To the Graduate Council:

I am submitting herewith a thesis written by Jarrod Dwayne Blue entitled “Soil nitrogen amendments and insect herbivory alter above-and belowground plant biomass in an old-field ecosystem”. I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology and Evolutionary Biology.

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Soil nitrogen amendments and insect herbivory alter above-and belowground plant biomass in an old-field ecosystem

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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 I investigate how nitrogen availability and insect herbivory interact to alter above- and belowground plant community biomass in an old-field ecosystem. In 2004, 36 experimental plots were established in which soil nitrogen (N) availability (at three levels) was manipulated and insect abundance (at two levels) in a completely randomized plot design. In 2009, after six years of treatment, I measured aboveground biomass and assessed root production at peak growth. Overall, I found a significant effect of soil N availability on both above- and belowground plant biomass while insects affected only aboveground biomass of subdominant plant species and coarse root production; there were no statistical interactions between N availability and insect herbivory for any response variable. 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 primarily limiting production in this ecosystem. Insect herbivory altered the aboveground biomass of the subdominant plant species and altered allocation patterns to coarse root production belowground. Overall, the results of six years of nutrient amendments and insect removals suggest strong bottom-up influences on total plant community productivity.

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This Thesis is prepared in manuscript format for future submission to the journal Oecologia, with coauthors Lara Souza, Aimee Classen, Jennifer Schweitzer, and Nathan Sanders. I completed all fieldwork. Lara Souza and Nathan Sanders supervised the project. Aimee Classen and Jennifer Schweitzer provided research concept feedback.

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. 2003; 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 2007; Gruner et al. 2008; Kohyani et al. 2009). In particular, bottom-up factors such as the addition or reduction of nitrogen (N) can result in dramatic increases in total aboveground biomass (Craine et al. 2003; Gruner et al. 2008) likely resulting from N limitation across ecosystems (LeBauer and Treseder 2006). Conversely, reducing N availability in the soil can lead to reductions in total aboveground biomass (Wedin and Tilman 1993; Throop et al. 2005). Herbivores, especially large mammals, can exert top-down control aboveground plant biomass by consuming plant biomass (Maron and Crone 2006; Gruner et al. 2008). Indeed, some 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), with some studies indicating that herbivory by insects reduces aboveground biomass (Schowalter 2000; McIntire and Hik 2005). A meta-analysis by Coupe and Cahill (2003) suggested that, on average, insects reduce primary

production 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 total aboveground biomass (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 affect total aboveground biomass 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 amendment 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 amendment on producer biomass, only one study focused on herbivory by invertebrates (a slug and a grass aphid). That study by 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 amendment on total aboveground biomass of intact plant communities in the field.

Another important, but often overlooked, aspect of many studies that have examined the effects of herbivory and nutrient amendment on producer biomass is belowground biomass, which, in some ecosystems, can account for >50% of total plant biomass (Candell et al. 1996; Schenk and Jackson 2002). One recent study looking at increased soil N availability on *Festuca campestris* found that fertilization led to higher root production, specifically higher investment in coarse roots relative to fine roots, indicative of root exploration for nutrients (McInenly et al. 2010).

In terrestrial ecosystems, root production often declines with foliar herbivory because tissue loss can result in reallocation of nutrients towards aboveground biomass for tissue regrowth (Brown 1994; Schadler et al. 2004). Other studies, however, have found that foliar herbivory can increase root productivity (Bardgett et al. 1998; Pucheta et al. 2004) and alter root turnover and nutrient release (Classen et al. 2007). For example, herbivory by spider mites increased root biomass in a nutrient rich environment (Nishida et al. 2009). However, the effects of nutrient amendment and aboveground herbivory on belowground biomass of entire plant communities in the field has been under 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 amendments (Van der Putten et al. 2001; Wardle et al. 2004). For example, increased abundance of root feeding insects enhanced nutrition quality of aboveground plant tissue, whereas increased abundance of aboveground insect herbivores reduced

belowground plant quality (Masters and Brown 1997). Moreover, while a growing number of studies have examined how aboveground processes, such as herbivory, might influence belowground processes, no studies to date have examined the relative and combined effects of foliar herbivory and nutrient availability on belowground biomass (Bardgett et al. 2005). Furthermore, nutrient amendments and insect herbivory can alter species interactions and overall plant community composition 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.

After six years of manipulating soil N (at three levels) and insect herbivory (at two levels) in an old-field ecosystem, I examined the effect of soil N fertilization, insect herbivory, and their interactive effects on above- and belowground biomass of the entire plant community as well as specific components of the aboveground community. Given that most plants are nutrient limited and that herbivores can consume approximately 15% of total plant NPP, I hypothesized that (*i*) total aboveground biomass would increase with fertilization but decrease with herbivory; (*ii*) total aboveground biomass would increase with fertilization only when herbivory was reduced; (*iii*) total belowground biomass would be reduced with fertilization and herbivory due to shifts in nutrient allocation; and (*iv*) dominant and subdominant plant species would respond differentially to fertilization and herbivory.

MATERIAL AND METHODS

A field experiment was established 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. And since 2003, many of the fields 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 1322 mm, an average January minimum temperature of 2.7°C, and average July maximum temperature of 31.2°C. Dominant plant species (those that comprise the greatest proportion of the biomass) at the site include *Solidago altissima*, *Verbesina occidentalis*, and *Verbesina virginica* (Wardle 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, Souza et al. (In review) 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 and other experiments have shown that *Solidago* species can have strong effects on the rest of the plant community (Schmitz 2003; Crustinger et al. 2008). Second, 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. In Review). Approximately 60 other sub-dominant plant species, both herbaceous and woody, are present at the site (Sanders et al. 2007; Table 1; all Figures and Tables in Appendix 1).

In April 2004, 36 plots (3 m × 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 (Note: in the

first two years of the study, propagule supply of an invasive plant species, *Lespedeza cuneata*, in 36 of the original 72 plots was manipulated; here I do not include those 36 plots in 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, soil N was manipulated and the presence of insects in randomly assigned plots. Soil N was manipulated by (1) adding N (applied as urea fertilizer, at a rate of 20 g m^{-2} yr^{-1}), (2) adding carbon (C) (applied as sucrose at a rate of 167 g m^{-2} yr^{-1}) and (3) unmanipulated control plots. Nitrogen manipulation rates in this 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 (Craine et al. 2007). In 2004, after fertilization, soil N availability (NO_3-N + NH_4-N) in the soil was five times greater in the N addition plots, and three times lower in the N reduction plots than in the control plots ($P < 0.0001$). 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).

I 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, Texas, 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. I sampled the plots using a combination of sweep-netting, vacuum sampling, and visual scanning, insect abundance was on average four times lower in the insect-reduced plots (Sanders et al. 2007), a reduction

consistent with that of other studies (e.g., Mulder et al. 1999). In addition, insecticide application had no confounding effect on plant growth for two reasons: insecticide application was equivalent to watering levels that were two orders of magnitude less than average rainfall at the study site, and NO_3-N and NH_4-N in the soil solution did not differ (t tests; $P > 0.45$ in all cases) between insecticide and control plots (Sanders et al. 2007).

I 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. I clipped aboveground biomass within each 0.5 m^2 quadrat to ground level and then sorted the clipped biomass into the following categories: dominant species (i.e.. *S. altissima*, *Verbesina* spp.) and subdominant species (combined all other species). Finally, I oven dried the clipped biomass samples at 60°C for approximately 36 hours and then weighed the samples to the nearest 0.1 g.

I assessed root production over the growing season of 2009 using root ingrowth core methods (Cuevas and Medina 1983; Steen 1984). Roots were removed 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. Roots were scanned using Win Rhizo Pro v. 2008a (1993-2008 by Regent Instruments, Inc.) for total root production as well as for root diameter. I further portioned total root production into two categories, fine roots (those < 2mm in diameter) and coarse roots (those > 2mm in diameter), to examine differential responses of roots that actively take up nutrients. In addition, all roots were

oven-dried at 60°C for approximately 48 hours, and all biomass data are presented as g dry mass per m^{-2}.

Statistical analyses

I analyzed the main and interactive effects of nutrient amendments and insect herbivory (as fixed effects), using independent two-way analysis of variance (ANOVA) models on the following response variables: total community aboveground biomass, biomass of dominant species, biomass of subdominant species, total belowground biomass production, as well as fine (<2mm) and coarse root (>2mm) production. A Tukey "honestly significant difference" (HSD) test was performed after each ANOVA to determine differences among treatments. Finally, I tested whether belowground biomass was an important covariate mediating aboveground biomass responses to nutrient amendments and herbivores using analysis of covariance (ANCOVA). All response variables were log-transformed prior to analyses to improve normality, but we show untransformed values in all figures. All analyses were conducted in JMP 7.0.1 © SAS Institute.

RESULTS

Aboveground Biomass

Overall, a significant effect was found of soil N amendment on total aboveground biomass and on the biomass of the subdominant plant species, while insect herbivory had a significant effect on only the biomass of subdominant plant species (Table 2). Total aboveground biomass was 19% greater in the N addition than in the N reduction plots, but neither differed from the control plots (Figure 1A). Herbivore reduction did not have a significant effect on total aboveground

biomass (Figure 1B; Table 2), and there was no significant nutrient × herbivore removal interaction on any response variable.

Aboveground biomass of dominant plant species responded only slightly to soil N amendment. There was a trend for the aboveground biomass of dominant species to be higher in both N addition plots and control plots relative to N reduction plots, but the result was not statistically significant ($P = 0.103$; Figure 1C; Table 2). Insects did not alter the aboveground biomass of dominant species (Figure 1D; Table 2), and there was no significant nutrient × herbivore removal interaction on the aboveground biomass of dominant species.

Both nutrient amendments and insect herbivory had significant effects on the biomass of subdominant plant species. Aboveground biomass of subdominant species was 66% higher in the N addition and control plots relative to the N reduction plots ($P = 0.049$; Figure 1E; Table 2). In addition, aboveground biomass of subdominant species was 52% higher in the insects present plots than in the insects reduced plots ($P = 0.032$; Figure 1F; Table 2).

Belowground Biomass

Total belowground biomass and the biomass of both coarse and fine roots responded to nutrient amendments while insect herbivory affected only the biomass of coarse roots. Nitrogen availability significantly promoted total root production ($P = 0.033$) (Figure 2A; Table 3). Belowground production in N reduction plots was on average 57% lower relative to the control and the N addition plots (Figure 2A). Coarse root production in N reduction plots was 54% and 44% lowered than in the control and N addition plots respectively (Figure 2C; Table 3). In addition, fine roots in the N reduction and N addition plots were 54% and 38% lower than in the control plots, respectively ($P = 0.008$) (Figure 2E; Table 3).

Insect herbivory did not influence total belowground biomass or fine root production, but did influence coarse root production (Figure 2B; Table 3). Coarse root biomass when insects were present was 41% lower than when insects were reduced ($P = 0.023$; Figure 2D; Table 3). Insect herbivory did not significantly affect the biomass of fine roots (Figure 2F; Table 3). Furthermore, there was no significant nutrient × herbivore removal interaction on the production of total belowground biomass, course root biomass, or fine root biomass (Table 3).

Both above- and belowground biomass responded similarly across nutrient treatments, with biomass in the N reduced plots being lower than on average than in the N addition plots. However, belowground biomass was not a significant covariate in the ANCOVA model in modifying aboveground response to herbivory and nutrients ($P = 0.23$; Table 4).

DISCUSSION

Bottom-up process (i.e. nutrient availability) shaped total aboveground biomass, but both top-down (i.e. insect herbivory) and bottom-up factors influenced the biomass of subdominant species in the community. In addition, bottom-up processes altered total belowground biomass production, coarse root, and fine root production. But top-down processes altered only coarse root production. Interestingly, and in contrast to research hypotheses, the nutrient effects 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). Finally, there was no statistical interaction between top-down and bottom-up processes for any of the belowground or aboveground response variables in this ecosystem. Put another way, the effects of herbivory did not depend on N availability in the soil, or vice versa.

Bottom-up Effects

The strongest overall effects of the study were found in the N amendment treatments (i.e., bottom-up effects). Interestingly, the aboveground biomass in the N addition plots did not differ from aboveground biomass in the control plots. This suggests that biomass production in this ecosystem is not primarily N limited. I can think of two lines of support for this claim. First, root biomass was not lower in N added plots than in the control plots. One would predict that if N availability limited production, then once N was elevated, plant biomass would increase, but this was not the case. However, in this study root production was lower when soil N was reduced than it was in either the control or N addition plots. Secondly, 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. For example, the abundance and biomass of N-fixers increased by phosphorus fertilization in a old-field in Connecticut (Finzi and Rodgers 2009).

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). However, nutrient availability may reduce the effect of dominant biomass on subdominant species by shifting competitive dynamics and ultimately altering community structure. In this study, nutrients had no effect on the biomass of dominant species, but significantly promoted aboveground biomass of subdominant species. This study showed that N fertilization led to a decline in aboveground biomass of subdominant species,

specifically of forbs. Future research in a resource-limited ecosystem may reveal whether the biomass of dominant species serves as a buffer to the effects of nutrient limitation on biomass of subdominant species

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, Stein et al. 2010). However, I found no significant effects of insect herbivory on total aboveground biomass or on the biomass of dominant plant species. But I did find significant effects of herbivory on the biomass of subdominant plant species. 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 aboveground biomass may be weak relative to nutrient amendment. First, herbivores may have been limited by their own predators or by intraguild processes, which might be more common in high productivity environments (Oksanen and Oksanen 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 treatments. Distinguishing among these possibilities would require experiments that have yet to be conducted in any system.

Insect herbivory in some instances may influence root production (Kaplan et al. 2008; Olson et al. 2008). Insect herbivory may serve as a stimulus for retranslocating nutrients from aboveground shoot production to belowground root production (Dyer and Bokhari 1976). Brown (1994) observed that foliar grazing by a chrysomelid beetle decreased root biomass. Likewise, grazing by sheep in grasslands led to a reduction of root mass and an increase in the allocation of nutrients to shoots of *Festuca reubra* and *Cynosurus criistatus* (Guitian and Bardgett 2000). However, in this study, insect herbivory did not have an effect on total belowground biomass production or fine root production, but insect herbivory did affect production of coarse roots. Invertebrate herbivores may not affect belowground biomass for the same reasons listed above.

This 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 and alter the dynamics of competing species (Crawley 1983; Tscharntke and Greiler 1995). Still others have indicated that pesticides simply reduce the density of (all) insects rather than completely exclude the herbivorous insects (e.g., Coupe and Cahill 2003), which was the case in this study. I predicted that herbivory would alter 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). I observed that insect herbivory did not affect biomass of dominant species; however, when insects were present, I found greater aboveground biomass of subdominant species relative to plots where insects were reduced, similar to results found by Schadler et al. (2008). Research results also support an earlier study by Carson and Root (2000), which found that herbivory by a chrysomelid beetle on *S. altissima*, increased biomass of subdominant species as a result of increased resource availability.

Conclusions

In this study, soil nutrient amendment had a significant effect on total aboveground biomass and affected belowground biomass in all size classes of roots. Insect herbivory, in contrast, had a significant effect on only the aboveground biomass of subdominant species and coarse root biomass. It appears that, in this old-field ecosystem at least, bottom-up processes dominated plant 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 different 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.

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APPENDIX

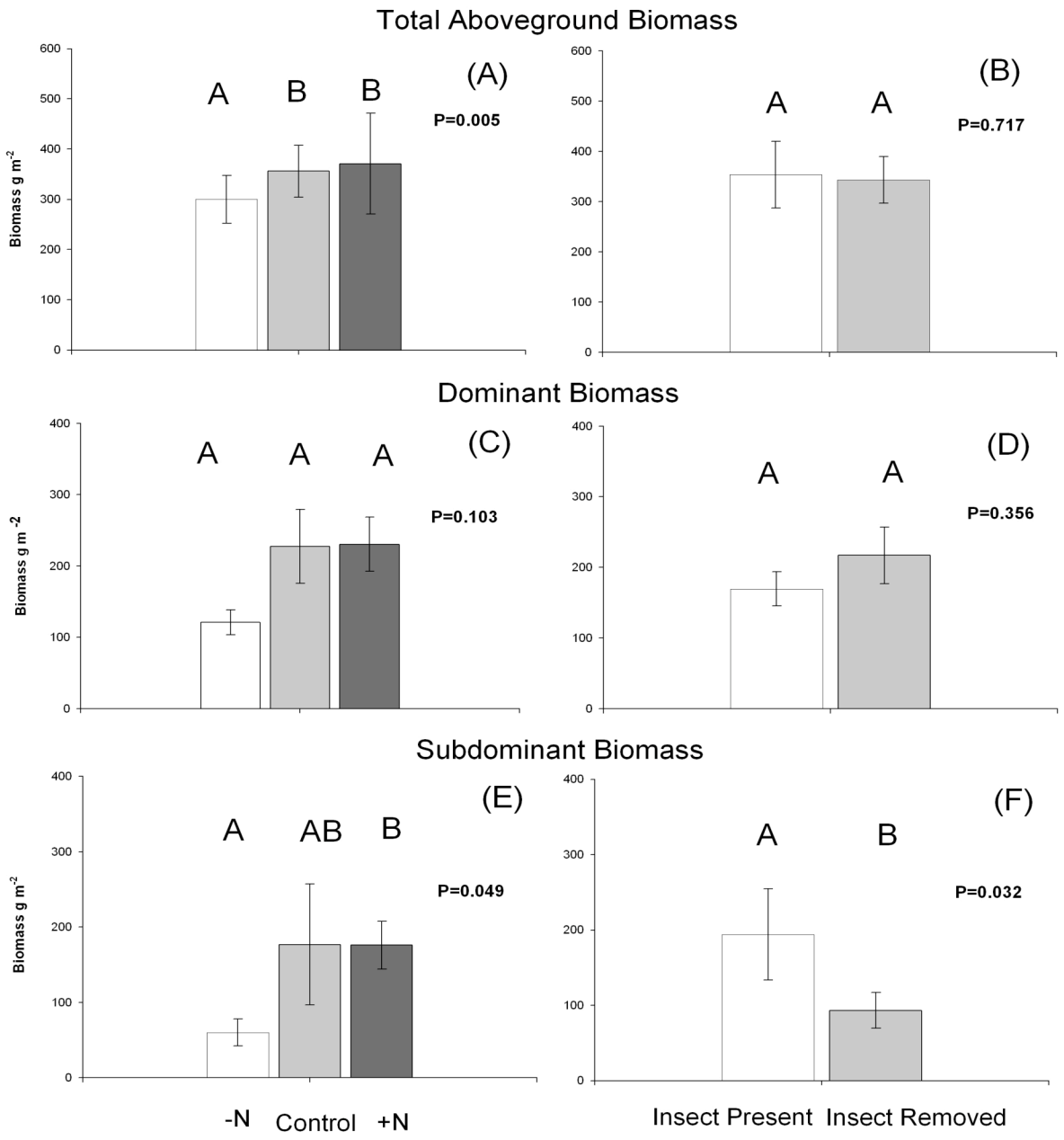

Figure 1. The effect of nitrogen (N) manipulation (3 levels) and insect herbivory (2 levels) on mean (± SE) total aboveground plant biomass (A-B), dominant plant biomass (C-D), and subdominant plant biomass (E-F). Different letters above bars indicate means that are statistically different from one another ($\alpha = 0.05$).

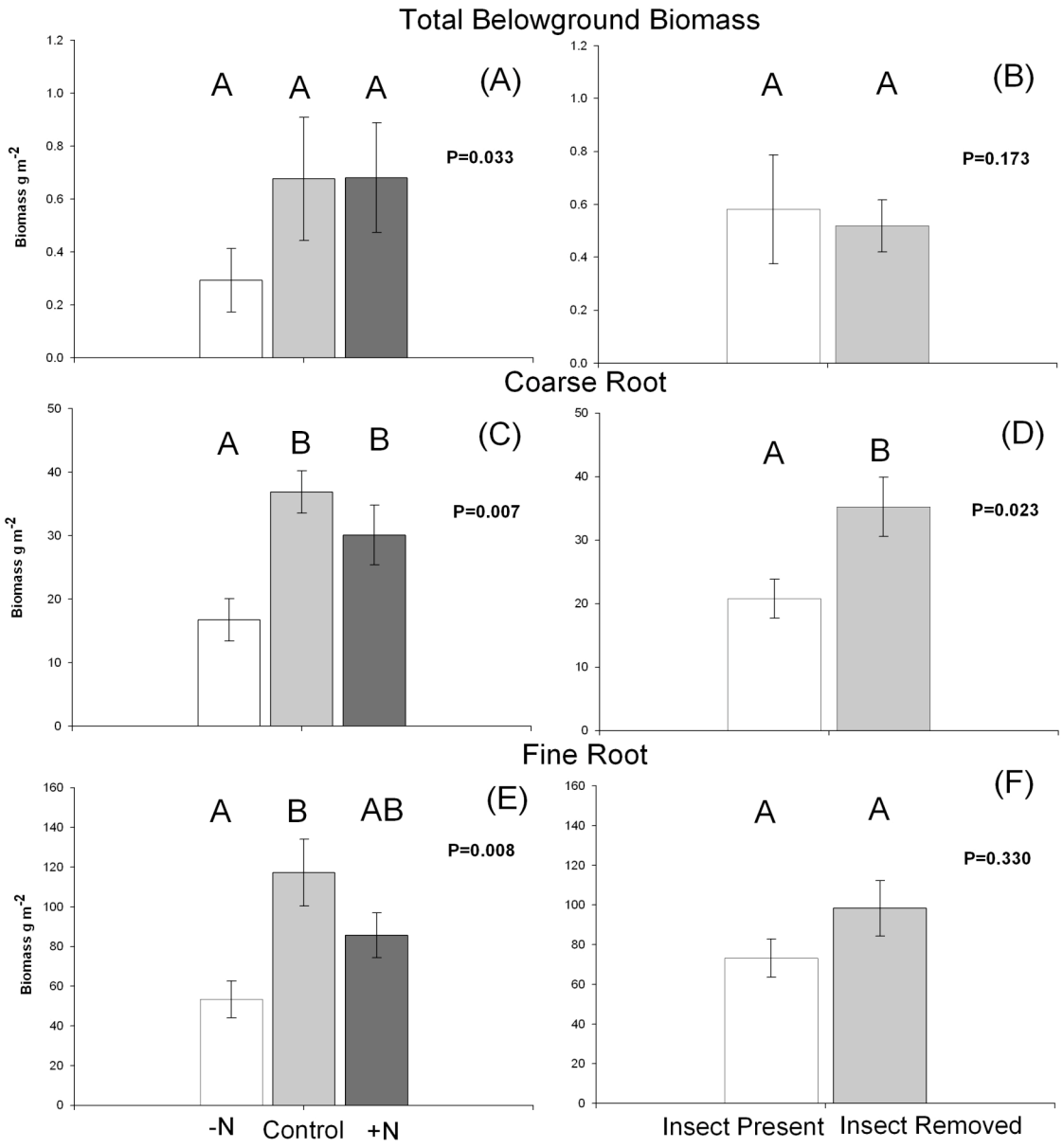

Figure 2. The effect of nitrogen (N) manipulation (3 levels) and insect herbivory (2 levels) on mean (± SE) total root biomass (A-B), biomass of coarse roots (> 2mm diameter) (C-D), and biomass of fine roots (<2 mm diameter) (E-F). Different letters above bars indicate means that are statistically different from one another (α= 0.05).

Table 1.
Observed plant species in the Summer of 2009 at the research site.

Scientific Name	Family	Functional Group	Life Cycle
Acalypha rhomboidea	*Euphorbiaceae*	C3 forb	Annual
Acer rubrum	*Aceraceae*	C3 Woody	Perennial
Acer Sachrum	*Sapindaceae*	C3 Woody	Perennial
Agrimonia parviflora	*Rosaceae*	C3 forb	Perennial
Allium vineale	*Liliaceae*	C3forb	Perennial
Andropogon virginicus	*Poaceae*	Graminoid	Perennial
Andropogon sp.	*Poaceae*	Graminoid	Perennial
Apocynum cannabinum	*Apocynaceae*	C3 forb	Perennial
Asclepias syriaca	*Asclepiadaceae*	C3 forb	Perennial
Aster pilosus	*Asteraceae*	C3 forb	Annual
Bromus commutatus	*Poaceae*	Graminoid	Annual
Bromus inermis	*Poaceae*	Graminoid	Perennial
Calystegia sepium	*Convolvulaceae*	C3 forb	Perennial
Campsis radicans	*Bignoniaceae*	C3 forb	Perennial
Carex complanata	*Cyperaceae*	Graminoid	Perennial
Carex sp.	*Cyperaceae*	Graminoid	Perennial
Cirsium discolor	*Asteraceae*	C3 forb	Biennial/Perennial
Coronilla varia	*Fabaceae*	N-fixer	Perennial
Croton glandulosus	*Euphorbiaceae*	C3 forb	Annual

Table 1 Continued.

Cuscuta sp.	*Convolvulaceae*	C3 forb	Perennial
Desmodium sp.	*Fabaceae*	N-fixer	Perennial
Diospyros virginiana	*Ebenaceae*	C3 Woody	Perennial
Diodia virginiana	*Rubiaceae*	C3 forb	Annual/Perennial
Duchesnea indica	*Rosaceae*	C3forb	Perennial
Elaeagnus umbellata	*Elaegnaceae*	C3 Woody	Perennial
Elephantopus carolinianus	*Asteraceae*	C3 forb	Perennial
Galium parisiense	*Rubiaceae*	C3forb	Annual
Hypericum punctatum	*Clusiaceae*	C3 forb	Perennial
Lespedeza cuneata	*Fabaceae*	N-fixer	Perennial
Ligustrum sp.	*Oleaceae*	C3 Woody	Perennial
Lonicera japonica	*Caprifoliaceae*	C3 Woody	Perennial
Oxalis stricta	*Oxalidaceae*	C3 forb	Perennial
Parthenocissus quinquefolia	*Vitaceae*	C3 forb	Perennial
Passiflora incarnata	*Passifloraceae*	C3 forb	Perennial
Prunus serotina	*Rosaceae*	C3 Woody	Perennial
Rubus argutus	*Rosaceae*	C3 Woody	Perennial
Rosa multiflora	*Rosaceae*	C3 Woody	Perennial
Rumex crispus	*Polygonaceae*	C3forb	Perennial
Setaria parviflora	*Poaceae*	Graminoid	Perennial
Smallanthus uvedalius	*Asteraceae*	C3 forb	Perennial

Table 1 Continued.

Smilax bona-nox	*Smilacaceae*	C3shrub	Perennial
Smilax glauca	*Smilacaceae*	C3shrub	Perennial
Solidago altissima	*Asteraceae*	C3 forb	Perennial
Solanum carolinense	*Solanaceae*	C3 forb	Perennial
Sorghum halepense	*Poaceae*	Graminoid	Perennial
Toxicodendron radicans	*Ancardiaceae*	C3 forb	Perennial
Trifolium campestre	*Fabaceae*	N-fixer	Annual/Biennial
Tridens flavus	*Poaceae*	Graminoid	Perennial
Trifolium repens	*Fabaceae*	N-fixer	Perennial
Ulmus sp	*Ulmaceae*	C3 Woody	Perennial
Veronia gigantean	*Asteraceae*	C3 forb	Perennial
Verbesina occidentalis	*Asteraceae*	C3 forb	Perennial
Verbesina virginica	*Asteraceae*	C3 forb	Perennial
Vitis vulpina	*Vitaceae*	C3 Woody	Perennial

Table 2. Results from ANOVA analyses of treatment effects (insect presence and nutrient manipulation) and their interaction on total aboveground biomass of the plant community, on total aboveground dominant (*Solidago altissima* and *Verbesina* spp.) plant biomass, and total subdominant plant biomass. Significant variables ($P < 0.05$) are in bold.

	Total aboveground Biomass				**Dominant biomass**				**Subdominant biomass**			
Factor	**Df**	**SS**	**F**	**P**	**df**	**SS**	**F**	**P**	**df**	**SS**	**F**	**P**
Insects	1	0.008	0.134	0.717	1	0.097	0.880	0.356	1	1.341	5.007	**0.033**
Nitrogen Availability	2	0.743	6.308	**0.005**	2	0.542	2.448	0.103	2	1.795	3.351	**0.049**
Insects × Nitrogen Availability	2	0.072	0.614	0.548	2	0.060	0.270	0.765	2	0.143	0.268	0.767
Error	31				31				30			

Table 3. Results from ANOVA analyses of treatment effects (insect presence and nutrient manipulation) and their interaction on community total root biomass, coarse root biomass, and fine root biomass. Significant variables ($P < 0.05$) are in bold.

	Total Belowground Biomass				Coarse root biomass				Fine root biomass			
Factor	**df**	**SS**	**F**	**P**	**df**	**SS**	**F**	**P**	**df**	**SS**	**F**	**P**
Insects	1	0.390	1.949	0.173	1	0.603	5.779	**0.023**	1	0.084	0.979	0.330
Nitrogen Availability	2	1.533	3.830	**0.033**	2	1.226	5.881	**0.007**	2	0.970	5.675	**0.008**
Insects × Nitrogen Availability	2	0.826	2.063	0.145	2	0.078	0.373	0.692	2	0.101	0.593	0.559
Error	35				34				29			

Table 4. Results from ANCOVA analysis using nutrient amendments and insect herbivory as main effects and plant belowground biomass as a covariate on total aboveground biomass.

Factor	df	SS	F	P
Insects	1	0.001	0.001	0.971
Nitrogen availability	2	0.677	1.509	0.242
Aboveground biomass	1	0.044	0.197	0.661
Insects × nitrogen availability	2	0.558	1.242	0.307
Insects × aboveground biomass	1	0.056	0.248	0.623
Nitrogen availability × aboveground biomass	2	0.219	0.489	0.619
Insects× nitrogen availability× aboveground biomass	2	0.316	0.704	0.505
Error	25			

VITA

Jarrod Dwayne Blue was born in December 1985 in Charlotte, North Carolina. He graduated with high honors and International Baccalaureate Diploma from Independence High School in Charlotte, North Carolina. He graduated from Davidson College, in 2008 with a Bachelors of Science in Biology. Jarrod received his Masters of Science degree in Ecology and Evolutionary Biology from the University of Tennessee in August 2010.