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EFFECTS OF EXPERIMENTAL WARMING ON PLANT REPRODUCTIVE PHENOLOGY IN A SUBALPINE MEADOW

MARY V. PRICE[1,2] AND NICKOLAS M. WASER[1,2]

[1]*Department of Biology, University of California, Riverside, California 92521 USA*
[2]*Rocky Mountain Biological Laboratory, Crested Butte, Colorado 81224 USA*

Abstract. Increasing "greenhouse" gases are predicted to warm the earth by several degrees Celsius during the coming century. At high elevations one likely result is a longer snow-free season, which will affect plant growth and reproduction. We studied flowering and fruiting of 10 angiosperm species in a subalpine meadow over 4 yr, focusing on plant responses to warming by overhead heaters. The 10 species reproduced in a predictable sequence during 3–4 mo between spring snowmelt and fall frosts. Experimental warming advanced the date of snowmelt by almost 1 wk on average, relative to controls, and similarly advanced the mean timing of plant reproduction. This phenological shift was entirely explained by earlier snowmelt in the case of six plant species that flowered early in the season, whereas four later-flowering species apparently responded to other cues.

Experimental warming had no detectable effect on the duration of flowering and fruiting, even though natural conditions of early snowmelt were associated with longer duration and greater overlap of reproduction of sequentially flowering species. Fruit set was greater in warmed plots for most species, but this effect was not significant for any species individually. We conclude that global warming will cause immediate phenological shifts in plant communities at high elevations, mediated largely through changes in timing of snowmelt. Shifts on longer time scales are also likely as plant fitnesses, population dynamics, and community structure respond to altered phenology of species relative to one another and to animal mutualists and enemies. However, the small spatial scale of experiments such as ours and the inability to perfectly mimic all elements of climate change limit our ability to predict these longer term changes. A promising future direction is to combine experiments with study of natural phenological variation on landscape and larger scales.

Key words: Colorado; climate change; experimental warming; flowering; fruiting; phenology; plant; snowmelt; subalpine meadow.

INTRODUCTION

Predicting plant community responses to global warming is not unlike forecasting effects of today's scandal on the fortunes of a political candidate in next year's election. In both cases complex feedbacks and contingent responses make it difficult to project into the future from past or present patterns. Unlike the political scientist, however, the natural scientist can use controlled experiments to help tease apart direct and indirect responses to change, in this case global climate change.

The anticipated increase in atmospheric levels of carbon dioxide and other "greenhouse" gases over the next century is expected not only to increase mean temperature at the earth's surface by ~2.5°C, but also to alter the entire global climate system through changes in sea level and uneven warming of the two hemispheres (Wigley and Raper 1992). Quite apart from its indirect effects on precipitation patterns, global warming can be expected to affect ecosystems directly through changes in soil moisture levels, nutrient fluxes, rate of plant growth (mediated by higher CO_2 levels as well as air temperature), and timing of plant growth (IPCC 1996). These direct effects of warming are likely to be striking at high elevation in temperate zones, where primary productivity is strongly limited by the snow-free growing season, and where spring snowmelt serves as a discrete environmental cue that initiates growth and flowering in many species (Sørensen 1941, Billings and Bliss 1959, Holway and Ward 1965, Inouye and McGuire 1991, Galen and Stanton 1993, 1995, Walker et al. 1995, Henry and Molau 1997). An obvious possibility for alpine and subalpine ecosystems is that global climate change will advance the timing of snowmelt and the onset of plant growth and sexual reproduction (flowering and fruiting in angiosperms). And, such phenological shifts might further affect plant communities by altering the relative fitnesses of species with different strategies of growth and reproduction.

To explore climate-induced changes in plant phenology and a reproductive component of fitness, we monitored responses over 4 yr to experimental warming of replicate plots in an otherwise undisturbed subalpine meadow. Additional heat input at the soil and snow

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surface, comparable to that expected from increased concentrations of greenhouse gases, was supplied by overhead infrared heaters. In the presence and absence of these heaters we monitored mean timing and duration of flowering and fruiting and proportional fruit maturation for 10 angiosperm species growing in the meadow.

Our study manipulated only one major aspect (surface warming) of global climate change. On the other hand, the study spanned multiple years and a gradient of environmental conditions. By comparing experimentally induced changes in phenology with changes related to natural variation in climate and microclimate within and among years, we were able to evaluate some limitations of the single-factor experiment.

METHODS

The study site

We worked in a subalpine meadow at the Rocky Mountain Biological Laboratory (RMBL) in west-central Colorado (38°53′ N, 107°02′ W, elevation 2920 m). Annual precipitation from 1984 to 1994 averaged 75 cm, ~80% in the form of snow (W. Barr, *unpublished data*). Melting of the winter snowpack is usually complete by late May or early June. Snowmelt typically gives way to a period of drought that breaks when moist subtropical air is drawn northward, causing thunderstorms over the mountains in July and August. The fall typically is dry. The RMBL area is characterized by forests of quaking aspen (*Populus tremuloides*) and conifers, mostly Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies bifolia*) [all taxonomic nomenclature follows Weber and Wittmann 1996], interspersed with dry meadows on rocky slopes and moist meadows in seeps and pockets of deep soil. The meadows are dominated by perennial angiosperms exhibiting diverse growth forms and reproductive patterns. Woody shrubs include mountain sagebrush (*Seriphidium vaseyanum*) on dry slopes, and cinquefoil (*Pentaphylloides floribunda*) and willows (*Salix* spp.) in moister areas. Semelparous (reproducing in a single episode) rosette-forming herbs include monument plant (*Frasera speciosa*) and scarlet gilia (*Ipomopsis aggregata*); iteroparous (repeatedly reproducing) herbs range from ephemeral bulbiferous species (e.g., *Claytonia lanceolata, Delphinium nuttallianum*) that flower and disappear from above ground soon after snowmelt, to vegetatively persistent species (e.g., *Potentilla pulcherrima, Erigeron speciosus, Helianthella quinquenervis*) whose aboveground tissues remain active throughout the summer. Grasses and sedges include rhizomatous and clump-forming species; common genera are *Elymus, Carex, Poa, Festuca, Stipa,* and *Bromopsis.*

Experimental design

In the summer of 1990 we established 10 experimental plots, each 3 × 10 m, in a subalpine meadow at the RMBL, separating each plot from its neighbors by >2 m (Fig. 1). Plots were numbered 1 to 10 from north to south. The long axis of each plot spanned a 1–2 m elevational gradient extending from the dry top of a small ridge (an ancient glacial moraine) down into a moist swale. The moraine curved so that the aspect of adjacent plots varied by ~5° on average; the northernmost plot faced southeast (130°) and the southernmost plot faced almost due east (78°).

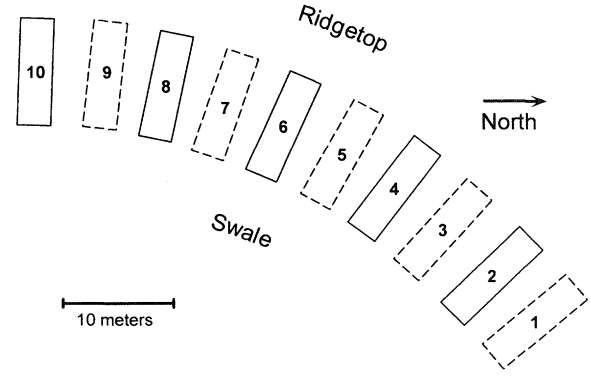

FIG. 1. Layout of the 10 study plots relative to the ridgetop of the ancient moraine and adjacent swale. Plots shown with dashed borders were warmed by overhead electric heaters.

Two electric heaters were suspended 2.5 m above odd-numbered plots, leaving even-numbered plots as unwarmed controls (Fig. 1). Parabolic reflectors above the heating elements caused nearly uniform delivery of 15 W/m^2 of infrared (IR) radiation over the central 80% of each warmed plot, 5 W/m^2 at the periphery and in a central band between the heaters, and no additional radiation to neighboring control plots. Heaters were activated in January 1991 and operated continuously thereafter. In May 1993 a third heater was added to each warmed plot, raising the incident IR flux to 22 W/m^2 and removing the central "cold spot." The downward radiant flux was chosen to effect the additional soil surface heating expected with a doubling of atmospheric CO_2 (Harte and Shaw 1995, Harte et al. 1995).

At the beginning of the experiment thermocouples were buried 5, 12, and 25 cm deep at three positions along the elevational gradient in each plot, and were connected to data loggers that automatically recorded temperature every 2 h. For further details see Harte et al. (1995).

Phenological measurements

For each plot, date of snowmelt in the four summers of 1991–1994 was estimated as the date at which soil temperature at a depth of 5 cm rose to +1°C. Visual inspection confirmed that this corresponds to a snow-free condition (J. Harte, *personal communication*). To obtain a single value for melt date of each plot we

averaged across its three replicate 5 cm deep thermocouples.

In each summer we measured reproductive phenology and fruit set for 10 plant species common enough to be represented by at least five flowering individuals in most plots. We chose species representative of the diversity of growth form, life history, and reproductive timing present in the angiosperm community, except that we excluded grasses and sedges. The chosen species were *Claytonia lanceolata* ("spring beauty," Portulacaceae), *Erythronium grandiflorum* ("avalanche lily," Liliaceae), *Mertensia brevistyla* ("bluebell," Boraginaceae), *Delphinium nuttallianum* ("Nelson's larkspur," Helleboraceae), *Lathyrus leucanthus* ("peavine," Fabaceae), *Potentilla pulcherrima* ("cinquefoil," Rosaceae), *Eriogonum subalpinum* ("buckwheat," Polygonaceae), *Ipomopsis aggregata* ("scarlet gilia," Polemoniaceae), *Campanula rotundifolia* ("harebell," Campanulaceae), and *Seriphidium vaseyanum* ("mountain sagebrush," Asteraceae). Nine of these species are herbaceous, sprouting days or weeks after snowmelt, whereas one is woody and retains some aboveground parts below the snowpack during winter. We identified a total of 66 angiosperm species (excluding grasses and sedges) in our plots (M. Price and N. Waser, *unpublished data*). Thus the chosen species comprise 15% of those present.

As soon as each of our 10 study species produced obvious flower buds, we tagged five mature individuals per plot in bud stage. We did not necessarily choose the same individuals in successive years. Indeed this was impossible for *I. aggregata,* which is 96–99% semelparous at the RMBL (Waser and Price 1989; A. K. Brody and N. M. Waser, *unpublished data*). To sample the elevational gradient from ridgetop to swale within a plot, we selected the uppermost and lowermost flowering individuals of each plant species, and three others spaced evenly in between. We adjusted our selection to match the elevational positions of individuals in each warmed plot with those of its unwarmed neighbor to the south. This ensured that we sampled the full phenological range within each plot.

We monitored focal individuals of the 10 plant species at weekly intervals during each summer for the presence of 6 phenological stages: unopened buds (recorded as stage 1), open flowers (stage 2), old flowers (stage 3 [post-anthesis but with petals, tepals, or petaloid sepals still attached]), initiated fruit (stage 4 [petals abscised but ovaries unexpanded]), expanding fruit (stage 5 [ovaries enlarged]), and dehisced fruit (stage 6). For each weekly census we calculated a single "phenological score" for each individual by averaging the stages present, unweighted by relative abundances of flowers (flowering heads in the case of *S. vaseyanum*) within each stage. For example, a plant with two buds (stage 1), three old flowers (stage 3), and one expanding fruit (stage 5), received a phenological score of 3.0. The unweighted average was chosen because exact counts of buds, flowers, and fruits for some species would have been too time-consuming to be feasible.

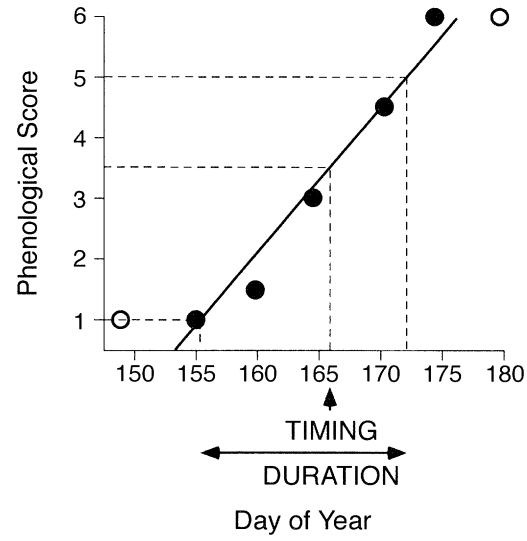

FIG. 2. An example of a phenological sequence, in this case for an individual *Claytonia lanceolata* in plot 1 in 1993. Phenological score indicates the mean stage (unweighted by flower number) for the individual on a given census date, where stages progress from unopened bud (stage 1) to dehiscing fruit (stage 6). Parameters describing the timing (TIMING) and duration (DURATION) of flowering are derived from linear regression of mean phenological score on day of year, for the period beginning with the last date at stage 1 and ending with the first date at stage 6 (●).

By fitting linear regressions to sequences of phenological scores for individual plants we derived two parameters that describe the mean timing and duration of reproduction. Regressions were performed only with plants for which we had at least three phenological scores beyond the bud stage. Also, we used only scores obtained during the period that began with the last census in which a plant had only buds, and ended with the first census in which the plant had dehisced all fruits (Fig. 2). Across 1487 individual regressions, linear fits were generally excellent ($R^2 = 0.89 \pm 0.12$ [mean $\pm$ 1 SD]) and we detected no systematic pattern of deviation from a straight-line relationship.

From regression equations for each plant we calculated several parameters (Fig. 2). The first variable is TIMING (also referred to as the *mean timing of reproduction*), the estimated date at which the plant reached a condition (phenological score = 3.5) midway between presenting only flower buds (stage 1) and presenting only dehisced fruits (stage 6). The second is DURATION (also referred to as *duration of reproduction*), the estimated time to progress from stage 1 to stage 5. We chose stage 5 because we sometimes missed stage 6; other academic duties lured us away from the field in the fall. TIMING and DURATION respectively indicate each individual's mean timing and duration of reproduction.

From plot means of the regression-based estimates of T-ONE (date of transition beyond bud stage) and T-FIVE (date to reach the expanding-fruit stage) we also could calculate mean phenological overlaps between pairs of species within each plot. OVERLAP was expressed as the time between the later value of T-ONE and the earlier value of T-FIVE for the species pair in question. We calculated overlaps only for each species and the species with the next-latest average value of TIMING, to reduce nonindependence problems associated with using each species' data in multiple comparisons.

In addition to phenological data, we recorded the total numbers of flowers and mature fruits produced by each plant whenever feasible. From these data we calculated FRUIT SET (also referred to as *proportional fruit maturation*) as the fraction of flowers on a plant that produced mature fruit.

We excluded data on phenological variables and/or FRUIT SET for some species and years, because we judged them to be unreliable. Thus, *S. vaseyanum* often flowered late in the season and suffered high levels of flower parasitism; parasitized heads did not develop normally. We obtained no values for proportional fruit maturation in this species, and some phenology data were discarded. It took us two seasons to correctly discriminate mature achenes of *E. subalpinum* held on the plant, and we obtained reliable data on fruit maturation for this species only after 1992. In *L. leucanthus,* high levels of fruit abcission and herbivory rendered data on fruit maturation from 1991 and 1992 unusable.

Analysis

We combined linear regression, ANCOVA, and ANOVA to analyze natural variation across plots, years, and species in phenology and proportional fruit maturation, as well as variation due to warming treatment. For most analyses we used the GLM procedure of SAS (SAS Institute 1990).

Most analyses involved several steps. First we tested the expectation that warming would advance the date of snowmelt. Next we considered whether warming affected TIMING, DURATION, OVERLAP, or FRUIT SET. We performed separate analyses for each variable, using means across replicate plant individuals, soil probes, or species pairs (in the case of OVERLAP) sharing a study plot. Mean OVERLAP values were based on different sets of species pairs in different years (5, 5, 5, and 6 pairs in 1991, 1992, 1993, and 1994, respectively), so each year was analyzed separately. For TIMING, DURATION, and FRUIT SET, separate analyses were performed for each species. Finally, we considered whether any treatment effects on phenological variables or FRUIT SET remained after the effect on date of snowmelt was removed statistically.

For several logistical reasons the 10 study plots were arranged in a regular alternation of control and warmed treatments (Fig. 1). This would cause any apparent treatment effect to include an effect of the position of each plot along the north-south array of plots (equivalent to the numbering of each plot, and hereafter referred to as *plot position*). To accommodate this in analyses we first asked whether there was any significant effect of plot position (treated as a continuous variable), and whether the effect differed by treatment, yielding a significant position × treatment interaction. We performed separate ANCOVAs on all 37 species-year combinations for TIMING and DURATION and all four years for mean OVERLAP values, and found significant effects (at $P < 0.05$) of plot position on TIMING in 18 of 37 cases, on DURATION in 13 of 37 cases, and on mean OVERLAP in three of four. In contrast, ANCOVA revealed significant position × treatment interaction effects on TIMING in only two of 37 cases, on DURATION in only five of 37, and on mean OVERLAP in zero of four cases. Thus plot position affected phenology for many species in many years and overlap patterns in most years, but did not act differentially by treatment. We therefore proceeded by statistically removing the effect of plot position. To do so we extracted residuals from linear regressions of snowmelt, phenology, or overlap variables on plot position, and used these residuals as dependent variables in randomized-blocks ANOVAs with warming treatment as a fixed effect and block (pair of adjacent warmed and control plots) as a random effect. In all cases, treatment effects were tested over the treatment × block interaction.

Treatment is expected to influence the mean timing of reproduction (TIMING) in large part because phenology in montane ecosystems is sensitive to snowmelt, and warming of plots significantly affected the date of snowmelt. We therefore explored relationships between phenology and date of snowmelt across all plots and years. To see whether any treatment effects remained after direct effects of accelerated snowmelt were removed, we next performed randomized-blocks ANOVAs as before, but on residuals from regressions of all phenology variables on date of snowmelt.

RESULTS

Natural variation in date of snowmelt

Total snowfall was equivalent to 69, 47, 99, and 68 cm of water in the winters (1 November–30 April) of 1990–1991, 1991–1992, 1992–1993, and 1993–1994, respectively (W. Barr, *unpublished data*). Mean date of snowmelt in control plots was positively correlated with total snowfall the previous winter ($r = 0.95$, df $= 2$, $P = 0.05$).

In all years of the study, snowmelt proceeded from north to south along the moraine (plot 1 to plot 10, Figs. 1, 3), in response to decreasing southerly exposure. Snowmelt was ~2 d later in each plot than in its lower-numbered northern neighbor (linear regres-

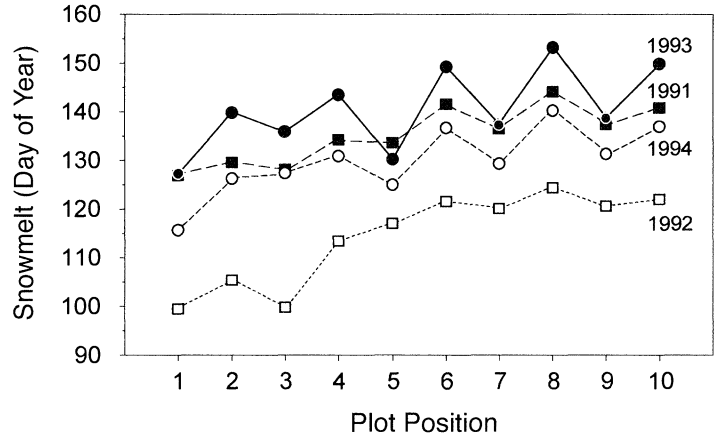

FIG. 3. Date of snowmelt in the experimental plots, whose orientation became progressively less south-facing from the northernmost plot 1 to the southernmost plot 10. Values are means across three samples per plot.

sion: [day of year on which snowmelt occurred] = 1.81 × [plot position] + 120.24; $F_{1,32} = 49.2$, $P = 0.0001$). ANCOVA indicated a significant effect of year as well (treated as fixed and tested over error; $F_{3,32} = 6.01$, $P = 0.002$), and no significant position × year interaction ($F_{3,32} = 0.84$, $P = 0.482$).

Effects of warming treatment on date of snowmelt

Because of the significant plot position effect and lack of interaction between plot position and treatment ($F_{1,36} = 0.02$, $P = 0.90$), we analyzed treatment effects on date of snowmelt with a randomized-blocks ANOVA on residuals from the plot position regression. This revealed a significant treatment effect on date of snowmelt (tested over block × treatment interaction; $F_{1,4} = 47.1$, $P = 0.002$). The treatment effect tended to vary among years (treatment × year interaction; $F_{3,24} = 3.10$, $P = 0.046$); the mean difference in date of snowmelt between control and warmed plots was positively correlated with total snowfall during the previous winter ($r = 0.88$). Over all years, snowmelt occurred on average 6.3 d earlier in warmed than control plots. In contrast, interplot variance in date of snowmelt was statistically indistinguishable between warmed and control treatments. For further details of soil responses to warming see Harte et al. (1995).

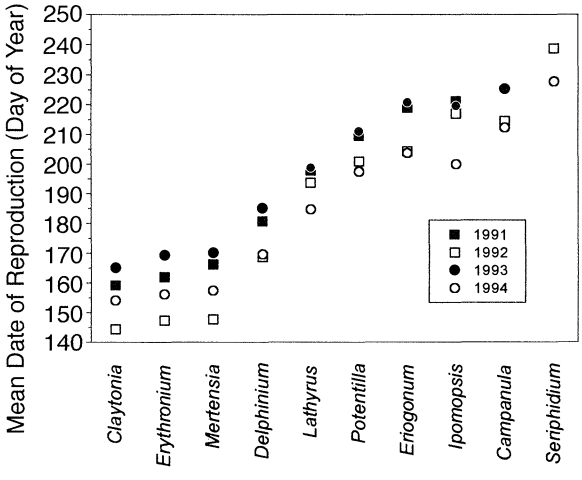

FIG. 4. Mean date of flowering and fruiting for 10 plant species in four different years. Values are means across replicate plots of the parameter TIMING.

Natural variation in mean timing of reproduction

The 10 species showed a consistent sequence of flowering and fruiting across years (Fig. 4). *Claytonia lanceolata, Erythronium grandiflorum,* and *Mertensia brevistyla* formed an early cohort; *Delphinium nuttallianum, Lathyrus leucanthus,* and *Potentilla pulcherrima* formed a middle cohort; and *Eriogonum subalpinum, Ipomopsis aggregata, Campanula rotundifolia,* and *Seriphidium vaseyanum* formed a late cohort. Year-to-year variation in mean timing of reproduction generally followed mean date of snowmelt, with 1992 and 1994 being early years and 1991 and 1993 late years (Figs. 3, 4).

Reproduction in all but two species proceeded from north to south along the moraine, as reflected in positive slopes for regressions of TIMING (with effects of year removed) on plot position (Table 1). The exceptions were *E. grandiflorum,* whose data in some years were unreliable because we did not record when frost damage arrested fruit development; and *I. aggregata,* whose indeterminate flowering, in years of sufficient summer moisture, continued until the first killing frost in the fall (see also Campbell and Halama 1993).

Effects of treatment on mean timing

The warming treatment advanced reproduction for all 10 species. The consistency of this pattern indicates a significant treatment effect on TIMING (by a binomial test, the probability of observing 10 of 10 positive responses by chance alone is only $P = 0.001$), although the effect was individually significant for four of the species (Table 1). All species with significant responses (*C. lanceolata, M. brevistyla, D. nut-*

TABLE 1. Responses of phenology and fruit set to plot position (Plot), date of snowmelt (Melt date), and experimental warming treatment (Treatment) in plants of a subalpine meadow.

		Regression of variable on:					
		Plot		Melt date		Treatment	
Species	Mean	Slope	*P*	Slope	*P*	Effect	*P*
TIMING							
C. lanceolata	156	**0.56**	0.016	**0.60**	0.001	**2.45**	0.016
E. grandiflorum	159	−0.16	0.096	**0.67**	0.001	0.44	0.326
M. brevistyla	161	**1.18**	0.001	**0.72**	0.001	**2.57**	0.003
D. nuttallianum	176	**0.94**	0.001	**0.52**	0.001	**1.89**	0.022
L. leucanthus	194	0.31	0.318	**0.37**	0.006	3.82	0.113
P. pulcherrima	205	0.39	0.092	**0.31**	0.001	**2.31**	0.046
E. subalpinum	212	0.48	0.230	**0.52**	0.001	4.34	0.090
I. aggregata	215	−0.23	0.584	0.05	0.776	3.57	0.217
C. rotundifolia	218	0.32	0.392	**0.34**	0.001	1.96	0.424
S. vaseyanum	234	0.23	0.133	**−0.28**	0.012	0.90	0.395
DURATION							
C. lanceolata	25	−0.44	0.056	**−0.31**	0.001	0.15	0.940
E. grandiflorum	23	**−0.64**	0.005	−0.17	0.152	−1.17	0.966
M. brevistyla	27	**−0.64**	0.002	**−0.25**	0.001	**−1.88**	0.025
D. nuttallianum	29	**−0.93**	0.002	**−0.29**	0.001	−0.53	0.644
L. leucanthus	37	−0.68	0.189	−0.02	0.929	5.46	0.172
P. pulcherrima	48	−0.14	0.609	**−0.26**	0.006	0.01	0.995
E. subalpinum	49	−0.63	0.283	0.04	0.680	5.06	0.126
I. aggregata	72	**−2.70**	0.022	**−1.16**	0.002	4.26	0.488
C. rotundifolia	34	−0.77	0.108	−0.04	0.738	4.56	0.113
S. vaseyanum	26	**−0.63**	0.015	**−0.45**	0.001	−0.89	0.572
FRUIT SET							
C. lanceolata	0.48	0.14	0.118	−0.001	0.777	−0.070	0.253
E. grandiflorum	0.25	0.03	0.071	0.008	0.100	−0.208	0.075
M. brevistyla	0.49	−0.001	0.826	**−0.004**	0.020	−0.026	0.400
D. nuttallianum	0.45	−0.006	0.420	−0.004	0.138	−0.044	0.463
L. leucanthus	0.12	0.02	0.206	**0.011**	0.030	−0.018	0.822
P. pulcherrima	0.76	0.009	0.051	0.001	0.696	−0.040	0.268
E. subalpinum	0.36	0.006	0.485	0.008	0.081	−0.091	0.153
I. aggregata	0.50	1.018	0.068	0.007	0.089	−0.071	0.388
C. rotundifolia	0.68	−0.022	0.164	−0.005	0.168	0.016	0.904

Notes: Mean = mean values, over all years, of mean timing (TIMING, expressed as day of year) and duration (DURATION, in number of days) of reproduction for 10 species, and of fruit set (FRUIT SET = proportion of flowers producing fruits) for nine species. Slope of regression = relationship between plot means and either plot position or date of snowmelt. Plot position regressions were performed on values with the effect of year removed. Treatment = effect of warming treatment, as determined from randomized-blocks ANOVA performed on plot means with effects of plot position and year removed. Effect = mean residual for control plots minus mean residual for warmed plots. Significant regression slopes and treatment effects are shown in boldface type.

tallianum, and *P. pulcherrima*) were cohorts flowering in the early or mid season (Fig. 4).

There was a significant ($P < 0.05$) positive relationship between TIMING and date of snowmelt for all species except *I. aggregata* and *S. vaseyanum.* In no case was there a significant interaction between date of snowmelt and treatment. The slope of the relationship between TIMING and date of snowmelt for a species was negatively correlated with TIMING for that species (Table 1; $r = -0.83$, df = 8, $P < 0.01$); in other words, late-flowering species were less responsive to timing of snowmelt than were species that flowered early.

Treatment had an inconsistent effect on TIMING beyond its effect on date of snowmelt, judging from randomized-blocks ANOVA on residuals from regressions of date of snowmelt on treatment. The additional treatment effect was positive in five species and negative in five, and was individually significant for only four species. Experimental warming advanced reproduction for *D. nuttallianum,* perhaps because the warmer soil (Harte et al. 1995) in warmed plots advanced the development of buds, flowers, and seeds (compare Wookey et al. 1993, Farnsworth et al. 1995, Fitter et al. 1995). Warming delayed reproduction for *E. grandiflorum, S. vaseyanum,* and *M. brevistyla.* The first of these species reproduces soon after snowmelt. Its buds and flowers appeared earlier in warmed plots but then were damaged in most years by late spring frosts, giving a false impression of stasis in development (ovaries in *E. grandiflorum* are particularly sensitive to cold nighttime temperatures after flowers have opened; J. Thomson, *personal communication*). Frost damage is unlikely for the later flowering *S. vaseyanum* and *M. brevistyla,* but the drier soil of warmed plots after the snowmelt period (Harte et al. 1995) may have slowed their flower development.

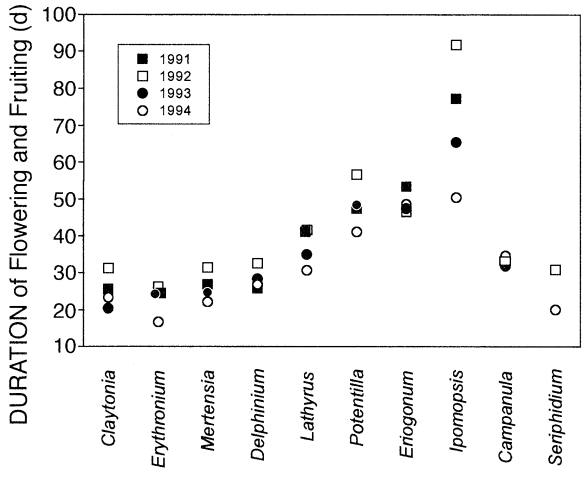

FIG. 5. Mean duration of flowering and fruiting for 10 plant species in four different years. Values are means across replicate plots of the parameter DURATION.

Natural variation in duration of reproduction

Flowering and fruiting lasted a mean of ~40 d, but species differed significantly in their duration of reproduction (DURATION; Fig. 5; $F_{9,24} = 26.0$, $P = 0.001$ for species effect, tested over the species × year interaction in factorial ANOVA with plot position effects removed). The mean DURATION for a species was not significantly correlated with its mean timing of reproduction ($r = 0.50$, df = 8, $P > 0.05$), although there was a tendency for DURATION to increase with TIMING over much of the season (Fig. 5).

For all species, DURATION was negatively related to plot position; the relationship was individually significant for five species (Table 1). This consistent pattern suggests that reproduction was compressed into shorter time periods as progressively later snowmelt shortened the growing season from plot 1 to plot 10. Indeed, DURATION was negatively related to date of snowmelt over all year-plot combinations for all species except *E. subalpinum,* significantly so for six species (Table 1).

Effects of treatment on duration of reproduction

With effects of plot position removed, there was no statistically significant treatment effect on DURATION for any species except *M. brevistyla,* for which warming extended flowering and fruiting (Table 1). The sign of the treatment effect was not consistent; in three species warming extended reproduction, and in six it compressed reproduction. Nor did treatment appear to have an influence beyond its effect on snowmelt, judging from lack of significance after date of snowmelt effects had been removed, although in 8 of 10 species the residual effect of warming was to compress reproduction.

Natural variation in reproductive overlap

ANCOVA revealed negative relationships in three of four years between plot position and mean OVERLAP. Effects were significant in 1991 and 1992 (Table 2). This indicates that reproductive overlap between sequentially flowering species tended to decrease along the moraine from northern plots, melting early, to southern plots, melting late. Similarly, when date of snowmelt was used as the covariate in ANCOVA, the regression slope was negative in all years (Table 2), indicating that reproductive overlap declined in plots with later snowmelt within each year. In no case was there a significant plot × treatment or melt date × treatment interaction.

Effects of treatment on overlap

Experimental warming had no significant effect on mean OVERLAP in any year. This was true whether the analysis was done on mean OVERLAP values before or after effects of plot position or snowmelt date

TABLE 2. Patterns of reproductive overlap between sequentially flowering species over four years in a Colorado subalpine meadow.

	OVERLAP			
Species pair	1991	1992	1993	1994
1 vs. 3	19.9	27.0	18.5	17.2
3 vs. 4	12.1	11.2	12.5	13.6
4 vs. 5	18.8	···	20.0	14.6
4 vs. 6	···	15.8	···	···
5 vs. 6	33.8	···	30.1	26.3
6 vs. 7	42.2	43.7	40.0	38.6
7 vs. 9	···	26.8	···	29.5
Mean OVERLAP	25.4	24.4	24.2	23.3
Plot slope	−0.47*	−1.07*	0.05	−0.70
Melt date slope	−0.27*	−0.34*	−0.02	−0.24

Notes: "Mean OVERLAP" is mean number of days of overlap calculated across all species pairs sharing a plot in a given year. "Plot slope" and "Melt date slope" are respectively the slopes of regressions of mean OVERLAP on plot number and date of snowmelt for each plot. Ellipses (···) = no data. Species 1 = *Claytonia lanceolata*; 3 = *Mertensia brevistyla*; 4 = *Delphinium nuttallianum*; 5 = *Lathyrus leucanthus*; 6 = *Potentilla pulcherrima*; 7 = *Eriogonum subalpinum*; 9 = *Campanula rotundifolia.* * $P < 0.05$.

TABLE 3. Effects of species and year on FRUIT SET in plants of a subalpine meadow. Species was treated as a fixed effect and year as a random effect. Species was tested over the species × year interaction.

Source of variation	df	MS	F	P
Species	8	1.08	4.00	0.025
Year	3	0.15	4.54	0.004
Species × Year	19	0.27	7.75	0.0001
Error	261	0.04		

had been removed (randomized-blocks ANOVAs, not shown).

Natural variation in fruit set

Proportional fruit maturation varied significantly across species and years (Table 3). 1992 was a year of relatively high FRUIT SET for five species, whereas 1994 was a year of low FRUIT SET for seven species (Fig. 6). The ranking of years was not concordant among species, however, causing a significant species × year interaction (Fig. 6, Table 3).

Proportional fruit maturation increased with plot position in six of nine species (Table 1), but this pattern is not significant by a binomial test ($P = 0.42$), and no species showed an individually significant response. Likewise, FRUIT SET varied inconsistently across species with date of snowmelt (Table 1), and the relationship was individually significant in only two cases (judging from regression across plots and years).

Effects of treatment on fruit set

Proportional fruit maturation was higher in warmed than control plots for eight of nine species (Table 1), a pattern that is significant by a binomial test ($P = 0.02$). However, this trend was inconsistent with the lack of response to natural variation in snowmelt. Furthermore, the overall pattern across species was insignificant by an alternative test (randomized-blocks ANOVA on all data with species and plot position effects removed, $P = 0.6$), and no species showed an individually significant response (randomized-blocks ANOVAs of residuals from regressions of FRUIT SET on plot position, Table 1).

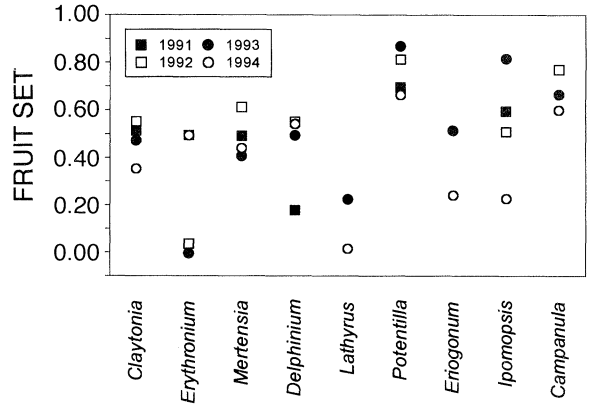

FIG. 6. Mean proportional fruit maturation for nine plant species in four different years. Values are means across replicate plots of the parameter FRUIT SET.

DISCUSSION

Natural patterns of phenology

Ecologists have been intrigued by the reproductive timing of flowering plants for at least a century (e.g., Robertson 1895). Over this period they have demonstrated conclusively that both genetics and environment contribute to phenological patterns. The natural phenological responses we observed are consistent with this conclusion.

The genetic aspect of phenology is evident in two kinds of observations. First, one often sees a strong phylogenetic signal within and across plant communities: species, genera, and higher taxa often exhibit characteristic seasonal timing (Robertson 1924, Clausen 1951, Rathcke and Lacey 1985, Kochmer and Handel 1986). In keeping with this, we observed a consistent sequence of reproduction among our 10 study species over 4 yr, as well as repeatable species differences in duration of reproduction. Second, one commonly sees that the phylogenetic signal is malleable, and that it can vary with the regime of artificial or natural selection (Clausen 1951, Ehrendorfer 1953, Stanford et al. 1962, Allard and Hansche 1964, Paterniani 1969, Rathcke and Lacey 1985, Tarasjev 1997). These observations suggest that a species' phenological position in the growing season, and its phenological response to environmental cues, are maintained by ongoing natural selection.

The environmental aspect of phenology is evident in immediate responses to temporal and spatial variation in climatic conditions (Robertson 1924, Sørensen 1941, Panje and Srinivasan 1959, Jackson 1966, Inouye and McGuire 1991, Friedel et al. 1993, Fitter et al. 1995, Sparks and Carey 1995, Tarasjev 1997). Thus it comes as no surprise that we also observed substantial variation in the timing and duration of reproduction of individual species that was correlated with year-to-year variation in winter snowfall and with the compass aspect of study plots. The single most important environmental variable in our subalpine meadow seems to be the date of snowmelt. The mean timing of reproduction for species flowering early in the season was most strongly related to date of snowmelt, suggesting that snowmelt provides a proximate cue or ultimate constraint for these species. Because most of our study species are herbaceous (as are most species in the meadow flora), and because the few woody species have no parts above the snow until almost the end of snowmelt, we conclude that the causal agent is truly snowmelt rather than cumulative energy input to aboveground plant tissues. Timing in species that flower later may be more strongly tied to vegetative growth, which is affected by factors uncoupled with snowmelt, and which we did not assess, such as summer

precipitation. The duration of reproduction was also sensitive to date of snowmelt, becoming shorter for all but one species when natural conditions of delayed snowmelt shortened the total growing season. Under such conditions individuals of different species growing in close proximity to one another also overlapped less in their reproductive phenology.

Effects of experimental warming

In a true greenhouse effect, surface warming occurs through conductive as well as radiant exchange with warmed air. Air movement at our exposed study site made it impossible to substantially warm the air over unenclosed plots, and it was not practical to enclose plots in open-top chambers or greenhouses (e.g., Wookey et al. 1993, Chapin et al. 1995, Henry and Molau 1997) because of powerful winter winds and heavy snowfalls. Thus experimental warming occurred entirely through downward IR flux. On the one hand, this method does not perfectly mimic real greenhouse warming, so we might expect some spurious plant responses (for example caused by uneven heating of the tops and bottoms of leaves). On the other hand, the method does mimic total energy input at the soil surface and provides input during both night and day. Thus we expect some experimental effects that faithfully represent what will occur with an increase in atmospheric greenhouse gases, including acceleration of snowmelt.

Indeed, our experiment advanced the date of snowmelt starting in the first spring after heaters were turned on. This advancement was related to altered mean timing of flowering and fruiting in a way that paralleled plant responses to natural variation in date of snowmelt. Experimental warming consistently advanced TIMING for all 10 species. Treatment effects were statistically significant primarily in species that flower early, suggesting, in concordance with natural patterns, that timing in late-flowering species is less strongly influenced by snowmelt. Overall we detected little effect of experimental warming on TIMING that could not be ascribed to effects of warming on date of snowmelt.

The experiment did not reproduce all effects of natural variation in snowmelt, however. For example, the duration of flowering and fruiting, and hence reproductive overlap with other species, failed to respond consistently to experimental warming. In contemplating this discrepancy it is instructive to consider that accelerated snowmelt in the experiment, and natural early snowmelt, did not share all the same causes. In the first case the mechanism was warming; in the second it included a shallow winter snowpack. A shallow snowpack has side effects, which include colder winter soil temperatures (less insulating snowpack) and drier soils in early summer (less water input during spring snowmelt). Such environmental correlates of snowpack might directly influence physiological processes that set the duration of flowering and fruiting, or might simply serve as reliable cues that plants use in adapting duration of reproduction (and as a consequence reproductive overlap with other species) to a variable growing season. In either case, correlates of snowpack might cause natural variation in DURATION and OVERLAP that our manipulation failed to reproduce, even though it did accelerate snowmelt.

If real global warming occurs without a correlated decrease in snowpack, it may be the manipulation, rather than the natural variation, that better predicts future effects (or lack thereof) on duration and overlap of reproduction. This is not assured, of course. In common with most experimental studies we mimicked only a single aspect of anticipated climate change, whereas actual change will have many dimensions in addition to warming. Higher CO_2 concentration is an important dimension that will increase plant photosynthetic rates and water-use efficiency (IPCC 1996). Another dimension is a differing amount, timing, and type of precipitation. And, there is reason to suspect that precipitation interacts with temperature and CO_2 to influence plant growth and phenology (Friedel et al. 1993, Wookey et al. 1993, IPCC 1996). In principle it is possible to simulate warming, CO_2 concentration, and precipitation in a single experiment. But there still is the problem that precipitation change at a given location is not predictable from present climate models (Schneider 1993), so it is not obvious in what directions to modify it.

Experimental effects on proportional fruit maturation also did not parallel responses to natural environmental variation. Whereas plot position and natural variation in date of snowmelt had slight (at best) effects on FRUIT SET, we detected a tenuous trend for this component of fitness to increase in warmed plots. This discrepancy is probably unsurprising, given the sensitivity of fruit set to a variety of abiotic and biotic environmental factors. If the experimental response represents a direct influence of warming on development of ovules, pollen tubes, or seeds, it may best predict the future effect of global warming in this case.

Predicted direct and indirect impacts of global warming

The phenological progression of reproductive events in angiosperms is of great practical importance in agriculture and of similar, although perhaps less obvious, importance to the functioning of natural ecosystems. In crop and natural systems alike, reproductive phenology dictates how an individual plant, in the process of producing iterated modules of flower buds, flowers, pistils, stamens, fruits, and seeds experiences an abiotic environment of nutrients, water, and irradiation and a biotic environment of competitors, pollinators, herbivores, and seed predators. Any change in phenology holds the potential to disrupt this interface between plant and environment.

The results presented here lend support to our initial expectation that global warming will consistently change phenological patterns in high-elevation and high-

latitude ecosystems (see also Henry and Molau 1997). A large share of the change will likely occur through shifted timing of cues used by plants to initiate reproductive events. The specific example involves acceleration of snowmelt and lengthening of the growing season. The predicted immediate response is that plant species will flower earlier, especially those that flower soon after snowmelt.

This prediction does assume that changed precipitation patterns do not counterbalance the warming effect on phenology. The prediction could fail if high elevations and latitudes also experience increased winter snowpacks that take longer to melt even though they begin to melt earlier. Current models of global climate change do suggest a general increase in winter precipitation at moderate to high latitudes, although regional predictions remain uncertain (Schneider 1993). The prediction of earlier flowering also might fail more spectacularly if climate change alters the correlations among cues used by plants to initiate reproduction and shifts the timing of appropriate combinations of cues. In this case phenology might change in unanticipated ways, even from one season to another.

Evolutionary changes in phenology over the longer term, which involve genetic change in cues used to initiate reproductive events or in responses to those cues, will depend on how climate change affects the relationship between phenology and individual plant fitness. Global warming might have immediate direct effects on plant fecundity, hinted at by our mixed evidence for increased proportional fruit maturation in warmed plots (see also Henry and Molau 1997). And warming is likely to have indirect effects as well on this component of fitness, because of phenological shifts that alter interactions with other species. These species include animal pollinators that are critical for sexual reproduction of many plants (e.g., Waser 1979, Bertin 1989), animals whose activities cause dispersal of seeds (e.g., Wheelwright and Orians 1982, Turnbull et al. 1983), herbivorous animals whose damage to reproductive and/or photosynthetic structures will affect pollination and seed maturation (e.g., Crawley 1989, Maschinski and Whitham 1989), and pre- and postdispersal seed predators whose activity can drastically reduce an individual plant's seed crop and seedling recruitment (Zimmerman 1980, Louda 1982, Pettersson 1991, Brody 1992). In addition, other plant species whose reproductive phenology overlaps that of the species in question can affect its fecundity by interacting with shared pollinators or with the other animals noted above that act as mutualists or antagonists to plants (e.g., Waser 1978, 1983, Wheelwright and Orians 1982, Rathcke 1983).

Unfortunately, we are not yet in a position to make more than very general statements about how global climate change might affect such ecological interactions, and thus plant fecundity. As discussed above (see *Discussion: Effects of experimental warming*), we manipulated only one factor, and the mechanisms of experimental and natural variation in snowmelt are not strictly comparable. As a result neither the experiment nor our study of annual variation allows a secure prediction of how global climate change will alter phenological overlap between plant species. We also face another major limitation: many of the ecological interactions listed above occur over a much larger spatial scale than that of any manipulation of climate change devised to date. For example, the pollinators of our study species are mostly strong-flying animals (e.g., bumble bees, solitary bees, butterflies, hummingbirds) whose foraging activities cover areas ranging from hectares to square kilometers. Even without these limitations it would be a daunting task to predict how global warming will change the relative phenologies of all the species that interact with a given plant species, and hence patterns of evolutionary response.

These observations suggest two sorts of conclusion. First, they illustrate the value of exploring natural variation in phenology in combination with experimental variation, as a way to partially circumvent the limitations of each approach by itself. In future, the ideal should be to expand the spatial scale over which natural variation is studied to the landscape level. Second, the combined natural and experimental responses of phenology that we have discussed, in spite of scale and other limitations, suggest that global warming will alter patterns of species interaction and thus fecundity. The result may be a host of shifts, involving on the one hand changes in individual fitness that lead to further evolutionary change in phenology, and on the other hand changes in population recruitment that alter population dynamics, relative abundances of plant species, and thereby community structure.

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