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COMPENSATORY RESPONSES TO LOSS OF WARMING-SENSITIVE PLANT SPECIES

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Abstract. Climate warming-induced plant species loss is likely to be nonrandom and based on species-specific susceptibility to changing climate. We examined the ecological consequences of losing shallow-rooted forbs, a group of species we predict to be adversely affected by climate change based on their response to experimental warming. After three years of experimental species removal, tap-rooted forbs and grasses were able to fully compensate for the loss of shallow-rooted forbs with increased biomass production. Moreover, the remaining plant community yielded a larger biomass response to nitrogen addition when shallow-rooted forbs were removed, possibly because removal led to increased soil moisture. We conclude that, although shallow-rooted forbs share a common response to warming, their loss did not affect community-level biomass. However, the loss of shallow-rooted forbs could result in increased sensitivity to perturbations, such as changing nutrient availability. Our results demonstrate that realistic, nonrandom scenarios of species loss do not necessarily follow the general pattern of decreased productivity and dampened response to nitrogen addition with species loss that is predicted by theory and many experimental results. Further examinations of nonrandom species loss in other ecosystems are needed to further improve our understanding of the consequences of human-driven species loss.

Key words: climate change; compensation; functional effect group; functional response group; nitrogen addition; nonrandom species loss; species-removal experiment; subalpine meadow.

Introduction

Human-induced environmental changes such as land use, climate change, nitrogen (N) deposition, atmospheric carbon dioxide (CO_2) enrichment, and the introduction of exotic invasive species are expected to have significant negative impacts on global biodiversity both now and in the future (Vitousek 1994, Pimm et al. 1995, Sala et al. 2000). In light of these current and impending changes, understanding the ecosystem consequences of losing biodiversity has become a major focus of ecological research (Chapin et al. 2000, Loreau et al. 2002, Hooper et al. 2005). Most experimental studies of the ecosystem consequences of plant species loss have focused on randomly assembled plant communities, where lower diversity treatments represent the random removal of species from the community (e.g., Naeem et al. 1994, Tilman et al. 1997, Hector et al. 1999, Reich et al. 2001, Tilman et al. 2001). However, changes in diversity as a result of human activities are not likely to be random; they are more likely to be targeted at species with traits that make them particularly vulnerable to change (Grime 2002, Solan et al. 2004, Zavaleta and Hulvey 2004, Hooper et al. 2005, Larsen et al. 2005, Schlapfer et al. 2005). Several studies have shown that ecosystem functioning responds differently to random vs. nonrandom species loss (e.g., Solan et al. 2004, Zavaleta and Hulvey 2004, Larsen et al. 2005, Schlapfer et al. 2005). Therefore, investigating how ecosystems may respond to nonrandom changes in diversity resulting from human activities is an important next step in predicting the ecosystem consequences of human-driven species loss (Grime 2002, Naeem and Wright 2003, Hooper et al. 2005, Srivastava and Vellend 2005).

Anthropogenic climate change is predicted to be an important driver of diversity change, especially in mountainous environments (Sala et al. 2000). Results from an ongoing 15-year warming experiment in a subalpine meadow in Colorado suggest that some plant species in that system may be more adversely affected by increasing temperatures than other species (Harte et al. 1995). We found that warming decreased the aboveground biomass and flowering success of shallow-rooted forbs (see Plate 1), yet increased or had no effect on the growth of tap-rooted forb species (de Valpine and Harte 2001, Saavedra et al. 2003). Although warming has not yet led to the complete disappearance of any plant species from this experimental system, spatial patterns across the experimental plots suggest that plant species richness is reduced under conditions of early snowmelt and enhanced soil nitrogen availability, both of which are occurring under the experimental heaters (Harte et al.

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PLATE 1. We investigated the effect of removing all shallow-rooted forb species (e.g., *Linum lewisii*, left), a functional group that we predict to be more adversely affected by warming relative to tap-rooted forb species (e.g., *Helianthella quinquenervis*, center), and grasses. Photo credits: M. S. Cross. The right-hand photo shows species removal and nitrogen addition field experiment at the Rocky Mountain Biological Laboratory, Gothic, Colorado, USA. Photo credit: Lin Jing.

1995, Shaw and Harte 2001; J. Harte, *unpublished data*). While it is difficult to know how every plant species in this meadow ecosystem will respond to future warming, the observation that manipulated warming reduces soil moisture in shallow soil layers and has had detrimental effects on several shallow-rooted forb species (Harte et al. 1995, de Valpine and Harte 2001, Saavedra et al. 2003) suggests that shallow-rooted forbs may be particularly vulnerable to being lost from this plant community.

To examine the impact that the nonrandom loss of shallow-rooted forb species may have on ecosystem functioning, we conducted an in situ species-removal experiment (Diaz et al. 2003). By working in otherwise unmanipulated ecosystems, species-removal experiments explore the consequences of nonrandom species loss in complex natural systems, while maintaining an ability to look at cause-and-effect relationships by directly altering community composition (Diaz et al. 2003). Previous removal studies of nonrandom plant species loss have focused on the loss of rare species (e.g., Lyons and Schwartz 2001, Smith and Knapp 2003), or on the loss of various combinations of functional groups and/or dominant species. To our knowledge, this is the first removal study that examines nonrandom plant species loss resulting from a specific anthropogenic activity.

While results from the warming experiment suggest that shallow-rooted forb species share traits that determine their response to climate warming ("functional response traits"), it is not clear whether they also share traits that affect key ecosystem processes such as productivity and nutrient cycling ("functional effect traits"). Understanding whether a group of species that share functional response traits also share functional effect traits is important in determining how the loss of a group of species due to climate warming might affect ecosystem functioning (Lavorel and Garnier 2002, Naeem and Wright 2003, Hooper et al. 2005). Ecosystem function is generally preserved when species that share functional effects traits differ in their response to environmental change since unaffected species within that group can often compensate for the loss of susceptible species (Chapin et al. 1997, Hooper et al. 2005). However, when species that share functional effect traits all respond negatively to a particular environmental change, full compensation for the loss of that group may not be possible if there are no remaining species to fill-in the available niche space (Diaz and Cabido 2001, Larsen et al. 2005).

We hypothesized that shallow-rooted forbs, which share a response to experimental warming, would also have a similar effect on productivity since they acquire their nutrients from a similar depth of soil, share a similar rooting morphology, and therefore may occupy a specific resource niche that may not be as accessible to species with other belowground nutrient acquisition strategies. Previous research has demonstrated that plant species can partition soil nutrient resources by soil depth, and that a greater diversity of rooting morphologies can result in more efficient use of soil resources and greater accumulation of biomass (Berendse 1982, McKane et al. 2002, Dimitrakopoulos and Schmid 2004). We therefore expected that the loss of shallow-rooted forb species would decrease total biomass since the remaining plant community would not be able to exploit the available soil resource niche space as thoroughly as would a community with a greater diversity of rooting morphologies. We also expected that the loss of shallow-rooted forbs would dampen the community's biomass response to an increase in soil nitrogen availability. We chose to perturb the system by altering nitrogen availability because we observed increased rates of net nitrogen mineralization in

response to experimental warming (Shaw and Harte 2001) and because future atmospheric deposition of nitrogen from anthropogenic activities is expected to increase in the study area (Burns 2004).

Methods

Study site

Our experiment was conducted in an ungrazed subalpine meadow at the Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado (38°53′ N, 107°02′ W; elevation, 2920 m), ~150 m from an ongoing warming experiment (Harte and Shaw 1995, Harte et al. 1995; see also Plate 1). The meadow plant community in our experimental plots is composed of long-lived and largely perennial herbaceous forbs and grasses (see Harte and Shaw [1995] and Harte et al. [1995] for additional soil and climate details).

Experimental design

In summer 2001, plant species removal and nitrogen addition treatments were established in 48 2×2 m plots, arranged in eight blocks of six contiguous plots. Blocks were spaced ~3 m apart within a section of hillside where slope, aspect, hydrologic regime, and plant community type were relatively uniform. Before assigning treatments to each plot, we collected pre-manipulation data on peak aboveground biomass (AGB) of grasses, deep tap-rooted forbs, and shallow-rooted forbs. We measured AGB nondestructively by calibrating estimates of aerial coverage (AC) to biomass via regressions for each plant group with off-plot harvests.

Plots within each block were randomly assigned to one of three plant species-removal treatments—removal of all AGB of shallow-rooted forb species (shallow removal, SR treatment), removal of random forb AGB (random removal, RR treatment), or control plots with no removal of biomass (control, CONT treatment)—for a total of two replicates of each species-removal treatment in each six-plot block. The RR treatment was included as a special type of control since the removal of species using this experimental approach is confounded with the loss of biomass. The RR treatment allowed us to distinguish between the effect of species loss and the effect of biomass loss since the RR treatment removed biomass without removing species. Forb species were classified into shallow- and tap-rooted categories based on field excavations of root morphology: shallow-rooted forbs were designated as those with fibrous rooting structures that were concentrated in the top 10 cm of the soil profile, whereas tap-rooted forbs were characterized by a coarse taproot structure that can access deeper soil resources (see Appendix A for species list). We randomly chose one replicate of each species-removal treatment within a block to be fertilized by inorganic nitrogen (+N treatment) while the other replicate remained at ambient nitrogen levels. Therefore, each block contained one replicate of each of six total treatment combinations: CONT, CONT+N, SR, SR+N, RR, and RR+N.

At the time of peak standing AGB in late July 2001, we removed aboveground vegetation of all shallow-rooted forb species from the SR plots by clipping plants at their base. Biomass in the RR plots was removed at the same time by clipping all of the forb AGB (regardless of rooting structure) within a set of randomly chosen 25×25 cm quadrats, until we had removed an equivalent amount of biomass to the amount removed from the other SR plots within that block. Before applying the removal treatments there were on average 18 forb species (minimum, 13 species; maximum, 24 species) in the central 1 m^2 of the plots, 13 of which were shallow-rooted species (minimum, 8 species; maximum, 17 species). Depending on pre-manipulation species composition within each plot, the SR treatments removed from 61.9% to 87.5% of all forb species. Therefore, the SR treatment manipulated both species richness and functional response group richness. Although grasses were present in the experimental plots, we chose not to target grasses for removal in any of the treatments since warming has had no effect on grass AGB in the warming meadow experiment (Harte and Shaw 1995). In 2002 and 2003, we continually weeded aboveground plant parts of all shallow-rooted forb species from the SR plots as soon as they emerged aboveground after snowmelt and could be identified to species. In the RR plots, the same 25×25 cm quadrats used to conduct the random removals in 2001 were kept free of forb biomass by weeding all throughout the growing season. In 2004, we discontinued weeding in both the SR and RR plots.

Inorganic nitrogen was applied to the soil surface of fertilized (+N) plots as ammonium-nitrate (NH_4NO_3) in solution. A total of 6 g N/m^2 was applied to each +N plot each year, divided into four equal doses of 1.5 L of NH_4NO_3 solution. This level of N addition is comparable to the approximate doubling of net N mineralization rates that has been observed in the heated plots relative to the controls in the warming meadow experiment (Shaw and Harte 2001). To account for the small amount of water addition that inevitably accompanies the application of fertilizer in solution, we added an equivalent amount of deionized water to non-fertilized plots, an amount that is negligible relative to incoming precipitation levels. The first nitrogen and water applications were applied just after snowmelt in spring 2002, with the remaining three doses applied roughly every 2–3 weeks thereafter. Nitrogen and water additions were continued in the same manner in 2003 and 2004.

We measured all response variables in the central 1 m^2 of each plot to reduce potential edge effects. We estimated aboveground plant productivity using peak standing AGB. Because all aboveground vegetation senesces at the end of each growing season in this system, peak standing AGB is a conservative estimate of annual aboveground production. We measured AGB

nondestructively by calibrating estimates of aerial coverage (AC) to biomass via regressions for each plant group (tap- and shallow-rooted forbs, and grasses) with off-plot harvests. We used maximum AC over the course of the growing season to calculate peak standing AGB for each plant group. We measured fine (<2 mm diameter) root biomass by taking three cores (3.5 cm diameter by 10 cm depth) per plot at the peak of the growing season in 2002 and 2003. Roots were hand-sorted into live and dead biomass based on tensile strength, friability, and color of all fragments ≥0.5 cm in length. We were unable to separate roots by species. We measured soil moisture at depths of 10 and 30 cm approximately once a week throughout the growing season in 2002 and 2003 using permanently installed gypsum blocks that were calibrated to percentage gravimetric soil moisture using soil samples taken directly from the plots.

Repeated-measures MANOVA on the biomass data often revealed a significant time by removal interaction (data not shown). Therefore we conducted separate ANOVA analyses for each year of the experiment with block, removal, and N addition as main effects, and a removal by N addition interaction term ($n = 8$ blocks). When a main effect or interaction term was significant ($P \leq 0.05$) or marginally significant ($0.05 < P \leq 0.10$) within our ANOVA model, we conducted the following planned a priori contrasts: (1) CONT vs. SR and RR vs. SR when the removal effect was significant; and (2) CONT vs. CONT+N, RR vs. RR+N, and SR vs. SR+N when there was a significant removal by N addition interaction. Data were analyzed using JMP 5.1 (SAS Institute 2003). All reported P values are for main effects and interaction terms from the ANOVA model specified previously, unless otherwise noted as being from a planned a priori contrast. All data are reported as means ± SE.

Results

Pre-manipulation data from 2001 show that total AGB and the amount of grass and tap-rooted forb AGB were equal across all plots before the experimental treatments were applied, with only a small difference ($P = 0.05$) in the average amount of shallow-rooted AGB initially found in plots designated for CONT and RR treatments (Fig. 1A). The removal treatments successfully shifted plant community composition (measured as the proportion of total biomass in each plant group), although it took nearly two years of weeding to remove almost all of the shallow-rooted forb AGB from the SR plots (Fig. 1C, black bars). This shift in composition held when weeding was discontinued in 2004 (Fig. 1D). While the RR treatment reduced total AGB relative to CONT levels, the ratio of shallow-rooted forb AGB to tap-rooted forb AGB in RR and CONT treatments remained equal throughout the experiment ($P > 0.50$ in all years; Fig. 1). The average amount of biomass removed from each of the removal treatments decreased over successive

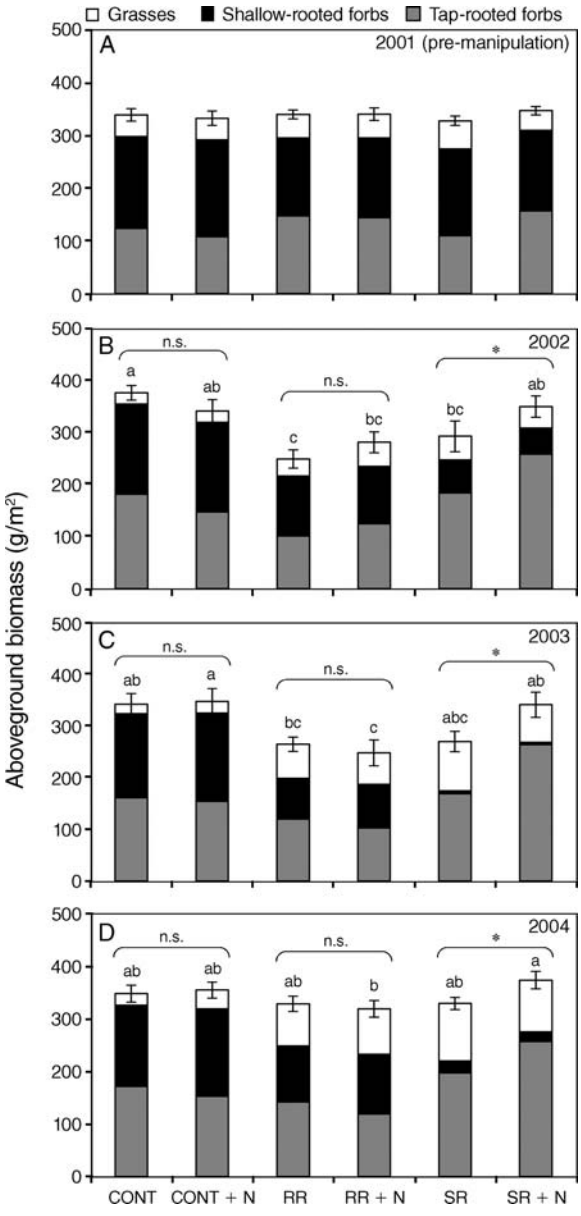


FIG. 1. Plant aboveground biomass (AGB) by treatment in (A) 2001 (pre-manipulation); (B) 2002 (with weeding and nitrogen [N] addition); (C) 2003 (with weeding and N addition); and (D) 2004 (no weeding, but N addition). The full height of bars indicates total AGB. Error bars are ±SE of total AGB for each treatment. Treatment abbreviations are: CONT, no removal, ambient N; CONT+N, no removal, added N; RR, random forb removal, ambient N; RR+N, random forb removal, added N; SR, shallow-rooted forb removal, ambient N; SR+N, shallow-rooted forb removal, added N. Different letters at the top of each bar denote significant differences among treatments at $P \leq 0.05$ using an ANOVA model with a block effect and the Tukey-Kramer hsd test to compare all pairs. Bracketed significance levels (n.s., not significant; $*P < 0.01$) refer to a priori contrasts for total AGB: CONT vs. CONT+N, RR vs. RR+N, and SR vs. SR+N.

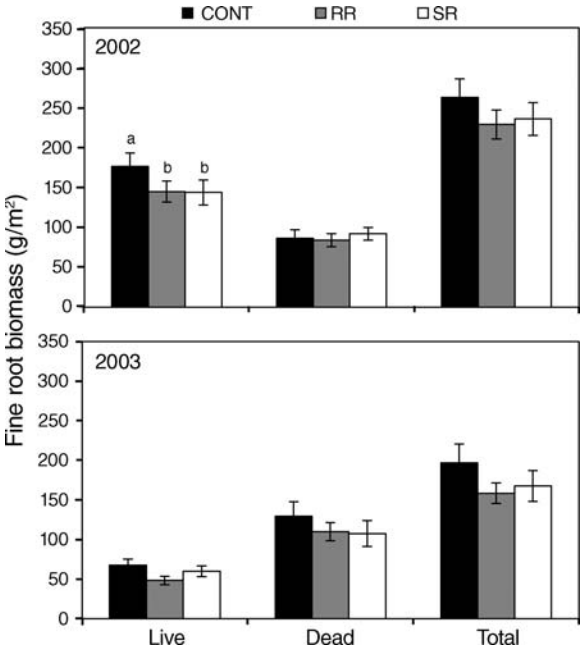


FIG. 2. Live, dead, and total fine root biomass in 2002 and 2003 for CONT (no removal, black bars), RR (random forb removal, gray bars), and SR (shallow-rooted forb removal, open bars). Data were pooled across nitrogen addition treatments. Different letters at the top of each bar denote significant differences among treatments at $P \leq 0.05$ using an ANOVA model with a block effect and a priori contrasts (CONT vs. SR, SR vs. RR). Error bars are ±SE.

years of the experiment (Appendix B). Although there were slight differences in the amount of biomass removed from SR and RR plots in 2001 and 2003, there was no difference in the cumulative amount of biomass removed from any of the SR and RR treatments over the duration of the experiment (Appendix B).

In plots where shallow-rooted forbs or random biomass were removed but no nitrogen was added, total AGB in 2003 was on average 25.9% ± 7.7% (SR) and 24.3% ± 4.6% (RR) lower than CONT AGB levels (Fig. 1C). Total AGB in the ambient nitrogen SR and RR plots recovered to CONT levels in 2004 when weeding was discontinued (Fig. 1D). Adding nitrogen to the RR+N plots did not change this pattern of reduced AGB in 2003 and recovery to CONT AGB levels in 2004 (Fig. 1C, D). However, when nitrogen was added to the SR+N plots, total AGB remained indistinguishable from AGB in both the CONT and CONT+N plots in 2002 through 2003, and was significantly higher than in RR+N plots in 2003 and 2004 (Fig. 1B–D). There was no significant effect of nitrogen addition on total AGB in either of the more diverse (in terms of both species and functional group richness) CONT or RR treatments in any year of the experiment, whereas nitrogen addition significantly increased total AGB in the less diverse SR plots in 2002, 2003, and 2004 (a priori contrast, $P < 0.01$ in each year; Fig. 1B–D).

Neither grasses nor shallow-rooted forbs showed a response to nitrogen addition in any of the removal or control treatments in any year of the experiment. Grasses did respond to the removal of shallow-rooted forbs with significantly increased AGB relative to the CONT treatment (a priori contrast, $P < 0.003$ in each year), but the response was the same in SR and RR treatments (a priori contrast, $P > 0.1$ in each year; Fig. 1B–D). Tap-rooted forbs did respond positively to the addition of inorganic nitrogen, but only in plots where shallow-rooted forbs had been removed (a priori contrast, $P < 0.01$ in each year; Fig. 1B–D).

In 2002, species and biomass removal significantly decreased live root biomass ($P = 0.05$), with live root biomass in the RR and SR plots 15.5% ± 8.1% and 17.7% ± 5.6% lower than in the CONT plots, respectively (Fig. 2). Live root biomass declined by 58.1% ± 3.1% between 2002 and 2003 across all treatments, while dead root biomass increased by 44.9% ± 9.7% between those same years, leading to an overall decline in total root biomass of 25.9% ± 3.6% between 2002 and 2003 (Fig. 2). In 2003, the effect of removal treatment on live root biomass was only marginal ($P = 0.10$), with RR plots having 27.1% ± 7.0% less live root biomass than CONT plots, and SR plots being intermediate between the two (Fig. 2). There was no effect of nitrogen addition on any of the root biomass measures in either 2002 or 2003.

Gravimetric soil moisture varied throughout the growing season, between soil depths, and between years (Fig. 3). There was no effect of removal treatment on average shallow (10 cm) soil moisture during the 2002 growing season (mid-May through mid-August; Fig. 3A); but average deep (30 cm) soil moisture in 2002 was significantly higher in SR plots (19.6% ± 0.5%) than in CONT plots (18.2% ± 0.2%), with RR soil moisture intermediate between the two (19.2% ± 0.5%) ($P = 0.04$; Fig. 3C). In summer 2003, average shallow soil moisture in SR plots (27.7% ± 0.6%) was significantly higher than in both CONT (25.7% ± 0.5%) and RR plots (26.1% ± 0.6%) ($P = 0.02$; Fig. 3B). Average deep soil moisture was also significantly affected by removal treatment in 2003, with SR and RR plots (30.1% ± 0.6% and 29.8% ± 0.6%, respectively) being significantly wetter than CONT plots (28.1% ± 0.3%) ($P = 0.01$; Fig. 3D).

DISCUSSION

We hypothesized that the loss of all shallow-rooted forb species would decrease the remaining plant community's total biomass and dampen the biomass response to an increase in soil nitrogen availability since the resulting community would not be able to exploit soil resources as efficiently as would a community with a greater diversity of rooting morphologies. However, we found that tap-rooted forbs and grasses were able to fully compensate for the loss of shallow-rooted forbs, an entire functional response group, in terms of total aboveground biomass (AGB; Fig. 1D). By 2004, total

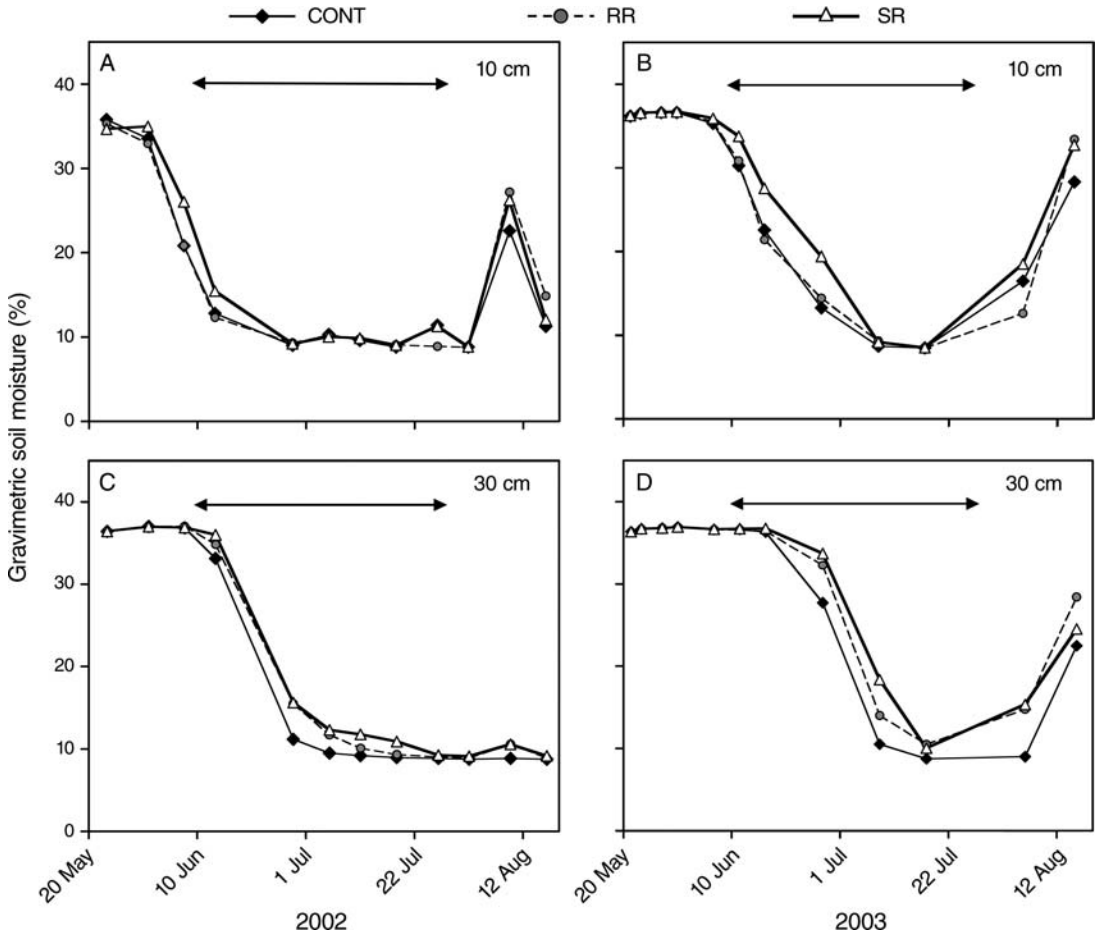


FIG. 3. Gravimetric soil moisture at 10 and 30 cm in 2002 (A, C) and 2003 (B, D) for CONT (no removal, diamonds, solid line); RR (random forb removal, circles, dashed line); and SR (shallow-rooted forb removal, triangles, heavy line). Data were pooled across nitrogen addition treatments. Horizontal arrows approximately indicate the peak six weeks of the growing season.

AGB in the less species- and functional group-rich shallow-rooted forb removal (SR) treatment was equal to total AGB in the more species- and functional group-rich control (CONT) and random removal (RR) treatments (Fig. 1D). We also found that the less diverse SR treatment responded to nitrogen addition with significantly increased growth of tap-rooted forbs, while the more diverse CONT and RR treatments showed no response to nitrogen addition (Fig. 1B–D). This response to nitrogen addition resulted in a faster rate of AGB compensation for the loss of shallow-rooted forbs in the SR+N treatment. These AGB responses represented true changes in total plant biomass, rather than shifting allocation between roots and aboveground tissue, since root biomass showed very little response to the experimental treatments beyond a small decrease in live root growth with the removal of both shallow-rooted forbs and random biomass in 2002 and 2003 (Fig. 2).

Comparisons between the SR and RR treatments allowed us to determine the importance of the loss of a group of species vs. the loss of biomass. Although we initially saw a decline in total AGB of the plant community in the less diverse ambient nitrogen SR treatment relative to the CONT treatment in 2002 and 2003, that decline must be attributed to the removal of biomass rather than the loss of shallow-rooted forbs since we observed a similar decline in AGB in the RR treatment (Fig. 1B, C). We anticipated that the more diverse RR treatment would be able to compensate for the loss of biomass more effectively than the less diverse SR treatment, but instead found that both the SR and RR treatments were equally productive as the CONT treatment in 2004 (Fig. 1D). The observation that the less diverse shallow-rooted forb removal plots were more responsive to added nitrogen can be directly attributed to the loss of shallow-rooted forbs as opposed to a loss of biomass because AGB did not increase in response to nitrogen addition in the RR+N plots where random biomass was removed (Fig. 1B–D). We conclude that the loss of shallow-rooted forbs, a group of species we predict to be adversely affected by climate change based on their response to experimental warming, did not have a strong effect on biomass production in this plant community over the duration of this study

due to compensatory growth by other remaining plants. It also appears that the ability of tap-rooted forbs to compensate for the loss of shallow-rooted forb biomass will likely be enhanced if future warming is accompanied by increased soil nitrogen availability. However, the loss of shallow-rooted forbs could have had a significant effect on other important ecosystem processes, such as soil nitrogen and carbon cycling (which we will discuss in a forthcoming paper).

Our findings fit into the spectrum of results from nonrandom removal experiments, which tend to show no systematic change in community-level biomass or its response to nitrogen addition with the removal of species or functional groups (e.g., Wardle et al. 1999, Symstad and Tilman 2001, Smith and Knapp 2003, Bret-Harte et al. 2004, Wardle and Zackrisson 2005). These removal studies tend to reveal that the identity of the removed species or functional group is more important than the number being removed (Wardle et al. 1999, Symstad and Tilman 2001, Bret-Harte et al. 2004), and indicate that relationships between diversity and productivity can vary significantly across ecosystem types and scales (Wardle and Zackrisson 2005). Several removal studies show at least some level of biomass compensation, although not always complete compensation, by remaining species and functional groups (e.g., Wardle et al. 1999, Symstad and Tilman 2001, Smith and Knapp 2003). While our study does not encompass a full gradient of species and functional group richness, it is interesting to note that our results do not follow the pattern of decreased productivity and a dampened response to nitrogen addition with species loss that is observed in many randomly assembled gradient experiments (e.g., Hector et al. 1999, Reich et al. 2001, Tilman et al. 2001). The findings from this and other removal studies appear to question whether conventional diversity-ecosystem functioning theory and experimental results, which are generally based on random species loss, are applicable to nonrandom scenarios of plant species loss.

The fact that this subalpine meadow plant community was able to fully compensate for the removal of shallow-rooted forb biomass suggests that while shallow-rooted forbs might be classified as a functional response group because of their similar response to warming, they do not appear to constitute a functional effect group in terms of their effect on biomass production over the duration of this study. Understanding this differentiation between species that share functional response traits and species that share functional effects traits is critical to being able to predict how the loss of a group of species due to anthropogenic activities might affect ecosystem functioning (Lavorel and Garnier 2002, Naeem and Wright 2003, Hooper et al. 2005). Other studies have demonstrated the poor ability of a priori functional group classifications to predict effects on ecosystem functioning (Wright et al. 2006). Our study shows how functional response groups do not necessarily correspond to functional effect groups of species, and that caution should be used when making predictions about how global change-induced species loss could affect community-level biomass production.

The loss of shallow-rooted forbs could have important consequences for ecosystem stability in terms of the system's "resistance," or ability to maintain function in response to a perturbation. Some research suggests a "diversity-begets-stability" relationship whereby a more diverse community is more resistant, or exhibits less change, in response to a perturbation due to an increased likelihood of having positively affected species which can compensate for declines in the growth of negatively affected species (e.g., Tilman 1996, Yachi and Loreau 1999, Tilman et al. 2006). Other research, however, presents theoretical and empirical evidence that less diverse plant systems can display greater resistance to a perturbation (Pfisterer and Schmid 2002). Only a few studies have directly manipulated both nitrogen availability and plant species diversity, with both Reich et al. (2001) and Fridley (2002) reporting that decreasing species diversity dampened the community's biomass response to nitrogen addition, and Bret-Harte et al. (2004) discovering that response to nitrogen addition was dependent on the identity of the plant group being removed. We found that the loss of shallow-rooted forbs resulted in an increased magnitude of biomass change in response to nitrogen addition (Fig. 1). This result suggests that the loss of shallow-rooted forbs from this plant community made the system less resistant to a perturbation in nitrogen availability. Whether the system would also be less resistant to other perturbations remains to be seen, but could be a concern.

A potentially complicating factor in interpreting the observed responses to nitrogen addition may be that water is also likely to be limiting plant growth in our system (de Valpine and Harte 2001). Our assumption that this meadow community is nitrogen-limited was based on the observation that several species had responded to added nitrogen with increased growth (de Valpine and Harte 2001). However, water is also considered to be an important resource (de Valpine and Harte 2001), and 2000–2003 was a period of severe drought throughout the southwestern United States (Breshears et al. 2005). The observed increase in soil moisture in the SR plots relative to CONT plots (Fig. 3) may have sufficiently alleviated water limitations in the SR+N plots and allowed the tap-rooted forbs in those plots to respond positively to nitrogen addition. However, this explanation does not account for the lack of response of tap-rooted forbs to nitrogen addition in the RR+N treatment, where soil moisture was mostly indistinguishable from that in the SR and SR+N treatment (Fig. 3). A more thorough exploration of how this plant community is limited by water and nitrogen is needed to further elucidate the complicated interplay between water and nitrogen limitations and the loss of shallow-rooted forbs. Therefore, while our results suggest that the ability of tap-rooted forbs to compensate for the loss of shallow-rooted forbs could be

enhanced if future warming is accompanied by increased nitrogen availability, this nitrogen addition effect may be mediated by soil water availability.

In summary, we found that the loss of shallow-rooted forbs did not have a negative effect on biomass production in this plant community over the duration of this study due to compensatory growth by other remaining plants. We also found that the loss of all shallow-rooted forbs increased the remaining plant community's biomass response to nitrogen addition. These results show that realistic nonrandom scenarios of species loss do not necessarily follow the pattern of decreased productivity and dampened response to nitrogen addition with species loss that is predicted by theory and experimental results from randomly assembled plant communities, and suggests that caution should be used in applying results from randomly assembled communities to natural communities undergoing nonrandom species loss. The effect of anthropogenic species loss on ecosystem function and stability will likely depend on the identity of species being lost, the extent to which remaining species can compensate for the lost species, and the amount of overlap between functional response and effect traits within a community. Additional experiments such as this one, that combine plausible species loss and perturbation scenarios, over even longer timescales are needed to improve our ability to predict the ecosystem consequences of human activity-driven declines in diversity.

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APPENDIX A

Plant species list and their classification as grass, shallow- or tap-rooted forb (*Ecological Archives* E088-047-A1).

APPENDIX B

A figure showing the amount of biomass removed from the treatment plots (*Ecological Archives* E088-047-A2).