later snowmelt date tended to extend duration, generally in that order of importance. The role of cooler soil and/or later snowmelt in extending duration in later flowering species is contrary to community-wide patterns of extended duration observed due to manipulated and natural climate warming. The inconsistencies of patterns of microclimate effects and constraints on duration for all but the early flowering species suggests that duration of flowering is under much weaker microclimate control than timing of flowering. The observation that best-fit microclimate models explained 20–80% more variance in timing than duration of flowering across species strongly supports this hypothesis.

CONCLUSION

We have provided multi-pronged evidence that earlier snowmelt date in conjunction with warmer soil temperatures, as is likely to occur with anthropogenic climate change, will substantially advance the timing of flowering and slightly lengthen the flowering cycle in an array of perennial subalpine meadow species, with strongest effects on early flowering forbs. The use of multiple experimental and natural gradient field methods facilitated identification of robust community-wide trends in phenology–microclimate relationships, particularly for timing of flowering, which displayed much stronger and more consistent relationships to microclimate than duration of flowering. The integration of methods also revealed the relative importance of different microclimate factors on flowering phenology, as well as differences in phenological responses to changing climate related to growth form (shrub vs. graminoid vs. forb) and life-history traits (early vs. later flowering species). Comparing and synthesizing results across ecological studies, and in particular among climate change studies, has been accorded increasing attention and rigor with the development and application of meta-analysis tools (e.g., Hedges and Olkin 1985, Arft et al. 1999, Gurevitch and Hedges 1999). Our research demonstrates the value of systematically comparing and synthesizing results of multiple experimental and natural gradient field methods within a single study.

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