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Authors: Smith, Jane G., Sconiers, Warren, Spasojevic, Marko J., Ashton, Isabel W., and Suding, Katharine N.

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Phenological Changes in Alpine Plants in Response to Increased Snowpack, Temperature, and Nitrogen

*Jane G. Smith**
Warren Sconiers†
Marko J. Spasojevic‡
Isabel W. Ashton§ and
Katharine N. Suding¶

*Corresponding author: Biology Department, New Mexico State University, MSC 3AF, Las Cruces, New Mexico 88003-0032, U.S.A. jgs@nmsu.edu
†Department of Entomology, Texas A&M University, TAMU 2475, College Station, Texas 77843-2475, U.S.A.
‡Department of Environmental Science and Policy, University of California, Davis, One Shields Avenue, Davis, California 95616, U.S.A.
§Northern Great Plains Inventory & Monitoring Network, National Park Service, 231 East St. Joseph Street, Rapid City, South Dakota 57701, U.S.A.
¶Department of Environmental Science Policy and Management, University of California, Berkeley, 137 Mulford Hall #3114, Berkeley, California 94720-3114, U.S.A.

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Abstract

Modified environmental conditions are driving phenological changes in ecosystems around the world. Many plants have already responded to warmer temperatures by flowering earlier and sustaining longer periods of growth. Changes in other environmental factors, like precipitation and atmospheric nitrogen (N) deposition, may also influence phenology but have been less studied. Alpine plants may be good predictors of phenological response patterns because environmental changes are amplified in mountain ecosystems and extreme conditions may make alpine plants particularly sensitive to changes in limiting factors like precipitation, temperature, and N. We tested the effects of increased snowpack, temperature, and N on alpine tundra plant phenology, using snow fence, open-top warming chamber, and N fertilization treatments at the Niwot Ridge Long Term Ecological Research (LTER) site. Flowering phenology of three abundant species was recorded during two growing seasons. Treatment responses varied among species and functional types. Forbs responded to warming by flowering earlier and responded to snowpack and N by flowering later; however, when both snow and N were increased simultaneously, phenology was unchanged. Graminoids flowered earlier in response to N addition. Our results demonstrate that changing environmental conditions influence plant phenology, and specifically highlight that N and multiple factor interactions can yield stronger responses than warming alone.

Introduction

Phenology is an organism characteristic highly responsive to changes in environmental conditions (Sparks and Menzel, 2002), and recent changes in global climate and other environmental factors are affecting the phenology of species around the world (Parmesan and Yohe, 2003; Parmesan, 2006; Miller-Rushing and Primack, 2008). Altered phenology may result in temporal asynchrony or reduced complementarity between species, modifying interspecific competition for resources or plant pollination success (Rathcke and Lacey, 1985; McKane et al., 1990; Inouye et al., 2002; Miller-Rushing and Inouye, 2009; Forrest et al., 2010). Earlier onset of growth and longer growing seasons may initially increase plant productivity at the cost of nutrient reserve depletion and reduced long-term productivity and reproductive effort (Wookey et al., 1993; Chapin and Shaver, 1996). Subsequent modifications of community composition may affect organisms at all trophic levels by influencing processes like nutrient cycling and net primary production (Rathcke and Lacey, 1985; Eviner and Chapin, 2003).

The majority of plant phenology research has been conducted in lowland areas (Hülber et al., 2010), but alpine tundra ecosystems may be particularly sensitive bellwethers of environmental change (Seastedt et al., 2004). Alpine plants are limited by a short growing season and extreme environmental conditions (Nadelhoffer et al., 1992; Bowman, 2001), making them highly vulnerable to modification of limiting factors (Bowman et al., 2006; Thuiller et al., 2005a, 2005b). Additionally, environmental changes are often amplified in alpine regions. In the northern U.S. Rocky Mountains, the annual rate of temperature increase is roughly two to three times that of the global average (Pederson et al., 2010), and the same pattern has been observed at high elevations throughout western North America (Diaz and Eischeid, 2007). Transport processes (e.g. wind or snowmelt) also amplify relatively small changes in factors like precipitation and nitrogen (N) deposition by material redistribution across the landscape (Seastedt et al., 2004).

To date, phenology research has focused primarily on changes in temperature and, less often, precipitation (e.g. Inouye et al., 2002; Huelber et al., 2006; Parmesan, 2006; Hülber et al., 2010; Lambert et al., 2010), while the influence of nutrient availability has been largely ignored. However, anthropogenic N deposition has amplified resource availability in many ecosystems (Galloway and Cowling, 2002; Howarth et al., 2002) and may influence phenology too (Vitousek et al., 1997; Diekmann and Falkengren-Grerup, 2002; Bowman et al., 2006; Cleland et al., 2006). While modification of any of these three environmental factors—precipitation, temperature, or N—has the potential to influence phenology alone, more realistically, simultaneous changes in multiple factors will induce more complex phenological

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responses (Forrest and Miller-Rushing, 2010). The effect on phenology of increased N availability and interactive effects between environmental factors have been understudied and are addressed in the research presented here.

In a manipulative experiment, we examined how increased snowpack (winter precipitation), temperature, and N availability influence the timing of flowering, flower abundance, and seedling germination in alpine tundra. Our research was conducted at the Niwot Ridge Long Term Ecological Research (LTER) site in the Colorado Rocky Mountains, where long-term data indicates increases in temperature, precipitation, and N deposition (Greenland and Losleben, 2001; Sievering, 2001; Clow, 2010). For two summers we recorded the first flowering date (FFD) and number of flowers of the most abundant species, and species composition in forty-eight 1 m^2 manipulation plots. During the second year, seedling abundance was also recorded. Our results demonstrate that changing global climate patterns and increased atmospheric N deposition may significantly alter flowering phenology and seedling germination of alpine tundra species, and specifically highlight the importance of N and how it may interact with other environmental factors to affect phenology.

Methods

EXPERIMENTAL AND TREATMENT DESIGN

We conducted a manipulative experiment in the alpine tundra at the Niwot Ridge LTER site (40°03′N, 105°35′W) in the Front Range of the Rocky Mountains, Colorado, U.S.A. Using a factorial design, we increased winter snowpack, summer air temperature, and N availability to examine the influence of these environmental factors on alpine plant phenology.

To manipulate snow cover, three 10 × 1 m snow fences were erected along a north–south line in an area of moist-meadow alpine tundra. The wind in this area comes primarily from the west and snow accumulation is wind driven. Snow fences have been used successfully at Niwot Ridge in the past to increase snowpack (Walker et al., 1999). The leeward side of each snow fence received increased winter precipitation (snow), while the windward side received approximately an ambient level of snow. Snow fences were in place from September to June for the winters of 2006/2007 and 2007/2008. We used snow rods to measure snow accumulation 3 m from the snow fence approximately twice a month in the winter of 2007/2008. The average depth of snow was 72 ± 2.4 cm in snow addition plots and 22 ± 3.5 cm in snow control plots. The fences were particularly effective in altering the depth of early season snowfall events and created 6–8 weeks more snow cover on the leeward side of the fence.

In a split-plot experimental design, snowpack manipulation plots (snow addition and control) were designated on opposites sides of three snow fences, and eight 1 m^2 temperature and N manipulation subplots were established within each snow manipulation plot (n = 3 snow fences × 2 snow plots × 8 subplots = 48). When wind hits the fence, it eddies and drops snow on the leeward side (snow addition plot) to a distance from the fence of approximately 10 times the height of the fence (10 × 1 m). Therefore, subplots on the leeward side of the fence were arranged in two rows of four, starting 1 m from the fence and all well within 10 m of the fence. To avoid shading and snow accumulation effects of the fence on the windward side (snow control plot), subplots were placed 2 m upwind from the fence. All subplots were separated by 1 m, and subplot edges were trenched to a depth of 15 cm two times per growing season to reduce root in-growth from adjacent tundra.

Increased temperature and N addition treatments were randomly assigned to subplots on each side of the fences so there were two replications of eight different treatments (all possible treatment combinations) within each snow-fence block. During the 2007 and 2008 growing seasons, temperatures were increased above ambient using open-topped chambers over the subplots (Marion et al., 1997) from June to early September. Despite some controversy over this method, in a review of warming experiments, Rustad et al. (2001) found no effect of using open-topped chambers on the magnitude or direction of response. In this remote site, open-top chambers were the most economical and feasible method to employ. Air temperature was monitored in all subplots within one snow-fence block, and soil temperature was measured at a 10 cm depth using Onset dataloggers in eight subplots. During the summer of 2007, the warmed subplots had an average air temperature of 10.0 °C ± 0.14 and soil temperature 8.0 °C ± 0.11. Air temperature in the control plots averaged 9.1 °C ± 0.12 and soil temperature 7.5 °C ± 0.25, a difference of approximately 1 °C and 0.5 °C, respectively.

Nitrogen was added in July 2006, June 2007, and June 2008 using Osmocote slow release fertilizer (urea 40-0-0 N-P-K) at a maximum rate of 8 g N m^{-2} yr^{-1}. We expect the actual N made available within each subplot was less than 8 g N m^{-2} yr^{-1} (we estimate 5 g N m^{-2} yr^{-1}) due to surface water flow, which is high at the beginning of the season due to snowmelt, and incomplete release of the slow-release pellets (Bowman et al., 1993). The application rate was lower than or equivalent to many other N fertilization experiments previously conducted at the site (Bowman et al., 1993, 1995; Seastedt and Vaccaro, 2001) but higher than the estimated minimum N input required to have a significant effect on plant biota in an adjacent community type (Bowman et al., 2006).

MEASUREMENTS

In 2007 we recorded FFD and length of flowering season for all species present in plots (20 forbs, 8 graminoids; see Appendix). Flowering has been found to be the phenophase of alpine plants most responsive to temperature changes (Hülber et al., 2010). Flower surveys were conducted every 2 to 9 days, but most (~70%) occurred 2 to 4 days apart and, within the range of FFDs for species considered here, the longest time between surveys was one six-day gap. Species were recorded as flowering when the first flower/inflorescence appeared from any individual of the relevant species in a subplot. Most species were considered flowering when petals were open enough for reproductive structures to be visible. *Bistorta* species have inflorescences with flowers too small for reproductive structures to be easily seen with the naked eye; these species were recorded as flowering when flowers' petals covered at least 50% of the inflorescence. Grass species were considered flowering when at least one spikelet of the inflorescence was no longer enclosed by the leaf sheath. In 2007 survey dates were 30 May; 4, 11, 13, 15, 19, 25, 28 June; 2, 6, 9, 12, 16, 19, 23, 26, 31 July; and 2, 6, 13, 22 August. In 2008 FFD observations were limited to five of the most abundant species at our site (see Appendix), those present in enough plots to provide adequate data for individual analyses. Flower surveys were conducted every 1 to 6 days, but most (~70%) occurred 1 to 4 days apart with only one six-day gap between surveys. In 2008 survey dates were 10, 13, 16, 17, 19, 24, 30 June; and 1, 3, 8, 11, 16, 21, 25, 26, 28 July.

In 2007 and 2008, the number of flowers/inflorescences of *Geum rossii*, *Bistorta bistortoides*, and *Deschampsia caespitosa* was counted in subplots shortly after peak flowering when new

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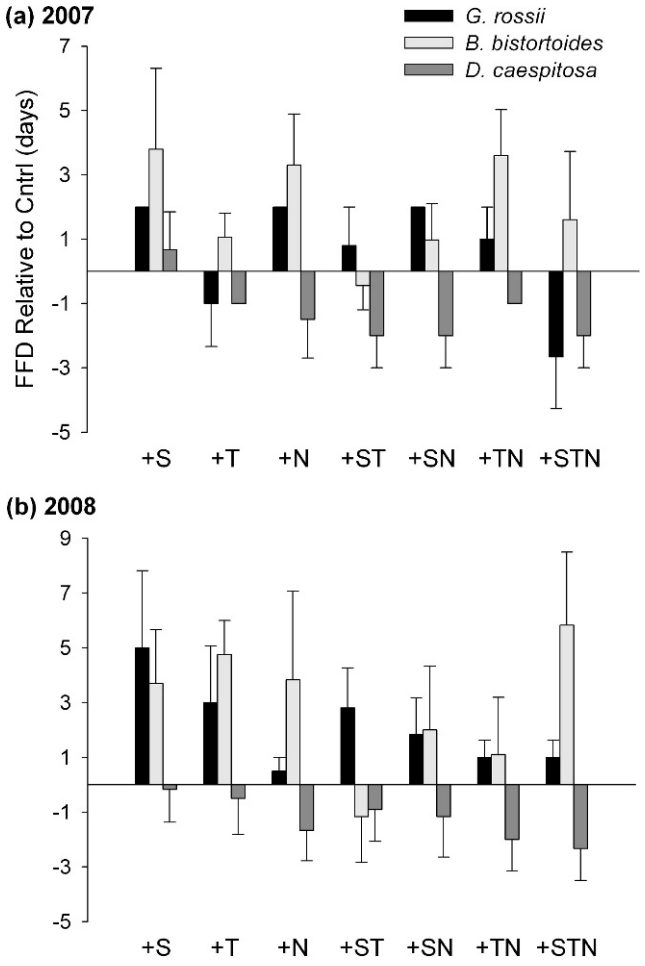


FIGURE 1. First flowering date (FFD) of forbs, *Geum rossii* and *Bistorta bistortoides*, and graminoid, *Deschampsia caespitosa*, in response to treatments of increased snowpack (S), temperature (T), and N and their combinations, relative to ambient (Cntrl) conditions in forty-eight 1 m^2 experimental subplots in moist-meadow alpine tundra. FFDs are treatment subplot means in (a) 2007 and (b) 2008.

flowers/inflorescences were unlikely to open but senesced flowers were still visible. In 2008 the number of seedlings present was counted in a 20 cm^2 area in the corner of each subplot. Seedlings were identified by cotyledons as *G. rossii*, *Bistorta* spp., and other forb spp.; no graminoid seedlings were present. *B. bistortoides* and *B. vivipara* cotyledons are indistinguishable and were included together as *Bistorta* spp.

In 2006–2008 species cover was determined in subplots using a nondestructive, point-quadrant frame sampling method.

STATISTICAL ANALYSIS

FFD, flower number, and seedling number were analyzed as a randomized complete block design using a split-plot, $2 \times 2 \times 2$ factorial design in which each snow fence constituted a block, snowpack was the whole plot treatment factor, and temperature and N were subplot factors. For flower number and seedling number, species' plot percent cover was included in the analysis as a covariate. Data from each year were analyzed separately. We were interested in the effects of all treatment factors and treatment factor interactions, significant or not, and analyzed data in a model that included all treatment factors alone and in combination: snowpack (S), temperature (T), N, and interactions between

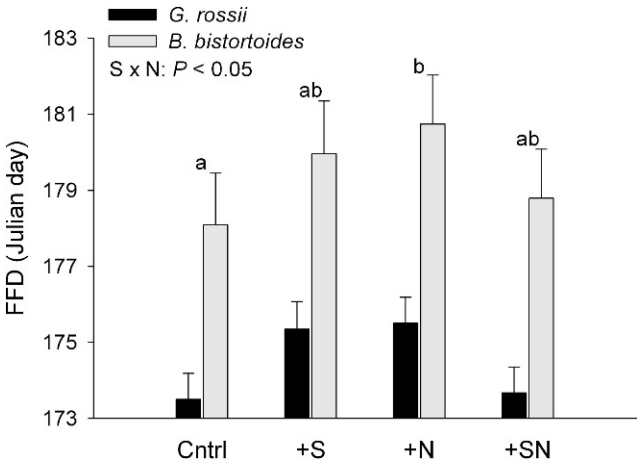


FIGURE 2. 2007 first flowering date (FFD) of *Geum rossii* and *Bistorta bistortoides* in response to a significant snowpack (S) × N interaction. Different lowercase letters indicate significant differences ($P < 0.05$) between bars for both species.

snowpack and temperature (S×T), snowpack and N (S×N), temperature and N (T×N), and snowpack, temperature, and N (S×T×N). All statistical analysis was done using SAS 9.2. Treatment differences were compared using ANOVA (PROC MIXED) in which treatment factors and block were fixed effects and the interaction between snowpack and block was a random effect. For example, the model used to test for variance in FFD of *G. rossii* in 2007 included factors of S, T, N, S×T, S×N, T×N, S×T×N, block, and S × block (random effect). For significant treatment factor interactions, a LSD test was used for pairwise comparisons, e.g. within a significant FFD S×N interaction, a LSD test was used to detect significant differences between FFDs driven by control, +S, +N, and +SN factors.

Despite the large number of species present across all plots, only a subset of species was found flowering in enough plots (≥75%) to be analyzed individually. For the analysis presented here, we focus on two forbs, *G. rossii* and *B. bistortoides*, and one graminoid, *D. caespitosa*, from that subset. These are three of the most abundant species throughout the tundra at Niwot Ridge and a limited historical record of FFD exists for them. We analyzed FFD and flower number from 2007 and 2008 and seedling number from 2008 for these three focal species.

Results

FIRST FLOWERING DATE

The 2007 and 2008 mean FFDs observed in subplots of all seven manipulation treatments compared to mean FFD in control subplots are displayed in Figure 1. However, not all statistically significant treatment factor effects are obvious from the subplot means alone. In 2007 two significant FFD response patterns were detected. First, *G. rossii* flowered two days earlier in response to warming (T: $P < 0.01$). Second, *G. rossii* and *B. bistortoides* flowered later in response to the addition of either snowpack or N alone, but remained similar to control plots where snow and N were added together (S×N: $P < 0.05$; Fig. 2). There was a marginally significant treatment effect on the FFD of *D. caespitosa* to flower earlier where N, temperature, or N and temperature together were increased (T×N: $P = 0.08$).

In the 2008 growing season, only one significant FFD response pattern was detected. *B. bistortoides* flowering was delayed where any one of snowpack, temperature, or N was added alone or where

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TABLE 1

Significant treatment factor effects on first flowering date (FFD) and seedling number (Sd. Num.) in the 2007 and 2008 growing seasons. Effects are from enhanced snowpack (S), temperature (T), and nitrogen (N) treatment factors (Trt) and interactions between them. Treatment effects are expressed as the difference from control plots in days or number of seedlings ± SE. For FFD, positive difference values indicate delayed flowering under treatment compared to control conditions and negative values indicate earlier flowering. An asterisk indicates effects that were only marginally significant statistically.

	Species	Effect	df	*F*	*P*	Trt	Diff.
FFD							
2007	*G. rossii*	T	1, 35	8.24	0.0069	+T	−2.0 ± 0.69
		S × N	1, 35	7.05	0.0118	+S	1.8 ± 0.99
						+N	2.0 ± 0.97
						+SN	0.2 ± 0.97
	B. bistortoides	S × N	1, 28	4.32	0.0470	+S	1.9 ± 1.95
						+N	2.6 ± 1.29
						+SN	0.7 ± 1.88
	**D. caespitosa*	T × N	1, 36	3.24	0.0803	+T	−1.8 ± 0.82
						+N	−2.1 ± 0.82
						+TN	−1.8 ± 0.82
2008	*B. bistortoides*	S × T × N	1, 24	8.40	0.0079	+S	3.5 ± 3.95
						+T	6.0 ± 2.86
						+N	2.8 ± 2.57
						+ST	0.4 ± 4.26
						+SN	1.0 ± 3.87
						+TN	1.0 ± 2.66
						+STN	6.0 ± 4.25
	**D. caespitosa*	N	1, 35	3.89	0.0564	+N	−1.3 ± 0.67
Sd. Num.							
2008	*G. rossii*	S × T × N	1, 35	5.17	0.0292	+S	0.8 ± 0.84
						+T	1.3 ± 0.82
						+N	0.8 ± 0.82
						+ST	−0.3 ± 0.81
						+SN	−0.4 ± 0.81
						+TN	0.1 ± 0.80
						+STN	0.1 ± 0.80

all three factors were applied in combination, but FFD remained similar to control plots where any two treatment factors were applied together (S×T×N: $P < 0.01$; Fig. 1, part b). There was also a marginally significant trend of *D. caespitosa* to flower earlier in response to N addition (N: $P = 0.056$). There were no significant treatment effects on FFD of *G. rossii*.

All significant results are summarized in Table 1. See Appendix for mean FFDs of all species recorded in 2007 and 2008.

FLOWER NUMBER

Treatments did not significantly alter flower/inflorescence number of *G. rossii*, *B. bistortoides*, or *D. caespitosa* in 2007 or 2008.

SEEDLING NUMBER

In 2008 one significant seedling abundance treatment response was detected. *G. rossii* seedling abundance was greater where any one of the treatment factors, snowpack, temperature, or N, was applied alone, but decreased or was similar to control plots where any two or three treatments were applied in combination (S×T×N: $P < 0.05$, Fig. 3, Table 1). There were no significant treatment effects on seedling abundance of *Bistorta* spp.

Discussion

Snowpack, temperature, and N manipulations all affected flowering phenology to different extents and with varying interactive effects depending on the functional characteristics of the species. Some of the phenological responses we observed, like earlier flowering in response to warming or later flowering in response to amended snowpack, were consistent with responses found in other alpine, arctic, and lowland experiments (e.g. Arft et al., 1999; Dunne et al., 2003; Cleland et al., 2006). However, phenological responses to N addition were more unexpected and contrasted with results found in lowland, grassland systems (Cleland et al., 2006). Interactions between treatment factors had the most surprising effects, but we found no thoroughly convincing explanation for the phenological responses observed and no relevant research with which to compare our results.

The first significant phenological pattern observed was that the forb, *G. rossii*, flowered earlier in response to warming. The graminoid, *D. caespitosa*, also tended to flower earlier in warmed plots, but the effect was only marginally significant statistically (Table 1). Other phenological studies in alpine, arctic, and lowland areas have observed the same flowering response to warmer temperature (Arft et al., 1999; Dunne et al., 2003; Parmesan and Yohe, 2003; Cleland et al., 2006). A historic phenological record of *G. rossii*, *B. bistortoides*, and *D. caespitosa* from Niwot Ridge and nearby Rocky Mountain National Park (RMNP) also indicates that FFD has become earlier over the last 50 years (Holway and Ward, 1965; May and Webber, 1982; Walker et al., 1995) while mean annual temperature has become warmer (Greenland and Losleben, 2001).

D. caespitosa exhibited a marginally significant trend toward earlier flowering in response to N addition in 2007 and more strongly in 2008 (Table 1). These results are contrary to those found in coastal grassland (Cleland et al., 2006), but are not necessarily surprising since similar plant functional types may employ different growth strategies under different environmental conditions. Most alpine plants rely on a conservative growth strategy (Chapin, 1980; Seastedt et al., 2004), but some graminoids may be able to use N opportunistically, allowing them to respond quickly to increased N availability and obtain growth and reproductive advantages in a longer growing season (Bowman, 2000; Bowman and Fisk, 2001). N fertilization has increased productivity and reduced species richness in ecosystems across North America (Suding et al., 2005), and in the alpine evidence

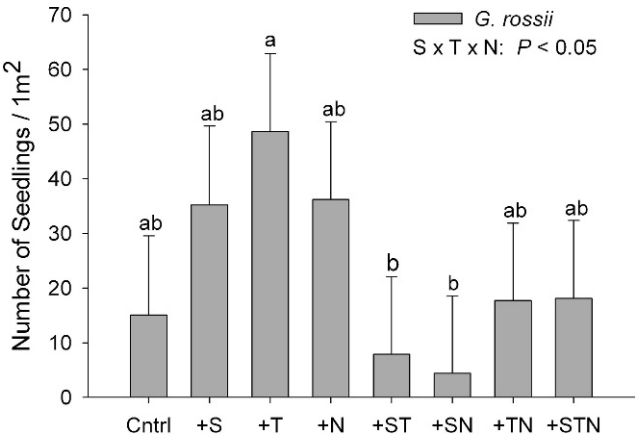


FIGURE 3. Seedling abundance of *Geum rossii* in response to a significant snowpack (S) × temperature (T) × N interaction. Significant differences ($P < 0.05$) are indicated by different lowercase letters.

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suggests that the more abundant species are superior N competitors (Miller and Bowman, 2003; Miller et al., 2007; Ashton et al., 2010). Studies from Niwot Ridge have shown graminoids acquire and use N to increase biomass more rapidly than neighboring forbs (Bowman et al., 1993, 1995, 2006; Bowman, 1994; Ashton et al., 2008), and long-term species composition surveys indicate that nitrophilous species have increased significantly over the last two decades (Korb and Ranker, 2001).

The third, most unexpected phenological pattern observed was that both forbs, *G. rossii* and *B. bistortoides*, flowered later when either snowpack or N alone was enhanced, but flowered simultaneously with control plots when snowpack and N were added together (Fig. 2, Table 1). Within this interaction, later flowering in response to snow augmentation is not surprising. Initiation of growth phenology in high-elevation mountain regions is most limited by the date of snowmelt (Holway and Ward, 1965; Inouye et al., 2002, 2003; Miller-Rushing and Inouye, 2009; Lambert et al., 2010), and other alpine studies have found that forbs flowered later in response to snow additions (Walker et al., 1995, 1999) or earlier in response to snow removals (Dunne et al., 2003). The later flowering of forbs in response to N augmentation, within the snow and N interaction, is also not surprising and is similar to results from a lowland experiment in which forb flowering also responded to N in the opposite direction from graminoids (Cleland et al., 2006).

The puzzling effect of the snowpack and N interaction on forb FFD is that although both factors alone delayed flowering, the two factors in combination seemed to elicit no response. One explanation could be simply that the treatment responses of *G. rossii* were erratic and unreliable. Comparing 2007 and 2008 treatment FFD means (Fig. 1), the responses of *G. rossii* are less consistent between years than those of *B. bitortoides* and *D. caespitosa*. However, the same snow and N interaction observed in *B. bistortoides* FFD reinforces the authenticity of *G. rossii's* response. We have no well-supported explanation for this snowpack and N interaction. It is conceivable that snow addition delays forb phenology by extending the date of snowmelt, and N addition indirectly delays forb phenology by amplifying graminoid productivity and depleting resource availability to forbs, but combined snow and N addition does not delay forb flowering because it limits graminoid growth onset and resource exploitation with later snowmelt and leaves more N available to forbs at growth onset to enhance productivity and flower earlier despite the snowmelt delay.

An even more complex interaction between treatment factors is visible in 2008 when *B. bistortoides* flowered later in response to addition of snowpack, temperature, or N alone, as well as to the combination of all three, but not to the combination of just two factors (Fig. 1, part b; Table 1). This response pattern could have a similar explanation to that proposed for the snow and N interaction observed in 2007, with the added element that warmer temperature impedes productivity and delays flowering of *B. bistortoides* by escalating evaporation and reducing water availability, an effect counterbalanced by moisture from increased snowpack or the advantage of greater nutrient availability from N addition. However, in 2008 *B. bistortoides* did not flower in 12 of 48 subplots and the data may be inadequate for reliable analysis.

There was no response in flower/inflorescence number of any species to any treatment. These results are not surprising because the flowers of most alpine plants are preformed belowground one or more years in advance of emergence, delaying a visible aboveground response to altered environmental conditions (Aydelotte and Diggle, 1997; Diggle, 1997; Mark, 1970; Meloche and Diggle, 2001). The International Tundra Experiment found that tundra plants had no visible increase in reproductive effort in response to warming until the later years of the four-year experiment, with the greatest magnitude response occurring in year four (Arft et al., 1999).

The response of *G. rossii* seedling abundance to treatment interactions was congruent with that of *B. bistortoides* FFD in 2008. The abundance of *G. rossii* seedlings increased in response to snowpack, temperature, and N amendment alone, but decreased or did not respond to any treatments applied in combination (Fig. 3, Table 1). It is not surprising that alpine seedling germination would respond positively to more amiable conditions of warmer temperature or increased water (snowpack) or nutrient (N) availability. Increased snowpack and delayed snowmelt may also improve seedling survival by preventing exposure to early season frost events (Inouye, 2000, 2008; Hülber et al., 2011). Treatment combinations, on the other hand, may have indirectly influenced seedling abundance by eliciting a germination response complementary to the productivity of adjacent mature plants with treatment response patterns similar to *B. bistortoides.* If *B. bistortoides*' single treatment factor-induced FFD delay was the result of an overall response of reduced productivity, access to more space, sunlight and nutrients may have amplified germination; *B. bistortoides*' multiple factor-induced FFD and productivity response would lead to germination similar to that found in control plots. However, there is no well-supported or truly satisfactory explanation for the observed phenology and germination responses to treatment interactions. Instead, these interactions highlight the limitation in our current understanding of the complex dynamics between the many factors driving phenology.

Changing environmental conditions are modifying the phenology of organisms in ecosystems around the world (Parmesan and Yohe, 2003; Parmesan, 2006; Miller-Rushing and Primack, 2008). Although the influence of precipitation and temperature patterns associated with global climate change has been investigated in a number of studies (e.g. Inouye et al., 2002; Huelber et al., 2006; Parmesan, 2006; Hülber et al., 2010; Lambert et al., 2010), the role of nutrient availability in phenology has remained largely unexplored. However, anthropogenic N deposition has amplified the availability of N in many ecosystems (Galloway and Cowling, 2002; Howarth et al., 2002) and our results suggest that N may play an important role in plant phenology, too. Our results also emphasize the significant phenological consequences of interactions between environmental factors and the need for further investigation into their dynamics. Alpine ecosystems may be sensitive bellwethers of change (Seastedt et al., 2004) that can be studied to elucidate and predict the phenological responses of organisms to modified conditions in other ecosystems. Many alpine plants, however, employ a conservative growth strategy (Seastedt et al., 2004) and preform leaves and buds (Mark, 1970; Aydelotte and Diggle, 1997; Diggle, 1997; Meloche and Diggle, 2001) so that phenological responses may require multiple growing seasons to fully materialize. Our research illustrates the importance of snowpack, temperature, and N, both alone and in combination, as drivers of alpine plant phenology, and the need for long-term experiments to illuminate the influence on different plant species and functional types of individual factors and the complex interactions between them.

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APPENDIX

First flower date (FFD) of alpine species in plots exposed to eight different treatments at Niwot Ridge LTER (Colorado Front Range) during the 2007 and 2008 growing seasons. A three-letter plot code indicates treatments of increased snowpack (S), temperature (T), and nitrogen (N) or control (X). Dates are reported as mean Julian day ± SE, where $n = 2$–6 one m^2 subplots with flowers present, "na" indicates cases where $n = 1$, and "—" indicates species not present in any plots of a treatment.

Species	XXX	SXX	XTX	XXN	STX	SXN	XTN	STN
2007								
Artemisia scopulorum	176 ± 1.2	175 ± 1.0	174 ± 1.2	174 ± 1.2	177 ± 0.7	175 ± 1.2	175 ± 1.0	177 ± 0.6
Bistorta bistortoides	177 ± 0.7	181 ± 2.5	178 ± 0.8	181 ± 1.6	177 ± 0.8	178 ± 1.1	181 ± 1.4	179 ± 2.1
Bistorta vivipara	190 ± 0.0	—	190 na	—	190 ± 0.0	190 ± 0.0	190 na	190 ± 0.0
Caltha leptosepala	160 ± 2.2	158 ± 2.1	160 ± 1.2	158 ± 1.7	156 ± 1.3	159 ± 1.7	159 ± 1.7	158 ± 2.4
Carex spp.	—	193 na	—	—	—	—	—	—
Carex scopulorum	176 ± 0.0	172 ± 2.0	174 ± 4.5	179 ± 1.4	173 ± 1.7	173 ± 1.5	176 na	175 ± 5.7
Castilleja occidentalis	183 ± 0.0	187 ± 0.0	184 ± 3.2	191 ± 4.2	181 ± 1.4	193 na	191 ± 7.0	204 ± 14
Chionophilia jamesii	187 na	187 na	187 ± 2.3	188 ± 1.0	185 ± 1.2	212 na	185 ± 2.0	187 ± 0.0
Deschampsia caespitosa	177 ± 0.6	178 ± 1.2	176 ± 0.0	176 ± 1.2	175 ± 1.0	175 ± 1.0	176 ± 0.0	175 ± 1.0
Dodecatheon pulchellum	—	—	187 na	—	187 na	190 na	—	—
Erigeron simplex	183 na	187 na	183 na	187 na	187 na	185 ± 2.0	—	—
Festuca brachyphylla	190 ± 7.0	193 ± 5.7	197 ± 4.5	190 ± 7.0	199 ± 2.2	190 na	194 ± 1.3	183 na
Gentianella amarella	209 ± 2.3	213 ± 5.5	205 ± 1.0	213 ± 1.0	204 ± 0.0	214 na	208 ± 4.0	207 ± 0.0
Gentianoides algida	214 ± 1.7	212 ± 1.8	212 ± 1.8	212 ± 2.0	212 ± 2.1	212 ± 0.0	212 ± 1.9	215 ± 3.0
Geum rossii	174 ± 1.3	176 ± 0.0	173 ± 1.3	176 ± 0.0	175 ± 1.2	176 ± 0.0	175 ± 1.0	171 ± 1.6
Juncus sp.	—	—	—	—	179 ± 2.0	—	—	—
Lewisia pygmaea	180 ± 3.3	180 ± 2.4	176 ± 0.0	176 ± 0.0	177 ± 0.9	176 ± 0.0	174 ± 4.3	179 ± 3.5
Lloydia serotina	—	—	—	—	176 na	—	—	—
Luzula spicata	176 na	179 ± 1.7	179 ± 2.0	183 ± 2.3	182 ± 1.9	185 ± 3.5	179 ± 0.0	—
Mertensia lanceolata	181 ± 2.0	—	179 na	—	—	—	182 ± 3.2	—
Pedicularis groenlandica	—	—	—	—	179 na	—	—	—
Poa alpina	225 na	225 na	—	—	—	—	—	—
Potentilla diversifolia	183 ± 0.0	179 na	180 ± 1.7	181 ± 1.3	176 na	183 na	184 ± 8.5	198 ± 1.5
Rhodiola integrifolia	171 ± 5.0	—	—	170 na	155 na	164 na	168 ± 2.0	164 na
Salix spp.	—	183 na	—	—		179 na	—	—
Stellaria longipes	188 ± 5.0	190 na	191 ± 1.0	196 ± 8.5	188 ± 0.9	204 na	191 ± 3.6	190 ± 0.0
Trifolium parryi	—	176 ± 0.0	179 ± 3.5	183 ± 4.0	178 ± 0.7	176 na	—	183 na
Trisetum spicatum	—	—	—	—	—	—	193 na	187 na
2008								
Bistorta bistortoides	190 ± 1.7	193 ± 2.0	194 ± 1.3	193 ± 3.2	188 ± 1.7	192 ± 2.3	191 ± 2.1	195 ± 2.7
Caltha leptosepala	166 ± 1.4	169 ± 0.6	168 ± 0.3	168 ± 1.1	169 ± 0.6	170 ± 1.5	166 ± 1.5	169 ± 0.6
Carex spp.	184 ± 1.0	184 ± 1.0	182 na	185 na	190 ± 6.6	189 ± 4.4	—	182 na
Deschampsia caespitosa	187 ± 1.6	186 ± 1.2	186 ± 1.3	185 ± 1.1	186 ± 1.2	185 ± 1.5	185 ± 1.1	184 ± 1.2
Geum rossii	182 ± 1.6	187 ± 2.8	185 ± 2.1	183 ± 0.5	185 ± 1.5	184 ± 1.3	183 ± 0.6	183 ± 0.6

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