Oecologia (2011) 167:771–780
DOI 10.1007/s00442-011-2028-7

COMMUNITY ECOLOGY - ORIGINAL PAPER

The variable effects of soil nitrogen availability and insect herbivory on aboveground and belowground plant biomass in an old-field ecosystem

Jarrod D. Blue · Lara Souza · Aimée T. Classen · Jennifer A. Schweitzer · Nathan J. Sanders

Received: 5 June 2010 / Accepted: 12 May 2011 / Published online: 31 May 2011

Abstract Nutrient availability and herbivory can regulate primary production in ecosystems, but little is known about how, or whether, they may interact with one another. Here, we investigate how nitrogen availability and insect herbivory interact to alter aboveground and belowground plant community biomass in an old-field ecosystem. In 2004, we established 36 experimental plots in which we manipulated soil nitrogen (N) availability and insect abundance in a completely randomized plot design. In 2009, after 6 years of treatments, we measured aboveground biomass and assessed root production at peak growth. Overall, we found a significant effect of reduced soil N availability on aboveground biomass and belowground plant biomass production. Specifically, responses of aboveground and belowground community biomass to nutrients were driven by reductions in soil N, but not additions, indicating that soil N may not be limiting primary production in this ecosystem. Insects reduced the aboveground biomass of subdominant plant species and decreased coarse root production. We found no statistical interactions between N availability and insect herbivory for any response variable. Overall, the results of 6 years of nutrient manipulations and insect removals suggest strong bottom-up influences on total plant community productivity but more subtle effects of insect herbivores on aspects of aboveground and belowground production.

Keywords Community structure · Insect herbivory · Old-field ecosystems · Soil nitrogen · Top-down

Communicated by Melinda Smith.

N.J.S. and A.T.C. conceived and designed the experiments. J.D.B., L.S., A.T.C. and N.J.S. performed the experiments. J.D.B., L.S., and N.J.S. analyzed the data. J.D.B., L.S., A.T.C., J.A.S., and N.J.S. wrote the manuscript.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-011-2028-7) contains supplementary material, which is available to authorized users.

J. D. Blue · L. Souza · A. T. Classen · J. A. Schweitzer · N. J. Sanders
Department of Ecology and Evolutionary Biology, University of Tennessee, 569 Dabney Hall, Knoxville, TN 37796, USA

N. J. Sanders (✉)
Department of Biology, Center for Macroecology, Climate, and Evolution, University of Copenhagen, 2100 Copenhagen Ø, Denmark
e-mail: nsanders@utk.edu

Introduction

Ecologists have long debated the relative importance of bottom-up (i.e., resource availability) and top-down (i.e., herbivory) effects on plant community structure and productivity (Elton 1927; Hairston et al. 1960; Sih et al. 1985; Power 1992; Worm et al. 2002; Borer et al. 2006). Over the past decade, the debate has moved away from arguments about which factors, top-down or bottom-up processes, have the biggest influence on primary productivity toward an increasing recognition that both processes can influence productivity across a variety of ecosystems (Borer et al. 2006; Hillebrand et al. 2007; Gruner et al. 2008; Kohyani et al. 2009). In particular, bottom-up factors such as the addition of nitrogen (N) can result in dramatic increases in total aboveground biomass (Craine et al. 2003; Gruner et al. 2008; Cleland and Harpole 2010), just as reductions in N availability can reduce aboveground biomass (Wedin and Tilman 1993; Throop 2005). The responses of a plant

community to N availability likely result from N limitation across ecosystems (LeBauer and Treseder 2008, Cleland and Harpole 2010). Herbivores, especially large mammals, can exert top-down control on aboveground plant biomass by consuming plant biomass (Maron and Crone 2006; Gruner et al. 2008). Indeed, on average terrestrial herbivores consume approximately 15% of net primary productivity (NPP) (Cyr and Pace 1993). The overall effects of herbivory by insects on total aboveground biomass, however, are mixed (Hunter 2001; Coupe and Cahill 2003). A recent meta-analysis by Coupe and Cahill (2003) suggested that, on average, insects reduce NPP by 13% in temperate herbaceous plant communities. But there was considerable variation among studies—some showed increases in, or no effects of, insect herbivory on NPP (Carson and Root 2000; Coupe and Cahill 2003; Chapman et al. 2003; Del-Val and Crawley 2005; Gao et al. 2008).

While it is clear that both herbivory and nutrient availability can sometimes affect NPP in plant communities, the relative and combined effects of herbivory and nutrient availability have been less well explored, especially with regard to herbivory by insects. In a recent meta-analysis, Gruner et al. (2008) found that producer community biomass increased with fertilization in marine, freshwater, and terrestrial ecosystems. In contrast, herbivores generally limited producer biomass in both freshwater and marine systems, but the effects of herbivory were inconsistent and non-significant overall in terrestrial ecosystems (Gruner et al. 2008). Additionally, most of the experimental studies analyzed by Gruner et al. (2008) showed only limited support for interactive effects of nutrient manipulation and herbivory on producer biomass. Moreover, of the 15 terrestrial studies reviewed by Gruner et al. (2008) that examined the interactive effects of herbivory and nutrient manipulation on producer biomass, only one focused on herbivory by invertebrates (a slug and a grass aphid). That study (Buckland and Grime 2000) found that herbivory by slugs (but not by aphids) decreased plant biomass across treatments (i.e., there was a main effect of herbivory in their models), but within each nutrient treatment there was no effect of herbivory on aboveground biomass. Given the ubiquity and importance of invertebrate herbivory on producer biomass (Coupe et al. 2009), it is somewhat surprising that so few studies have examined the interactive effects of invertebrate herbivory and soil nutrient manipulation on total aboveground biomass of intact plant communities in the field.

Nutrient manipulations and herbivory can also alter species interactions and overall plant community structure and functional diversity (Wardle et al. 2000; Hooper et al. 2005). Thus, dominant and subdominant plants may respond differently to nutrients and insect herbivory, especially if herbivores preferentially select dominant or subdominant plants and/or the dynamics of competition between dominant and subdominant plants depend on nutrient availability (Collins et al. 2008). In other words, dominance patterns in plant communities can be maintained by herbivores preferentially consuming subdominant species and/or by ambient nitrogen availability keeping subdominant species at lower abundances relative to dominant species.

Another important, but often overlooked, aspect of many studies that have examined the effects of herbivory and nutrient manipulation on producer biomass is belowground biomass, which, in some ecosystems, can account for >50% of total plant biomass (Canadell et al. 1996; Schenk and Jackson 2002). Recent reviews (Gruner et al. 2008; Cleland and Harpole 2010) of the effects of fertilization on plant communities do not mention any potential effects on belowground biomass, perhaps because there are so few studies. The effects of foliar herbivory on root production are mixed. In some cases, root production declines with foliar herbivory because tissue loss can result in reallocation of nutrients towards aboveground biomass for tissue regrowth (Brown 1994; Schädler et al. 2004). Other studies, however, have found that foliar herbivory can increase root production (Bardgett et al. 1998; Pucheta et al. 2004) and alter root turnover and nutrient release (Classen et al. 2007). For example, aboveground herbivory by spider mites increased root biomass in a nutrient-rich environment (Nishida et al. 2009). However, the effects of nutrient manipulation and aboveground herbivory on belowground biomass of intact plant communities in the field have rarely been examined.

Though aboveground and belowground compartments of ecosystems are often linked (Wardle et al. 2004), belowground responses may not simply mirror aboveground responses to herbivory and nutrient manipulations (Van der Putten et al. 2001; Wardle et al. 2004). While a growing number of studies have examined how aboveground processes, such as herbivory or nutrient amendment (e.g., nitrogen deposition), might influence belowground processes (Nadelhoffer 2000; Bardgett et al. 2005), to our knowledge, no studies to date have examined the relative and combined effects of foliar insect herbivory and soil nutrient availability on belowground biomass or the differential response of fine and coarse roots. After 6 years of manipulating soil N (at three levels) and insect herbivory (at two levels) in an old-field ecosystem, we examined the effect of soil N fertilization, insect herbivory, and their interactive effects on aboveground biomass and belowground biomass production of the entire plant community as well as specific components (dominant species and subdominant species) of the aboveground community. Given that most plants are nutrient limited and that herbivores can consume approximately 15% of total plant NPP (Cyr and Pace 1993), we tested two hypotheses. Firstly, aboveground

biomass is more responsive to soil nutrient amendment than to insect herbivory. Moreover, we predict that some components of the plant community may respond more strongly to the nutrient amendment and herbivory than others based on species-specific variation in allocation strategies, the differential effects of herbivory on competitively dominant and subdominant species, or nutrient requirements and uptake rates. Secondly, belowground biomass is more strongly altered in the soil nutrient amendment than herbivore treatments, with fine roots showing the most plastic responses.

Materials and methods

We established a field experiment in the spring 2004 within a ~10-ha old-field community at Oak Ridge National Environmental Research Park near Oak Ridge, Tennessee, USA (35°58′N, 84°17′W). Agricultural practices were discontinued at the site in 1943. Since 2003, many of the fields (including the one in which our experiment is embedded) have been mowed annually to manage for open-space and wildlife habitat. The soil, classified as a Typic Hapludult, has a silty clay loam texture and is moderately well drained (Phillips et al. 2001). Precipitation is evenly distributed throughout the year, with an annual mean rainfall of 1,322 mm, an average January minimum temperature of 2.7°C, and an average July maximum temperature of 31.2°C. Dominant plant species at the site include *Solidago altissima*, *Verbesina occidentalis*, and *V. virginica* (Wardle et al. 1999; Hooper et al. 2005). *Solidago altissima*, *V. occidentalis*, and *V. virginica* have been identified as dominant plant species based on two sets of studies. First, surveys of 17 neighboring old fields showed that *S. altissima* and *V. virginica* and *V. occidentalis* made up 40% of the total aboveground biomass (Souza et al. 2011). Approximately 60 other sub-dominant plant species, both herbaceous and woody, are present at the site (Sanders et al. 2007; Appendix 1). Second, Souza et al. (2011) experimentally manipulated the presence of *S. altissima* and both *V. occidentalis* and *V. virginica*, and found that both *Solidago* and *Verbesina* altered the structure of the subdominant community, while other experiments have shown that *Solidago* species can have strong effects on the rest of the plant community (Schmitz 2003; Crutsinger et al. 2008).

In April 2004, 72 plots (3 × 3 m, including a 0.5-m buffer around each plot) were established within an existing old-field community, with 2-m spacing between plots. In the first 2 years of the study, we also manipulated propagule supply of an invasive plant species, *Lespedeza cuneata*, in 36 of the original 72 plots; here, we do not include those 36 plots in our analyses because of the potential effects of that species on the response variables of interest in this study. A 3-m-tall fence was erected around the experimental site to exclude deer. In a fully crossed, completely randomized plot design, we manipulated soil nitrogen (N) and the abundance of insects in randomly assigned plots. We manipulated soil N by (1) adding N (applied as urea fertilizer, at a rate of 20 g m^{-2} $year^{-1}$), (2) adding carbon (C) (applied as sucrose at a rate of 167 g m^{-2} $year^{-1}$) and (3) unmanipulated control plots. Nitrogen manipulation rates in our experiment are similar to other studies addressing the role of N fertilization on dynamics in grasslands and old fields (McLendon and Redente 1992; Larson and Siemann 1998). The addition of C in the form of sucrose provides microbial communities with a surplus source of labile C ultimately leading to N immobilization (Wang et al. 2004; Craine et al. 2007). In 2005, 1 year after the first application of the nutrient treatments, soil N availability (NO_3-N + NH_4-N) in the soil was 2× greater in the N addition plots (11.69 ± 1.00 ppm), and 5× lower in the N reduction plots (1.17 ± 1.00 ppm) than in the control plots (6.80 ± 0.84 ppm) ($P < 0.0001$). Urea additions increased both NO_3-N and NH_4-N ($P < 0.0001$), but sucrose additions decreased NO_3-N ($P < 0.0001$) and had no effect on NH_4-N ($P = 0.50$) (Sanders et al. 2007). Similar effects of urea and sucrose on soil have been observed in other field studies (Wilson and Gerry 1995; Morghan and Seastedt 1999). Nitrogen availability in the nitrogen addition plots was consistently higher than either the control or sucrose addition plots.

We manipulated the abundance of insects at two levels: (1) unmanipulated controls (in which insects were present) and (2) the reduction of insects. Insects were reduced by permethrin insecticide (Hi-Yield Kill-A-Bug; Voluntary Purchasing Group, Bonham, TX, USA) applied with a backpack sprayer at a rate of 0.23 L m^{-2} every 2–3 weeks during the growing season. The use of pyrethroid-based insecticides effectively reduced insect abundance, as in other studies (Root 1996; Schmitz 2006). When we sampled the plots using a combination of sweep-netting, vacuum sampling, and visual scanning, we found that insect abundance was on average 4× lower in the insect reduced plots (6.6 individuals m^{-2}) relative to the control plots (28.4 individuals m^{-2}; Sanders et al. 2007). Based on observations at the field site since 2004 (Lane 2006; Sanders et al. 2007), and detailed studies on plant–insect interactions conducted at the site (Crawford et al. 2007), we are confident that herbivores were by far the most abundant trophic group. For example, Lane (2006) surveyed the insect community for 2 years using a series of standard techniques, and Crawford et al. (2007) performed intensive surveys for herbivorous arthropods on several key plant taxa in the system. Additionally, of the insect taxa that were most frequently detected in the insect reduced plots, only one was a herbivore—an aphid that proved difficult for us to

remove or reduce using the insecticide treatment and vacuum sampler. Finally, several pilot experiments demonstrated that neither plant growth nor NO_3-N and NH_4-N in the soil solution differed between insect reduced and control plots (Sanders et al. 2007).

We determined the aboveground biomass at the end of the growing season of 2009 (September) by randomly placing a 0.5 m × 1 m quadrat within each experimental plot. We clipped aboveground biomass within each 0.5-m^2 quadrat to ground level and then categorized the clipped biomass as dominant species (i.e., *Solidago altissima*, *Verbesina* spp.), the invasive species *Lespedeza cuneata*, or subdominant species (combined all other species). We oven-dried the clipped biomass at 60°C for approximately 36 h and then weighed the samples to the nearest 0.1 g.

We assessed root production over the growing season of 2009 using root ingrowth core methods (Cuevas and Medina 1983; Steen 1984). We removed roots from a volume of soil prior to the growing season and the re-growth of roots into the root-free soil was measured after 15 weeks (Lauenroth 2000; Bessler et al. 2009). Root ingrowth cores (5 cm diameter × 15 cm depth) were established in May, at the beginning of the growing season and removed in August. Roots were extracted from cores using a hydropneumatic elutriator, and a 250-μm sieve. We scanned roots using Win Rhizo Pro v. 2008a (1993–2008; Regent Instruments) and recorded total root production as well as root diameter. We further portioned total root production into two categories, fine roots (those <2 mm in diameter) and coarse roots (those >2 mm in diameter). Smaller diameter roots have higher surface area to volume ratios; thus, we assume that differential responses of root diameters in the same volume of soil could indicate a shift in nutrient uptake by the plant community from the soil (Eissenstat 1992). In addition, we oven-dried all roots at 60°C for approximately 48 h, and all biomass data are presented as g dry mass per m^{-2}. We did not obtain belowground production data for one plot (a N addition, insects removed plot).

Statistical analyses

We analyzed the main and interactive effects of nutrient manipulations and insect herbivory (as fixed effects), using independent two-way analysis of variance (ANOVA) models on the following response variables: total aboveground biomass, biomass of the dominant species, biomass of subdominant species, total belowground biomass, fine (<2 mm) root biomass and coarse root (>2 mm) biomass. The nutrient × herbivore removal was not significant for any of the response variables examined here. We then used a post-hoc Dunnett's test to compare each of the treatment means to the control mean. All response variables were log-transformed prior to analyses to improve normality, but we show untransformed values in all figures. We conducted all analyses in JMP 7.0.1.

Table 1 Results from analysis of variance examining the effects of nitrogen manipulation, the presence of insects, and their interaction on log-transformed total aboveground biomass of the plant community, log-transformed aboveground biomass of dominant species (*Solidago altissima* and *Verbesina* spp.), and log-transformed biomass of subdominant plant species

Factor	*df*	SS	*F*	*P*
Total aboveground biomass				
Nutrients	2	5.585	6.876	0.003
Insects	1	0.006	0.014	0.906
Nutrient × insects	2	0.177	0.218	0.805
Error	30			
Aboveground biomass of dominant species				
Nutrients	2	2.942	2.476	0.100
Insects	1	0.660	1.110	0.300
Nutrient × insects	2	0.462	0.389	0.681
Error	30			
Aboveground biomass of subdominant species				
Nutrients	2	9.253	3.091	0.060
Insects	1	6.942	4.638	0.039
Nutrient × insects	2	0.587	0.196	0.823
Error	30			

Results

Aboveground biomass

Overall, we found a significant effect of soil N manipulation on total aboveground biomass and on the biomass of the subdominant plant species, while insect herbivory decreased the aboveground biomass of subdominant species (Table 1). Total aboveground biomass was more than 2× greater in the N addition and control plots than in the N reduction plots (Fig. 1a). The aboveground biomass of dominant plant species was nearly 2× higher in both N addition plots and control plots relative to N reduction plots, but the result was only marginally statistically significant ($P = 0.10$; Fig. 1b; Table 1). Aboveground biomass of subdominant species was more than 3× higher in the N addition and control plots than in the N reduction plots ($P = 0.06$; Fig. 1b; Table 1).

There were no significant nutrient × herbivore removal interactions on any response variable. Herbivore reduction did not have a significant effect on total aboveground biomass (Fig. 2a; Table 1). Insects did not alter the aboveground biomass of dominant species (Fig. 2b; Table 1). In addition, the biomass of subdominant species

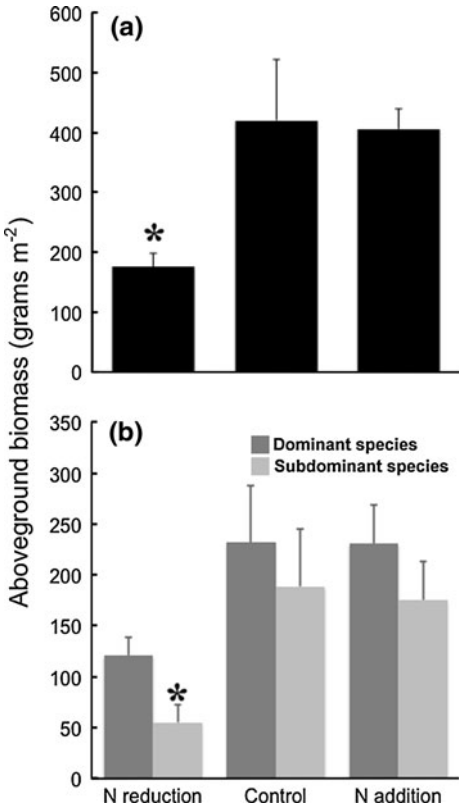

Fig. 1 The effect of nitrogen (N) manipulation on **a** total aboveground biomass and **b** biomass of dominant and subdominant species. *Bars* mean (+SE). In (**a**), the *asterisk* indicates that the mean biomass in N reduction plots differed from the control mean according to a Dunnett's post-hoc test. In (**b**), the *asterisk* indicates that the mean aboveground biomass of subdominant species was significantly lower in the N reduction plots than was the biomass of subdominant species in the control plots

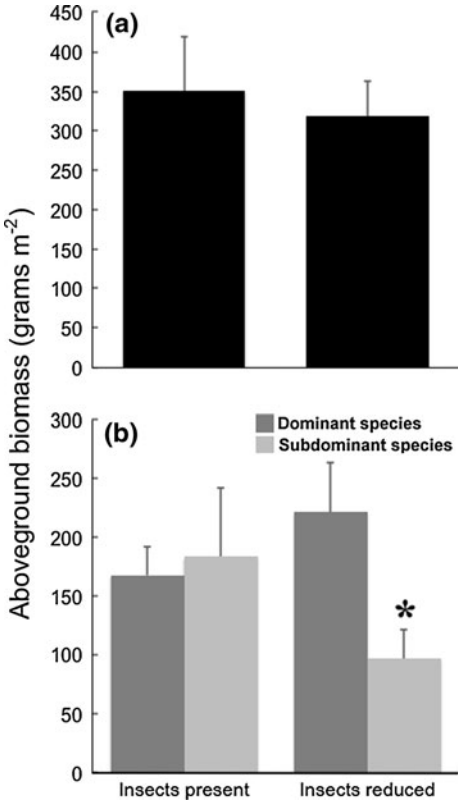

Fig. 2 The effect of reductions in insects on **a** total aboveground biomass and **b** biomass of dominant and subdominant species. *Bars* mean (+SE). In (**b**), the *asterisk* indicates that the biomass of subdominant species was significantly lower than the biomass of subdominant species when insects were present, according to a post-hoc Dunnett's test

was 1.9× greater in plots where insects were present relative to where they were removed ($P = 0.04$; Fig. 2b; Table 1).

Belowground biomass production

Total belowground biomass produced and the biomass of both coarse and fine roots produced responded to nutrient manipulations while insect herbivory affected only the production of coarse root biomass. Total belowground biomass production was approximately 1.7× greater in the N addition than in the N reduction plots, and nearly 2× higher in control plots relative to the N reduction plots ($P = 0.006$) (Fig. 3b; Table 2). Coarse root production was approximately 2× greater in the N addition and control plots than in the N reduction plots (Fig. 2b; Table 2). In addition, fine root production was 1.6× and more than 2× greater in the N addition and control plots, respectively, than in the N-reduction plots (Fig. 3b; Table 2). The proportion of coarse and fine roots did not differ among treatments; across all treatments coarse roots made up ~25% of the belowground biomass and fine roots made up ~75% of the total belowground biomass produced.

Insect herbivory did not influence total belowground biomass or fine root production, but did influence coarse root production (Fig. 4a; Table 2), though in every case there were trends suggesting that root production was higher when insects were removed than when they were present. However, this relationship was only significant for coarse root production, where the production of coarse roots was approximately 1.7× greater when insects were removed relative to when they were present (Fig. 4b). In contrast to the effect of nutrients on coarse and fine root production, the proportions of the total biomass contributed by coarse and fine roots did depend on whether insects were reduced ($P = 0.02$). When insects were present, coarse roots made up, on average, 21.8% of the total belowground production, but when insects were reduced, coarse roots made up approximately 27% of the belowground production. In no case was there a significant nutrient × herbivore removal interaction on the production of total belowground biomass, coarse root biomass, or fine root biomass (Table 2).

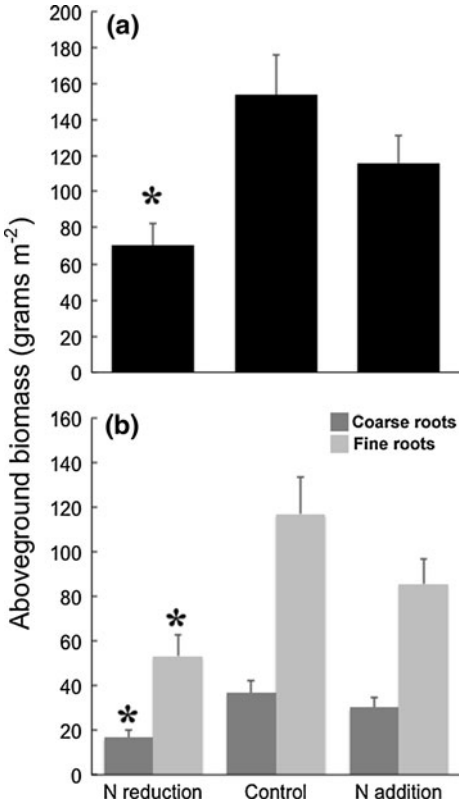

Fig. 3 The effect of nitrogen (N) manipulation on **a** total belowground biomass and **b** biomass of coarse and fine roots. *Bars* mean (+SE). In (**a**), the *asterisk* indicates that the mean total belowground biomass produced in N reduction plots differed from the control mean according to a Dunnett's post-hoc test. In (**b**), the *asterisk* indicates that the mean belowground biomass of coarse roots and fine roots produced differed from the respective mean biomass produced in the control plots

Discussion

There was no statistical interaction between top-down and bottom-up processes for any of the belowground or aboveground response variables in this old-field ecosystem. Put another way, the effects of herbivory did not depend on N availability in the soil, or vice versa, a result largely consistent with previous studies (Gruner et al. 2008). Instead, we found that bottom-up process (i.e., nutrient availability) shaped total aboveground biomass and biomass of subdominant species in this old-field ecosystem. In addition, bottom-up processes altered total belowground biomass production, coarse root, and fine root production. Top-down processes, herbivory by insects, led to higher aboveground biomass of subdominant plant species and reduced coarse root production. Interestingly, and in contrast to our expectations, the effects of nutrient manipulation were mostly in the N reduction plots indicating that ambient levels of soil N do not limit production (i.e., fertilization did not significantly increase biomass) in this ecosystem.

Table 2 Results from analysis of variance examining the effects of nitrogen manipulation, the presence of insects, and their interaction on log-transformed total root biomass, log-transformed coarse root biomass, and log-transformed fine root biomass

Factor	*df*	SS	*F*	*P*
Total root biomass				
Nutrients	2	5.191	6.268	0.005
Insects	1	0.779	1.882	0.181
Nutrient × insects	2	0.398	0.481	0.623
Error	29			
Coarse root biomass				
Nutrients	2	6.501	5.881	0.007
Insects	1	3.195	5.780	0.023
Nutrient × insects	2	0.413	0.373	0.692
Error	29			
Fine root biomass				
Nutrients	2	5.145	5.675	0.008
Insects	1	0.444	0.980	0.330
Nutrient × insects	2	0.537	0.593	0.559
Error	29			

Bottom-up effects

The strongest overall effects of the study were apparent in the N reduction plots (i.e., bottom-up effects). Interestingly, aboveground biomass in the N addition plots did not differ from aboveground biomass in the control plots, suggesting that biomass production in this ecosystem is not primarily N limited. Root biomass was not lower in N added plots than in the control plots. We would predict that if N availability limited production, then once N was elevated, plant biomass would increase. But this was not the case in this study; instead root production was lower when soil N was reduced than it was in either the control or N addition plots. In addition, previous research in a nearby old-field ecosystem demonstrated that symbiotic N-fixation rates in local old fields can be quite high and the entire plant community can indirectly benefit via reduced community demands on soil N supplies (Garten et al. 2008). Given the increase in soil N from fixation, it is possible that biomass production in this old-field ecosystem may be primarily limited by a nutrient other than N, such as phosphorus.

Dominant species are known to affect the structure of plant communities, mainly by suppressing the establishment and/or success of subdominant species (Wardle and Barker 1997; Wardle et al. 1999; Diaz et al. 2003). Nutrient availability may promote the effect of dominant biomass on subdominant species by shifting competitive dynamics and ultimately altering community structure. In our study, experimentally reducing N availability had no effect on the biomass

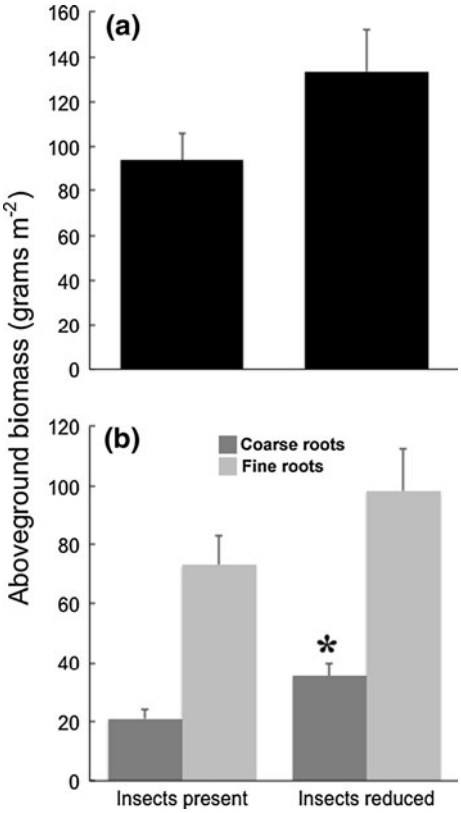

Fig. 4 The effect of reductions in insects on **a** total belowground biomass and **b** the biomass of coarse and fine roots produced. *Bars* mean (+SE). In (**b**), the *asterisk* indicates that the mean biomass of coarse roots produced was significantly higher than the mean biomass of the plots in which insects were present, according to a post-hoc Dunnett's test

of competitively dominant species, but significantly reduced the aboveground biomass of subdominant species. One possible explanation is that in the N-limited plots, the cover and biomass of an N-fixing invasive plant species, *Lespedeza cuneata*, increases relative to control plots (Sanders et al. 2007). In fact, recent studies have shown that *Lespedeza cuneata* outcompetes both native dominant and subdominant species under N-limitation (Brandon et al. 2004, Allred et al. 2010). Indeed, the greater foliar cover of *Lespedeza cuneta* in N-reduced plots ($P = 0.04$) compared to N-added plots could have contributed towards the decline of subdominant species in N-reduced plots (note that the biomass of *L. cuneata* is not included in any of our estimates of subdominant biomass). Likewise, lower foliar cover of *Lespedeza cuneta* in N-added plots compared to N-reduced plots could have contributed towards greater biomass of subdominant species in N-added plots.

Top-down effects

Insect herbivory can influence plant biomass production and community structure (Coupe and Cahill 2003; Scherber et al. 2006; Unsicker et al. 2006; Schädler et al. 2008; Stein et al. 2010). However, we found no significant effects of insect herbivory on total aboveground biomass or on the biomass of dominant plant species. But we did find that, when insects were present, the biomass of subdominant species was nearly twice as high as when they were absent. Because aboveground herbivores often preferentially select high quality host plants, they can have dramatic effects on biomass of particular species (Hunter 2001), but still have little or no effect on total aboveground biomass of the entire plant community (e.g., Stein et al. 2010). Gruner et al. (2008) listed several reasons why the effects of herbivory on total aboveground biomass may be weak relative to nutrient manipulation. First, herbivores may have been limited by their own predators or by intraguild processes, which might be more common in high productivity environments (Oksanan and Okasanen 2000). Second, some degree of compensation for herbivory, either by individual plant species or by the entire community, may occur such that if the biomass of one species goes down, the biomass of another (or others) increases. Third, taxa other than aboveground herbivorous insects (e.g., gastropods, voles, belowground herbivores) may consume more biomass in this ecosystem, and they were likely not affected by our treatments. Distinguishing among these possibilities would require experiments that, to our knowledge, have yet to be conducted in any system.

Our intent is not to downplay the role of insect herbivores as influences on plant communities, because numerous studies have shown that they can affect plant population dynamics, alter the dynamics of competing species, and reduce total aboveground biomass (Crawley 1983; Tscharntke and Greiler 1995; Coupe and Cahill 2003). Though we found no effect of insect herbivory on total aboveground biomass, we predicted that herbivory would differentially affect the aboveground biomass of dominant and subdominant species in this ecosystem. This would especially be the case if herbivores selectively targeted dominant species, releasing subdominant species from competitive exclusion (Schmitz 2003). However, we found that insect herbivory did not affect biomass of dominant species but instead led to increases in the biomass of subdominant species relative to plots where insects were reduced, similar to results in previous studies (Carson and Root 2000; Schädler et al. 2008). If the biomass of subdominant species increases, but the biomass of dominant species does not decrease, then overall biomass has to be higher when herbivores are present. But we found no effect of herbivores on total biomass or on the biomass of dominant species. One possibility is that herbivores could have reduced the biomass of particular dominant species (such as *Solidago altissima*), which has an especially strong effect on the biomass of subdominant species in this system

(Souza et al. 2011). Unfortunately, our data do not allow us to test this compelling hypothesis.

Numerous studies have shown that vertebrate herbivores can affect root production (reviewed by Bardgett et al. 1998), but fewer have examined the effects of insect herbivory (Kaplan et al. 2008; Olson et al. 2008; Schädler et al. 2008, Coupe et al. 2009). Insect herbivory may serve as a stimulus for re-translocating nutrients from aboveground shoot production to belowground root production (Dyer and Bokhari 1976). Alternatively, Brown (1994) found that foliar grazing by a chrysomelid beetle decreased root biomass, and Coupe et al. (2009) found that insect herbivory reduced the production of small, deep roots but did not affect shallow root production after 5 years. In our study, insect herbivory did not affect total belowground biomass production or fine root production, but it did lead to a decrease in coarse root production. These results are congruent with work on a single species—*Eucalyptus globulus*—which showed that herbivory aboveground can lead to reduced biomass production of coarse roots belowground (Eyles et al. 2009). One potential explanation is that when photosynthate aboveground is lost to herbivores, resources are reallocated from belowground tissues, such as coarse roots, to aboveground tissues to compensate the loss of photosynthate aboveground (Marshall and Waring 1985). Tissue loss due to aboveground herbivory can result in compensatory response, most noticeably observed in reduced biomass allocation to coarse roots due to a greater energy needed for coarse root production relative to fine root production (Marshall and Waring 1985).

Conclusions

In this study, reducing the availability of soil N reduced total aboveground biomass and belowground production of both coarse and fine roots. Insect herbivory increased the biomass of subdominant species and decreased the biomass of coarse roots. It appears that, in this old-field ecosystem at least, bottom-up processes dominated plant production, and herbivory by insects had subtle, but detectable, effects on both aboveground biomass and belowground production. Limited studies to date have explored the long-term effects of soil N availability in concert with insect herbivory on plant productivity. Thus, further research is needed to tease apart how bottom-up and top-down processes may interact (or may not) under different resource manipulations, and with different suites of herbivores across ecosystems. One possibility is that perhaps there are no generalities among systems in the interactions between foliar herbivory aboveground and the effects of nutrient availability belowground.

Acknowledgments We thank Phillip Allen, Jacqueline Areson, Lauren Breza, Claire Brown, Windy A. Bunn, Karianne Chung, Melissa Cregger, Cavenne Engle, Colleen Iversen, Jean-Philippe Lessard, Laura Marsh, Martin Nuñez, Mariano Rodriguez-Cabal, Noelia Barrios, Tara Sackett, Tander Simberloff, Haley Smith, Katie Stuble, Heather Tran, Jeramy Webb, Jake Weltzin, and Phoebe Wright for help with field and laboratory work. Jake Weltzin was integral in establishing the experiment. The experiments described here complied with the current laws of the US. The work was partially supported by grants from Department of Ecology and Evolutionary Department at the University of Tennessee to J.B.

References

Allred BW, Fuhlendorf SD, Monaco TA, Will RE (2010) Morphological and physiological traits in the success of the invasive plant *Lespedeza cuneata*. Biol Invasions 12:39–49

Bardgett RD, Wardle DA, Yeates GW (1998) Linking aboveground and belowground interactions: how plant responses to foliar herbivory influence soil organisms. Soil Biol Biochem 30:1867–1878

Bardgett RD, Bowman WD, Kaufmann R, Schmidt SK (2005) A temporal approach to linking aboveground and belowground ecology. Trends Ecol Evol 20:634–641

Bessler H, Temperton VM, Roscher C, Buchmann N, Schmid B, Schulze E, Weisser W, Engels C (2009) Aboveground overyielding in grassland mixtures in associated with reduced biomass partitioning to belowground organs. Ecology 90:1520–1530

Borer ET, Halpern BS, Seabloom EW (2006) Asymmetry in community regulation: effects of predators and productivity. Ecology 87:2813–2820

Brandon AL, Gibson DJ, Middleton BA (2004) Mechanisms for dominance in an early successional old field by the invasive non-native *Lespedeza cuneata* (Dum. Cours.) G. Don. Biol Invasions 6:483–493

Brown DG (1994) Beetle folivory increases resource availability and alters plant invasion in monocultures of goldenrod. Ecology 75:1673–1683

Buckland SM, Grime JP (2000) The effects of trophic structure and soil fertility on the assembly of plant communities: a microcosm experiment. Oikos 91:336–352

Canadell J, Jackson RB, Ehleringer JR, Mooney HA, Sala OE, Schulze ED (1996) Maximum rooting depth of vegetation types at the global scale. Oecologia 108:583–595

Carson WP, Root RB (2000) Herbivory and plant species coexistence: community regulation by an outbreaking phytophagous insect. Ecol Monogr 70:73–99

Chapman SK, Hart SC, Cobb NS, Whitham TG, Koch GW (2003) Insect herbivory increases litter quality and decomposition: an extension of the acceleration hypothesis. Ecology 84:2867–2876

Classen AT, Chapman SK, Whitham TG, Hart SC, Koch GW (2007) Genetic-based plant resistance and susceptibility traits to herbivory influence needle and root litter nutrient dynamics. J Ecol 95:1181–1194

Cleland EE, Harpole WS (2010) Nitrogen enrichment and plant communities. Ann NY Acad Sci 1195:46–61

Collins SL et al (2008) Rank clocks and plant community dynamics. Ecology 89:3534–3541

Coupe MD, Cahill JF (2003) Effects of insects on primary production in temperate herbaceous communities: a meta-analysis. Ecol Entomol 28:511–521

Coupe MD, Stacey JN, Cahill JF (2009) Limited effects of aboveground and belowground insects on community structure and function in a species-rich grassland. J Veg Sci 20:121–129

Craine JM, Reich PB, Tilman D, Ellesworth D, Fargione J, Knops J, Naeem S (2003) The role of plant species in biomass production and response to elevated CO_2 and N. Ecol Lett 6:623–630

Craine JM, Morrow C, Fierer N (2007) Microbial nitrogen limitation increases decomposition. Ecology 88:2105–2113
Crawford KM, Crutsinger GM, Sanders NJ (2007) Host-plant genotypic diversity mediates the distribution of an ecosystem engineer. Ecology 88:2114–2120
Crawley MJ (1983) Herbivory: the dynamics of animal–plant interactions. Blackwell, Oxford
Crutsinger GM, Souza L, Sanders NJ (2008) Intraspecific diversity and dominant genotypes resist plant invasions. Ecol Lett 11:16–23
Cuevas E, Medina E (1983) Root production and organic matter decomposition in a tierra firme forest of the upper Rio Negro basin. In: Bohm W, Kutshera L, Lichtenberger E, Gumpenstein V (eds) Root ecology and its practical application. Gumpernstein, Austria. pp 653–666
Cyr H, Pace ML (1993) Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. Nature 361:148–150
Del-Val E, Crawley MJ (2005) What limits herb biomass in grasslands: competition or herbivory. Oecologia 142:202–211
Diaz S, Symstad AJ, Chapin FS, Wardle DA, Huenneke LF (2003) Functional diversity revealed by removal experiments. Trends Ecol Evol 18:140–146
Dyer MI, Bokhari UG (1976) Plant-animal interactions: studies of the effects of grasshopper grazing on blue grama grass. Ecology 57:762–772
Eissenstat DM (1992) Costs and benefits of constructing roots of small diameter. J Plant Nutr 15:763–782
Elton CS (1927) Animal ecology. Sidgwick and Jackson, London
Eyles A, Pinkard EA, Mohammed C (2009) Shifts in biomass and resource allocation patterns following defoliation in *Eucalyptus globulus* growing with varying water and nutrient supplies. Tree Phyl 29:753–764
Gao Y, Wang D, Ba L, Bai Y, Liu B (2008) Interactions between herbivory and resource availability on grazing tolerance of *Leymus chinensis*. Environ Exp Bot 63:113–122
Garten CT Jr, Classen AT, Norby RJ, Brice DJ, Weltzin JF, Souza L (2008) Role of N_2-fixation in constructed old-field communities under different regimes of [CO_2], temperature, and water availability. Ecosystems 11:125–137
Gruner DS, Smith JE, Seabloom EW, Sandin SA, Ngai JT, Hillebrand H, Harpole WS, Elser JJ, Cleland EE, Bracken MES, Borer ET, Bolker BM (2008) A cross-system synthesis of consumer and nutrient resource control on producer biomass. Ecol Lett 11:740–755
Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. Am Nat 94:421–425
Hillebrand H, Gruner DS, Borer ET, Bracken MES, Cleland EE, Elser JJ, Harpole WS, Ngai JT, Seabloom EW, Shurin JB, Smith JE (2007) Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. Proc Natl Acad Sci USA 104:10904–10909
Hooper DU, Chapin FS III, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge D, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35
Hunter MD (2001) Insect population dynamics meets ecosystem ecology: effects of herbivory on soil nutrient dynamics. Agric For Entomol 3:77–84
Kaplan I, Halitschke R, Kessler A, Rehill BJ, Sardanelli S, Denno RF (2008) Physiological integration of roots and shoots in plant defense strategies links aboveground and belowground herbivory. Ecol Lett 8:841–851
Kohyani PT, Bossuyt B, Bonte D, Hoffmann M (2009) Differential herbivory tolerance of dominant and subordinate plant species along gradients of nutrient availability and competition. Plant Ecol 201:611–619
Lane KE (2006) The structure and dynamics of arthropod communities in an old-field ecosystem. Thesis, Humboldt State University, Arcata
Larson JL, Siemann E (1998) Legumes may be symbiont-limited during old-field succession. Am Midl Nat 140:90–95
Lauenroth WK (2000) Methods of estimating belowground net primary production. In: Sala OE, Jackson RB, Mooney HA, Howarth RW (eds) Methods in ecosystem science. Springer, New York, pp 58–69
LeBauer DS, Treseder KK (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems in globally distributed. Ecology 89:371–379
Maron JL, Crone E (2006) Herbivory: effects on plant abundance, distribution and population growth. Proc R Soc Lond B 273:2575–2584
Marshall JD, Waring RH (1985) Predicting fine root production and turnover by monitoring root starch and soil temperature. Can J For Res 15:791–800
McLendon T, Redente EF (1992) Effects of nitrogen limitation on species replacement dynamics during early secondary succession on a semiarid sagebrush site. Oecologia 91:312–317
Morghan KJR, Seastedt TR (1999) Effects of soil nitrogen reduction on nonnatibe plants in restored grasslands. Restor Ecol 7:51–55
Nadelhoffer KJ (2000) The potential effects of nitrogen deposition on fine-root production in forest ecosystems. New Phytol 147:131–139
Nishida T, Izumi N, Katayama N, Ohgushi T (2009) Short-term response of abuscular mycorrhizal association to spider mite herbivory. Popul Ecol 51:329–334
Oksanan L, Okasanen T (2000) The logic and realism of the hypothesis of exploitation ecosystems. Am Nat 155:703–723
Olson DM, Davis RF, Wackers FL, Rains GC, Potter T (2008) Plant-herbivore-carnivore interactions in cotton, Gossypium hirsutum: linking belowground and aboveground. J Chem Ecol 10:1341–1348
Phillips DH, Foss JE, Stiles CA, Trettin CC, Luxmoore RJ (2001) Soil-landscape relationships at the lower reaches of a watershed at Bear Creak near Oak Ridge, Tennessee. Castena 44:205–222
Power ME (1992) Top-down and bottom-up forces in foodwebs: do plants have primacy? Ecology 73:733–746
Pucheta E, Bonamici I, Cabido M, Diaz S (2004) Belowground biomass and productivity of a grazed site and a neighboring ungrazed exclosure in a grassland in central Argentina. Austral Ecol 29:201–208
Root RB (1996) Herbivore pressure on goldenrods (*Solidago altissima*): its variation and cumulative effects. Ecology 77:1074–1087
Sanders NJ, Weltzin JF, Crutsinger GM, Fitzpatrick MC, Nuñez MA, Oswalt CM, Lane KE (2007) Insects mediate the effects of propagule supply and resource availability on a plant invasion. Ecology 89:2383–2391
Schädler M, Alphei J, Scheu S, Brandl R, Auge H (2004) Resource dynamics in an early-successional plant community are influenced by insect exclusion. Soil Biol Biochem 36:1817–1826
Schädler M, Rottstock T, Brandl R (2008) Do nutrients and invertebrate herbivory interact in an artificial plant community? Basic Appl Ecol 9:550–559
Schenk HJ, Jackson RB (2002) The global biogeography of roots. Ecol Monogr 72:311–328
Scherber C, Mwangi PN, Temperton VM, Roscher C, Schumacher J, Schmid B, Weisser WW (2006) Effects of plant diversity on invertebrate herbivory in experimental grassland. Oecologia 147:489–500
Schmitz OJ (2003) Top predator control of plant biodiversity and productivity in an old field ecosystem. Ecol Lett 6:156–163
Schmitz OJ (2006) Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. Ecology 87:1432–1437

Sih A, Crowley P, McPeek M, Petranka J, Strohmeier K (1985) Predation, competition, and prey communities: a review of field experiments. Annu Rev Ecol Syst 16:269–311

Souza L, Weltzin JF, Sanders NJ (2011) Differential effects of two dominant plant species on community structure and invasibility in an old field ecosystem. J Plant Ecol 3 (in press)

Steen E (1984) Variation of root growth in a grass ley studied with a mesh bag technique. Swed J Agric Res 14:93–97

Stein C, Unsicker SB, Kahmen A, Wagner M, Audorff V, Auge H, Prati D, Weisser WW (2010) Impact of invertebrate herbivory in grasslands depends on plant species diversity. Ecology 91:1639–1650

Throop HL (2005) Nitrogen deposition and herbivory affect biomass production and allocation in an annual plant. Oikos 111:91–100

Tscharntke T, Greiler HJ (1995) Insect communities, grasses, and grasslands. Annu Rev Entomol 40:535–558

Unsicker SB, Baer N, Kahmen A, Wagner M, Buchmann N, Weisser (2006) Invertebrate herbivory along a gradient of plant species diversity in extensively managed grasslands. Oecologia 150:233–246

Van der Putten WH, Vet LEM, Harvey JA, Wackers FL (2001) Linking aboveground and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. Trends Ecol Evol 16:547–554

Wang WJ, Baldocka JA, Dalala RC, Moody PW (2004) Decomposition dynamics of plant materials in relation to nitrogen availability and biochemistry determined by NME and wet-chemical analysis. Soil Biol Biochem 36:2045–2058

Wardle DA, Barker GA (1997) Competition and herbivory in establishing grassland communities: implications for plant biomass, species diversity and soil microbial activity. Oikos 80:470–480

Wardle DA, Bonner KI, Barker GM, Yeates GW, Nicholson KS, Bardgett RD, Watson RN, Ghani A (1999) Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. Ecol Monogr 69:535–568

Wardle DA, Bonner KI, Barker GM (2000) Stability of ecosystem properties in response to abovegroundground functional group richness and composition. Oikos. 89:11–23

Wardle DA, Bardgett RD, Klironomos JN, Setälä H, Van der Putten WH, Wall DH (2004) Ecological linkages between aboveground and belowground biota. Science 304:1629–1633

Wedin D, Tilman D (1993) Competition among grasses along nitrogen gradient- initial conditions and mechanisms of competition. Ecol Monogr 173:199–229

Wilson SD, Gerry AK (1995) Strategies for mixed-grass prairie restoration: Herbicide, tilling, and nitrogen manipulation. Restor Ecol 3:290–298

Worm B, Lotze HK, Hillebrand H, Sommer U (2002) Consumer versus resource control of species diversity and ecosystem functioning. Nature 417:848–851