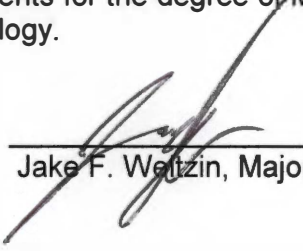


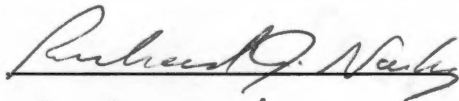
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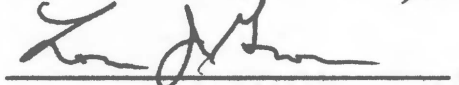
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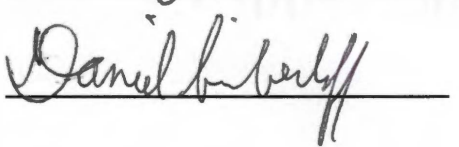


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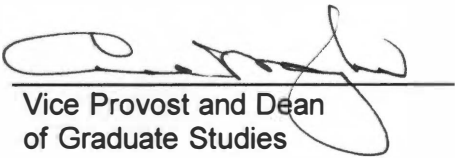
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**Effects of elevated CO₂ on a forest understory community dominated by two
invasive plants**

A thesis presented for the Master of Science Degree
The University of Tennessee, Knoxville

Russell Travis Belote

August 2003

DEDICATION

I dedicate this thesis to my lost friend, Brandon Paul Wolfe, who inspired me to independently choose my own path and to “be a lizard,” but also taught me to be mindful of others along the way.

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ABSTRACT

Rising levels of atmospheric carbon dioxide (CO₂) and invasions by non-native organisms are predicted to change patterns and processes of native ecosystems in the near future. However, no studies to date investigated both (1) the effects of elevated CO₂ on invasive species in natural settings and (2) how interactions between invaders may drive the response of an entire community to CO₂ enrichment. In this thesis, I examine the effects of elevated CO₂ on an understory plant community dominated by two invasive species (Chapter 2) and determine the nature of interactions and mechanisms mediating the interactions between two co-dominant invasive plants (Chapter 3).

I examined species composition, aboveground production, and cover of the understory plant community in ambient and elevated CO₂ treatments in an ongoing, free-air CO₂ enrichment (FACE) facility on the Oak Ridge National Environmental Research Park, Tennessee. Five 25-m diameter plots have received either ambient [CO₂] or elevated [CO₂] since 1998. The understory plant community in these plots is dominated by several non-native plant species including *Lonicera japonica* and *Microstegium vimineum*, two highly invasive plants in the Southeastern U.S. *L. japonica* responded similarly between 2001 and 2002 with a three-fold increase in production in plots receiving elevated [CO₂]. In contrast, production of *M. vimineum* was greater in plots receiving ambient [CO₂] in 2001, a relatively wet year, but did not differ between [CO₂] treatments in 2002, a drier year. In 2001, species diversity and evenness were greater in elevated CO₂ plots, but total understory production did not differ between [CO₂] treatments. In 2002, diversity and evenness did not differ between [CO₂] treatments, but total understory production was greater in plots

receiving elevated [CO₂]. These results suggest that community responses to increases in atmospheric [CO₂] – in terms of production and diversity – will depend on individual species responses, but will likely be mediated by other resources. Moreover, rising [CO₂] may enhance the performance of some, but not all, invasive plants.

The co-dominance of the two invasive species, *L. japonica* and *M. vimineum*, raised intriguing questions related to invasion biology: Is the pattern of co-dominance between these two species explained by facilitative interactions? Results of a 'press' removal experiment indicated that the relationship between the two species was mutually detrimental, though *M. vimineum* had a competitive advantage over *L. japonica*, because its growth form enabled it to acquire light to the detriment of the prostrate *L. japonica* (Chapter 3). In contrast to our prediction that greater water availability might release the two species from competition, increased soil water availability only benefited *M. vimineum*, which further reduced the light available to *L. japonica*. Water and light were important resources mediating the interactions between the two species. However, the growth forms and phenology of each plant may determine the extent and nature of their interactions and govern their response under elevated [CO₂].

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LIST OF ACCRONYMS

ANOVA	analysis of variance
ANPP	aboveground net primary productivity
CO ₂	carbon dioxide
CRDS	completely randomized design with sampling
DCA	detrended correspondence analysis
DOE	Department of Energy
DOY	day of year
<i>E</i>	evenness
FACE	free air carbon dioxide enrichment
GLM	general linear model
<i>H'</i>	Shannon-Weaver diversity index
MANOVAR	multivariate analysis of variance with repeated measures
NPS	National Park Service
ORNERP	Oak Ridge National Environmental Research Park
PAR	photosynthetic active radiation
PCA	principal components analysis
ppm	parts per million
RCI	relative competition index
RUBISCO	ribulose-1,5-bis-phosphate carboxylase
<i>S</i>	species richness
TDR	time domain reflectometry
VWC	volumetric water content

CHAPTER 1

Introduction

Unprecedented changes in atmospheric chemistry and the global movement of species across once impenetrable geographical barriers are the results of an exponentially increasing human population and its use and interchange of natural resources (Vitousek 1994). Specifically, carbon dioxide concentrations ($[\text{CO}_2]$) are increasing in the atmosphere and may double this century (Houghton et al. 2001). Elevated $[\text{CO}_2]$ may lead to increasing temperatures and shifts in precipitation regimes, which will alter the structure and function of managed and natural ecosystems. Second, invasions by non-indigenous species have altered the structure and functioning of ecosystems by changing the nutrient and water availability of systems, altering species composition, and reducing diversity of communities (Luken and Thieret 1997; Parker et al. 1999).

Recently, ecologists have suggested that the combined effects of increasing $[\text{CO}_2]$ and invasions by exotic plants on native ecosystems may be more detrimental than the individual effects of either factor (Dukes and Mooney 1999; Simberloff 2000; Weltzin et al. 2003). Moreover, the impact non-indigenous plants will have on agricultural and natural ecosystems in the future may be mediated by facilitative interactions with other invasive species (Simberloff and Von Holle 1999). However, no studies to date have investigated both (1) the effects of elevated CO_2 on invasive species in natural settings and (2) how interactions between invaders may drive the response of an entire community to CO_2 enrichment. In this thesis, I examine the effects of elevated CO_2 on an understory plant community dominated by two invasive

species (Chapter 2) and determine the nature of interactions and mechanisms mediating the interactions between two co-dominant invasive plants (Chapter 3).

Elevated CO₂

Increasing concentrations of CO₂ in the atmosphere are likely to affect vegetation directly. Many controlled environment studies conducted in pots demonstrate that elevated [CO₂] enhances the growth of many plant species by increasing rates of photosynthesis (Poorter and Navas 2003). Other documented responses included decreased stomatal conductance (Field et al. 1995), reduced production of RUBISCO (Sage 1994), and reduced photorespiration (Cousins et al. 2001). In contrast to the number of studies investigating individual species responses to CO₂ enrichment, there have been relatively few investigations of the response of *in situ* communities to elevated [CO₂] (Koch and Mooney 1996).

Recently, studies investigating plant community responses to elevated [CO₂] in more realistic settings have been conducted with the advent of open top chamber and free air carbon dioxide enrichment (FACE) facilities (Potvin and Vasseur 1997; Vasseur and Potvin 1998; Norton et al. 1999; Niklaus et al. 2001; Shaw et al. 2002). Results of these “natural” field experiments, however, are often unpredictable and conflicting, because responses of species depend on confounding factors, including variation in availability of resources (Bazzaz and Miao 1993; Owensby et al. 1999; Smith et al. 2000; Shaw et al. 2002) and interspecific interactions (Stewart and Potvin 1996; Dukes 2002). Therefore, our ability to predict effects of elevated [CO₂] on species composition, diversity, or invasibility is limited. Additional research is needed on intact natural communities to learn more about how elevated [CO₂] will affect species productivity, composition, and diversity, and processes such as invasions.

Invasions by non-indigenous plants

Biological invasions threaten global biological diversity, the integrity of natural ecosystems, and the goods and services that ecosystems provide to humanity (Mack et al. 2001). Invasions by non-indigenous plants can alter biotic and abiotic factors by directly competing with native species (Callaway and Aschehoug 2000) or by changing other aspects of ecosystems, such as fire regimes (Mack and D'Antonio 1998), water availability (Sala et al. 1996), or nitrogen cycling (Vitousek and Walker 1989). Two questions that have become the cornerstone of contemporary invasion biology are (1) Which species will invade?, and (2) Which ecosystems are vulnerable to invasion? Despite recent considerable and still-increasing theoretical and experimental research, answers to these questions remain unclear but are important in understanding plant invasions and forecasting the impact of invasive plants. Predicting the future effects of plant invasions may be further complicated by interactions among invasive species. Simberloff and Von Holle (1999) suggest facilitation between invasive species may enhance the spread and impact of non-indigenous species on native ecosystems in an "invasional meltdown." To date, however, very few studies have investigated interactions between invasive plant species.

Elevated CO₂ and plant invasions

Increases in atmospheric [CO₂] could promote, and may have already contributed to the success of, invasive species (Dukes and Mooney 1999; Weltzin et al. 2003). Dukes (2000) compared the mean weight gain ratios of native and non-indigenous plant species grown under ambient and elevated [CO₂] and found that the responses of native and non-indigenous plant species were statistically

indistinguishable from one another. While it appears that there is nothing intrinsically novel about invasive plants that makes them responsive to increases in $[CO_2]$ when grown in monoculture, invasive plants may possess novel traits that allow them to invade native ecosystems, and elevated $[CO_2]$ might give them an added advantage when invading habitats. For example, Smith et al. (2000) determined that elevated $[CO_2]$ may increase propagule pressure of invasive species in a desert ecosystem. Specifically, they found that red brome (*Bromus madritensis* ssp. *rubens*), a non-indigenous annual grass that has invaded many areas of the Mojave and Sonoran deserts, increased its density and production of aboveground biomass and seeds under elevated $[CO_2]$ during a wet El Niño year. However, responses of invasive plants to elevated CO_2 within natural communities are largely unknown (Dukes 2000). Although predicting the impact of biological invaders or elevated $[CO_2]$ already poses a challenge to ecologists, it is prudent and timely to investigate what is likely to be an even greater challenge: predicting the effects of elevated $[CO_2]$ on invasive plants within ecological systems.

Elevated CO_2 and plant invasions: a research agenda

Körner (2000) recently noted the infrequency of CO_2 enrichment studies that were conducted in “realistic” settings. He suggested that experiments conducted *in situ* may be the only appropriate way to gain insights into the future response of terrestrial ecosystems to elevated CO_2 . Similarly, Simberloff and Von Holle (1999) noted the paucity of studies directly investigating the interactions among invasive species. The goals of my project were (1) to examine the response of an *in situ* understory community to elevated $[CO_2]$ and (2) to determine how interactions

between the two co-dominant invasive species within this community might influence the response of the community to elevated [CO₂].

As part of a large-scale FACE facility at Oak Ridge Environmental Research Park, I conducted a field experiment to investigate the effect of elevated [CO₂] on an *in situ* understory plant community in a closed canopy eastern deciduous forest (Chapter 2). The understory community was co-dominated by two invasive plant species, *Lonicera japonica* Thunb. and *Microstegium vimineum* (Trin.) A. Camus. This presented a unique opportunity to investigate whether changes in [CO₂] would facilitate the success of invasive plants. Within communities, plant responses to elevated CO₂ are often mediated by interacting biotic (e.g. competition) and abiotic factors (e.g. soil water availability) (Reynolds 1996; Dukes 2002). Therefore, to determine the nature of interactions between the two invasive plants and the mechanisms driving those interactions, I conducted two experiments under ambient [CO₂], (1) a press removal and watering experiment between *L. japonica* and *M. vimineum* and (2) a light gradient experiment with *L. japonica* (Chapter 3). In Chapter 4, I synthesize the results of these experiments and provide directions for future research.

CHAPTER 2

Effects of elevated [CO₂] on an eastern deciduous forest understory community

This chapter is a revised version of a paper by the same name to be submitted to the journal *New Phytologist* by R. Travis Belote, Jake F. Weltzin, and Richard J. Norby.

My use of “we” in this chapter refers to the co-authors and myself.

Introduction

It is well known that carbon dioxide concentrations ([CO₂]) are increasing in the atmosphere and may double this century from pre-industrial levels (Houghton et al. 2001). Elevated [CO₂] are likely to have direct effects on vegetation (Poorter and Navas 2003), while also causing changes in climate, which may affect patterns and processes of plant communities. Direct and indirect effects that elevated CO₂ will have on plants in natural ecosystems in the future are mostly unknown, because the majority of studies to date have been conducted in controlled environments with plant monocultures grown in pots. These studies demonstrate that elevated CO₂ enhances the growth of most plant species, especially those using the C₃ photosynthetic pathway (Poorter et al. 1996; Poorter and Navas 2003). However, they may not provide realistic information on how plants will respond in natural communities, where the availability of resources is spatially and temporally heterogeneous, and where species interact (Körner and Bazzaz 1996; Körner 2000).

With the advent of open top chamber and free air carbon dioxide enrichment (FACE) facilities, more studies are beginning to investigate responses of plant communities to elevated CO₂ in more realistic settings (e.g., Potvin and Vasseur

1997; Vasseur and Potvin 1998; Norton et al. 1999; Niklaus et al. 2001; Shaw et al. 2002). Community responses to CO₂ have generally been described in terms of total production (Koch and Mooney 1996) or changes in community composition (Körner and Bazzaz 1996). Increases in the productivity of communities in response to CO₂ enrichment depend on species composition (Niklaus et al. 2001; Reich et al. 2001) and interspecific interactions (Stewart and Potvin 1996; Dukes 2002). However, elevated CO₂ can alter plant community composition even when total productivity is unaffected (Roy et al. 1996; Norton et al. 1999; Niklaus et al. 2001). Compositional responses to elevated CO₂ have included shifts in species abundance (Vasseur and Potvin 1998), increased evenness and diversity of communities (Potvin and Vasseur 1997; Leadley et al. 1999; Niklaus et al. 2001), and increased success of invasive species (Dukes and Mooney 1999; Smith et al. 2000; Weltzin et al. 2003).

However, mixed and sometimes contradictory results have been observed in these studies under variations of resource availability, including light (Bazzaz and Miao 1993), water (Owensby et al. 1993), and nitrogen (Roy et al. 1996; Cannell and Thornley 1998). Specifically, resource limitations (e.g., water, nitrogen) typically attenuate the response of plants to elevated [CO₂] (Poorter and Pérez-Soba 2001), but may accentuate differences between different plant species or functional groups growing in natural communities. Owensby et al. (1993 and 1999) found that elevated CO₂ increased biomass of a C₄-dominated community during dry years. Smith et al. (2000) determined that red brome (*Bromus madritensis* ssp. *rubens*), a non-native annual grass, increased its density and production of aboveground biomass and seeds under elevated [CO₂] during a wet El Niño year. Alternatively, elevated CO₂ may actually diminish the response of plants to other environmental factors (Shaw et

al. 2002), although mechanisms contributing to this response are unclear. It is clear, however, that our ability to predict the future effects of elevated CO₂ on species composition, diversity, and invasibility is limited (Körner 2000).

The present study was designed to determine the response of an *in situ* understory plant community to elevated CO₂. We examined community and species responses in 2001 and 2002 to elevated [CO₂] in the understory of the FACE facility at Oak Ridge National Environmental Research Park (Norby et al. 2002).

Specifically, we predicted that total production would be greater in plots receiving elevated [CO₂] than plots receiving ambient [CO₂], because C₃ species were common in the understory. In addition, because of the variety of growth forms and functional groups (e.g., C₃ herbaceous and woody dicots and monocots, and C₄ monocots), we predicted that community composition would change in response to CO₂ enrichment. Finally, the community was co-dominated by several non-native invasive plant species, so it presented a unique opportunity to investigate whether changes in [CO₂] would facilitate the success of invasive plants.

Methods

Site description

Research was conducted at the FACE facility, Oak Ridge National Environmental Research Park, Oak Ridge, Tennessee (35° 54' N; 84° 20' W). The research site is a planted sweetgum (*Liquidambar styraciflua* L.) monoculture established in 1988 on an old terrace of the Clinch River (elevation 230 m asl). The sweetgum trees were approximately 17 m tall in 2002, with a closed canopy that reduced the light in the understory 70-95% during the growing season (Belote, unpublished data). The soil, classified as an Aquic Hapludult, has a silty clay loam

texture and is moderately well drained and slightly acidic (water pH approximately 5.5-6.0) (SCS 1967; van Miegroet et al. 1994). Precipitation is generally evenly distributed throughout the year with an annual mean of 1322 mm. The mean annual temperature at the site is 13.9°C. Additional details about the physical and biological characteristics of the site are in Norby et al. (2001; 2002).

The understory was sparse at plantation establishment, but by the growing season of 2000 plant cover in the understory was continuous and co-dominated by two non-native invasive plant species, Nepal grass (*Microstegium vimineum* (Trin.) A. Camus) and Japanese honeysuckle (*Lonicera japonica*). *M. vimineum*, a shade-tolerant C₄ annual grass, was first reported in Tennessee in 1917 and since then has spread throughout most of the eastern United States (Fairbrothers and Gray 1972). *L. japonica*, a C₃ evergreen woody vine, was introduced in 1806 and has become naturalized throughout the southeastern United States (Leatherman 1955). Other understory taxa at the FACE site include small clumps or scattered individuals of blackberry (*Rubus* spp.), goldenrod (*Solidago canadensis* L.), and box elder seedlings (*Acer negundo* L.).

Experimental design

FACE technology applies elevated CO₂ to natural systems without the confounding effects on light, temperature, and precipitation (Hendrey et al. 1999). In 1998, five 25-m diameter plots consisting of two CO₂ treatments were established in the sweetgum plantation (Norby et al. 2002). Four plots are surrounded by 24 vertical vent pipes spaced 3.3 m apart suspended from 12 aluminum towers. Two of the plots receive elevated [CO₂] (target = 565 ppm) delivered to the vent pipes by blowers

while two control plots receive ambient [CO₂] (= 365 ppm). One ambient [CO₂] plot with no vent pipes or other infrastructure serves as a control for the presence of the CO₂ delivery apparatus (Norby et al. 2002). The CO₂ treatment was initiated in April 1998 and has been maintained each year from April to November. Nighttime fumigation was discontinued in 2001 because it interfered with soil respiration measurements.

Sampling methods

In March 2001, we randomly distributed four 0.5 m² subplots within each of the five plots. For the 2002 season, we relocated each subplot to new random locations. At each subplot in each year, we determined foliar cover (%) and aboveground net primary productivity (ANPP; g/m²/yr) for all plant species. Cover was estimated in mid-May and late August to capture seasonal differences in plant community composition; maximum intra-annual species foliar cover was used in analyses. In early September, we determined ANPP within each subplot by clipping all individual herbaceous species at ground level. ANPP of woody perennials (e.g., *L. japonica*) was determined by marking new shoots in early spring and clipping the subsequent seasonal growth during the destructive harvest. All plant tissue samples were oven dried at 65°C to constant mass. We summed all species within each year to determine total understory ANPP. Shannon-Weaver (H') diversity index (Shannon and Weaver 1949), species richness (S), and evenness (E) were calculated for each subplot based on ANPP.

Six time domain reflectometry (TDR, Soil Moisture Equipment Corp., Santa Barbara, CA, USA) probes were permanently installed within each 25-m diameter plot

to determine volumetric water content (%; VWC) in the top 20 cm of soil. We recorded VWC 8 and 10 times during the growing season in 2001 and 2002, respectively. We measured photosynthetically active radiation (PAR; $\mu\text{mol}/\text{m}^2/\text{s}$) 1 meter above subplots between 11 a.m. and 1 p.m. on clear days using a handheld line integrating ceptometer (AccuPAR, Decagon Devices, Inc., Pullman, WA, USA) twice in each of the 2001 and 2002 growing seasons.

Statistical analysis

We analyzed total and species ANPP and biomass, species cover, H' , S , E , and PAR for effect of CO_2 treatment with an unbalanced completely randomized design with sampling (CRDS), where each subplot was considered a sample within the plots (Filion et al. 1999). Data were analyzed with a mixed model analysis of variance (ANOVA; procedure MIXED; SAS Institute 1999) with the model:

$$y_{ijk} = \mu + \text{CO}_2 \text{ treatment}_i + \text{Rep}(\text{CO}_2)_{ij} + \text{subplot}(\text{Rep}(\text{CO}_2))_{ijk},$$

where μ is the overall mean, CO_2 treatment is a fixed effect, plot replicate is the random effect, and subplots are the residual error that explain the measured dependent variable (y_{ijk}) (Filion et al. 1999). To minimize the number of statistical tests, we conducted species-specific comparisons (of ANPP and cover) for only the 5 dominant species (present in at least 25% of the subplots and with > 8 % cover across treatments and years).

Data were tested for normality and homogeneity of variance with the Shapiro-Wilk W -Statistic and Levene's test, respectively (Shapiro and Wilk 1965; Levene 1960). Continuous and proportional data that did not meet these assumptions were

log transformed or arcsine-square root transformed before analysis, respectively. We excluded one outlying observation from the 2001 dataset.

We used principal components analysis (PCA) to analyze and display vegetation data based on maximum foliar cover within subplots. Species present in less than 5% of the subplots were removed from the dataset before ordination, which left 29 and 22 species for ordination in 2001 and 2002, respectively. The correlation matrix was used because of the high diversity of variances among species within the understory (Johnson 1998). Because distortion problems can occur with PCA (Beals 1984), we also examined the data using detrended correspondence analysis (DCA). However, the results of the DCA analyses were similar to PCA so we focused our interpretation on the latter. We conducted Pearson correlations of axes I and II scores with annual means of PAR and VWC, and maximum foliar cover of dominant species, within year, to determine environmental variables and species accounting for differences in the plant community, respectively.

VWC measurements from the six locations within each plot were averaged for each sampling date. We analyzed VWC for main and interactive effects of CO₂ and time (i.e., day of year = DOY) with a repeated measures multivariate analysis of variance (MANOVA; Pillai's Trace in SAS procedure GLM; SAS Institute 1999).

Results

Community and species production

Total understory ANPP in 2001 did not differ between [CO₂] treatments ($P = 0.97$), but in 2002 was 27% greater under elevated [CO₂] than ambient [CO₂] ($P =$

0.14; Fig. 1[†]). In both years of this study, *L. japonica* comprised at least 24% of total community ANPP. Production of *L. japonica* was 3 and 2.5 times greater in plots that received elevated [CO₂] than ambient [CO₂] in 2001 and 2002, respectively (Table 1). In 2001, cover of *L. japonica* was 2 times greater under elevated than ambient [CO₂], but in 2002 cover of *L. japonica* did not differ between treatments.

M. vimineum accounted for at least 64% of total production in both years of the study. Production of *M. vimineum* was 68% greater under ambient than elevated [CO₂] in 2001, but did not differ between treatments in 2002 (Table 1). Cover of *M. vimineum* was 44% greater under ambient than elevated CO₂ in 2001, but did not differ in 2002.

Production of *Rubus* did not differ between CO₂ treatments in either year, but cover of *Rubus* was greater under elevated than ambient CO₂ in both years (Table 1). Production of *S. canadensis* in ambient and elevated CO₂ plots did not differ in either year. *S. canadensis* cover was greater under elevated than ambient CO₂ in 2001, but not in 2002. Foliar covers of subdominant species in the understory are in Table 3.

Community structure and diversity

Principal components analysis (PCA) reflected differences in species composition and abundance under ambient and elevated CO₂ (Fig. 2). In 2001, axis I and II explained 15% and 11% of the variation, respectively. Axis I scores were negatively correlated with cover of *L. japonica*, *Rubus* spp. and *S. canadensis* ($r \leq -0.43$, $P \leq 0.07$) and positively correlated with cover of *M. vimineum* ($r = 0.61$, $P = 0.006$).

[†] All figures and tables are located in the Appendix.

In 2002, axes I and II explained 14% and 13% of variation, respectively; the ordination for 2002 is not shown because patterns were similar to 2001. Axis I scores were positively correlated with *L. japonica* ($r = 0.52$, $P = 0.02$) and negatively correlated with *M. vimineum* ($r = -0.50$, $P = 0.02$) in 2002. Axis II scores were negatively ($r = -0.50$, $P = 0.03$) and positively ($r = 0.67$, $P = 0.001$) correlated with *A. negundo* and *S. canadensis*, respectively. In both years, neither mean annual PAR or VWC were correlated with axis I or II quadrat scores ($P \geq 0.24$).

In 2001, species richness (S) did not differ between CO_2 treatments, but species evenness (E) and diversity (H') of species production were greater under elevated than ambient $[\text{CO}_2]$ (Table 1). In 2002, S , E , and H' did not differ between CO_2 treatments.

Soil moisture and photosynthetically active radiation

Soil volumetric water content (VWC) did not differ between plots under ambient CO_2 and elevated CO_2 in 2001 or 2002 ($P \geq 0.24$). VWC varied throughout the year, depending on precipitation, but the pattern differed substantially between years (Fig. 3). In 2001, VWC was relatively constant throughout June and July, but increased in August (DOY effect, $P = 0.0007$), whereas in 2002 VWC peaked in May and declined throughout the growing season (DOY, $P = 0.0001$). In both years, patterns of soil moisture between treatments did not vary through time ($\text{CO}_2 \times \text{DOY}$, $P \geq 0.51$). Photosynthetically active radiation ($\mu\text{mol}/\text{m}^2/\text{s}$) above subplots did not differ between CO_2 treatments on any sampling date in 2001 and 2002 ($P \geq 0.34$) (Table 2).

Discussion

Total production of the understory in response to elevated CO₂ varied between years, and was mediated by species-specific responses to CO₂ enrichment and inter-annual variation in environmental conditions. Specifically, opposite responses of the two dominant plant species, *L. japonica* and *M. vimineum*, to CO₂ enrichment masked potential differences in total production in 2001. This opposing response of species to CO₂ has also been observed in other communities (Potvin and Vasseur 1997; Norton et al. 1999), and has been attributed to differential responses of C₃ and C₄ plants (Reynolds 1996). In the understory of the sweetgum plantation, the dominant C₃ plant, *L. japonica*, exhibited higher rates of production in elevated CO₂, which is consistent with observed responses of other C₃ species (Poorter and Navas 2003) and this species in particular (Sasek and Strain 1991). Production of *M. vimineum*, the dominant C₄ species, was actually lower under elevated CO₂. Negative responses to elevated CO₂ of other species has been observed elsewhere (Arp et al. 1993; Norton et al. 1999), and is usually attributed to competitive interactions with more responsive species (Reynolds 1996; see *Species Interactions* section below).

In 2002, we did not observe this opposing response between *L. japonica* and *M. vimineum*. In fact, although production of *L. japonica* was three times greater under elevated than ambient CO₂, *M. vimineum* did not differ between treatments. This result is not particularly unusual, because rates of photosynthesis of C₄ species are often CO₂ saturated at current [CO₂] and exhibit minimal responses to elevated CO₂ in controlled environments (Poorter and Navas 2003) and in field settings (Owensby et al. 1999). In this case, 2002 was a particularly dry year, which likely

explains the 64% decrease in *M. vimineum* production from 2001 to 2002 under ambient CO₂. This decrease in production of *M. vimineum* resulted in the decline in total production within ambient plots. Elevated CO₂ can alter water budgets at the individual (Huxman and Smith 2001) and ecosystem (Field et al. 1995) level in grassland systems (Owensby et al. 1999; Dukes 2002). *M. vimineum* may have had greater water savings under elevated CO₂ treatments in 2002, and was thus able to maintain rates of production similar to 2001. While no data exist to support this hypothesis, other C₄ plants respond positively to CO₂ enrichment as a result of increased water savings (Knapp et al. 1993). Moreover, the response of other C₄ plants to elevated CO₂ in dry years lead to increases in total community production in a grassland community (Owensby et al. 1999).

The differential response of species to CO₂ in each year also were responsible for observed differences in composition under elevated CO₂. Differences in diversity between the CO₂ treatments in 2001 and 2002 were driven by the response of *M. vimineum*. Diversity was higher in elevated CO₂ plots in 2001, as a result of differences in species evenness, which was driven by the decreased production and dominance of *M. vimineum*. Elevated CO₂ has altered species diversity in other systems by increasing evenness (i.e., decreasing dominance) within communities by favoring certain species or functional groups (Potvin and Vassuer 1997; Leadley et al. 1999; Niklaus et al. 2001).

Species interactions

Species interactions were likely important mediators of plant community responses to elevated CO₂ (Tilman 1982; Lüscher et al. 1996). In another

experiment conducted under ambient [CO₂], *M. vimineum* asymmetrically competed with *L. japonica* (Chapter 3). In the current study, elevated [CO₂] may have shifted this interaction in favor of *L. japonica*, which coincides with the pattern in other systems where CO₂ enrichment favors C₃ species over C₄ species (Reynolds 1996). While *L. japonica* responded similarly during both the wet (2001) and dry (2002) growing seasons, the response of *M. vimineum* to interactions of soil water availability, competition with *L. japonica*, and potential water savings under elevated CO₂ are not clear. Others have reported potential interactions between soil water availability, CO₂ enrichment, and interspecific competition as important factors mediating community responses to elevated CO₂ (Owensby et al. 1993). Specifically, in a grassland community, species that were inferior competitors in mesic habitats responded negatively to increased soil moisture caused by elevated CO₂ (Leadley et al. 1999). We need to conduct more experiments to determine the relationship between elevated CO₂ and limited availability of water on the interactions between *L. japonica* and *M. vimineum*.

Response of invasive species to elevated CO₂

An increase in atmospheric [CO₂] may increase the success of non-native invasive plants by directly enhancing their growth or by altering the availability of resources (Dukes and Mooney 1999; Smith et al. 2000; Weltzin et al. 2003). However, studies examining the response of invasive plants to elevated CO₂ are rarely conducted in natural communities (Dukes 2000). This study provides evidence that *L. japonica* responds positively to CO₂ enrichment, not only in monoculture (Sasek and Strain 1991), but also in natural communities. Thus, as [CO₂] continue to

rise, *L. japonica* may become more abundant and pose additional threats to native ecosystems.

M. vimineum is also considered a problematic invasive plant (Redman 1995), but it responded differently to elevated CO₂, possibly as a result of variations in soil moisture. Moreover, inter-annual variation in production of *M. vimineum* was an important driver of understory composition and diversity. Thus, abundance and impact of *M. vimineum* in a future CO₂-enriched atmosphere may be mediated by predicted changes in precipitation patterns and soil water availability (Houghton et al. 2001).

Conclusion

This study demonstrates that community responses to elevated CO₂ are dependent on the responses of individual species. However, other environmental factors, such as water availability and species interactions, are important mediators of community and species responses to CO₂ enrichment. Interannual variation in the production of *M. vimineum* affected total understory production, community composition, and diversity. Thus, opposing species responses masked differences in total understory production but accentuated differences in diversity during the year when soil water availability was high. These data, coupled with previous studies (Sasek and Strain 1991), suggest that certain invasive species may become more abundant as atmospheric CO₂ continues to increase. However, increases in [CO₂] are likely to affect patterns of precipitation and temperature, so responses of invasive species and their recipient communities to increased [CO₂] are likely to be mediated by subsequent changes in other environmental factors.

CHAPTER 3

Positive and negative interactions of non-indigenous species: invasional meltdown or just plain competition?

This chapter is a revised version of a paper by the same name to be submitted to the journal *Ecology* by R. Travis Belote and Jake F. Weltzin.

My use of “we” in this chapter refers to the co-author and myself.

Introduction

Interspecific interactions including competition, interference, and facilitation are important determinants of composition, distribution, and abundance of species within natural communities (Goldberg and Barton 1992; Keddy 2001; Bruno et al. *in press*). Mechanisms determining the nature of interspecific interactions and how those interactions affect community structure are dependent on life history strategy, phenology, physiology, and morphology of potentially interacting species (Tilman 1987). Moreover, interactions of species change along environmental gradients, both biotic (e.g., presence of herbivores) and abiotic (e.g., resource availability) (Huston 1979). The effect that resource availability has on species interactions, and how those interactions affect the structure and function of communities and ecosystems (i.e. species abundance and distribution) has been a major topic of ecology (Clements et al. 1929; Tilman 1982; Keddy 2001).

Over the last several decades, ecologists have become increasingly interested in how invasions by non-indigenous organisms affect managed or natural ecosystems (Elton 1958; Mack et al. 2000). Invasions by non-indigenous species are considered one of the greatest threats to global biological diversity, second only to

habitat destruction (Vitousek 1997). While resource availability may be the ultimate determinant of invasive plant establishment and success within ecosystems (Davis et al. 2000), invading species may possess novel traits, such as the ability to fix nitrogen, that allow them to use resources more efficiently in native communities (Shea and Chesson 2002). Moreover, asymmetric competition for shared resources between exotics and native species may be an important factor determining invasions (Callaway and Aschehoug 2000) and their impact on native communities (Parker et al. 1999).

Negative interactions between species, both native and exotic, is proposed as a mechanism supporting the long held paradigm that species rich-communities are more resistant to invasions than species poor communities (Elton 1958; Naeem et al. 2000). However, direct interactions between invasive plants may be important in determining the structure and function of native communities. Elton (1958), and more recently Simberloff and Von Holle (1999), suggested facilitation between invasive species may enhance the spread and impact of non-indigenous species on native ecosystems in an "invasional meltdown." Specifically, exotic plants may facilitate other invasions by altering abiotic factors of ecosystems, such as fire regimes (Mack and D'Antonio 1998), water availability (Sala et al. 1996), or nitrogen cycling (Vitousek and Walker 1989). However, the ability of an exotic species to invade and impact habitats may often be due to its superior competitive ability within communities (Shea and Chesson 2002), which could result in resistance to further invasions (i.e., supporting the classical invasional paradigm). Interactions between invasive species, whether facilitative or mutually detrimental (i.e., competitive), have rarely been investigated (Simberloff and Von Holle 1999).

This study was designed to determine the patterns of interactions (i.e., competition or facilitation) and the mechanisms driving those interactions, between two invasive plant species. *Lonicera japonica* Thunb., an invasive C₃ evergreen vine and *Microstegium vimineum* (Trin.) A. Camus, an invasive C₄ annual grass have invaded habitats throughout the eastern United States (Barden 1987; Hunt and Zaremba 1992; Robertson et al. 1994; Redman 1995). Both *L. japonica* and *M. vimineum* are considered shade tolerant (Carter and Teramura 1988; Horton and Neufeld 1998) and are regarded by local land managers of Oak Ridge National Environmental Research Park (ORNERP; Drake et al. *in press*) and Great Smoky Mountains National Park (NPS 1999), as serious threats to native understory communities. Specifically, *L. japonica* and *M. vimineum* together comprised over 85% of the total production within an eastern deciduous forest understory community located on the ORNERP (Chapter 2). Interactions between *M. vimineum* and *L. japonica* are likely to determine community structure and diversity in the understory communities already invaded by these species, as well as other habitats yet to be invaded. However, mechanisms determining interactions between the two invasive plants are unknown.

We established an *in situ* substitutive “press” removal experiment (Bender et al. 1984; Inouye 2001) to determine the nature of interactions between *M. vimineum* and *L. japonica* for 2 years within the understory of a closed canopy eastern deciduous forest. We predicted that soil water availability was a contested belowground resource limiting the production of both species in the forest understory. Therefore, we determined how experimental increases in soil water availability affected the interactions between the two species.

Data from the first growing season of the removal experiment suggested that *M. vimineum* interfered with *L. japonica*, regardless of soil moisture. We hypothesized that this pattern was caused by reductions in light under the canopy of *M. vimineum*. *M. vimineum* forms relatively dense canopies (4000 individuals/m²) about 40 cm tall during the peak of the growing season at this site (Belote, unpublished data) and elsewhere on the ORNERP (Cole 2003). The canopy of *M. vimineum* can overtop *L. japonica*, which in the absence of support hosts, has a prostrate growth form (Larson 1999). Therefore, in a second experiment, we used shade cloth to establish a light gradient to determine the effects of shading on the performance of *L. japonica*.

Methods

Study site

Research was conducted in the understory of a sweetgum (*Liquidambar styraciflua* L.) plantation established in 1988 on a terrace of the Clinch River (elevation 230 m asl) at the Oak Ridge National Environmental Research Park, Oak Ridge, Tennessee (35° 54' N; 84° 20' W). The *L. styraciflua* trees are approximately 17 m tall, with a closed canopy, which reduces the light in the understory between 70 and 95% during the growing season (Belote, unpublished data). The soil has a silty clay loam texture, is moderately well drained, and slightly acidic (water pH approximately 5.5-6.0) (SCS 1967, van Miegroet et al. 1994). Precipitation is evenly distributed throughout the year with an annual mean of 1322 mm. The mean annual temperature at the site is 13.9°C. The understory plant cover is continuous and co-dominated by *L. japonica* and *M. vimineum*. *L. japonica* and *M. vimineum*, on average, account for approximately 50% and 40% of the total biomass throughout the

understory, respectively (Chapter 2). Other common understory taxa at the site include *Rubus* spp. L., *Solidago canadensis* L., and seedlings of *Acer negundo* L.

Competition experiment

In April 2001, we established 24 1-m² plots within the sweetgum understory and randomly assigned one of three vegetation treatments and one of two watering treatments to each plot. Vegetation and watering treatment combinations were replicated four times in a fully crossed factorial design (3 vegetation treatments X 2 watering treatments X 4 replicates, $N = 24$).

Vegetation treatments were established from the *in situ* plant community and included (1) monocultures of *L. japonica*, (2) monocultures of *M. vimineum*, and (3) *L. japonica* and *M. vimineum* grown in mixture. *L. japonica* monocultures were established by pulling or clipping shoots of *M. vimineum* and all other taxa by hand, and were maintained throughout the experiment by hand weeding. *M. vimineum* monocultures were established by removing *L. japonica* with an application of herbicide in April and hand-clipping throughout the growing season. Mixture vegetation treatments were established by removing all plant species other than *L. japonica* and *M. vimineum* from each plot with a spot application of herbicide or by hand weeding. In the mixture plots we carefully disturbed the soil with our hands to mimic the soil disturbance caused by vegetation removal in the monoculture plots. Each vegetation treatment was randomly assigned one of two watering treatments that consisted of (1) ambient precipitation (= ambient) and (2) a weekly addition of water equivalent to a 27 mm precipitation event (= wet) between late April and mid-September 2001 and 2002.

Within each plot, we collected vegetation data from the central 0.25-m² area to provide a 0.25 m buffer area around sampled vegetation. We visually estimated cover (%) of *L. japonica* and *M. vimineum* based on a modified Daubenmire cover class (Mueller-Dombois and Ellenberg 1974) prior to treatment initiation in April 2001 and again in June and September of 2001, and May, June, and August of 2002. On each sampling date, we determined average canopy height (mm) of *M. vimineum* with a ruler at two random locations within each plot. At experiment termination in September 2002, we determined aboveground biomass (g/m²) of both species by clipping them at ground level and drying them at 60°C to constant mass.

Volumetric water content (VWC; %) in the top 15 cm of soil was recorded biweekly four to six days after watering events in all plots during the growing season, with permanently placed time domain reflectometry (TDR) rods (Soil Moisture Equipment Corp., Santa Barbara, CA, USA). We measured PAR ($\mu\text{mol}/\text{m}^2/\text{s}$) 0.5 meters above each plot at midday on clear days using a handheld line integrating ceptometer (AccuPAR, Decagon Devices, Inc., Pullman, WA, USA) 3 times during each of the 2001 and 2002 growing seasons.

Light gradient experiment

Because low light levels (in an understory already shaded by the *L. styraciflua* canopy) may have constrained the growth of *L. japonica*, we initiated a light gradient experiment to test the effects of a reduction in PAR on cover and production of *L. japonica*. We measured PAR above and below the canopy of *M. vimineum* at random locations in the understory three times during the 2002 growing season, and determined that *M. vimineum* reduced PAR between 80% and 90%. In May 2002, we

established 12 1-m² plots of *L. japonica* monoculture, and randomly assigned each plot to 1 of 3 shade treatments created with shade cloth. Monocultures of *L. japonica* were established in the same manner as in the competition experiment, and were maintained throughout the experiment by removing other plant species by hand. We clipped vegetation along the perimeter of each plot to prevent prostrate shoots of *L. japonica* from entering plots. Commercially available shade cloth of different densities was erected 0.3-m above the center of each plot to establish light treatments of (1) ambient understory PAR (= non-shaded), (2) 40% of ambient PAR (= medium), and (3) 2% of ambient PAR (= dark). Medium and dark plots were completely covered with 1.5-m x 1.5-m squares of shade cloth to include a 0.25-m buffer around each plot. Light reduction treatments were verified by determining PAR above and below the shade cloth three times during the growing season.

We estimated cover of *L. japonica* at experiment initiation (May 2002) and again in June and July 2002. At experiment termination in August 2002, aboveground biomass (g/m²) of *L. japonica* was destructively harvested at ground level, dried at 60°C to constant mass, and weighed. We determined VWC three times during the growing season with a handheld TDR probe (Hydrosense; Decagon Devices, Inc., Pullman, WA, USA). Temperature was recorded every hour in each plot for 10 continuous days during the growing season using temperature data loggers placed on the soil surface in the center of each plot (Stowaway tidbit; MicroDAQ, Ltd., Warner, NH, USA). All vegetation and environmental data were recorded in the center 0.25-m² area of each plot.

Statistical analysis

We analyzed cover and biomass of *L. japonica*, and cover, height and biomass of *M. vimineum*, for main and interactive fixed effects of vegetation and watering treatments by sampling date with a two-way ANOVA (procedure GLM; SAS Institute 1999). VWC was analyzed by year for effects of vegetation and watering treatments, and sampling date as the repeated measure, with a repeated measures multivariate analysis of variance (MANOVA; Pillai's Trace in SAS procedure GLM; SAS Institute 1999). Because *L. japonica* is evergreen, we used a paired t-test (procedure TTEST; SAS Institute 1999) to determine whether cover of *L. japonica* differed between the September 2001 and the May 2002 sampling dates. To elucidate patterns between canopy development of *M. vimineum* and abundance of *L. japonica*, we used Pearson correlation to analyze height of *M. vimineum* with cover of *L. japonica* within mixture plots, across all sampling dates.

We calculated relative competition indices (RCI) (Gurevitch et al. 2002) based on aboveground biomass of both species within each watering treatment to determine whether competition intensity differed between species and with water availability.

RCI of each observation (i) was calculated as:

$$RCI_i = (B_{i \text{ monoculture}} - B_{\mu \text{ mixture}}) / B_{i \text{ monoculture}}$$

where $B_{i \text{ monoculture}}$ is the aboveground biomass (g/m^2) of either *L. japonica* or *M. vimineum* grown in monoculture, and $B_{\mu \text{ mixture}}$ is the mean biomass of each species grown in mixture. Positive RCI values indicate detrimental effects of the other species on the species of interest when grown in mixture (i.e., species have greater biomass when grown in monoculture than in mixture). For example, an RCI value of 0.70 can be interpreted as a 70% reduction in biomass of species i when grown in

mixture relative to monoculture. Alternately, negative values indicate facilitation, where species have greater biomass when grown in mixture than in monoculture. We analyzed RCI for main and interactive effects of each species and watering treatment using a two-way ANOVA (procedure GLM; SAS Institute 1999).

Cover of *L. japonica*, and PAR and VWC collected from the light gradient experiment, were analyzed for each sampling date using a one-way ANOVA (procedure GLM; SAS Institute 1999) to test for fixed effects of shade treatment. Similarly, we used a one-way ANOVA to analyze biomass of *L. japonica* at experiment termination. Mean daily temperature data were averaged across the sampling period for each plot and were analyzed with a one-way ANOVA.

All data from both experiments were tested for normality and homogeneity of variance with the Shapiro-Wilk *W*-Statistic and Levene's test, respectively (Shapiro and Wilk 1965; Levene 1960); data that did not meet these assumptions were either log-transformed or arcsine-square root transformed before analysis as appropriate. Because cover values were converted to the midpoint of each class, they did not meet assumptions of normality and were rank-transformed (Zar 1984) before analyses.

Results

Competition experiment

Predictably, cover of *L. japonica* and cover of *M. vimineum* did not differ between vegetation treatments prior to treatment initiation in April 2001 (Table 4, Fig. 4). On all subsequent dates, cover of *L. japonica* was greater in monoculture plots (without *M. vimineum*) than in mixture plots (with *M. vimineum*). However, on all but one sampling date, cover of *L. japonica* within vegetation treatment also depended on

watering treatment (vegetation x water interaction, Table 4). Specifically, cover of *L. japonica* in monoculture plots was greater in wet than ambient plots on three sampling dates, and cover of *L. japonica* in mixture plots was lower in wet than ambient plots on two sampling dates (Fig. 4). Cover of *L. japonica* in mixture plots was greater in May 2002 than September 2001 (paired t-test; $P \leq 0.05$), but cover of *L. japonica* in the monoculture plots did not differ in this manner ($P \geq 0.18$).

Cover of *M. vimineum* differed little between vegetation treatments and watering treatments (Table 4, Fig. 5). In June 2002, cover of *M. vimineum* in monoculture plots was less in wet than ambient treatments (Fig. 5). Height of *M. vimineum* did not differ ($P \geq 0.53$) between treatments on any date (data not shown). In mixture plots, height of *M. vimineum* was negatively correlated ($r = -0.65$, $P < 0.0001$) with *L. japonica* cover across all dates.

Biomass of *L. japonica* at experiment termination was 3 times greater in monoculture than when grown in mixture with *M. vimineum* ($P < 0.0001$), but did not differ between watering treatments ($P = 0.72$, Fig. 3; vegetation x water interaction, $P = 0.17$). Biomass of *M. vimineum* was 47% greater in monoculture than in mixture ($P = 0.01$), and was 35% greater in wet than ambient precipitation plots ($P = 0.03$, Fig. 6; vegetation x water interaction $P = 0.83$).

RCI

RCI of *L. japonica* (0.63) was greater than RCI of *M. vimineum* (0.32) depending on watering treatment (water x vegetation interaction, $P = 0.01$). RCI of *L. japonica* was greater in wet mixture plots (0.74) than ambient mixture plots (0.53) ($P = 0.01$). RCI of *M. vimineum* was greater in ambient mixture plots (0.38) than wet mixture plots (0.25) ($P = 0.08$).

Soil moisture and PAR

Soil VWC depended on watering treatment and time of year (water treatment $\times$ time, $P \leq 0.0001$). On 9 of 10 dates in 2001, and all 7 dates in 2002, soil VWC was greater in wet plots than ambient plots (Fig. 7). In 2001, VWC peaked in May and August (time, $P = 0.0001$), whereas in 2002, VWC peaked in May and declined throughout the growing season. Photosynthetically active radiation did not differ ($P = 0.49$) between treatments on any sampling date (data not shown).

Light gradient experiment

Cover of *L. japonica* did not differ between plots at the time the shade treatment was established in May 2002 (Fig. 8). By June, cover of *L. japonica* was greater in non-shaded plots than plots receiving the darkest treatment. By late July, *L. japonica* in the dark plots had lost most of its leaves and cover in those plots was less than the medium and non-shaded plots. At experiment termination aboveground biomass of *L. japonica* was lower in the dark shade treatment ($66 \pm 8 \text{ g/m}^2$; $P \leq 0.09$) than the medium ($111 \pm 16 \text{ g/m}^2$) or non-shaded ($113 \pm 26 \text{ g/m}^2$) treatments, which did not differ ($P = 0.93$).

Photosynthetically active radiation (PAR) differed between treatments depending on date (Table 5). Specifically, in May and June 2002, PAR was greater in non-shaded plots than shaded plots, but did not differ between the medium and dark plots. In July, PAR in the non-shaded plots did not differ from the medium shade plots, but they were both greater than the dark plots. Soil VWC did not differ between shade treatments on any date in May ($36 \pm 1\%$; $P = 0.24$), June ($38 \pm 1\%$; $P = 0.76$), and July ($28 \pm 1\%$; $P = 0.65$). Mean daily temperature was greater ($P \leq 0.003$) in the

non-shaded plots ($23.5 \pm 0.1^{\circ}\text{C}$) than either the medium plots ($22.8 \pm 0.1^{\circ}\text{C}$) and dark plots ($22.9 \pm 0.1^{\circ}\text{C}$), which did not differ ($P = 0.67$).

Discussion

Interpreting the nature of interactions between *L. japonica* and *M. vimineum* depends on the measure of abundance employed, a finding not uncommon to competition experiments (Gurevitch et al. 2002). Specifically, cover estimates demonstrated that *M. vimineum* interferes (i.e., amensalism) with *L. japonica*, whereas biomass data revealed a mutually detrimental relationship (i.e., competition) between the two species. However, it is clear that *M. vimineum* is a superior competitor to *L. japonica*, probably because reductions in light by *M. vimineum* negatively affected *L. japonica*. Moreover, *M. vimineum* more strongly interfered with *L. japonica* in plots that received weekly additions of water, again because of reductions in the availability of light below the *M. vimineum* canopy. I will explore these patterns and mechanisms further in the following paragraphs.

Based on cover, *M. vimineum* interfered with *L. japonica* but was unaffected by the presence of *L. japonica*. Interestingly, in their review of the literature on interactions between exotic species, Simberloff and Von Holle (1999) found no studies documenting amensalistic interactions between non-indigenous species. In terms of biomass production, which is a more precise measure of abundance, interactions between *L. japonica* and *M. vimineum* were mutually detrimental, but still asymmetric in favor of *M. vimineum*. Moreover, *M. vimineum* performed better in wet than ambient plots regardless of the presence of *L. japonica*.

Relative competition indices for both species were positive, which indicates mutually detrimental interactions between the two species. However, the RCI for

each species depended on the availability of water. For example, *L. japonica* was more detrimentally affected by *M. vimineum* in wet plots than ambient plots. Thus, in contrast to our hypothesis, additions of water did not release the two species from competition, but rather gave *M. vimineum* an added advantage over *L. japonica*. Therefore, we reject the hypothesis that interactions between these two species are caused by competition for water. However, our interpretation is consistent with the theory that increases in resource availability will likely benefit the better competitor (Huston 1979), which in this case is *M. vimineum*.

Mechanisms of species interaction

There are several mechanisms that explain the observed pattern of asymmetric competition between *M. vimineum* and *L. japonica*. First, the reduction in light below the canopy of *M. vimineum* may reduce the available light below the tolerance of *L. japonica*. Results from the light gradient experiment demonstrated that cover of *L. japonica* was reduced by shading commensurate with *M. vimineum* canopy. This hypothesis is further supported by the trend in decreases in cover of *L. japonica* as the *M. vimineum* canopy developed. Based on these patterns, we cannot reject the hypothesis that light limits the abundance of *L. japonica* under the canopy of *M. vimineum*.

Supplemental watering may have increased light interception by *M. vimineum* in the wet plots. While this was not specifically measured, this interpretation is supported by patterns of *M. vimineum* biomass in wet plots and supports the hypothesis that light reductions under *M. vimineum* is the factor limiting *L. japonica*. In fact, the effect of resource availability on competitive intensity has long been a

debated topic in ecology. The discussion centers on the interactions between belowground and aboveground resources and whether or not competition intensity increases with productivity (i.e., soil resource availability) (Grime 1973; Newman 1973; Tilman 1987; Keddy 2001). This study supports the theory that competition for aboveground resources (i.e., light) is more intense in areas of greater belowground resources (i.e., soil water availability). However, the data are limited with regard to the role of competition for belowground resources in unproductive sites, because soil moisture was not experimentally reduced to specifically test the effects of limited soil water availability.

While the debate on the importance of resource availability in determining the nature of competition has been important in ecology, the physiology and morphology of species may also explain the observed patterns of interactions (Tilman 1987). In this case, the ability of *L. japonica* to use circumnutation hosts (i.e., vegetation with erect forms, such as tall herbs, or shrubs, or tree seedlings) for support when growing to acquire light has been proposed as a mechanism by which *L. japonica* competes with other species (Dillenburg et al. 1993), and may be a factor related to its "invasiveness" (Larson 1999). Because other species were removed at the onset of the experiment, no support hosts were available to *L. japonica*. As a consequence, the prostrate growth form of *L. japonica* limited its ability to obtain light below the dense *M. vimineum* canopy. There are other reports of plants with prostrate growth forms that are overtopped by competitors due to their inability to acquire light resources (Grime 1965; Reader and Best 1989).

In a separate experiment, we experimentally added circumnutation support hosts to mixtures of *L. japonica* and *M. vimineum*. We observed that within a single

growing season, circumnutation activity of *L. japonica* and end of season biomass increased in plots with added support hosts (Belote, unpublished data). Over several growing seasons, the presence of support hosts may enable *L. japonica* to overtop *M. vimineum* and eventually exclude it. *M. vimineum* cannot establish in areas where *L. japonica* has established thickets (Barden 1987) and shading by other plants has been shown to reduce performance of *M. vimineum* (Cole 2003). However, circumnutation throughout the sweetgum understory is relatively low compared to more open stands of trees nearby, which suggests light may actually limit circumnutation by *L. japonica*. Because we cannot reject the hypothesis that *L. japonica* is limited by circumnutation support hosts, more rigorous experimentation is needed to determine mechanisms governing this response. Finally, *M. vimineum* may produce an allelopathic substance that inhibits the growth of *L. japonica*; this hypothesis is yet to be tested.

The different phenologies of *L. japonica* (evergreen vine) and *M. vimineum* (annual grass) are important in determining the interactions and coexistence of the two species. Specifically, interactions between *L. japonica* and *M. vimineum* depend on temporal variation in abundance of *M. vimineum*. After *M. vimineum* senesces at the end of the growing season, *L. japonica* is released from the negative effects of *M. vimineum*. This explains the decrease in *L. japonica* throughout both growing seasons, the increase in *L. japonica* cover during the first sampling period of 2002, and the negative correlation between height of *M. vimineum* and cover of *L. japonica* across sampling periods when grown in mixture. *M. vimineum* interference with *L. japonica* may be causing temporal niche partitioning between the two species by forcing *L. japonica* to utilize the sub-optimal time between fall and early spring for

growth and reproduction (Carothers and Jaksic 1984). While some species have evolved life history strategies or phenologies to reduce negative interactions with competitors, *L. japonica* and *M. vimineum* have been sympatric in North America for only about 80 years. However, we do not know if these species interact in their native ranges, or the possible importance of the interactions to the ecology and evolution of each. Moreover, reproductive variables (i.e., flowering time and seed production) were not measured in this study; assessment of such may provide important insights into predicting longer term population effects of interactions between the species.

Evidence for invasional meltdown?

In a provocative article, Simberloff and Von Holle (1999) suggested that positive interactions between non-indigenous species may facilitate further invasions, which may intensify the impact of invasive species on native ecosystems. Non-indigenous plants with novel traits that profoundly altered functions of ecosystems are the best example of invasive plants facilitating other invasive plants (e.g., *Myrica faya*, Vitousek and Walker 1989; *Tamarix*, Sala et al. 1996), but little other evidence exists for facilitation among non-indigenous plants. The co-dominance of these two species within understory communities may appear to support the facilitative theory of exotics species or “invasional meltdown” (Simberloff and Von Holle 1999). However, interactions between *L. japonica* and *M. vimineum* are amensalistic or competitive and not facilitative. Competition between the two species may actually limit the performance of both species, the invasion by other non-indigenous species, or the establishment of native species.

While both species are regarded by land managers as negatively impacting native vegetation, little data exist supporting the claims. This is the first study to provide experimental and mechanistic evidence of *M. vimineum*'s negative effects and competitive ability. More experiments are needed to determine how interactions between *L. japonica* and *M. vimineum* may impact diversity and function of native ecosystems already and yet invaded by these two species.

CHAPTER 4

Conclusions

Community response to elevated CO₂

Results from my research indicate that ecosystem and community responses to future increases in [CO₂] will depend not only on responses of individual species, but also on species interactions and abiotic environmental factors (e.g. soil moisture). Consistent with other work that observed opposing responses of different plant species to elevated [CO₂] (Norton et al. 1999), opposite responses of *L. japonica* and *M. vimineum* masked potential differences in total understory production but accentuated compositional (e.g., species diversity) differences during the wet year (2001). Specifically, elevated CO₂ caused a three-fold increase in production of *L. japonica* in both the wet and dry years, whereas *M. vimineum* varied between years. During the wet year, *M. vimineum* produced twice as much biomass in ambient CO₂ plots than elevated CO₂ plots, but did not differ between CO₂ treatments in the dry year. These results confirm research in other studies of elevated CO₂ on communities that found that community responses to elevated CO₂ are often unpredictable, in part because of the availability of other resources (Owensby et al. 1993 and 1999; Smith et al. 2000).

Heterogeneity of resources in space and time is an important determinant of species composition and production (Tilman 1982). However, our ability to predict responses of natural systems to elevated CO₂ is limited in that resource availability can both enhance and dampen the effects of elevated CO₂. In some communities, positive species responses to elevated CO₂ were observed only when availability of

water was high (Smith et al. 2000). In other systems, community responses to CO₂ occurred only when the availability of water was limited (Owensby et al. 1999; Chapter 2). The photosynthetic pathway of the dominant species may explain the contradictory results regarding water availability: specifically, C₃ species may positively respond to elevated CO₂ by increasing the acquisition of carbon only when water resources are abundant (Huxman and Smith 2001). In contrast, photosynthesis rates of C₄ species are usually CO₂-saturated at current [CO₂] (Ghannoum et al. 2000), and may only benefit from elevated CO₂ through increased water use efficiency during dry years (Clark et al. 1999). Similar results, for reasons as yet understood, can occur for other resources, such as light (Bazzaz and Miao 1993; Poorter and Pérez-Soba 2001) or nitrogen (Roy et al. 1996; Cannell and Thornley 1999). Recently, Shaw et al. (2002) suggested that elevated CO₂ might actually diminish the otherwise positive effects of water, nitrogen, and warming on California grassland production. The mechanisms driving this latter pattern are not fully understood, but it is clear that more long term studies with multiple factors are needed to better understand potential effects of increasing atmospheric CO₂ on communities (Morgan 2002).

Plant invasions and interactions under elevated CO₂

Invasive species are not intrinsically more responsive to elevated CO₂ (Dukes 2000). However, invasive species may possess novel characteristics that allow them to invade communities (Shea and Chesson 2002), and elevated CO₂ may give them an added advantage over native species (Weltzin et al. 2003). Moreover, responses of invasive species to elevated CO₂ may mediate the response of entire communities, in terms of production and diversity (Chapter 2). However, few studies have

investigated or documented the response of invasive species to elevated CO₂ in community settings (Dukes and Mooney 1999; Dukes 2000; Smith et al. 2000; Weltzin et al. 2003). Smith et al. (2000) determined that elevated [CO₂] may increase propagule pressure of an invasive annual grass in a desert ecosystem, but only during years that receive abundant rainfall. In this study, *L. japonica*, a problematic invasive plant in the southeastern U.S., exhibited a three fold increase in production under elevated CO₂ (Chapter 2). This observation, coupled with results of previous studies (Sasek and Strain 1991), suggest that this invasive vine may become more abundant as atmospheric CO₂ continues to increase, provided its response is not limited by other resources. The response of the other dominant invasive plant, *M. vimineum*, to elevated CO₂ altered total understory production and diversity, depending on soil water availability. Therefore, as atmospheric CO₂ increases, shifts in patterns of precipitation and soil moisture (Houghton et al. 2001) may mediate the response of invasive species (Smith et al. 2000; Chapter 2).

Interspecific interactions are important determinants of composition, distribution, and abundance of species within natural communities (Goldberg and Barton 1992; Keddy 2001) and may mediate responses of species to elevated CO₂ (Dukes 2002). Moreover, the co-dominance of the two invasive species, *L. japonica* and *M. vimineum*, raised intriguing questions related to invasion biology: Is the pattern of co-dominance between these two species explained by facilitative interactions (Simberloff and Von Holle 1999)? Results of a 'press' removal experiment indicated that the relationship between the two species was mutually detrimental, though *M. vimineum* had a competitive advantage over *L. japonica*, because its growth form enabled it to acquire light to the detriment of the prostrate *L.*

japonica (Chapter 3). In contrast to our prediction that greater water availability might release the two species from competition, increased soil water availability only benefited *M. vimineum*, which further reduced the light available to *L. japonica*. Therefore, facilitation between the two species does not explain their co-dominance in the understory community.

The phenology of each species appeared to play an important role in their coexistence and may lead to detrimental impacts to native vegetation. Specifically, the evergreen characteristics of *L. japonica* may prevent it from being excluded by its use of a separate temporal niche. This temporal niche separation may be important in determining the impact the two species. To date, little is known about the individual effects of *L. japonica* and *M. vimineum* on native communities. However, if the two species are occupying separate temporal niches, then their combined effects throughout the year may have negative impacts on native understory species. While this is only speculation, it is apparent that interactions, between invasive species, as mediated by species phenology and their use of resources, should be an important area of research.

It is unclear exactly how elevated CO₂ might affect interactions between plants. Results from Chapter 2 indicated that elevated CO₂ favors *L. japonica*, which may affect its interactions with *M. vimineum*. Under elevated CO₂, *L. japonica* may be able to better compete with *M. vimineum*, eventually forming thickets and possibly excluding *M. vimineum* (Barden 1987). However, this change from coexistence under current [CO₂] to competitive exclusion under elevated CO₂, is obviously speculative. More research is needed to determine whether *L. japonica* is favored over *M. vimineum* in elevated CO₂, and how soil water availability may alter the interactions of

the two species under elevated CO₂. Furthermore, models could be developed to characterize the time dependent interactions of *L. japonica* and *M. vimineum*, and possibly predict changes in the interactions of *L. japonica* and *M. vimineum* under elevated CO₂.

Future directions

Future research should investigate the role of multiple and possibly interacting factors of global change, including elevated CO₂, water availability, increased temperature, nitrogen deposition, altered disturbance regimes, and invasions by exotic species on managed and natural ecosystems. Predicting how ecosystems will respond to global change should be based on empirical data acquired through longer term, manipulative multi-factorial experiments (Shaw et al. 2002) conducted in realistic settings (Körner 2000). Models that incorporate empirical data may help determine long term effects that global change may have on species interactions and ecosystem responses (Cannell and Thornley 1998). Furthermore, global change, including increases in [CO₂] and invasions by non-indigenous species, may affect ecosystems on all scales from genetic composition of populations (Burger and Lynch 1995) to landscape distributions of species (Turner et al. 2001). Investigations should address landscape level changes, such as habitat fragmentation, while considering that shifts in genetic components of populations may have important implications regarding responses to other aspects of global change.

Understanding the importance of increasing atmospheric [CO₂] and invasions by non-indigenous species is complex (Mooney and Hobbs 2000). This is mainly because species within communities may respond differently to spatial and temporal variations in availability of resources. Moreover, because species composition is

important to community level responses to CO₂, introductions of non-indigenous species, and the loss of native species, will likely affect how ecosystems respond to increasing atmospheric CO₂.

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APPENDIX

Table 1. Mean (± 1 SE) ANPP (g/m²/yr) and cover (%) of 5 dominant (mean cover > 8%) understory plant species in ambient and elevated CO₂ plots for 2001 and 2002. Richness, evenness, and diversity (based on ANPP) in subplots were calculated based on all species.

	2001			2002		
	Ambient	Elevated	<i>P</i> -value	Ambient	Elevated	<i>P</i> -value
<i>A. negundo</i>						
ANPP	3.6 $\pm$ 2.5	2.3 $\pm$ 3.1	0.78	1.3 $\pm$ 0.8	1.3 $\pm$ 1.0	0.95
Cover	10.9 $\pm$ 6.3	11.5 $\pm$ 8.1	0.96	8.0 $\pm$ 3.7	4.4 $\pm$ 4.6	0.70
<i>L. japonica</i>						
ANPP	11 $\pm$ 4	36 $\pm$ 5	0.03	17 $\pm$ 7	42 $\pm$ 9	0.11
Cover	21 $\pm$ 4	63 $\pm$ 5	0.008	37 $\pm$ 12	55 $\pm$ 15	0.42
<i>M. vimineum</i>						
ANPP	121 $\pm$ 11	72 $\pm$ 15	0.07	78 $\pm$ 14	70 $\pm$ 17	0.74
Cover	85 $\pm$ 5	67 $\pm$ 6	0.09	81 $\pm$ 8	60 $\pm$ 10	0.19
<i>Rubus</i> spp.						
ANPP	0.6 $\pm$ 0.6	3.2 $\pm$ 0.8	0.42	1.3 $\pm$ 1.9	4.8 $\pm$ 2.3	0.59
Cover	3.0 $\pm$ 3.0	16.0 $\pm$ 4.0	0.08	3.0 $\pm$ 5.2	19.1 $\pm$ 6.4	0.07

Table 1. Continued

	2001			2002		
	ambient	elevated	<i>P</i> -value	ambient	elevated	<i>P</i> -value
<i>S. canadensis</i>						
ANPP	0.6 ± 3.3	17.6 ± 4.4	0.43	0.05 ± 0.89	2.9 ± 1.1	0.76
Cover	1.6 ± 3.9	22.2 ± 4.9	0.02	4.0 ± 3.0	5.4 ± 3.7	0.79
Richness	5.4 ± 0.9	7.0 ± 1.2	0.38	4.2 ± 0.5	5.0 ± 0.6	0.37
Evenness	0.35 ± 0.04	0.54 ± 0.07	0.07	0.47 ± 0.05	0.56 ± 0.06	0.33
H'	0.6 ± 0.1	1.0 ± 0.1	0.09	0.7 ± 0.1	0.9 ± 0.1	0.27

Table 2. Mean (± 1 SE) photosynthetically active radiation (PAR; $\mu\text{mol}/\text{m}^2/\text{s}$) at the top of the sweetgum canopy and at 1 m above subplots in plots receiving ambient $[\text{CO}_2]$ and elevated $[\text{CO}_2]$. PAR did not differ between CO_2 treatments on any date ($P \geq 0.34$).

Date	Top of tree canopy	CO ₂ treatment	
		Ambient	Elevated
Aug. 2001	1451 $\pm$ 32	80 $\pm$ 20	78 $\pm$ 25
Sept. 2001	1316 $\pm$ 24	83 $\pm$ 24	102 $\pm$ 30
May 2002	1593 $\pm$ 77	180 $\pm$ 24	214 $\pm$ 29
June 2002	1672 $\pm$ 14	167 $\pm$ 46	71 $\pm$ 56

Table 3. Mean ($\pm$ SE) maximum cover (%) of understory taxa (s=seedling) in plots receiving ambient [CO₂] and elevated [CO₂] at sweetgum FACE site in 2001 and 2002.

Species	2001		2002	
	Ambient	Elevated	Ambient	Elevated
<i>Acer saccharum</i> (s)	1.5 $\pm$ 1.5	0.2 $\pm$ 0.2	3.8 $\pm$ 3.1	0
<i>Allium</i> spp.	3.1 $\pm$ 3.1	0.9 $\pm$ 0.5	0	0
<i>Asplenium platyneuron</i>	0.1 $\pm$ 0.1	0	0	0
<i>Aster dumosus</i>	0	0.5 $\pm$ 0.3	0	0
<i>Bignonia capreolata</i>	0.6 $\pm$ 0.3	0	2.1 $\pm$ 1.5	0
<i>Carex laevivaginata</i>	0.1 $\pm$ 0.1	1.4 $\pm$ 1.0	0	0
<i>Cerastium glomeratum</i>	0	0	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1
<i>Clematis virginiana</i>	1.5 $\pm$ 1.5	0	0	0
<i>Fraxinus pennsylvanica</i> (s)	16.5 $\pm$ 7.1	0	3.8 $\pm$ 3.1	2.2 $\pm$ 2.2
<i>Galium aparine</i>	0.6 $\pm$ 0.3	2.0 $\pm$ 1.0	0	0
<i>Geum canadense</i>	1.6 $\pm$ 1.4	0.4 $\pm$ 0.2	0	0
<i>Juncus tenuis</i>	0.1 $\pm$ 0.1	0.2 $\pm$ 0.2	0.6 $\pm$ 0.3	0.4 $\pm$ 0.4
<i>Juniperus virginiana</i> (s)	0	1.1 $\pm$ 1.1	0	0
<i>Lespedeza cuneata</i>	0	2.5 $\pm$ 2.5	0	0
<i>Lobelia</i> spp.	0	0.2 $\pm$ 0.2	0	0
<i>Myotosis macrosperma</i>	0.4 $\pm$ 0.3	0.4 $\pm$ 0.2	0	0.1 $\pm$ 0.1

Table 3. Continued

Species	2001		2002	
	Ambient	Elevated	Ambient	Elevated
<i>Oxalis stricta</i>	0.2 ± 0.1	0.2 ± 0.2	0	0
<i>Panicum clandestinum</i>	0.1 ± 0.1	5.4 ± 5.4	0	0
<i>Panicum</i> spp.	0.1 ± 0.1	0.5 ± 0.5	0.6 ± 0.6	0.8 ± 0.5
<i>Parthenocissus quinquefolia</i>	0.3 ± 0.3	0.5 ± 0.5	0.3 ± 0.2	6.9 ± 4.9
<i>Potentilla simplex</i>	3.5 ± 1.5	0.2 ± 0.2	2.6 ± 1.5	2.3 ± 1.2
<i>Prunus serotina</i> (s)	3.3 ± 1.9	0.2 ± 0.2	0	0
<i>Quercus velutina</i> (s)	1.5 ± 1.5	0	0	0
<i>Sanicula</i> spp.	0.5 ± 0.3	2.7 ± 2.4	0.7 ± 0.6	0.4 ± 0.4
<i>Solidago erecta</i>	0	3.6 ± 2.5	0	0
<i>Solidago</i> spp.	0	1.1 ± 1.1	0	4.8 ± 2.8
<i>Solidago speciosa</i>	0	4.1 ± 2.3	0.1 ± 0.1	0.8 ± 0.5
<i>Taraxacum officinale</i>	0.2 ± 0.1	0	0	0
<i>Toxicodendron quercifolia</i>	0.3 ± 0.1	3.0 ± 2.5	1.5 ± 1.5	5.7 ± 4.6
<i>Ulmus</i> spp.	0.1 ± 0.1	0.5 ± 0.5	0.4 ± 0.4	0.1 ± 0.1
<i>Vitis</i> spp.	1.5 ± 1.5	0.7 ± 0.3	0.3 ± 0.3	0.4 ± 0.4

Table 4. ANOVA *P*-values for main and interactive effects of two vegetation treatments (Veg; monoculture and mixture) and two watering treatments (Water; ambient precipitation and weekly additions of water) on cover (%) of *L. japonica* and *M. vimineum*. Means are in Figures 1 and 2.

Species	Year	Date	Source		
			Veg	Water	Veg X Water
<i>L. japonica</i>	2001	April	0.81	0.84	0.27
		June	<0.0001	0.56	0.05
		Sept.	<0.0001	0.88	0.003
	2002	May	0.01	0.44	0.01
		June	<0.0001	0.67	0.15
		Aug.	<0.0001	0.52	0.04
<i>M. vimineum</i>	2001	April	0.29	0.45	0.36
		June	0.006	0.09	0.01
		Sept.	0.18	0.99	0.99
	2002	May	0.25	0.41	0.41
		June	0.57	0.57	0.57
		Aug.	0.29	0.05	0.99

Table 5. Mean ($\pm$ SE) photosynthetically active radiation (PAR; $\mu\text{mol}/\text{m}^2/\text{s}$) in light gradient experiment of *L. japonica* during sampling periods, 2002.
 Note: Means with different superscript letters differed significantly within sampling period ($P < 0.05$).

Sampling period	Shade treatment		
	Non-shaded	Medium	Dark
May	45.2 $\pm$ 17.5 ^a	11.2 $\pm$ 2.2 ^b	1.3 $\pm$ 0.1 ^b
June	27.2 $\pm$ 7.9 ^a	6.1 $\pm$ 0.4 ^b	1.4 $\pm$ 0.2 ^b
July	33.8 $\pm$ 2.2 ^a	24.9 $\pm$ 12.7 ^a	2.5 $\pm$ 0.5 ^b

Figure 1. Total understory community ANPP ($\text{g/m}^2/\text{yr}$) in plots receiving ambient $[\text{CO}_2]$ (A) and elevated $[\text{CO}_2]$ (E) treatments at the sweetgum FACE site in 2001 and 2002. Symbols represent subplots within replicates of CO_2 treatments; horizontal bars are means. *P*-values are in results.

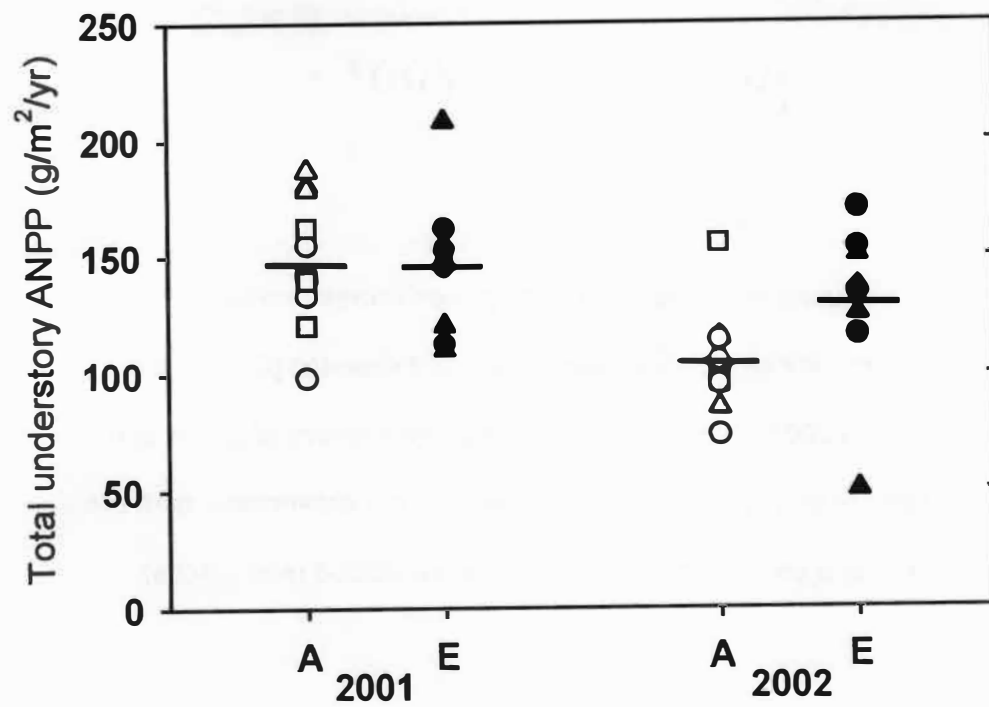


Figure 2. Ordination of quadrat scores (top) and species scores (bottom) of the understory plant community receiving ambient [CO₂] and elevated [CO₂] at the sweetgum FACE site in 2001. Taxa are coded using first 4 letters of genus and species, respectively, or only genus where species were not determined; taxa are in Table 1 or Table 3. Taxa correlated with axis scores are bolded (see results).

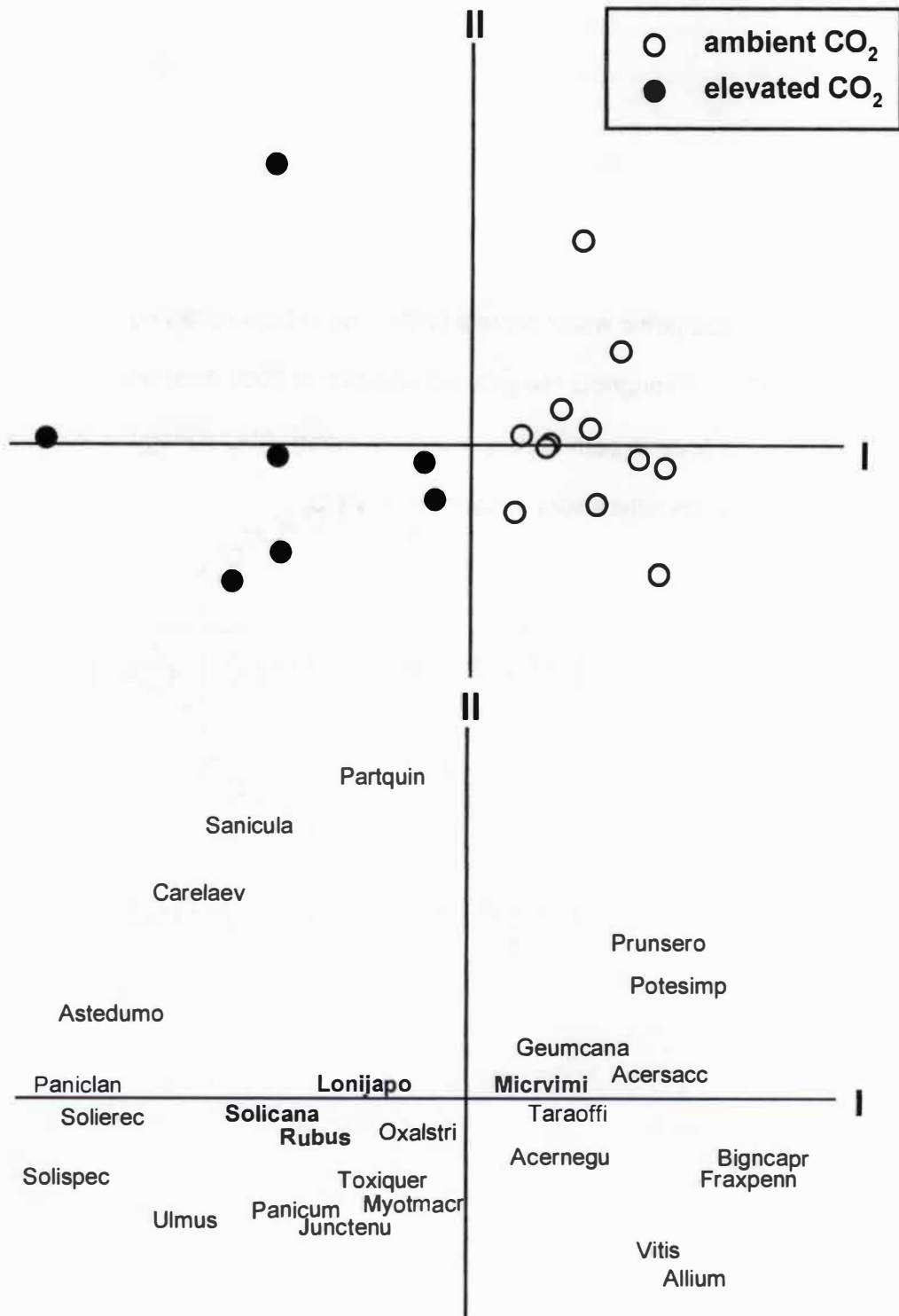


Figure 3. Soil volumetric water content (VWC; %) in plots receiving ambient [CO_2] and elevated [CO_2] throughout the growing seasons of 2001 (top) and 2002 (bottom). Broken horizontal lines in both figures represent mean VWC during the 2001 growing season to emphasize differences in patterns of VWC.

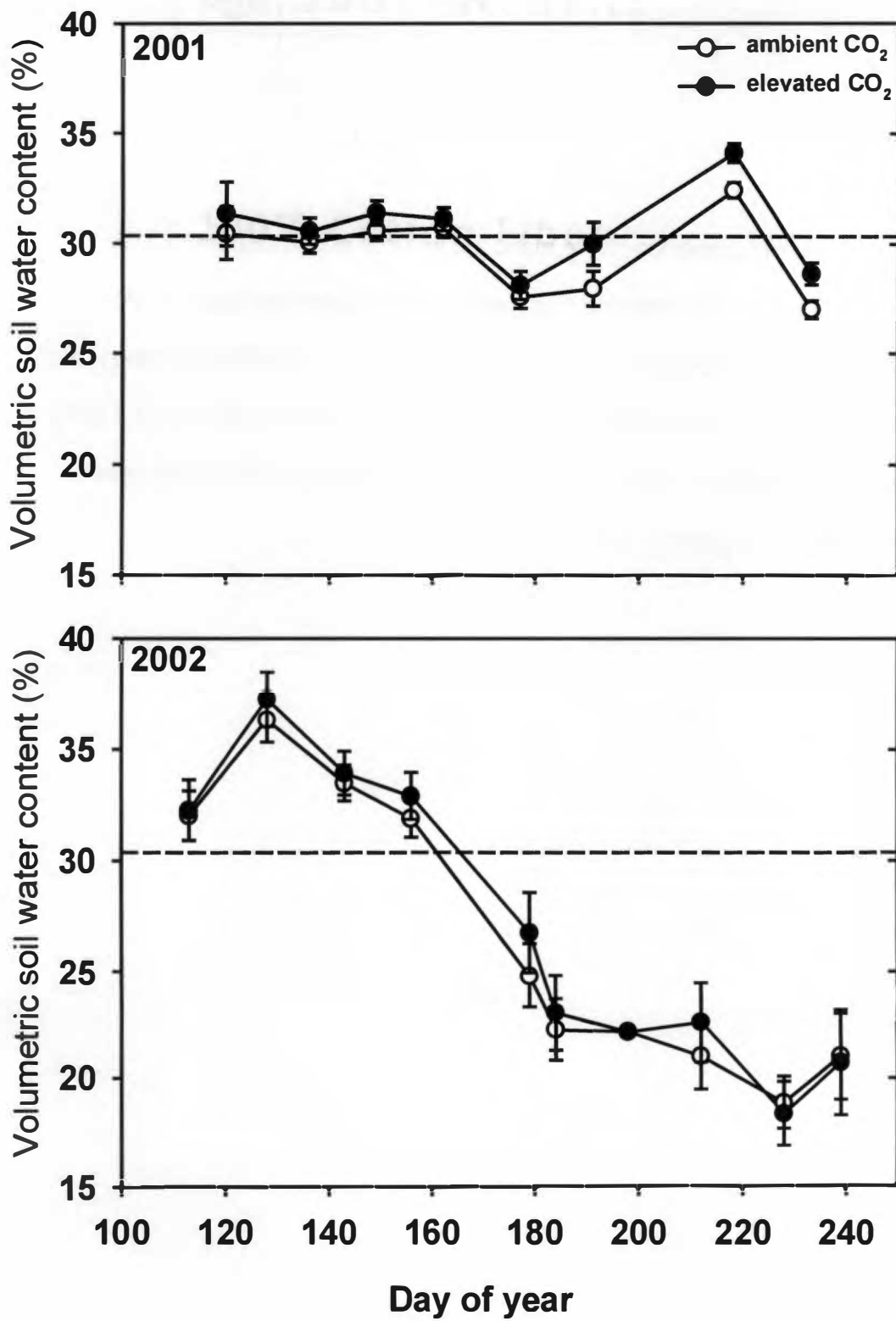


Figure 4. Cover of *L. japonica* (%) in monoculture (top) and in mixture with *M. vimineum* (bottom) in two watering treatments at three sampling dates in 2001 and 2002 (see Table 1). April 2001 data were recorded prior to treatment initiation. For each date, asterisks indicate means within vegetation treatment differed ($P < 0.05$) between water treatment; solid lines are included to emphasize intra- and inter-annual trends in evergreen *L. japonica*.

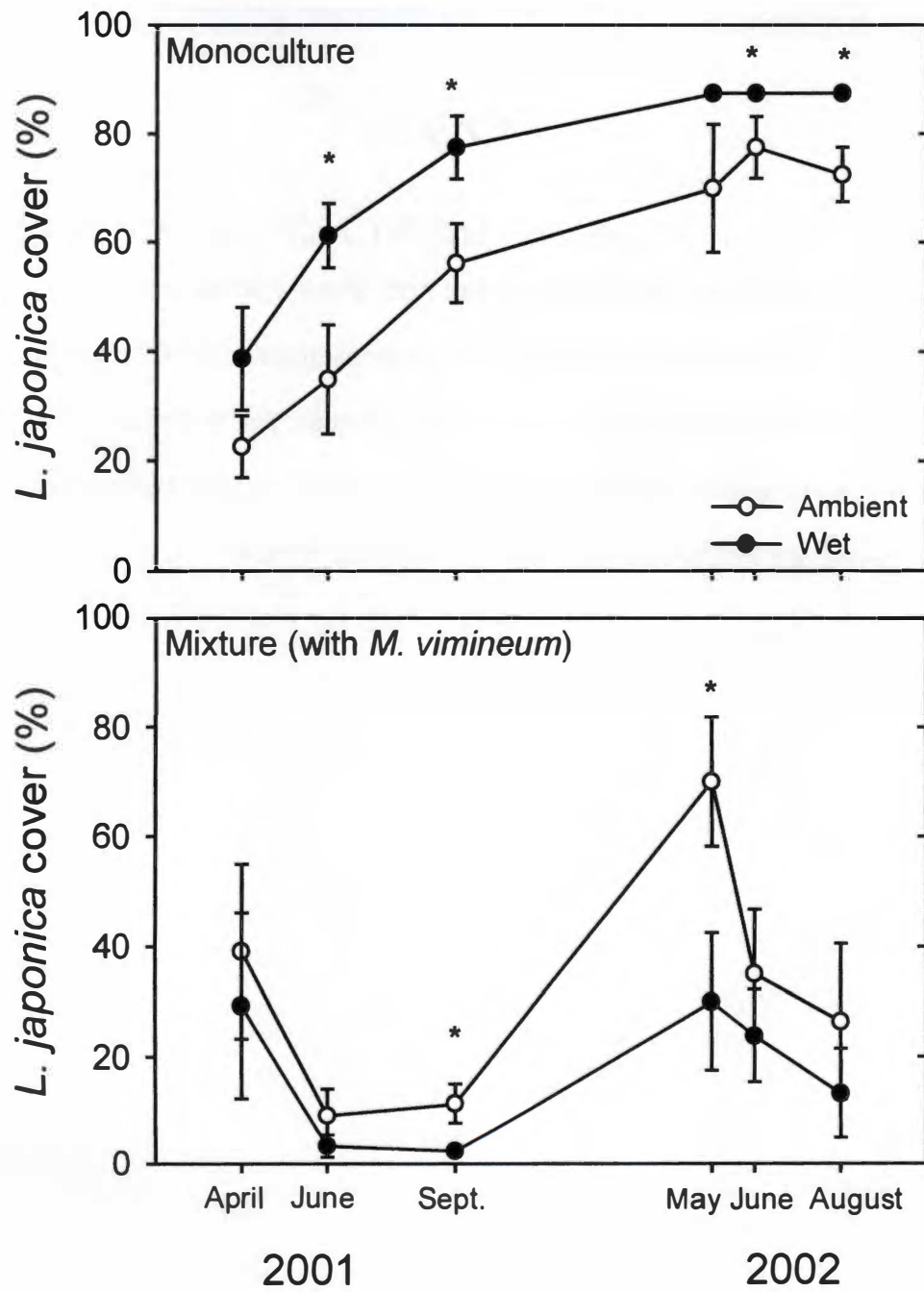


Figure 5. Cover of *M. vimineum* (%) in monoculture (top) and in mixture with *L. japonica* (bottom) in two watering treatments at three sampling dates in 2001 and 2002. April 2001 data was recorded prior to treatment initiation. For each date, asterisk indicate means within vegetation treatment differed ($P < 0.05$) between water treatment. Solid lines are included to emphasize intra-annual trends.

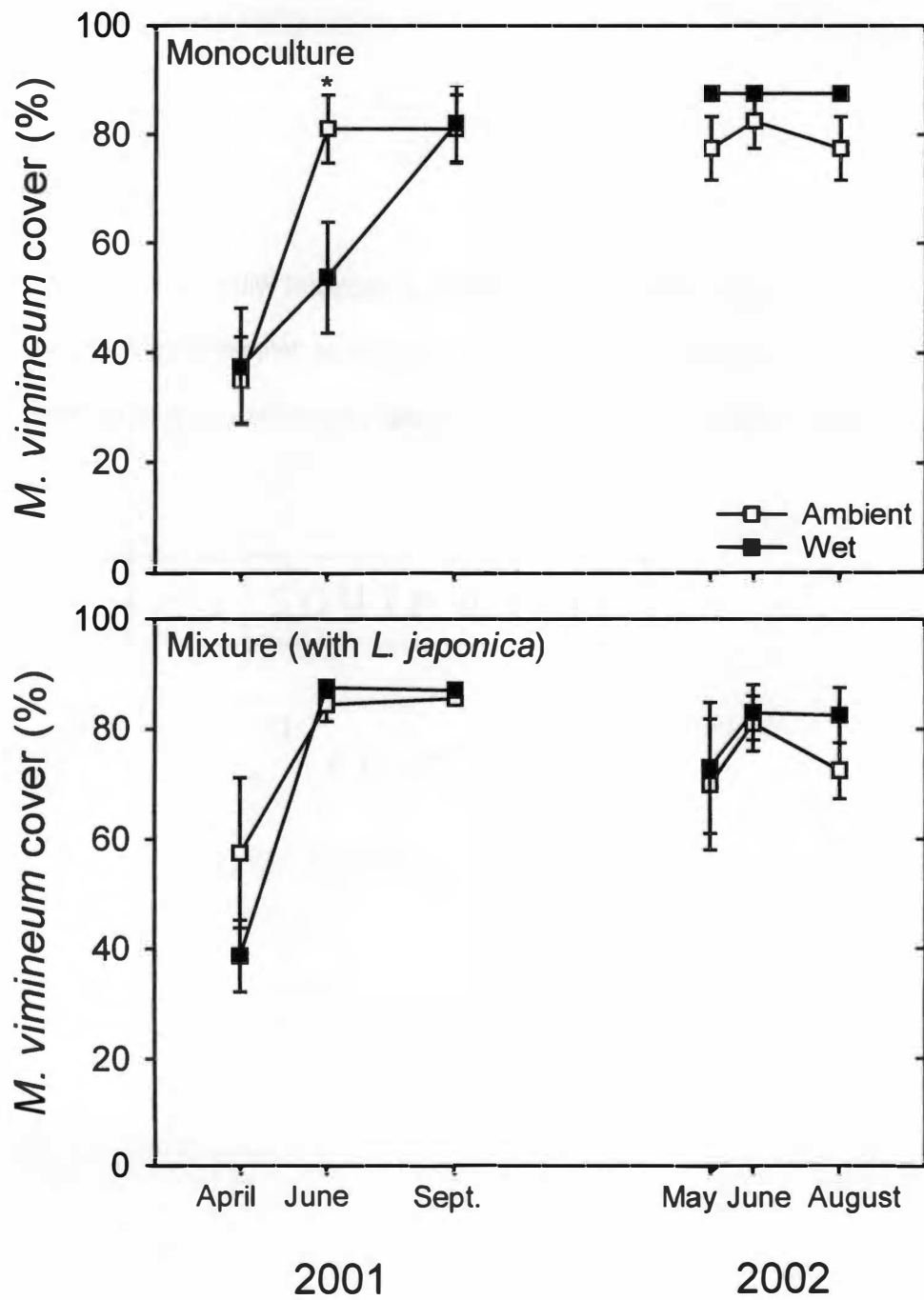


Figure 6. Biomass of *L. japonica* (top) and *M. vimineum* (bottom) within ambient and wet water treatments in monoculture plots and in mixture plots. Within vegetation treatments, means that differed ($P < 0.05$) between water treatment are marked with an asterisk.

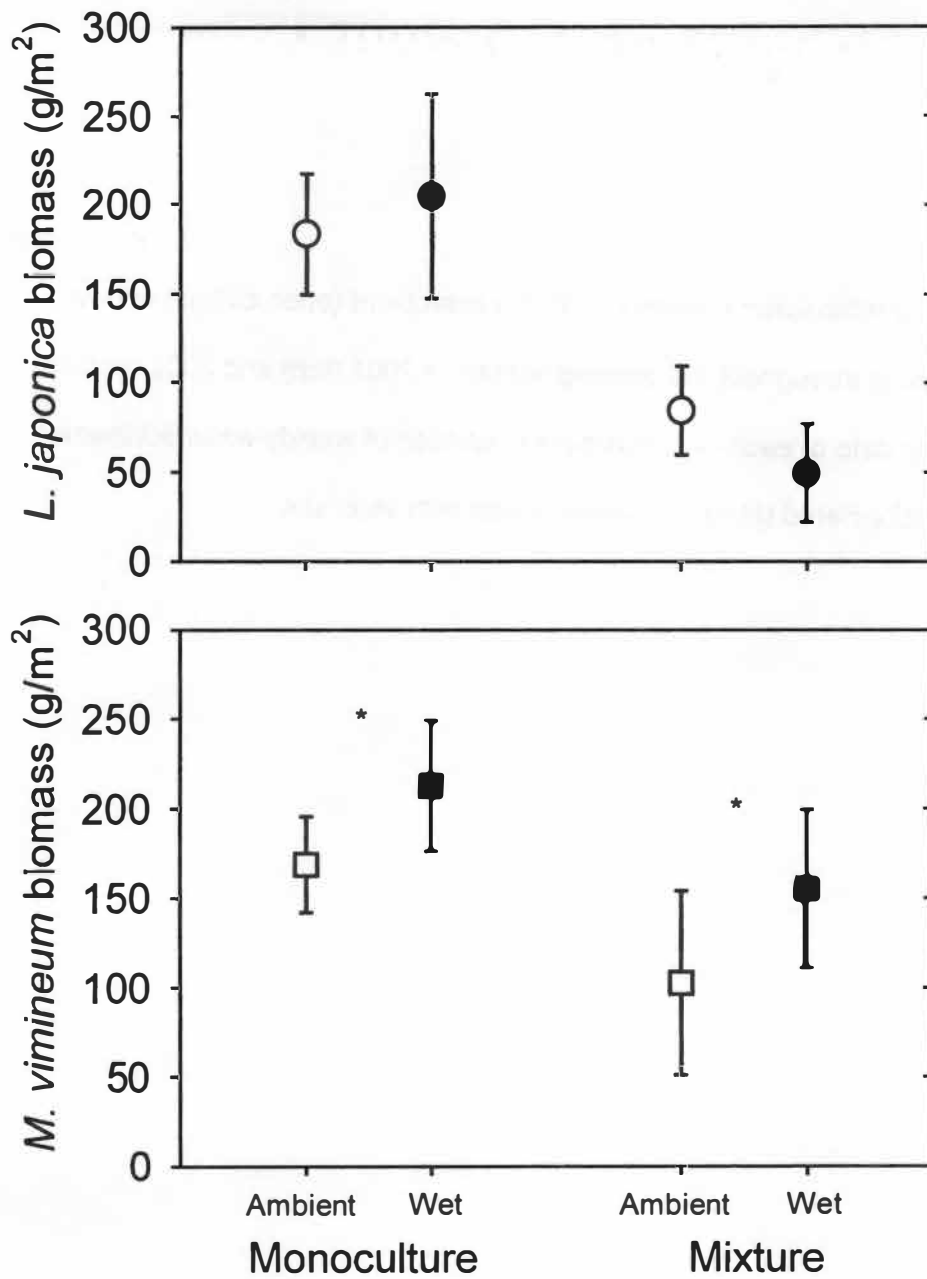


Figure 7. Soil volumetric water content (VWC; %) in ambient (open circles) and wet (closed circles) plots throughout the growing season in 2001 (top) and 2002 (bottom). The first sampling date of each year was before initiation of weekly water additions. Dates where VWC differed ($P < 0.05$) are indicated with asterisks.

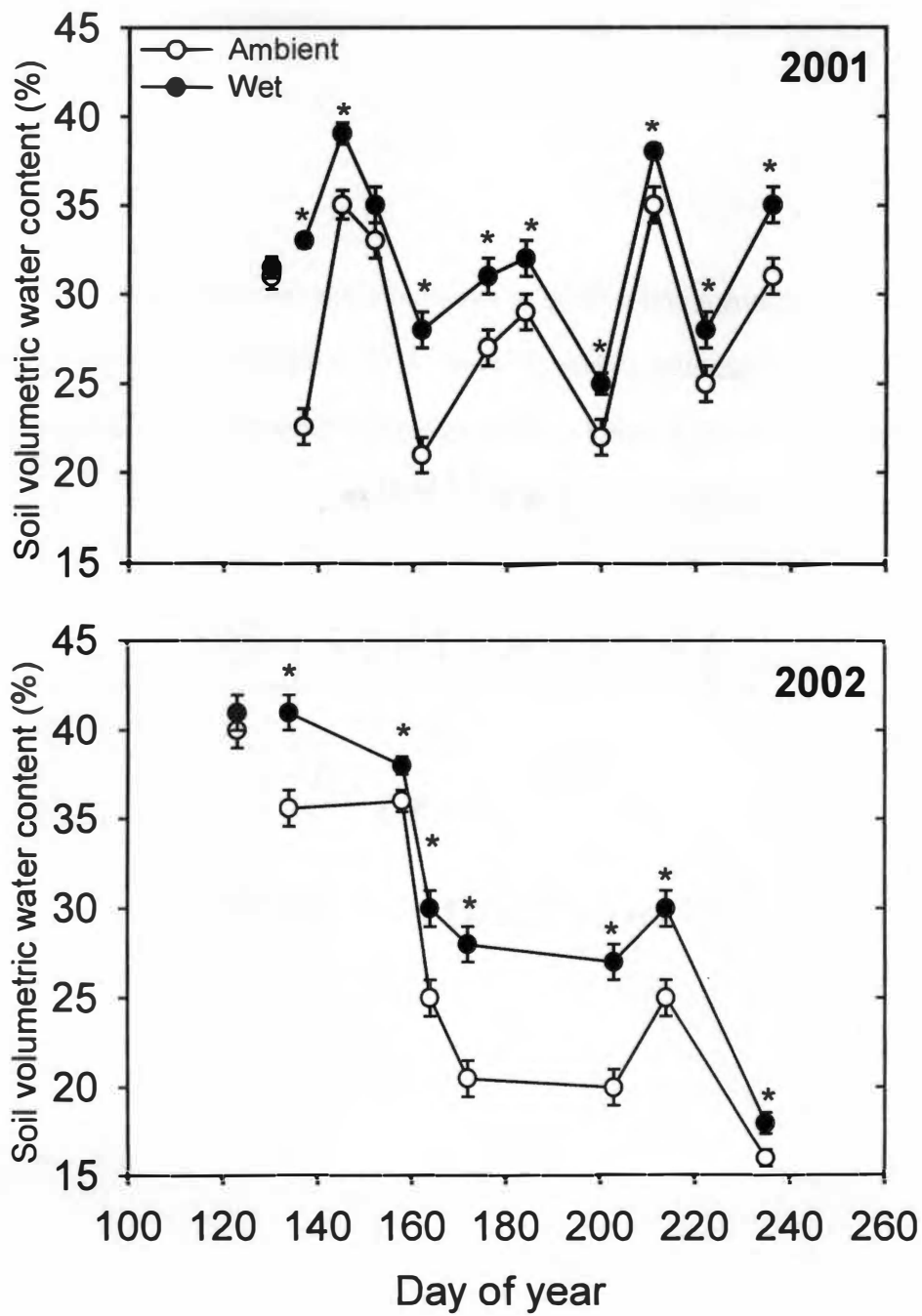
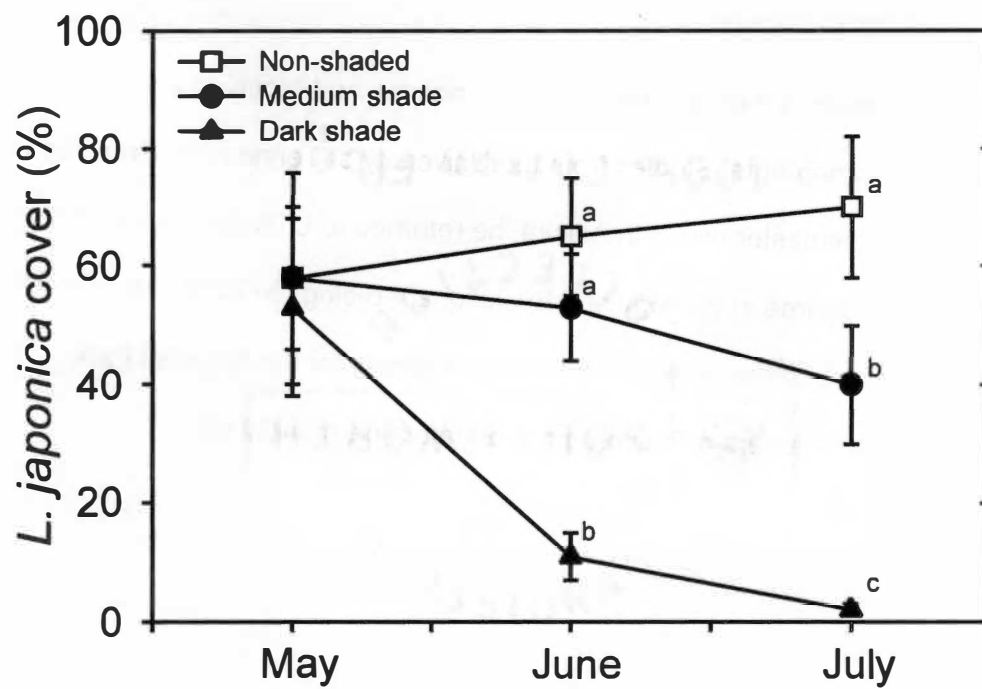


Figure 8. Cover of *L. japonica* under three shade treatments: ambient understory photosynthetically active radiation (= Non-shaded), 40% of ambient understory PAR (= Medium shade), and 2% of ambient understory PAR (= Dark shade). On each date, means with different lowercase letters were different ($P < 0.05$).



VITA

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