

# Response of an understory plant community to elevated [CO<sub>2</sub>] depends on differential responses of dominant invasive species and is mediated by soil water availability

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## Summary

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- Rising atmospheric CO<sub>2</sub> concentrations are likely to have direct effects on terrestrial ecosystems. Here, we describe effects of elevated concentrations of CO<sub>2</sub> on an understory plant community in terms of production and community composition.
- In 2001 and 2002 total and species-specific above-ground net primary productivity (ANPP) were estimated by harvesting above-ground biomass within an understory community receiving ambient [CO<sub>2</sub>] and elevated [CO<sub>2</sub>] at Oak Ridge National Laboratory's free-air carbon dioxide enrichment (FACE) facility.
- During a wet year, community composition differed between plots receiving ambient [CO<sub>2</sub>] and elevated [CO<sub>2</sub>], but total ANPP did not differ. By contrast, during a drier year, community composition did not differ, but total ANPP was greater in elevated than ambient [CO<sub>2</sub>] plots. These patterns were driven by the response of two codominant species, *Lonicera japonica* and *Microstegium vimineum*, both considered invasive species in the south-eastern United States. The ANPP of *L. japonica* was consistently greater under elevated [CO<sub>2</sub>], whereas the response of *M. vimineum* to CO<sub>2</sub> enrichment differed between years and mediated total community response.
- These data suggest that community and species responses to a future, CO<sub>2</sub>-enriched atmosphere may be mediated by other environmental factors and will depend on individual species responses.

**Key words:** CO<sub>2</sub> enrichment, invasive species, understory communities, *Lonicera japonica*, *Microstegium vimineum*.

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## Introduction

It is well known that the concentration of carbon dioxide ([CO<sub>2</sub>]) in the atmosphere is increasing and may double this century from preindustrial levels (Houghton *et al.*, 2001). Elevated [CO<sub>2</sub>] is likely to have direct effects on vegetation (Poorter & Navas, 2003), while also causing changes in climate, which may affect patterns and processes of plant communities. To date, controlled CO<sub>2</sub>-enrichment studies demonstrate that elevated [CO<sub>2</sub>] enhances the growth of most plant species grown in monoculture, especially those using the C<sub>3</sub> photosynthetic pathway (Poorter *et al.*, 1996; Poorter & Navas, 2003). However, they might 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 & 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 [CO<sub>2</sub>] in more realistic settings (Potvin & Vasseur, 1997; Vasseur & Potvin, 1998; Norton *et al.*, 1999; Niklaus *et al.*, 2001; Shaw *et al.*, 2002). Community responses to CO<sub>2</sub> enrichment have generally been described in terms of total production (Koch & Mooney, 1996) or changes in community composition (Körner & Bazzaz, 1996). Increases in the productivity of

communities in response to CO<sub>2</sub> enrichment depend on species composition (Niklaus *et al.*, 2001; Reich *et al.*, 2001) and interspecific interactions (Stewart & Potvin, 1996; Dukes, 2002). However, elevated [CO<sub>2</sub>] 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 [CO<sub>2</sub>] have included shifts in species abundance (Vasseur & Potvin, 1998), increased evenness and diversity of communities (Potvin & Vasseur, 1997; Leadley *et al.*, 1999; Niklaus *et al.*, 2001), decreased diversity (Zavaleta *et al.*, 2003), and increased success of invasive species (Dukes & 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 & Miao, 1993), water (Owensby *et al.*, 1993) and nitrogen (Roy *et al.*, 1996; Cannell & Thornley, 1998). Specifically, resource limitations (e.g. water or nitrogen) typically attenuate the response of plants to elevated [CO<sub>2</sub>] (Poorter & Pérez-Soba, 2001), but may accentuate differences between different plant species or functional groups growing in natural communities. Owensby *et al.* (1993, 1999) found that elevated [CO<sub>2</sub>] increased biomass of a C<sub>4</sub>-dominated community during dry years. Smith *et al.* (2000) determined that red brome (*Bromus madritensis* ssp. *rubens*), a nonnative annual grass, increased its density and production of above-ground biomass and seeds under elevated [CO<sub>2</sub>] during a wet, El Niño year. Alternatively, elevated [CO<sub>2</sub>] 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 [CO<sub>2</sub>] 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 [CO<sub>2</sub>]. We examined community and species responses in 2001 and 2002 to elevated [CO<sub>2</sub>] in the understory of the FACE facility at Oak Ridge National Environmental Research Park, TN, USA (Norby *et al.*, 2002). We predicted that total production would be greater in plots receiving elevated [CO<sub>2</sub>] than plots receiving ambient [CO<sub>2</sub>], because C<sub>3</sub> species were common in the understory. In addition, because of the variety of growth forms and functional groups (e.g. C<sub>3</sub> herbaceous and woody dicots and monocots, and C<sub>4</sub> monocots), we predicted that community composition would change in response to CO<sub>2</sub>-enrichment. Specifically, we predicted that production of dominant C<sub>3</sub> species would be greater under elevated [CO<sub>2</sub>], because photosynthesis of C<sub>3</sub> plants is limited by current [CO<sub>2</sub>]. Because C<sub>4</sub> photosynthesis is saturated at current [CO<sub>2</sub>], we predicted that the production of C<sub>4</sub> species would not differ between ambient and elevated [CO<sub>2</sub>]. Finally, the community was codominated by several nonnative invasive plant species, so it presented a unique opportunity to investigate whether changes in [CO<sub>2</sub>] would facilitate the success of invasive plants.

## Materials and Methods

### Site description

Research was conducted at the FACE facility, Oak Ridge National Environmental Research Park, Oak Ridge, TN, USA (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 above sea level). 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, 2003; Norby *et al.*, 2003). The soil, classified as an Aquic Hapludult, has a silty clay loam texture and is moderately well drained and slightly acidic (water pH approx. 5.5–6.0) (Soil Conservation Service, 1967; van Miegrout *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 described in Norby *et al.* (2001, 2002).

The understory was sparse in 1997 when the FACE plots were laid out, but by the growing season of 2000 plant cover in the understory was continuous and codominated by two nonnative invasive plant species, Nepal grass (*Microstegium vimineum* (Trin.) A. Camus) and Japanese honeysuckle (*Lonicera japonica* Thunb.). *Microstegium vimineum*, a shade-tolerant C<sub>4</sub> annual grass, was first reported in Tennessee in 1917 and since then has spread throughout most of the eastern USA (Fairbrothers & Gray, 1972). *Lonicera japonica*, a C<sub>3</sub> evergreen woody vine, was introduced in 1806 and has become naturalized throughout the south-eastern USA (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.), and about 25 other herbaceous and woody species.

### Experimental design

Free-air CO<sub>2</sub> enrichment (FACE) technology applies elevated [CO<sub>2</sub>] to natural systems with minimal effects on light, temperature and precipitation (Hendrey *et al.*, 1999). In 1998, five 25-m diameter plots consisting of two [CO<sub>2</sub>] treatments were established in the sweetgum plantation (Norby *et al.*, 2002). Four plots were surrounded by 24 vertical vent pipes spaced 3.3 m apart suspended from 12 aluminum towers. Two of the plots received elevated [CO<sub>2</sub>] (target = 565 p.p.m.) delivered to the vent pipes by blowers, while two control plots received ambient [CO<sub>2</sub>]. Mean [CO<sub>2</sub>] in elevated plots was 548 p.p.m. and 552 p.p.m. in 2001 and 2002, respectively. One ambient [CO<sub>2</sub>] plot with no vent pipes or other infrastructure served as a control for the presence of the [CO<sub>2</sub>] delivery apparatus (Norby *et al.*, 2002). The [CO<sub>2</sub>] treatment was initiated in April 1998 and was

maintained each year from April to November. Night-time fumigation was discontinued in 2001 because it interfered with soil respiration measurements.

### Sampling methods

In March 2001, we randomly distributed four 0.5-m<sup>2</sup> 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 above-ground net primary productivity (ANPP; g m<sup>-2</sup> yr<sup>-1</sup>) 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. The 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, which was determined by repeatedly weighing biomass samples. We summed all species within each year to determine total understory ANPP. The Shannon–Weaver ( $H'$ ) diversity index (Shannon & 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. The VWC was recorded eight and ten times during the growing season in 2001 and 2002, respectively. We measured photosynthetically active radiation (PAR;  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) 1 m above subplots between 11:00 hours and 13:00 hours 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 analysed total and species ANPP and biomass, species cover,  $H'$ ,  $S$ ,  $E$  and PAR for effect of [CO<sub>2</sub>] treatment with an unbalanced completely randomized design with sampling (CRDS), where each subplot was considered a sample within the plots (Filion *et al.*, 2000). Data were analyzed with a mixed model analysis of variance (ANOVA; procedure MIXED; SAS Institute, 1999) with the model:

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

( $\mu$  is the overall mean; [CO<sub>2</sub>] treatment is a fixed effect; plot replicate is the random effect; 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 five 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 (Levene, 1960; Shapiro & Wilk, 1965). 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 analyse 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.

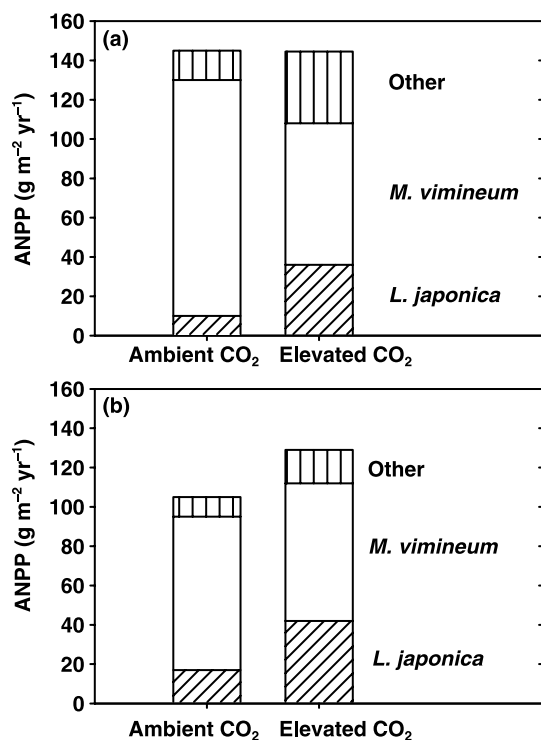
The VWC measurements from the six locations within each plot were averaged for each sampling date. We analysed VWC for main and interactive effects of [CO<sub>2</sub>] and time (i.e. day of year, DOY) with a repeated measures multivariate analysis of variance (MANOVA; Pillai's Trace in SAS procedure GLM; SAS Institute, 1999).

## Results

### Community and species production

Total understory ANPP in 2001 did not differ between [CO<sub>2</sub>] treatments ( $P = 0.97$ ), but in 2002 it was 27% greater under elevated [CO<sub>2</sub>] than ambient [CO<sub>2</sub>] ( $P = 0.14$ ; Fig. 1). In both years of this study, *L. japonica* comprised at least 24% of total community ANPP. The productivity of *L. japonica* was 3.3 and 2.5 times greater in plots that received elevated [CO<sub>2</sub>] than ambient [CO<sub>2</sub>] in 2001 and 2002, respectively (Fig. 1; Table 1). In 2001, cover of *L. japonica* was 3.0 times greater under elevated than ambient [CO<sub>2</sub>], but in 2002 the *L. japonica* cover did not differ between treatments (Table 1).

*Microstegium vimineum* accounted for at least 64% of total production in both years of the study. The productivity of *M. vimineum* was 68% greater under ambient than elevated [CO<sub>2</sub>] in 2001, but did not differ between treatments in 2002 (Fig. 1; Table 1). The *M. vimineum* cover was 44% greater under ambient than under elevated [CO<sub>2</sub>] in 2001, but did not differ in 2002.



**Fig. 1** Contribution of *Microstegium vimineum*, *Lonicera japonica*, and other species to total understory community ANPP (g m<sup>-2</sup> yr<sup>-1</sup>) in plots receiving ambient [CO<sub>2</sub>] and elevated [CO<sub>2</sub>] treatments at the sweetgum free-air CO<sub>2</sub> enrichment (FACE) site in a wet year, 2001 (a) and dry year, 2002 (b). Standard errors and *P*-values for *M. vimineum* and *L. japonica* are given in Table 1; the *P*-values for total understory production can be found in the Results section.

The productivity of *Rubus* did not differ between [CO<sub>2</sub>] treatments in either year, but *Rubus* cover was greater under elevated than ambient [CO<sub>2</sub>] in both years (Table 1). The productivity of *S. canadensis* in ambient and elevated [CO<sub>2</sub>] plots did not differ in either year. *Solidago canadensis* cover was greater under elevated than ambient [CO<sub>2</sub>] in 2001, but not in 2002. Production and cover of *A. negundo* did not differ between treatments in either years (Table 1). Foliar covers of subdominant species in the understory given are in Table 2.

### Community structure and diversity

Principal components analysis reflected differences in species composition and abundance under ambient and elevated [CO<sub>2</sub>] in 2001, but the dissimilarity between treatments was less pronounced in 2002 (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* ( $r = -0.43$ ,  $P = 0.07$ ) and positively correlated with cover of *M. vimineum* ( $r = 0.61$ ,  $P = 0.006$ ).

In 2002, axes I and II explained 14% and 13% of variation, respectively (Fig. 2). 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 nor VWC were correlated with axis I or II quadrat scores ( $P = 0.24$ ).

Species	Year	[CO <sub>2</sub> ] Treatment	ANPP (g m <sup>-2</sup> yr <sup>-1</sup> )	<i>P</i>	Cover (%)	<i>P</i>
<i>Acer negundo</i>	2001	Ambient	4 ± 2	0.78	11 ± 6	0.96
		Elevated	2 ± 3		12 ± 8	
	2002	Ambient	1 ± 1		8 ± 4	
		Elevated	1 ± 1		4 ± 5	
<i>Lonicera japonica</i>	2001	Ambient	11 ± 4	0.03	21 ± 4	0.008
		Elevated	36 ± 5		63 ± 5	
	2002	Ambient	17 ± 7		37 ± 12	
		Elevated	42 ± 9		55 ± 15	
<i>Microstegium vimineum</i>	2001	Ambient	121 ± 11	0.07	85 ± 5	0.09
		Elevated	72 ± 15		67 ± 6	
	2002	Ambient	78 ± 14		81 ± 8	
		Elevated	70 ± 17		60 ± 10	
<i>Rubus</i> spp.	2001	Ambient	1 ± 1	0.42	3 ± 3	0.08
		Elevated	3 ± 1		16 ± 4	
	2002	Ambient	1 ± 2		3 ± 5	
		Elevated	5 ± 2		19 ± 6	
<i>Solidago canadensis</i>	2001	Ambient	1 ± 3	0.43	2 ± 4	0.02
		Elevated	18 ± 4		22 ± 5	
	2002	Ambient	0 ± 1		4 ± 3	
		Elevated	3 ± 1		5 ± 4	

Data are means ± SE;  $n = 3$  for ambient [CO<sub>2</sub>] and  $n = 2$  for elevated [CO<sub>2</sub>].

**Table 1** Above-ground net primary productivity (ANPP) and cover of five dominant (mean cover > 8%) understory plants in free-air CO<sub>2</sub> enrichment plots receiving ambient [CO<sub>2</sub>] and elevated [CO<sub>2</sub>] in a wet year (2001) and dry year (2002)



**Table 2** Maximum cover of understory taxa in plots receiving ambient [CO<sub>2</sub>] and elevated [CO<sub>2</sub>] at the sweetgum free-air CO<sub>2</sub> enrichment site in 2001 and 2002

Species	2001 (%)		2002 (%)	
	Ambient	Elevated	Ambient	Elevated
<i>Acer saccharum</i> (s)	1.5 ± 1.5	0.2 ± 0.2	3.8 ± 3.1	0
<i>Allium</i> sp.	3.1 ± 3.1	0.9 ± 0.5	0	0
<i>Asplenium platyneuron</i>	0.1 ± 0.1	0	0	0
<i>Aster dumosus</i>	0	0.5 ± 0.3	0	0
<i>Bignonia capreolata</i>	0.6 ± 0.3	0	2.1 ± 1.5	0
<i>Carex laevivaginata</i>	0.1 ± 0.1	1.4 ± 1.0	0	0
<i>Cerastium glomeratum</i>	0	0	0.1 ± 0.1	0.1 ± 0.1
<i>Clematis virginiana</i>	1.5 ± 1.5	0	0	0
<i>Fraxinus pennsylvanica</i> (s)	16.5 ± 7.1	0	3.8 ± 3.1	2.2 ± 2.2
<i>Galium aparine</i>	0.6 ± 0.3	2.0 ± 1.0	0	0
<i>Geum canadense</i>	1.6 ± 1.4	0.4 ± 0.2	0	0
<i>Juncus tenuis</i>	0.1 ± 0.1	0.2 ± 0.2	0.6 ± 0.3	0.4 ± 0.4
<i>Juniperus virginiana</i> (s)	0	1.1 ± 1.1	0	0
<i>Lespedeza cuneata</i>	0	2.5 ± 2.5	0	0
<i>Lobelia</i> sp.	0	0.2 ± 0.2	0	0
<i>Myotosis macrosperma</i>	0.4 ± 0.3	0.4 ± 0.2	0	0.1 ± 0.1
<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> sp.	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> sp.	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> sp.	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> sp.	0.1 ± 0.1	0.5 ± 0.5	0.4 ± 0.4	0.1 ± 0.1
<i>Vitis</i> sp.	1.5 ± 1.5	0.7 ± 0.3	0.3 ± 0.3	0.4 ± 0.4

s, seedling. Data are means ± SE;  $n = 3$  for ambient [CO<sub>2</sub>] and  $n = 2$  for elevated [CO<sub>2</sub>].

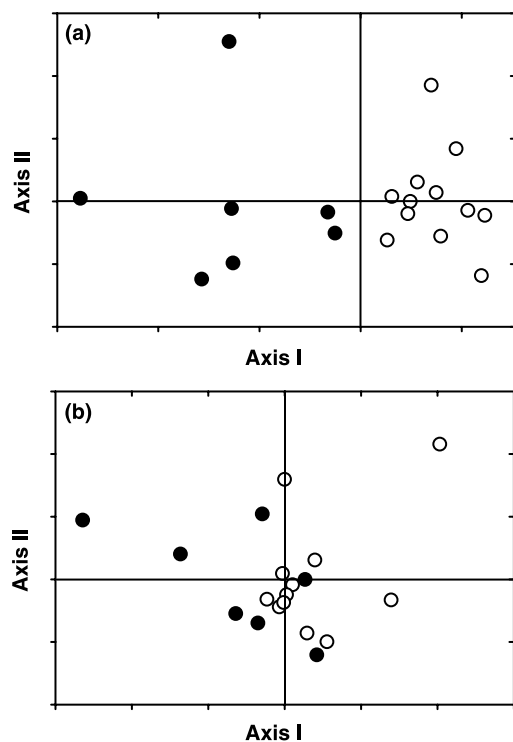
In 2001, species richness ( $S$ ) did not differ between [CO<sub>2</sub>] treatments, but species evenness ( $E$ ) and diversity ( $H'$ ) of species production were greater under elevated than ambient [CO<sub>2</sub>] (Table 3). In 2002,  $S$ ,  $E$  and  $H'$  did not differ between [CO<sub>2</sub>] treatments.

#### Soil moisture and photosynthetically active radiation

Soil volumetric water content did not differ between plots under ambient [CO<sub>2</sub>] and elevated [CO<sub>2</sub>] in 2001 or 2002 ( $P = 0.24$ ). The 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 (CO<sub>2</sub> × DOY,  $P = 0.51$ ). Photosynthetically active radiation ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) above subplots did not differ between [CO<sub>2</sub>] treatments on any sampling date in 2001 and 2002 ( $P = 0.34$ ) (Table 4).

#### Discussion

Results indicate that ecosystem and community responses to future increases in [CO<sub>2</sub>] will depend on responses of individual species, as well as abiotic environmental factors (e.g. soil moisture). Consistent with other work that observed opposing responses of different plant species to elevated [CO<sub>2</sub>] (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 composition and diversity) differences during the wet year (2001). Specifically, elevated [CO<sub>2</sub>] caused a threefold 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 [CO<sub>2</sub>] plots than elevated [CO<sub>2</sub>] plots, but did not differ between [CO<sub>2</sub>] treatments in the dry year. These results confirm research in other studies of elevated [CO<sub>2</sub>] on communities that found that community responses to elevated [CO<sub>2</sub>] are often unpredictable, in part because of the availability of other resources (Owensby *et al.*, 1993, 1999; Smith *et al.*, 2000).



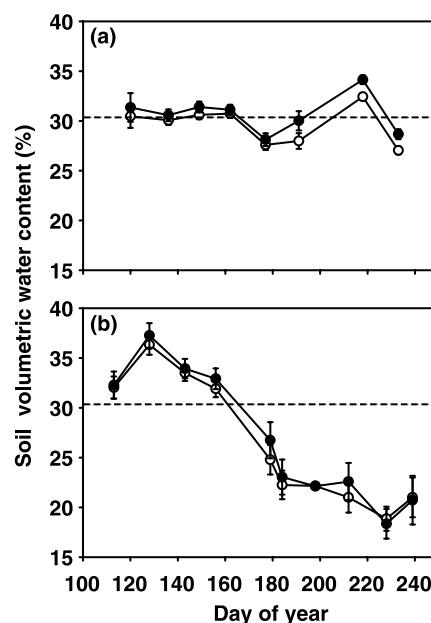
**Fig. 2** Principal components analysis ordination of quadrat scores of the understory plant community receiving ambient [CO<sub>2</sub>] (open circles) and elevated [CO<sub>2</sub>] (closed circles) at the sweetgum free-air CO<sub>2</sub> enrichment (FACE) site in a wet year, 2001 (a) and dry year 2002 (b).

**Table 3** Richness, evenness, and Shannon–Weaver's diversity index ( $H'$ ) of subplots, calculated based on above-ground net primary productivity of all species in plots receiving ambient [CO<sub>2</sub>] and elevated [CO<sub>2</sub>]

Year	[CO <sub>2</sub> ]		Richness	<i>P</i>	Evenness	<i>P</i>	$H'$	<i>P</i>
	Treatment							
2001	Ambient		5.4 ± 0.9		0.35 ± 0.04		0.6 ± 0.1	
	Elevated		7.0 ± 1.2	0.38	0.54 ± 0.07	0.07	1.0 ± 0.1	0.09
2002	Ambient		4.2 ± 0.5		0.47 ± 0.05		0.7 ± 0.1	
	Elevated		5.0 ± 0.6	0.37	0.56 ± 0.06	0.33	0.9 ± 0.1	0.27

Data are means ± SE;  $n = 3$  for ambient [CO<sub>2</sub>] and  $n = 2$  for elevated [CO<sub>2</sub>].

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 [CO<sub>2</sub>] is limited in that resource availability may either enhance or dampen the effects of elevated [CO<sub>2</sub>]. For example, in some communities, positive species responses to elevated [CO<sub>2</sub>] were observed only when availability of water was high (Smith *et al.*, 2000). In other systems, community responses to CO<sub>2</sub> enrichment occurred only when the availability of water was limited (Owensby



**Fig. 3** Soil volumetric water content (VWC; %) in plots receiving ambient [CO<sub>2</sub>] (open circles) and elevated [CO<sub>2</sub>] (closed circles) throughout the growing seasons of 2001 (a) and 2002 (b). Broken horizontal lines in both figures represent mean VWC during the 2001 growing season to emphasize differences in patterns of VWC.

**Table 4** Photosynthetically active radiation at the top of the sweetgum canopy and at 1 m above subplots in plots receiving ambient [CO<sub>2</sub>] and elevated [CO<sub>2</sub>]

Date	Top of tree canopy (μmol m <sup>-2</sup> s <sup>-1</sup> )	CO <sub>2</sub> Treatment (μmol m <sup>-2</sup> s <sup>-1</sup> )	
		Ambient	Elevated
Aug. 2001	1451 ± 32	80 ± 20	78 ± 25
Sept. 2001	1316 ± 24	83 ± 24	102 ± 30
May 2002	1593 ± 77	180 ± 24	214 ± 29
June 2002	1672 ± 14	167 ± 46	71 ± 56

Data are means ± SE;  $n = 3$  for ambient [CO<sub>2</sub>] and  $n = 2$  for elevated [CO<sub>2</sub>]. Photosynthetically active radiation (PAR) did not differ between CO<sub>2</sub> treatments on any date ( $P = 0.34$ ).

*et al.*, 1999). The photosynthetic pathway of the dominant species may explain the contradictory results. Specifically, C<sub>3</sub> species may positively respond to elevated [CO<sub>2</sub>] by increasing the acquisition of carbon only when water resources are abundant (Huxman & Smith, 2001). By contrast, photosynthesis rates of C<sub>4</sub> species are usually CO<sub>2</sub>-saturated at current [CO<sub>2</sub>] (Ghannoum *et al.*, 2000), and may only benefit from elevated [CO<sub>2</sub>] through increased water-use efficiency during dry years (Clark *et al.*, 1999) especially when growing in a community setting (Owensby *et al.*, 1999). Contradictory results, for reasons not yet understood, can occur for other

resources, such as light (Bazzaz & Miao, 1993; Poorter & Pérez-Soba, 2001) or nitrogen (Roy *et al.*, 1996; Cannell & Thornley, 1998). Recently, Shaw *et al.* (2002) suggested that elevated [CO<sub>2</sub>] might actually diminish the otherwise positive effects of water, nitrogen and warming on California grassland production. The mechanisms driving these patterns are not fully understood, but may include differential species responses to availability of resources (Reich *et al.*, 2001), spatial or temporal variation in resource availability (Tilman, 1982), nitrogen immobilization by soil microbes (Morgan, 2002), or species interactions (Arp *et al.*, 1993; Belote, 2003) both above and below ground. It is clear that more long-term studies with multiple factors in naturalistic settings are needed to better understand potential effects of increasing atmospheric [CO<sub>2</sub>] on communities (Körner, 2000; Morgan, 2002).

The differential response of species to elevated [CO<sub>2</sub>] in each year also were responsible for observed differences in composition and diversity under elevated [CO<sub>2</sub>]. Based on PCA ordinations, opposing responses of the dominant species accentuated compositional differences during the wet year (2001). During the drier year (2002) differences in composition were not as pronounced. Variation in compositional shifts under elevated [CO<sub>2</sub>] caused by differential responses of species between years is not uncommon in community-level CO<sub>2</sub>-enrichment investigations (Vasseur & Potvin, 1998; Norton *et al.*, 1999; Niklaus *et al.*, 2001; Marissink & Hansson, 2002).

Differences in diversity between the [CO<sub>2</sub>] treatments in 2001 and 2002 were driven by the response of *M. vimineum*. Diversity was higher in elevated [CO<sub>2</sub>] plots in 2001, as a result of differences in species evenness, which was driven by the decreased production and dominance of *M. vimineum*. Similarly, elevated [CO<sub>2</sub>] has altered species diversity in other systems by increasing evenness (i.e. decreasing dominance) within communities by favoring certain species or functional groups (Potvin & Vasseur, 1997; Leadley *et al.*, 1999; Niklaus *et al.*, 2001). However, a recent report suggests that in some systems species diversity may decrease under elevated [CO<sub>2</sub>] through species interactions, where small-stature annual forbs are excluded by dominant grasses (Zavaleta *et al.*, 2003).

Species interactions may have been important mediators of plant community responses to elevated [CO<sub>2</sub>] in the understory community. Others have reported interspecific competition as an important factor mediating community responses to elevated [CO<sub>2</sub>], especially when certain species benefit from elevated [CO<sub>2</sub>] to the detriment of other co-occurring species (Owensby *et al.*, 1993; Leadley *et al.*, 1999; Zavaleta *et al.*, 2003). In the present study, elevated [CO<sub>2</sub>] may have favored *L. japonica* to the detriment of *M. vimineum*, which coincides with the pattern in other systems where CO<sub>2</sub>-enrichment favors C<sub>3</sub> species over C<sub>4</sub> species (Reynolds, 1996). While *L. japonica* responded similarly during both the wet (2001) and dry (2002) growing seasons, the response of *M. vimineum* to variation in soil water availability, possible

competition with *L. japonica*, and potential water savings under elevated [CO<sub>2</sub>] are not clear. We need to conduct more experiments to determine the relationship between elevated [CO<sub>2</sub>] and limited availability of water on the potential interactions between *L. japonica* and *M. vimineum*.

### Response of invasive species to elevated [CO<sub>2</sub>]

An increase in atmospheric [CO<sub>2</sub>] may increase the success of nonnative invasive plants by directly enhancing their growth or by altering the availability of resources (Dukes & Mooney, 1999; Smith *et al.*, 2000; Weltzin *et al.*, 2003). However, studies examining the response of invasive plants to elevated [CO<sub>2</sub>] are rarely conducted in natural communities (Dukes, 2000). This study provides evidence that *L. japonica* responds positively to CO<sub>2</sub> enrichment, not only in monoculture (Sasek & Strain, 1991), but also in natural communities. Thus, as [CO<sub>2</sub>] continues to rise, *L. japonica* may become more abundant and pose additional threats to native ecosystems.

*Microstegium vimineum* is also considered a problematic invasive plant (Redman, 1995), but it responded differently between years to elevated [CO<sub>2</sub>], possibly as a result of variations in soil moisture. Moreover, interannual 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, CO<sub>2</sub>-enriched atmosphere may be mediated by predicted changes in precipitation patterns and soil water availability (Houghton *et al.*, 2001).

This study demonstrates that community responses to elevated [CO<sub>2</sub>] are dependent on the responses of individual species. However, other environmental factors, such as water availability, are important mediators of community and species responses to CO<sub>2</sub> enrichment. Interannual variation in the production of *M. vimineum* affected total understory production, community composition, and diversity. Thus, opposing species responses masked potential 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 & Strain, 1991), suggest that certain invasive species may become more abundant as [CO<sub>2</sub>] continues to increase. However, increases in [CO<sub>2</sub>] are likely to affect patterns of precipitation and temperature, so responses of invasive species and their recipient communities to increased [CO<sub>2</sub>] are likely to be mediated by subsequent changes in other environmental factors.

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