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PLANT RESPONSES TO EXPERIMENTAL WARMING IN A MONTANE MEADOW

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Abstract. We studied the effects of a seven-year warming experiment on 11 forb species in the Rocky Mountains of Colorado in 1996 and 1997. Previous work on this experiment focused on ecosystem and community responses to warming. Our purpose here is to report on species responses. We found significant positive responses to warming for two species and negative responses for four species in terms of abundance, size, flowering, or frost damage. Because previous results from the warming experiment showed that artificial warming decreases soil moisture and increases nitrogen mineralization, we used nitrogen and water addition experiments on the two dominant forbs to determine whether species responses in the warming experiment could be due to shifts in resource availability. We found that *Erigeron speciosus* was limited more clearly by water than by nitrogen and *Helianthella quinquenervis* was limited by both nitrogen and water. These responses are consistent with the hypothesis that a primary effect of warming on plants occurs via changes in soil resource availability, but more complicated factors including competition are likely to be important to warming effects as well. Because previous work on this experiment indicated that annual forb detrital production is a key component of the carbon cycle of this system, we also asked which species responded to warming with changes in aboveground biomass. Over 1996 and 1997, four of nine perennial species had significantly lower biomass in the warmed plots, and in 1997 one species had significantly higher biomass. The biomass differences of *Erigeron* and *Helianthella* were almost equal and opposite, but while the decline in *Erigeron* was statistically significant the increase in *Helianthella* was smaller and not significant. In one year, a major effect of warming was to protect *Helianthella* from frost damage, which illustrates the importance of extreme weather events. Our study points to the potential importance of understanding ecosystem responses to climate change in terms of species responses.

Key words: carbon cycle; climate change; Erigeron speciosus; Helianthella quinquenervis; *montane forbs; plant physiological ecology; resource limitation; Rocky Mountains, Colorado.*

INTRODUCTION

Two related goals of studying biotic responses to climate change are to understand changes in species distributions and abundances (Field et al. 1992, Jensen et al. 1992, Pacala and Hurtt 1993, Bazzaz 1996, Chapin and Shaver 1996) and to understand ecosystem feedbacks to climate change, particularly via carbon uptake or loss (Houghton et al. 1983, Pastor and Post 1988, Vitousek 1990, Ojima et al. 1991, Hobbie 1992, Oechel et al. 1993, 1994, Smith and Shugart 1993, Chapin et al. 1995, Woodwell 1995, Lashof et al. 1997). An important link between these two topics concerns the level of detail of species responses necessary to predict ecosystem responses. Climate models often use a ''one big leaf'' representation of ecosystems, but species responses may not combine to produce such simple behavior under climate perturbations (Chapin and Shaver 1985, 1996, Hobbie 1992, Bazzaz 1996). Indications of the complex role of species in ecosystems come from studies showing that particular species characteristics can change ecosystem dynamics (Vitousek 1990, Johnson and Damman 1991, Hobbie 1992, Oechel et al. 1994, Chapin et al. 1996, Lauenroth et al. 1997) and that range shifts during past climate change were species specific (Davis 1989, Graham 1992, Webb 1992). Species responses to climate change will be difficult to understand both because correlational studies of species ranges may not be predictive (Pacala and Hurtt 1993) and because species may respond to the distribution rather than just the mean of climate conditions (Clark 1988, Overpeck et al. 1990, Bazzaz et al. 1996).

An ongoing artificial warming experiment in the Rocky Mountains of Colorado has allowed investigation of ecosystem responses to one of the most direct aspects of predicted climate change, increased radiative heat flux. Work to date on this experiment has focused on community and ecosystem responses including

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PLATE 1. View of warming experiment in 1992. Each row of heaters is suspended above the middle of the 10-m axis of a treatment plot. Control plots are between treatment plots. Photograph by Natalie J. Demong.

aboveground biomass, soil respiration, net uptake or loss of carbon from the system, and nitrogen mineralization (Harte and Shaw 1995, Harte et al. 1995, Torn and Harte 1996, Saleska et al. 1999, Shaw et al. 2000, Shaw and Harte 2001, *in press*). Leaf-level physiological responses have also been studied (Loik and Harte 1996, 1997). Our primary purpose in this study was to investigate responses of individual forb species to the experimental warming. We report on growth, abundance, and flowering responses of 11 forb species.

In addition we investigated the resource limitations driving responses of the two dominant forb species with separate experiments. Previous results from the warming experiment showed that two primary microclimate effects of warming are a decrease in soil moisture and an increase in nitrogen mineralization (Harte et al. 1995; Shaw and Harte, *in press*). A simple hypothesis for species responses to warming is that they are consistent with direct effects of changes in limiting resources. Under this hypothesis, a species that is more nitrogen limited than water limited should respond favorably to warming and vice versa. We tested this hypothesis for *Erigeron speciosus* and *Helianthella quinquenervis* with nitrogen and water addition experiments outside of the warming experiment.

Our species-level study is related to ecosystem studies of this experiment because those studies showed that annual forb detrital input to the soil carbon pool is a key component of the carbon cycle of this system. Harte and Shaw (1995) found that in the warmed plots, aboveground biomass (AGB) of forbs decreased, AGB of shrubs increased, and AGB of grasses was unchanged. Aboveground biomass is ~54% forb, 16% shrub, and 30% grass (1992–1994 averages from Harte and Shaw 1995). Shrub AGB consists almost entirely of sagebrush (*Artemisia tridentata*), while forb AGB is composed of a community of ~30 species in the portion of the experiment where effects were strongest. Saleska et al. (1999) measured warming effects on the net carbon flux of the system and found that the differences in plant carbon uptake, which are related to AGB, were several times larger than differences in soil respiration. Effects on these processes together showed a possible carbon loss from the warmed plots relative to control plots because plant carbon uptake decreased. Because warming effects on plant carbon uptake are important in this carbon cycle (Saleska et al. 1999), and because forbs as a group are a key part of the gross plant response to warming (Harte and Shaw 1995), measurement of species-level forb size and abundance could improve understanding of how warming affects the carbon cycle of this system.

METHODS

Study site and warming treatment

Our experiments were conducted at Rocky Mountain Biological Laboratory, Gunnison County, Colorado (38° 53′ N, 107° 02′ W; elevation 2920 m) in an ungrazed montane meadow. The warming experiment consists of 10 experimental plots, each 3 × 10 m, with every other plot warmed by overhead infrared heaters year-round. The heaters are suspended 1.5 m over treatment plots by towers and cables, have reflective shields designed to provide uniform radiation, and remain on throughout the year (see Plate 1). They produced 15 W/m^2 incident on the soil surface from January 1991 until May 1993, when they were turned up to 22 W/m^2 (Harte et al. 1995, Saleska et al. 1999). Their radiation wavelength is between 800 and 1100 nm, which means visible light and photosynthetically active radiation are negligible (Harte et al. 1995, Saleska et al. 1999). Predictions for a doubled-CO_2 atmosphere include a combination of radiative and convective warming (IPCC 1996). This experiment does not include a convective component (i.e., warmer air) but uses nearly twice the predicted radiative component in order to approximate the midrange of predictions of soil warming that would be produced by both (Harte et al. 1995, IPCC 1996, Saleska et al. 1999). The warming is main-

TABLE 1. Warming experiment biomass calibrations.

Species	Type	Regression	r^2	n
Helianthella quinquenervis (Asteraceae)	flowering	$M = 0.12 + 0.055 \times \text{Height}$	0.76	16
	aborted	$M = -0.55 + 0.073 \times \text{Height}$	0.95	4
	nonflowering	$M = -1.07 + 0.13 \times (\text{No. leaves}) + 0.052 \times (\text{Max leaf})$	0.87	20
Erigeron speciosus (Asteraceae)	flowering	$M = -0.25 + 0.022 \times \text{Height} + 0.013 \times (\text{No. leaves})$	0.81	25
	nonflowering	$M = -0.48 + 0.040 \times \text{Height} + 0.008 \times (\text{No. leaves})$	0.82	15
Potentilla hippiana (Rosaceae)	flowering	$M = \exp(-0.31 + 0.020 \times (\text{No. flowers and buds}))$	0.52	25
	nonflowering	$M = \exp(-4.0 - 0.27 \times (\text{No. leaves}) + 0.15 \times (\text{Max leaf}))$	0.63	25
Lathyrus leucanthus (Leguminosae)	all	$M = \exp(-2.3 + 0.081 \times (\text{No. leaf pairs})$	0.79	25
Eriogonum subalpinum (Polygonaceae)	flower stalks	$M = \exp(-5.8) \times (\text{Height})^{1.7}$	0.75	24
	ground cover	$M = 0.060 + 0.018 \times \text{Area}$	0.95	25
Galium boreale (Rubiaceae)	all (1996)	$M = -0.073 + 0.019 \times \text{Height} + 0.016 \times (\text{No. flower groups})$	0.92	10
	all (1997)	$M = -0.064 + 0.010 \times \text{Height} + 0.073 \times (\text{No. stem splits})$	0.87	15
Arenaria congesta (Caryophyllaceae)	all	$M = \exp(-3.5 + 0.075 \times \text{Height})$	0.60	25
Delphinium nelsonii (Helleboraceae)	flowering	$M = \exp(-3.2 + 0.074 \times \text{Height})$	0.76	25
Mertensia fusiformis (Boraginaceae)	flowering	$M = -0.29 + 0.022 \times \text{Height} + 0.029 \times (\text{No. leaves})$	0.60	15
Potentilla gracilis (Rosaceae)	flowering	$M = 0.27 + 0.077 \times (\text{No. flowers and buds})$	0.82	15
	nonflowering	$M = -0.94 - 0.044 \times (\text{No. leaves}) + 0.081 \times (\text{Max leaf})$	0.73	15

Notes: Biomass regression for aborted *Helianthella* flowering shoots is based on a small sample of four individuals because the significance of flower abortion was not apparent until the end of the study. *P. gracilis* and *M. fusiformis* biomass calibrations are based on data from 1997 only. For *Galium,* No. flower groups and No. stem splits are measures unique to *Galium*'s growth form. For *Helianthella* and the *Potentilla* species, Max leaf is the length of the largest leaf of nonflowering shoots. *Eriogonum* area measurement is in arbitrary units of areal coverage. For all species, *M* is dry mass in grams, heights are in centimeters, and *n* is sample size.

tained year-round because under doubled CO_2 warming is predicted to occur year-round, but the larger predicted temperature differences in winter than summer were not simulated with the heaters (IPCC 1996). The primary effect of the winter warming treatment is to advance snowmelt; it does not affect winter soil temperature under the snowpack (Harte et al. 1995).

Soil moisture and temperature are monitored every 2h at depths of 0.05, 0.12, and 0.25 m with gypsum blocks and thermocouples connected to automatic data loggers. The site and previous results of the warming experiment have been described by Harte et al. (1995), Harte and Shaw (1995), Loik and Harte (1996, 1997), Torn and Harte (1996), Price and Waser (1998), Saleska et al. (1999), Shaw et al. (2000), Shaw and Harte (2001, *in press*). Air temperatures from 15 June to 15 August averaged 11.9° and 11.0°C in 1996 and 1997, respectively. A similar average from 1991 to 1998 is 11.6°C. During the same period, soil moisture (measured as grams of water per gram of dry, seived soil) averaged 0.195 and 0.222 g/g in 1996 and 1997, compared to the 1991–1998 average of 0.211 g/g. Thus 1996 and 1997 represent a warm, dry season and a cool, wet season, respectively, relative to the average over the course of the experiment.

The 10 m axis of the plots spans a microclimate gradient from the dry top of a small moraine hill (the dry zone) to a wetter swale habitat (the wet zone). The dry zone contains ~30 forb species, eight grass and sedge species, and two shrub species. The dominant shrub is sagebrush, which occurs there near the limit of Great Basin desert shrub habitat, and the dominant grass is *Festuca thurberi.* The most dramatic soil microclimate and biogeochemical effects of the warming treatment occur in the dry zone (Harte and Shaw 1995, Harte et al. 1995, Saleska et al. 1999), and we used this part of the plots for the current study. In the dry zone, relative to control plots, soil in the warmed plots ranges from 0% to 25% drier and from 0° to 6°C warmer diurnally during the snow-free season, winter snow melts ~10 d earlier (Harte et al. 1995), and nitrogen mineralization increased by ~0.14 $g \cdot m^{-2} \cdot d^{-1}$ (Shaw and Harte, *in press*). During all years of the study from 1993 onward, aboveground forb biomass has been lower and aboveground shrub biomass higher in the warmed plots relative to the control plots, but the magnitude of the difference has varied from year to year. During 1993 and 1994 these differences were particularly large (Harte and Shaw 1995).

Survey methods

In each plot we surveyed the populations of seven forb species (all perennial) in 1996 and 11 forb species (nine perennial and two annual) in 1997 in a 4 m^2 quadrat in the dry zone. These species represent the most abundant and largest forbs in the dry zone. We surveyed one additional species (*Potentilla gracilis*) because it is a substantial component of forb biomass on one plot.

For perennial species, we counted flowering and nonflowering shoots (or both together) and measured correlates of biomass (e.g., height, number of leaves; see Table 1) from an unbiased subsample of shoots on each plot. The unbiased subsamples generally contained 5–

15 randomly chosen shoots of each type of each species in 1996 and 15 shoots (or as many as were available) of each in 1997, with the exception of *Helianthella*, for which we conducted more extensive subsampling in 1997 in an attempt to minimize sampling error. We also distinguished between initiated flowering and completed flowering of *Helianthella* to measure frost damage in 1997, which causes initiated flower stalks to abort (D. W. Inouye, *personal communication*). *Helianthella* flowering is important to detritus production because its flowering stalks are large (up to 1 m tall) and contain four to eight times more biomass than a nonflowering rosette of basal leaves.

Most perennial study species (except *Delphinium nelsonii* and *Mertensia fusiformis*) produce many shoots per individual, so distinguishing genetic individuals from aboveground observations is difficult. Therefore our measurement of abundance represents a combination of true abundance of genetic individuals and the number of aboveground shoots for each individual. For the annuals *Polygonum douglasii* and *Collomia linearis* we measured abundance only. A flowering index was calculated for each species either as a rate (proportion flowering: total shoots) or as a number per gram of biomass (number of flowers per gram of biomass or number of flower stalks per gram of biomass).

In general we calibrated our nondestructive correlates of biomass with actual biomass using 15–25 individuals of each category of each species pooled from both years from outside of the plots. We measured our correlates, cut, dried, and weighed the plants, and used linear regression to provide a conversion equation between nondestructive measurements and biomass (Table 1). Exceptions to our protocol include correlations for aborted *Helianthella* shoots and for *Galium.* Sample size for aborted *Helianthella* shoots is small because the importance of frost damage and hence aborted shoots was not appreciated until late in this study. A new calibration for *Galium* was developed in 1997 to separate the biomass calibration from the flowering estimate, which was not done in the 1996 calibration.

With the exception of *Lathyrus,* all perennial surveys occurred when species were clearly at or near peak biomass, which was qualitatively assessed under the assumption that aboveground growth was complete when plants were setting seed and/or showing early signs of senescence. *Lathyrus* has no uniform growing season (i.e., it has indeterminate flowering and varying senescence times), so in 1997 we conducted two surveys of *Lathyrus*: a midseason survey of plants that were already senescing and a late-season survey of the rest of the population, which was generally senescing by mid-August. In 1996 we obtained only an early-season survey of *Lathyrus.*

Analysis of warming experiment surveys

For each species, we tested for warming effects on abundance per square meter, average size, flowering index, and net biomass per square meter by analysis of variance. When flowering index was the proportion of individuals flowering, we used the arcsine of the square root of the proportion. We chose net biomass for analysis of multiyear effects with repeated measures ANOVA because it is an integrated response variable combining abundance and size. For the perennials, we assumed that absence from a plot reflects initial conditions and should be interpreted as a missing data item, except in the case of *Arenaria,* for which one plot went from several shoots in 1996 to zero in 1997.

Because of the relatively low statistical power forced on us by the difficulty of replicating the warming treatment, we conducted a power analysis of our experimental design to choose appropriate significance (Type I error) levels. Statistical power is the probability of detecting a true effect (1 − Type II error rate). For a *t* test with five replicates, if there is a real treatment effect of one standard deviation, then rejecting the null hypothesis with $\alpha = 0.05$ gives only a 29% chance of detecting the effect. Increasing α to 0.10 increases the chance to 42%, and increasing α to 0.20 increases the chance to 59%. If the true difference is only one half of a standard deviation, these chances become 11%, 19%, and 32%, respectively. Recognizing that Type I and Type II error rates together provide information to weigh evidence provided by a low-replication experiment (Kendall and Stuart 1973, Neter et al. 1990, Thomas 1997), we choose $\alpha < 0.10$ as indicating a statistically significant effect and $0.10 < \alpha < 0.20$ as indicating a marginally significant effect.

To test the statistical significance of the suite of biomass responses we found in the warming experiment, we used a binomial model to calculate the probability of the net number of significant responses (or more) arising from chance alone. This approach determines the significance of the net number of responses but does not distinguish which particular responses are least likely to be spurious. We used $\alpha = 0.05$ as a significance criterion for the suite of responses in the binomial model.

Nitrogen–water experiments

Among the observed effects of the experimental warming are a decrease in soil moisture, an increase in nitrogen mineralization rate, an increase in soil temperature, and an advancement in the date of snowmelt (Harte and Shaw 1995, Harte et al. 1995, Shaw and Harte, *in press*). Of these, we chose to test moisture and nitrogen as possible direct causes of species responses to warming. Amount and timing of snowmelt could also affect species responses (Galen and Stanton 1993, 1995), but we did not test for direct snowmelt effects in this study.

To test resource limitation hypotheses on *Erigeron* and *Helianthella,* we conducted independent experiments in 1997 with a two-way water addition and nitrogen addition design. These two species are the

largest biomass components of the dry zone and both showed possible treatment effects. *Erigeron* showed a clear decline in abundance in the warmed plots relative to the control plots. *Helianthella* showed a change in initiated flowering that varied across years and was only marginally statistically significant but important in magnitude. Therefore we tested the hypotheses that *Erigeron* is more water limited than nitrogen limited and that *Helianthella* is both water and nitrogen limited such that its response to warming may vary between years.

The *Helianthella* experiment was located on a northeast-facing 5° slope located ~0.9 km southwest of the warming experiment. Vegetation on the slope is similar to that on the warming meadow but has slightly higher moisture conditions than found on the dry zone of the warming meadow. The *Erigeron* experiment was located on a southwest-facing 15° slope located 0.8 km northwest of the warming experiment. This slope is also similar in vegetation to the warming meadow, but is slightly steeper and rockier. Although these sites do not perfectly replicate the warming meadow site or each other, they were among the most similar nearby sites available for our use.

For each nitrogen–water experiment, we used a block design with 20 replicates. Each unit consisted of a 0.0625 m^2 (0.25 × 0.25 m) plot with a focal plant or clump of plants. Each block consisted of four units separated by 1–2 m, and each unit was randomly chosen to receive nitrogen, water, both, or neither (control). Blocks were separated by 5–20 m and were spaced evenly across each site. At the start of the experiment the focal plots were nondestructively measured to estimate initial biomass. We used 15 replicates of similar plots of plants to calibrate these measurements by cutting, drying, weighing, and using linear regression. Our calibrations explained 58% of the variation in initial biomass for *Helianthella* and 91% for *Erigeron.* Neither species had initiated flowering at the start of the experiment.

We reduced competition in these experiments by clipping all other plants in the 0.0625-m^2 plots to soil level at the start of the experiment and approximately every 10 d thereafter. This was done to isolate the simple abiotic factors of water and nitrogen availability. Had we not reduced competition, it would be unclear whether a significant effect of resource additions, if found, depends in some way on the presence of competition. By removing competitors, an effect of resource additions would suggest that direct resource effects alone, regardless of competition, could explain the effects on the warming experiment. There are numerous other factors that could affect responses to the warming treatment, including complicated combinations of competition (Goldberg and Barton 1992), multiple resource limitation, and environmental and temporal heterogeneity. A significant response to the resource additions does not rule out the importance of other factors in the warming experiment, but crossing other treatments with resource additions was beyond the scope of this study.

We chose regimes for adding water and nitrogen to approximately mimic the differences found on the warming meadow (Harte et al. 1995; Shaw and Harte, *in press*), with an error factor of two to account for imperfect application, drainage, and the desire to err on the side of overapplication. For the watering treatment, we applied 0.6 L of water to the 0.0625-m^2 plot around each plant, which is equivalent to ~0.01 m of rain, about every 5 d. Watering treatments were applied on 24 and 30 June and 5, 11, 15, 21, 25, and 30 July. For the nitrogen treatment, we applied ammonium nitrate to achieve nitrogen addition of 4 g/m^2 every 14 d. Application was made by mixing 11.4 g ammonium nitrate with 1 L water and applying 0.0625 L of the mixture evenly to the soil over each plot. Nitrogen was applied on 17 June and 3, 15, and 30 July. We considered the small amount of water used for nitrogen delivery to be negligible. Despite gradual application, some surface runoff nearly always occurred on these sloped sites, so in practice less water and nitrogen were applied than we had planned, justifying our incorporation of an error factor in our treatment levels. Surface runoff never extended close to other plots. Since *Helianthella* flowering shoots were initiated soon after the start of the experiment, only the initial treatment applications could have affected *Helianthella* flowering. A similar early-season limit to effects on *Erigeron* flowering may occur as well but is less clear since *Erigeron*'s growth form is similar for flowering and nonflowering shoots prior to flower development.

We harvested all experimental plants in late August. For each unit we counted flowering and nonflowering shoots and the number of inflorescences produced by each flowering shoot. We harvested inflorescences and flowering and nonflowering shoots separately, and for *Helianthella* we separated flowering shoots into aborted shoots and nonaborted shoots. We dried and weighed each of the three (*Erigeron*) or four (*Helianthella*) categories of plant biomass.

Analysis of nitrogen–water experiments

For *Erigeron*, we tested for effects on biomass and flowering rate with two-way ANOVA with either log(final mass) or flowering rate (proportion of shoots with flowers) as the response variable, water addition, nitrogen addition, and block as categorical variables, and log(initial mass) as a covariate. Blocks were treated as random, and block by treatment interactions were not included (Neter et al. 1990, Newman et al. 1997). We used net number of inflorescences as another measure of investment in flower production because a single shoot could commonly produce three or four inflorescences and we recorded up to seven inflorescences on a single shoot. Initial mass rather than log(initial mass) was used as a covariate for this analysis because

it resulted in more normal residuals than log(initial mass). For *Helianthella,* we analyzed biomass similarly as for *Erigeron,* but block effects were not significant and so were not used in the model. We analyzed *Helianthella* flowering using number of initiated flowering shoots as a response variable with number of basal rosettes at the start of the experiment as a covariate. Since few of the initiated shoots completed flowering due to frost damage, we were unable to evaluate effects on completed inflorescence production.

Results

Abundance, size, flowering, and frost damage

Six of 11 species responded to warming with significant changes in either abundance, average size, flowering, or frost damage (Fig. 1). The results are best considered on a species-by-species basis. The two largest biomass components of the forb community are *Erigeron* and *Helianthella. Erigeron* had lower abundance in both years ($P = 0.04$ and 0.10 in 1996 and 1997, respectively) and higher flowering rate and average size in 1997 ($P < 0.001$ and $P = 0.01$, respectively). The 1997 size distribution estimated using all 30 (15 flowering and 15 nonflowering) subsamples from each plot shows that control plots had more individuals of every size (data not shown), which suggests that the abundance effect is stronger than the size effect. The clearest effect of warming on *Helianthella* involved protection of initiated flowering stalks during an early summer frost event. On 3 July 1997, air temperature reached a low of −5°C. Typically at that time temperatures do not drop below 0°C. Significantly fewer initiated stalks were aborted on warmed plots ($P < 0.01$, means of 72% and 6% of initiated stalks were aborted in the control and warmed plots, respectively). Relation of *Helianthella* flowering to aboveground biomass is discussed below.

Delphinium and *Mertensia* are the two principal early-flowering species on the dry zone of the warming meadow, and both responded negatively to the warming treatment. *Delphinium* had fewer individuals ($P < 0.01$) and more fruits per biomass ($P = 0.07$), but no difference in average size. The effect on *Delphinium* abundance appears to dominate the effect on fruits per biomass (there were 4.6 vs. 1.3 individuals/m^2 in control vs. heated plots, respectively), and the fruit difference may be an artifact of the persistence of only the most robust individuals in the warmed plots. *Mertensia* had no difference in abundance, fewer flowers per gram of biomass ($P = 0.08$), and possibly smaller adults ($P = 0.12$) in the warmed plots. *Lathyrus* is the most abundant nitrogen-fixer in the warming experiment. Early season *Lathyrus* was less abundant in the warmed plots in 1996 ($P = 0.09$) but not in 1997, and *Lathyrus* was smaller in the warmed plots in 1997 ($P = 0.02$, sizes not censused in 1996), an effect driven by smaller late-season plants ($P = 0.01$). The only clear response of *Eriogonum subalpinum* was that flowering shoots were significantly larger on warmed plots ($P = 0.05$ and 0.01 for 1996 and 1997, respectively).

Five species, *Potentilla hippiana, Galium boreale, Arenaria congesta,* and the annuals *Polygonum douglasii* and *Collomia linearis,* showed no significant responses to warming in terms of abundance, size, or flowering. However, *Potentilla hippiana* had statistically marginal increases in abundance ($P = 0.13$) and size ($P = 0.18$) in 1997.

Biomass responses

Over both years, four of nine perennial species showed differences in net aboveground biomass between warmed and control plots at $P < 0.10$ (Fig. 2; *Erigeron, Lathyrus, Delphinium,* and *Mertensia* all declined in warmed plots; repeated measures results were used for species surveyed in both years, 1997 data for those that were not), an overall pattern that is highly significant ($P = 0.008$ in the binomial model). In year-by-year analyses, five of nine species showed significant effects in 1997 (the same four declined and *Potentilla hippiana* increased; $P < 0.001$ in the binomial model), and two of seven showed significant effects in 1996 (*Erigeron* and *Lathyrus* both declined; $P = 0.15$ in the binomial model; *Delphinium* and *Mertensia* were not surveyed in 1996). The means shown in Fig. 2 include zeros from plots with none of a given species so that average total biomass is the sum of the species averages, but the symbols indicating significant warming effects are from significance tests without zeros. The four most productive species nearly offset each other in their biomass differences, and there was no significant effect of warming on the sum of forb aboveground biomass that we measured in either 1996 or 1997.

Helianthella flowering is of special interest because it varied across years and is associated with large biomass input into litter. In 1996 ~10% more *Helianthella* flowered in warmed plots than in control plots, and the resulting difference in biomass (also caused by larger average individuals) was approximately equal and opposite to the biomass difference caused by the lower *Erigeron* biomass in the warmed plots (see Fig. 2). In contrast, in 1997 more individuals initiated flowering in the control plots than in the warmed plots, apparently setting the stage for a large aboveground biomass difference. However, this difference was not realized because of high abortion rates on control plots from the frost event. The initiated flowering differences were statistically insignificant in 1996 and marginal ($P = 0.16$) in 1997.

Responses to nitrogen and water

Due to high herbivory on *Helianthella,* we lost 29 of 80 experimental units, leaving 9 control, 14 water, 13 nitrogen, and 15 nitrogen-plus-water replicates. *Helianthella* initiated more flowering shoots in response

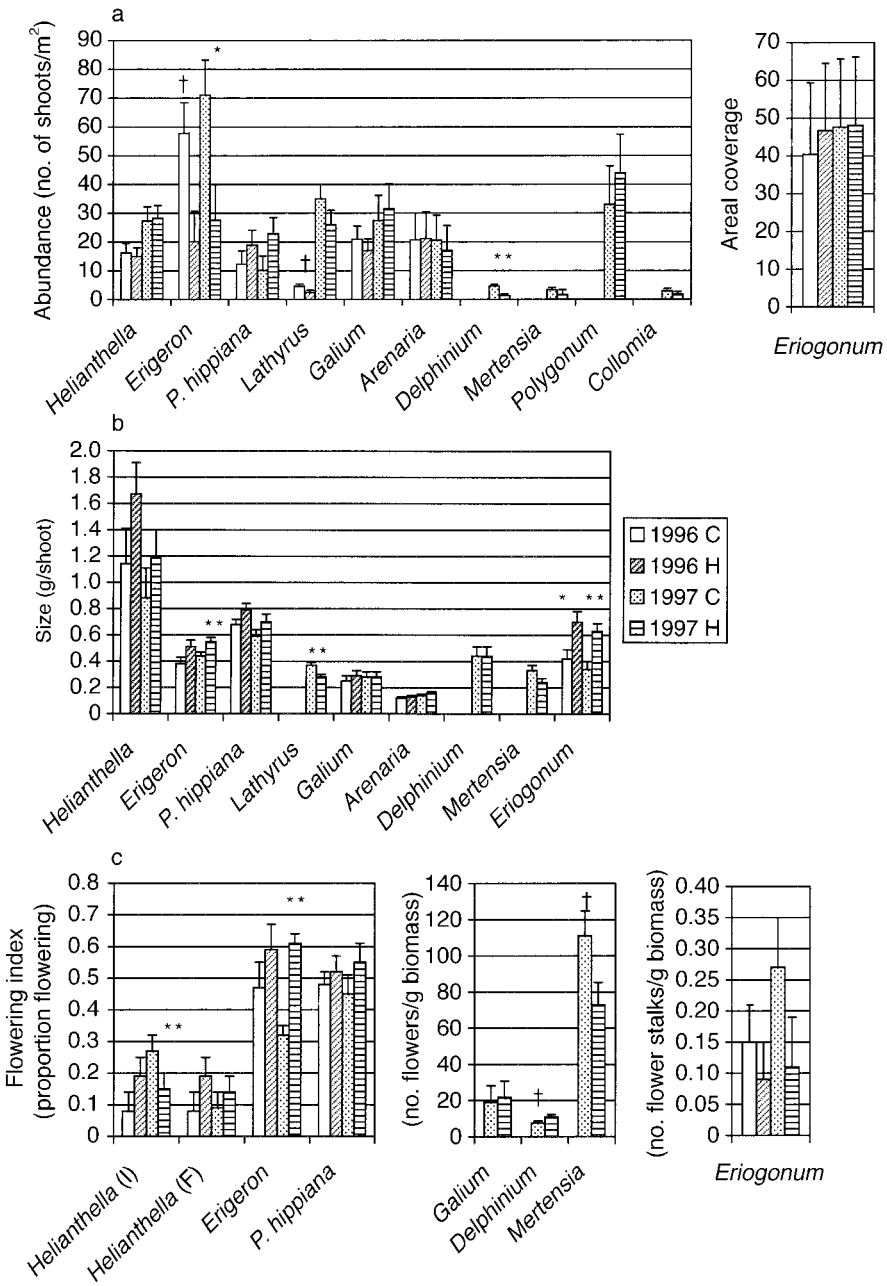

FIG. 1. Results of the warming experiment for (a) abundance, (b) size, and (c) flowering of forb species in the Rocky Mountains in Colorado (means + 1 SE). (a) *Lathyrus* abundance in 1996 reflects an early season census only. *Eriogonum* areal coverage is in arbitrary units from our sampling grid. (b) *Helianthella, Erigeron,* and *Potentilla hippiana* data are weighted means of flowering and nonflowering plants. *Lathyrus* data show only late-season plants. *Galium* and *Arenaria* data do not distinguish between flowering and nonflowering individuals. *Delphinium* and *Mertensia* data show only flowering individuals. *Eriogonum* data show size of flowering shoots only, since size of ground cover is a direct conversion of abundance, shown in (a). (c) Flowering index is a proportion of aboveground shoots with flowers for *Helianthella, Erigeron,* and *P. hippiana,* flowers per gram of biomass for *Galium* and *Mertensia,* flowering stalks per gram of nonflowering (ground-cover) biomass for *Eriogonum,* and flowers that set seed per gram of biomass for *Delphinium.* For *Helianthella,* initiated (I) and finished (F) flowering are given separately. Significance symbols (daggers [†] or asterisks [*]) for *Helianthella* flowering indicate a significant effect of warming on flower abortion rate in 1997. ''C'' and ''H'' stand for ''control'' and ''heated.''
†$P < 0.10$, *$P < 0.05$, and **$P < 0.01$.

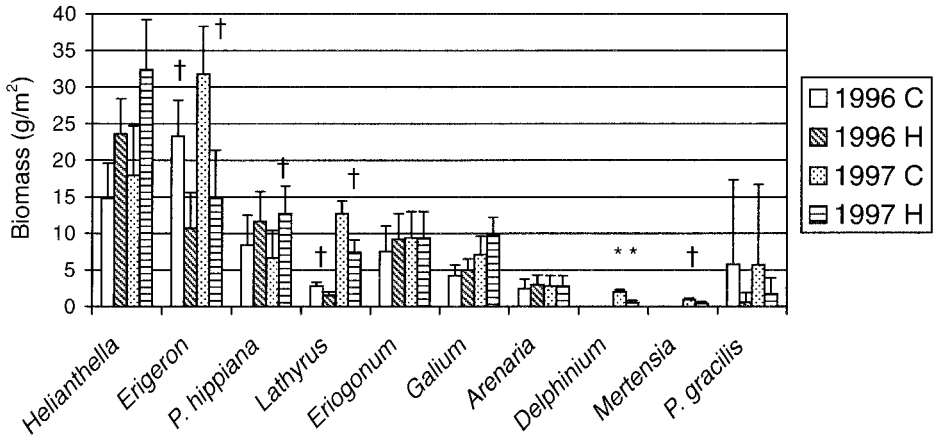

FIG. 2. Results of the warming experiment on biomass of each species in 1997 (mean + 1 SE). For graphical purposes, calculations include zeros so that mean net biomass is the sum of the mean species biomasses as shown. Significance tests treat zeros as missing values. Significance symbols are as in Fig. 1. *Potentilla gracilis* occurs on only four plots but is included because it is 23% of the biomass in plot 3.

to both nitrogen and water addition with marginal statistical significance ($P = 0.06$ and 0.08, respectively, corrected for the covariate of initial number of basal rosettes, which was significant at $P < 0.01$; Table 2, Fig. 3). The magnitude of these effects was similar (adjusted means of 2.4 and 1.5 shoots with and without water and 2.4 and 1.4 shoots with and without nitrogen, respectively; means were adjusted for the linear covariate of initial number of basal rosettes). There was no interaction effect. The *Helianthella* used in this experiment were severely frost damaged, probably by the same early summer frost event that damaged *Helianthella* in the warming experiment. As a result, completed flowering was low and did not differ significantly between treatments.

Neither water nor nitrogen had a significant effect on aboveground *Helianthella* biomass. This null result is not surprising because few plants completed flowering after frost damage and completed flowering largely determines aboveground biomass. In some cases abortion of a flowering stalk occurred when the stalk was only 0.1–0.2 m tall, making it not much larger than a nonflowering basal rosette of leaves.

Erigeron responded to both nitrogen and water additions, but its response to water was larger than its response to nitrogen and involved both biomass and flower production (Table 3, Fig. 3). Final biomass increased significantly ($P = 0.03$) with water addition and marginally significantly ($P = 0.08$) with nitrogen addition. Block and initial mass were both highly significant ($P < 0.001$ for each). Water addition but not nitrogen addition significantly increased both flowering rate and net number of inflorescences produced by *Erigeron* ($P = 0.03$ in both cases).

TABLE 2. Results of *Helianthella* nitrogen–water experiment.

Source	df	Type III SS	*F*	*P*
Initiated flowering stalks				
Water	1	10.30	3.13	0.08
Nitrogen	1	12.54	3.81	0.06
Water × Nitrogen	1	0.02	0.01	0.93
Initial count	1	22.19	6.75	0.01
Completed flowering stalks				
Water	1	0.02	0.03	0.87
Nitrogen	1	0.81	1.02	0.32
Water × Nitrogen	1	1.27	1.62	0.21
Initial count	1	0.42	0.54	0.47
Log(Final Biomass)				
Water	1	0.27	1.13	0.29
Nitrogen	1	0.03	0.11	0.74
Water × Nitrogen	1	0.10	0.42	0.52
Log(Initial biomass)	1	9.41	38.59	0.0001

Notes: Initial count is the number of aboveground shoots at the start of the experiment. Few plants completed flowering due to heavy frost damage.

DISCUSSION

Six of 11 forb species in the dry zone of the warming experiment responded significantly in terms of abundance, size, flowering, or frost damage. Two of these were favorable responses to warming (lower frost damage in *Helianthella* and larger flowering stalks of *Eriogonum*). The rest were negative overall (decreased abundance in *Erigeron* and *Delphinium*, decreased flowering in *Mertensia*, and decreased size in *Lathyrus*). Five of the nine perennial species showed evidence of an aboveground biomass response, with four declines and one increase. Of these five, *Erigeron* is the most abundant and showed the strongest decline. Effects on *Helianthella* remain unclear but are potentially important because of its large role in litter production, which in the years of this study largely counterbalanced the *Erigeron* difference between warmed and control plots. The responses of individual species were larger than the net forb response to warming.

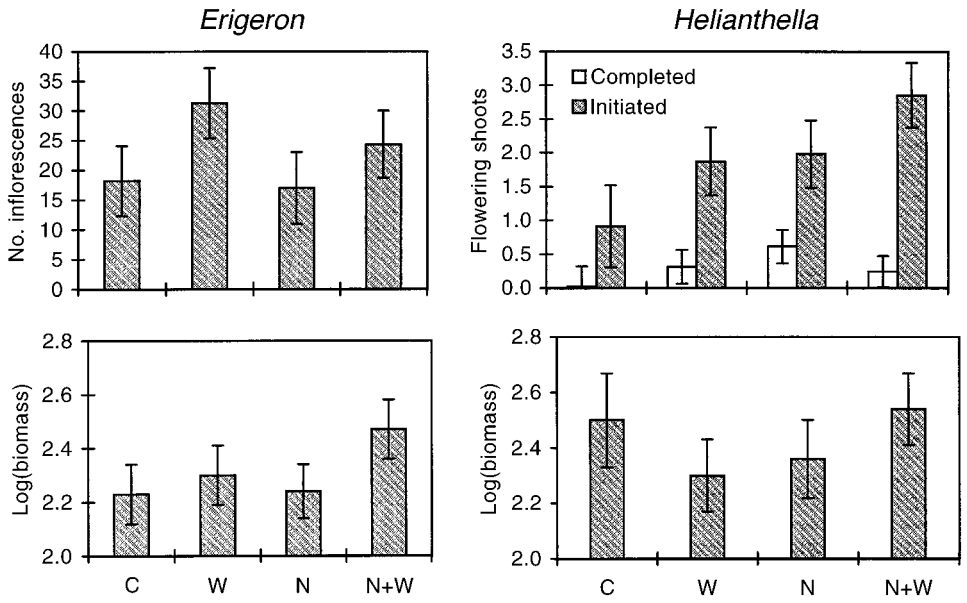

FIG. 3. Effects of nitrogen and water additions on *Helianthella* and *Erigeron* flowering and biomass (means ± 1 SE). For *Erigeron*, inflorescensce number responses are adjusted for the covariate of initial mass. For *Helianthella*, flowering shoot responses are adjusted for the covariate of initial count of basal rosettes. The covariate corrections are different for the initiated shoot and completed shoot data. For both species, log(final biomass) is adjusted for the covariates of log(initial biomass). Treatment abbreviations are: C = control; W = water addition; N = nitrogen addition; N + W = nitrogen and water addition.

Results from the nitrogen–water experiments are consistent with the hypothesis that resource shifts caused by the warming could drive the responses of *Erigeron* and *Helianthella*, but other factors are likely to be important as well. We found evidence that both nitrogen and water addition increase *Helianthella* flowering. The magnitude of the responses was similar to the statistically unclear flowering differences found in the warming experiment. It is possible that in the warming experiment increased nitrogen mineralization and decreased soil moisture have contrasting effects on *Helianthella* such that the net effect is small or varies between years. It is perhaps surprising that we obtained a flowering response at all in the nitrogen–water experiment since this must represent plasticity in flowering during the short window between snowmelt and initiation of flowering stalks. Longer term *Helianthella* growth and flowering in the warming experiment may

TABLE 3. Results of *Erigeron* nitrogen–water experiment.

Source	df	Type III SS	*F*	*P*
Log(Final Biomass)				
Water	1	0.65	5.37	0.03
Nitrogen	1	0.38	3.18	0.08
Water × Nitrogen	1	0.06	0.51	0.48
Block	19	7.84	3.43	0.0003
Log(Initial mass)	1	5.15	42.85	0.0001
Flowering rate				
Water	1	0.21	4.76	0.03
Nitrogen	1	0.03	0.59	0.45
Water × Nitrogen	1	0.004	0.10	0.76
Block	19	2.55	2.98	0.001
Log(Initial mass)	1	0.0002	0.004	0.95
Net inflorescences produced				
Water	1	1 797.15	5.36	0.03
Nitrogen	1	18.70	0.06	0.81
Water × Nitrogen	1	25.85	0.08	0.78
Block	19	17 327.02	2.72	0.003
Initial mass	1	3 964.22	11.23	0.002

Notes: Flowering rate is the proportion of shoots with inflorescences. Net inflorescences is the total number of inflorescences produced by an experimental unit of shoots.

be more complicated, since we do not know whether flowering responses represent only a short-term shift in resource allocation from roots to shoots or also a longer term shift in growth affecting both roots and shoots.

In terms of aboveground biomass *Erigeron* responded significantly to water and marginally significantly to nitrogen, and in terms of flower production it responded significantly to water but not to nitrogen. The biomass response to water is consistent with the biomass decline of *Erigeron* in response to warming. However, the marginal biomass response to nitrogen suggests that other factors are also important in the warming experiment. The positive response of *Erigeron* flowering to water addition but not nitrogen addition, if interpreted as a reflection of overall robustness, is also consistent with the overall decline of *Erigeron* in response to warming. However, it is unclear why an exception to the negative response of *Erigeron* to warming was that it flowered more in the warmed plots in 1997, which is inconsistent with its flowering in response to water but not nitrogen. It is possible that *Erigeron*'s higher flowering in warmed plots was due to frost damage on the control plots (D. W. Inouye, *personal communication*), but we did not measure this. The resource addition experiments provide a first indication of specific factors involved in plant responses to the experimental warming, but there are likely to be other important factors including competition in the warming experiment which merit further study.

The focus on forbs in this study was partly motivated by previous findings that warming decreased aboveground forb biomass and increased aboveground shrub biomass in 1993 and 1994 (Harte and Shaw 1995), that warming effects were several times stronger on plant carbon uptake than on soil respiration (Saleska et al. 1999), and that forbs make up over half of aboveground biomass. A major part of the forb biomass response is clearly the decline in *Erigeron.* However, results presented here for 1996 and 1997 are difficult to compare to the 1993 and 1994 results because we did not find a statistically significant change in net forb biomass, although the trend was consistent with results from 1993 and 1994. There is high interannual variability in climate conditions in this system, so the variability in warming effects is not surprising. Our results suggest that *Helianthella* plays an important role in the interannual variability of forb aboveground biomass. When *Helianthella* flowered more in warmed than control plots in 1996 and 1997, its aboveground biomass largely offset the consistently lower biomass of *Erigeron.* If *Helianthella* were to flower more in control than warmed plots—as apparently would have happened in 1997 if not for frost damage—we would expect significantly less aboveground forb biomass in warmed plots due to the combined differences of *Helianthella* and *Erigeron.* We have no evidence that there could be significantly higher aboveground forb biomass in warmed plots in any years.

The response of *Helianthella* is further complicated because it remains unclear how flowering reflects carbon uptake. For example, if *Helianthella* does flower more in the warmed plots over the long run, this could represent only a shift of carbon from roots to shoots or also an increase in carbon acquisition to both roots and shoots. In the former case, increased flowering would represent a flow of carbon previously stored in plant tissue into soil organic matter, which could be respired out of the system. In the latter case, increased carbon fixation would include an uptake of carbon into root tissue. Our focus on forb species has identified longer term *Helianthella* responses as important for understanding the carbon cycle of this system. The approximately equal and opposite biomass responses of two of the next most abundant species, *Potentilla hippiana* and *Lathyrus leucanthus,* also merit further study. It remains unclear whether *Erigeron* and *Helianthella* and/or *P. hippiana* and *Lathyrus* represent different functional groups, although *Lathyrus* is the only legume among these.

Our findings support evidence from other studies about responses to climate and resource shifts. Studies of arctic moist tussock tundra and arctic wet sedge tundra with manipulations of nitrogen, temperature, and light have shown that responses were species specific and that responses to temperature tended to balance each other and occur via effects on soil microclimate (Chapin et al. 1995, Chapin and Shaver 1996, Hobbie and Chapin 1998, Shaver et al. 1998). Two unanswered questions are how long-term survival and reproduction are related to short-term growth responses (Bazzaz et al. 1996) and how warming affects belowground growth.

Two complex aspects of climate–ecosystem interactions are the multiplicity of climatic factors involved (Oechel et al. 1994, Bazzaz et al. 1996, Shaver et al. 1998) and the potential importance of climate variability or extreme events (Overpeck et al. 1990, Walker et al. 1994, Bazzaz et al. 1996). This study examined one of the most direct predicted effects of climate change, increased temperature, but did not examine possible changes in precipitation or other factors. However, the importance of soil moisture suggests that if real climate change does include a change in precipitation regime—one of the least certain aspects of climate predictions—the response of the community studied here could be different (Harte and Shaw 1995, Harte et al. 1995, Loik and Harte 1997, Saleska et al. 1999). The frost damage to *Helianthella* in 1997 illustrates the potential importance of climate variability. Warming protected *Helianthella* from a frost event, thus allowing successful flowering and aboveground biomass production. This protective effect of the heaters may have been a direct effect of warming—higher temperatures preventing frost—but we cannot rule out a phenolog-

ical effect. Warming advances the phenology of *Helianthella*, so if phenology affects frost susceptibility, it is possible that the warmed plants avoided frost damage because they were past a vulnerable developmental stage.

Our study supports the possibility that, at least in the short term, ecosystem responses to climate change can be predicted by understanding how climate change will affect resource availability and how resource availability will affect the major species in a plant community. We investigated only the simplest direct effects of resource availability on two important species in our community, but other processes are likely to be important as well. Connections between species-level and ecosystem-level effects may be important for understanding biotic responses to climate change.

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