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Biomass and Root Mass

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Appendix E - UNIVERSITY HONORS PROGRAM
SENIOR PROJECT - APPROVAL

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PROJECT TITLE: Biomass and root mass vary due to changes in $[CO_2]$ in an understory plant community: variation depending on individual species and mediated by soil water availability

I have reviewed this completed senior honors thesis with this student and certify that it is a project commensurate with honors level undergraduate research in this field.

Signed: _____. Faculty Mentor

Date: 3 May 2004

General Assessment - please provide a short paragraph that highlights the most significant features of the project.
please see attached sheet

Comments (Optional):

[redacted]

Summary

-- Rising concentrations of atmospheric CO_2 [CO_2] are likely to have direct effects on terrestrial ecosystems via direct and indirect effects on plant communities. Here, we describe effects of [CO_2] on understory plant community concentration and production.

-- In 2000 to 2003, total and species-specific aboveground biomass were estimated by harvesting plots within a deciduous forest understory plant community receiving ambient [CO_2] and elevated [CO_2] at Oak Ridge National Laboratory's Free-Air Carbon dioxide Enrichment (FACE) facility. We estimated root biomass to 25 cm depth by extracting soil cores to and separating roots from soil by hand.

-- Total understory aboveground biomass did not differ between plots exposed to elevated and ambient [CO_2] in 2000, 2001, or 2002. In 2003 biomass was greater under elevated [CO_2], depending on the availability of soil moisture. Total root biomass of *Liquidambar styraciflua* and all other roots in fine (< 1 mm) and coarse (≥ 1 mm) size classes, differed little between [CO_2] treatments in all years.

--Results suggest that a CO_2-enriched atmosphere may affect biomass production over the long term, and that community responses may be mediated by individual species responses, species interactions, and availability of soil moisture.

Key Words: CO_2 enrichment, understory community, biomass production, roots, shoots, soil moisture

Biomass and root mass vary due to changes in [CO_2] in an understory plant community: variation depending on individual species and mediated by soil water availability

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Introduction

It is well known that the concentration of carbon dioxide ($[CO_2]$) in the atmosphere is increasing and may double this century relative to preindustrial levels (Houghton *et al.*, 2001). Elevated $[CO_2]$ is likely to have direct effects on vegetation (Poorer & Navas, 2003), while also causing changes in climate (Houghton, et al. 2001), which may affect patterns and processes of plant communities. Controlled CO_2-enrichment studies have demonstrated that elevated $[CO_2]$ enhances the growth of most plant species--particularly those using the C_3 photosynthetic pathway--grown in monoculture (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 homogeneous, and where species interact (Körner & Bazzaz, 1996; Körner, 2000).

With the advent of open-top chamber and Free-Air Carbon dioxide Enrichment (FACE) facilities, there have been of late more studies that investigated responses of plant communities to elevated $[CO_2]$ in more realistic settings (Potvin & Vasseur, 1997; Vasseur & Potvin, 1998; Norton *et al.*, 1999; Niklaus *et al.*, 2001; Shaw *et al.*, 2002; Navas *et al.*, 2004). Community responses to CO_2 –enrichment have generally been described in terms of changes in total production (Koch & Mooney, 1996), community composition (Körner & Bazzaz, 1996; Belote *et al.*, 2004), biological diversity (Zavaleta et al., 2003), and succession (Potvin & Vasseur, 1997; Vasseur & Potvin, 1998). Increases in the productivity of communities in response to CO_2-enrichment depend on species composition (Niklaus *et al.*, 2001; Reich *et al.*, 2001) and interspecific interactions (Stewart & Potvin, 1996; Dukes, 2002). However, elevated $[CO_2]$ can alter plant community composition even when total productivity is unaffected (Roy *et al.*, 1996; Norton *et al.* 1999, Niklaus *et al.*, 2001; Belote *et al.*, 2004).

The present study was designed to determine the response of an *in situ* understory plant community to elevated [CO_2]. Between 2000 and 2003, we examined community and species responses to elevated [CO_2] in the understory of the sweetgum (*Liquidambar styraciflua* L.) FACE facility in East Tennessee, USA (Norby *et al.*, 2002). We predicted that total aboveground biomass production would be greater in plots receiving elevated [CO_2] than plots receiving ambient [CO_2]. In addition, because of the variety of growth forms and functional groups (e.g., C_3 herbaceous and woody dicots and monocots, and C_4 monocots), we predicted that community composition would change in response to CO_2-enrichment, with C_3 species favored by [CO_2] in wet years and C_4 species favored during dry years. We also examined root biomass to 25 cm depth, and distinguished between *Liquidambar styraciflua* roots and all other roots. We predicted that elevated CO_2 would stimulate production of fine roots (< 1 mm diameter).

Materials and Methods

Site description

Research was conducted at the sweetgum FACE facility, Oak Ridge National Environmental Research Park, Oak Ridge, Tennessee, USA (35°54'N; 84°20'W). The research site is a planted sweetgum monoculture established in 1988 on an old terrace of the Clinch River (elevation 230 m above sea level). The sweetgum trees were approximately 18 m tall in 2003, with a closed canopy that reduced the light in the understory 70–95% during the growing season. The soil, classified as an Aquic Hapludult, has a silty clay loam texture and is moderately well drained and slightly acidic. 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) and Belote et al. (2004).

The understory was sparse in 1997 when the FACE plots were established, but by the growing season of 2000 plant cover in the understory was continuous and codominated by two non-native invasive plant species, Nepal grass (*Microstegium vimineum* (Trin.) A. Camus) and Japanese honeysuckle (*Lonicera japonica* Thunb.). *Microstegium vimineum*, a shade-tolerant C_4 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_3 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* spp. L.), and box elder seedlings (*Acer negundo* L.), and about 25 other herbaceous and woody species (Belote et al. 2004).

Experimental design

Free-air CO_2 enrichment (FACE) technology applies elevated [CO_2] 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_2] 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 and suspended from 12 aluminum towers. Two of the plots received elevated [CO_2] (target = 565 ppm) delivered to the vent pipes by blowers, while two control plots received ambient [CO_2]. Mean [CO_2], averaged across the year in plots that received supplemental [CO_2], was 548 ppm and 552 ppm in 2001 and 2002 respectively (Norby, personal communication). One ambient [CO_2] plot with no vent pipes or other infrastructure served as a control for the

presence of the [CO_2] delivery apparatus (Norby *et al.*, 2002). The [CO_2] 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

We determined above ground plant biomass for *L. japonica*, *M. vimineum*, and all other species combined in September 2000 by clipping all plants at ground level within each of five 1.0-m^2 subplots located at random within each of the five plots. In subsequent years (i.e., 2001-2003), we determined above ground biomass for all species present in fewer, smaller subplots (to reduce the time required for sampling in this more intensive manner). In March 2001, we randomly distributed four 0.5-m^2 subplots within each of the five plots. Prior to both the 2002 and 2003 growing seasons, we relocated each subplot to new random locations. In early September of each year, we determined above ground biomass within each subplot by clipping individuals of each species at ground level. Plant tissue samples were oven-dried at 65°C to constant mass. We summed species within each year to determine total understory biomass.

We determined root biomass of sweetgum and all other species combined at two soil depths in 2001-2003 by extracting soil cores from each subplot and separating roots into size and species classes by hand. Within 2 days after the subplots were clipped each September, we obtained soil cores using a slide-hammer bulk density corer (4.77 cm diameter, 12.5 cm deep) from 0-12.5 cm and 12.5-25 cm depth, at each of three regular locations within the subplot (longitudinally oriented at equal distances from other cores and the edge of the subplot). Cores from each depth were composited into a single sample that was refrigerated until processing. Cores were soaked in water for ~1 hour and gently palpated to soften prior to wet-sieving over a 2-mm mesh screen. Roots were hand-sorted into two size classes (< 1mm, and ≥ 1 mm) within

each of two species groups, sweetgum and 'other.' Sweetgum roots were separated on the basis of color and morphology (based on live sweetgum roots collected from locations adjacent to but outside of the FACE plots concurrent with sampling), and all other roots were pooled into the 'other' category. Root samples were dried at 52°C for 24 hours before weighing, and were summed within species, size class, and depth categories as appropriate for analysis.

Between 2000-2002, we sampled six pairs of time–domain reflectometry (TDR; Soil Moisture Equipment Corp., Santa Barbara, CA, USA) probes permanently installed within each 25-m diameter plot to determine volumetric water content (%; VWC) in the top 20 cm of soil. VWC was recorded eight and ten times during the growing season in 2001 and 2002, respectively. In 2003, soil VWC was recorded for each subplot (at three random locations within each subplot averaged for analysis) three times throughout the growing season with a hand-held TDR probe (14 cm probe length; Hydrosense, Decagon Devices, Inc., Pullman, Washington, USA).

We measured photosynthetic photon flux density (PPFD; μmol m^{-2} s^{-1}) 1 m above subplots between 1100 hours and 1300 hours on clear days using a handheld line integrating ceptometer (AccuPAR; Decagon Devices, Inc., Pullman Washington, USA) two to three times in each of the 2001 through 2003 growing seasons. In 2003 [CO_2] at 1 m above each subplots was measured twice during the growing season using a portable infrared gas analyzer (IRGA, Li-COR LI-800; Li-COR, Inc., Lincoln, Nebraska, USA); samples were collected by drawing air through the IRGA with a battery-operated air pump and sampling 10 subsamples at one second intervals averaged by subplot for subsequent analysis.

Statistical analysis

We analyzed total and species-specific above ground biomass data, and root biomass data, by year 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.*, 2000). Data were analyzed with a mixed model analysis of variance (ANOVA; procedure MIXED; SAS Institute, 1999) with the model:

$$y_{ijk} = \mu + CO_2\ \text{treatment}_i + \text{Rep}(CO_2)_{ij} + \text{subplot}(\text{Rep}(CO_2))_{ijk}$$

where μ is the overall mean; [CO_2] 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 biomass for only the five dominant species (with mean biomass greater ≥ 5 g m^{-2} across treatments and years). We analyzed VWC, PPFD, and [CO_2] with the CRDS model for each respective sample date.

Residuals for all datasets were tested for normality with the Shapiro–Wilk W-statistic (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 for biomass from the 2001 dataset.

Results

Above ground and root biomass

Total understory above ground biomass for plots with elevated [CO_2] (179 ± 11.2 g m^{-2}) did not differ from ambient [CO_2] (204 ± 13.2 g m^{-2}, $P = 0.26$) in 2000, 2001 ($P = 0.22$), or 2002

($P = 0.16$) (Figure 1). However, in 2003 total understory above ground biomass was greater ($P = 0.07$) in elevated [CO_2] than ambient [CO_2].

Between 2000 and 2003, *Lonicera japonica* comprised between 40% and 60% of total understory aboveground biomass (Figure 1). *L. japonica* biomass more than doubled in the elevated [CO_2] plots relative to the ambient [CO_2] plots in 2001 and nearly doubled in 2003, but did not differ between [CO_2] treatments in 2000 or 2002 (Table 1). *Microstegium vimineum* accounted for about one-third of biomass in all years of the study (Figure 1). In 2001 *M. vimineum* biomass doubled in elevated [CO_2], but did not differ between [CO_2] treatments in 2000, 2002 or 2003 (Table 1).

The biomass of *Rubus* spp. nearly tripled under elevated [CO_2] in 2001, but did not differ between [CO_2] treatments in 2002 or 2003 (Table 1). The biomass of *Solidago* spp. differed between treatments in all years, although differences between elevated and ambient [CO_2] differed substantially between years. Biomass of *A. negundo* did not differ between treatments in any year. Aboveground biomass of subdominant species (with total biomass < 5 g m^{-2}) are in Table 2.

Root biomass in most depths, species, and size-class categories between 2001 and 2003 seldom differed between [CO_2] treatments (Table 3). In 2001, mass of coarse sweetgum roots (i.e., ≥ 1 mm diam.)—and coarse sweetgum plus other roots—at the 12.5-25 cm soil depth was about 4 times greater under elevated than ambient [CO_2] ($P = 0.10$). In 2003, mass of roots other than sweetgum, at both soil depths and in size classes both coarse and coarse plus fine (< 1 mm diam.), were at least 2 times greater under elevated than ambient [CO_2] ($P \leq 0.07$).

Soil moisture, and understory light and [CO_2]

Soil volumetric water content (VWC) did not differ between plots under ambient [CO_2] and elevated [CO_2] in 2001 or 2002 (Belote et al. 2004). In 2001, VWC was relatively constant throughout June and July, but increased in August, whereas in 2002 VWC peaked in May and declined substantially throughout the growing season (Belote et al. 2004). In 2003, VWC did not differ between [CO_2] treatments and remained relatively constant throughout the growing season (Table 4). Photosynthetic photon flux density (PPFD; μmol m^{-2} s^{-1}) above subplots did not differ between [CO_2] treatments on any sampling date in 2001 and 2002 (Belote et al. 2004) or in 2003 (Table 5). [CO_2] at 1 m above subplots in 2003 was greater in plots with elevated [CO_2], than ambient [CO_2] in both August (798 ± 53 ppm vs 432 ± 43 ppm, respectively; $P = 0.01$) and September (780 ± 36 ppm vs. 416 ± 29 ppm, respectively; $P = 0.004$).

Discussion

Results indicate that from 2000 to 2002, total above ground biomass remained approximately the same, while in 2003, the total above ground biomass was greater in elevated [CO_2] than in ambient [CO_2]. This can be explained in part because individual species respond differently to the [CO_2] treatments in their production of biomass. This is consistent with other work that observed differential or opposing responses of different plant species to elevated [CO_2] (Garbutt *et al.*, 1990; Coleman & Bazzaz, 1992; Norton *et al.*, 1999; Laing *et* al., 2002). While *Acer negundo* did not differ between treatments in any year, and total above ground biomass of *Solidago* spp was substantially greater under elevated [CO_2] treatments in each year, the other three dominant species demonstrate an interesting pattern. The biomass of both *Rubus* spp. and *Microstegium vimineum* was only significantly greater under elevated [CO_2] in 2001, while it was only in 2002 that *Lonicera japonica* biomass did not differ between treatments. In 2001, the greater above ground biomass of *M. vimineum* and the other species combined under ambient

[CO_2] conditions were masked by the greater above ground biomass of *L. japonica* under elevated [CO_2] treatments. In 2002, the only year when L. japonica did not approximately double in above ground biomass under elevated [CO_2] treatments, the biomass of *M. vimineum* and the other species combined did not differ between treatments either, maintaining approximate equilibrium between ambient and elevated [CO_2] conditions. In 2003, on the other hand, the greater above ground biomass of *Lonicera japonica* and the other species combined under elevated [CO_2] conditions, was not masked by the above ground biomass of *Microstegium vimineum*, which remained approximately equal under both treatments, resulting in a total aboveground biomass greater under elevated [CO_2] conditions as compared to ambient [CO_2] conditions. This suggests that in some cases the dominant plant response to differing [CO_2] treatments may be the determining factor behind a community's response under different [CO_2] conditions.

Moveover, differences in biomass production by the different species were not necessarily predictable based on their photosynthetic pathways: although *M. vimineum*, a C_4 grass, was little affected by elevated [CO_2], and the C_3 vine, *L. japonica*, and C_3 herbaceous dicot, *Solidago* spp. responded positively to elevated [CO_2] in most years, the two C_3 woody plants, *A. negundo* and *Rubus spp.* responded little or not at all to elevated [CO_2]. This is consistent with several other populations and community-level studies that have found that the response of species cannot necessarily be predicted based on functional group classification (Körner, 2000; Zavaleta, *et al.*, 2003).

Under other circumstances, the cumulative effects of many individual species contribute to the total production in biomass and changes in species composition. The year 2001 had the greatest number of species demonstrating greater above ground biomass under elevated [CO_2] as

compared to ambient [CO_2]. This was also the only year that coarse roots for sweetgum and sweetgum plus other roots differed significantly between treatments. These differing conditions may be related to soil water availability. The year 2001, like 2003 was considered to be a 'wet' year as compared to 2002, suggesting a tenuous interconnection between soil moisture availability and [CO_2] in affecting biomass and root mass growth. These results confirm research in other studies of elevated [CO_2] on communities that found that community responses to elevated [CO_2] are often unpredictable, in part because of the availability of other resources (Owensby *et al.*, 1993, 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 [CO_2] were observed only when availability of water was high (Smith *et al.*, 2000). In other systems, community responses to CO_2 enrichment occurred only when the availability of water was limited (Owensby *et al.*, 1999). The photosynthetic pathway of the dominant species may explain the contradictory results. Specifically, C_3 species may positively respond to elevated [CO_2] by increasing the acquisition of carbon only when water resources are abundant (Huxman & Smith, 2001). By contrast, photosynthesis rates of C_4 species are usually CO_2-saturated at current [CO_2] (Ghannoum *et al.*, 2000), and may only benefit from elevated [CO_2] 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 & Perez-Soba, 2001) or nitrogen (Roy *et al.*, 1996; Cannell & Thornley, 1998). Temperature also has an interconnected effect with [CO_2] on species (Coleman & Bazzaz, 1992; Laing *et* al., 2002, recent papers from New Phytologist). Recently, Shaw *et al.* (2002) suggested that elevated [CO_2]

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 variations in resource availability (Tilman, 1982), nitrogen immobilization by soil microbes (Morgan, 2003). Moreover, or species interactions (Arp *et al.*, 1993) both above ground and below ground, may affect a strong competitive interaction between *Microstegium vimineum* and *Lonicera japonica*, where both mutually negatively affected biomass production, as Belote *et al.* (2004) observes. However, of the two species *M. vimineum* was the superior competitor and interfered with *L. japonica*, regardless of soil moisture availability, by over-growing the prostrate vine and depriving it of light or other resources (Belote *et al.*, *in review*), but, effects under elevated [CO_2] are unknown. 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_2] on communities (Körner, 2000; Morgan, 2002).

Time may be a factor in plant community response to [CO_2]. In the first three years of this experiment, from 2000-2002, there was no difference between total biomass in either [CO_2] treatment, but by the fourth year in this study the elevated [CO_2] treatment had a greater total understory biomass than the ambient [CO_2] treatment. This could be attributed to a cumulative effect through the years. Root biomass showed a similar trend: in 2001 and 2002, roots other than sweetgum coarse and coarse plus fine categories did not differ, but in 2003 they approximately doubled under elevated [CO_2]. This may suggest a parallel growth between above and below ground biomass or an interaction between the dominant sweetgum trees and understory plant development.

Differences in above ground and root biomass are not attributable to environmental factors such as light and soil moisture which did not differ between treatments, although soil moisture availability did differ each year. Overall, differences in biomass both above and below ground can be attributed to changes in [CO_2] treatments. Over time, elevated [CO_2] resulted in increased total biomass for understory communities. This suggests that changes in atmospheric composition could increase production and standing biomass of forest understory communities. However, the benefits of this incrase in production must be weighed against changes in the species composition of the understory community. For example, elevated [CO_2] may benefit invasive plants at the expense of native species (Smith *et al.*, 2000; Sasek & Strain 1990; Weltzin *et al.*, 2003).

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Figure caption

Figure 1. Aboveground biomass of FACE plots receiving ambient [CO_2] ($N = 3$) and elevated [CO_2] ($N = 2$) in 2001 through 2003.

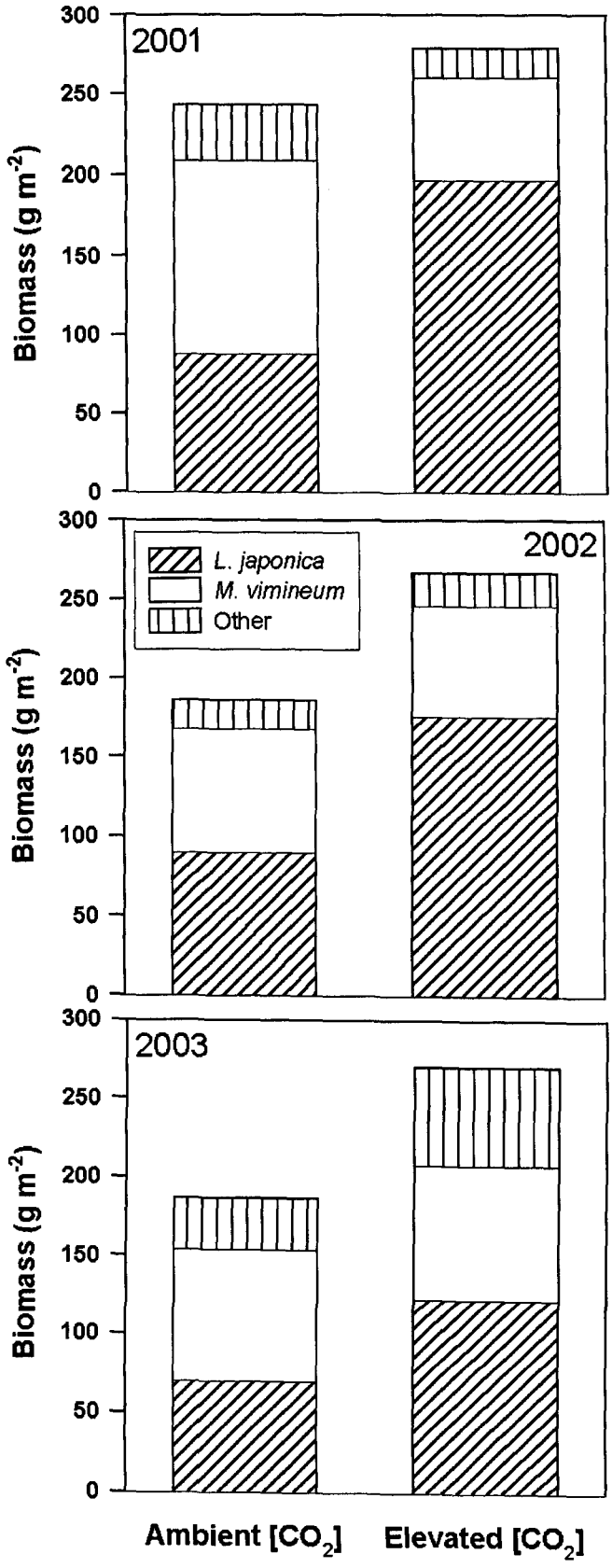
2001
2002
2003
L. japonica
M. vimineum
Other
Biomass (g m-2)
300
250
200
150
100
50
0
Ambient [CO2]
Elevated [CO2]

Table 1. Aboveground biomass (mean ± 1 SE) of five dominant understory plants (with mean biomass ≥ 5 g m^{-2} averaged across treatments and years) in FACE plots receiving ambient [CO_2] (N = 3) and elevated [CO_2] (N = 2) in 2001 through 2003.

Species	Year	[CO_2] treatment	Biomass (g m^{-2})	P
A. negundo	2001	Ambient	12.9 ± 9.2	
		Elevated	7.6 ± 7.6	0.87
	2002	Ambient	5.4 ± 2.7	
		Elevated	4.4 ± 4.4	0.86
	2003	Ambient	9.2 ± 3.7	
		Elevated	15.4 ± 15.4	0.40
L. japonica	2000	Ambient	73.7 ± 7.2	
		Elevated	92.9 ± 12.3	0.30
	2001	Ambient	87.7 ± 5.7	
		Elevated	197.4 ± 33.1	0.03
	2002	Ambient	90.2 ± 15.7	
		Elevated	176.0 ± 77.2	0.25
	2003	Ambient	70.2 ± 12.8	
		Elevated	123.4 ± 16.8	0.08
M. vimineum	2000	Ambient	82.1 ± 7.9	
		Elevated	58.0 ± 12.3	0.18
	2001	Ambient	120.5 ± 5.5	
		Elevated	64.0 ± 13.8	0.05
	2002	Ambient	78.3 ± 8.7	
		Elevated	70.3 ± 25.6	0.74
	2003	Ambient	84.1 ± 9.3	

Rubus spp.		Elevated	85.1 ± 4.4	0.95
	2001	Ambient	1.3 ± 0.4	
		Elevated	9.6 ± 4.4	0.06
	2002	Ambient	1.3 ± .6	
		Elevated	4.8 ± 3.8	0.29
	2003	Ambient	14.7± 9.1	
Solidago spp.		Elevated	13.0 ± 5.8	0.36
	2001	Ambient	0.6 ± 0.3	
		Elevated	22.3 ± 1.5	0.004
	2002	Ambient	0.0 ± 0.0	
		Elevated	4.3 ± 2.5	0.03
	2003	Ambient	0.3 ± 0.3	
		Elevated	8.7 ± 4.7	0.06

Table 2. Aboveground biomass (mean ± 1 SE) of subdominant (< 5.0 g m^{-2}) understory taxa (s = seedling) in FACE plots receiving ambient [CO_2] ($N = 3$) and elevated [CO_2] ($N = 2$) in 2001 through 2003.

	2001		2002		2003	
Species	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated
Acer saccharum (s)	0.4 ± 0.4	0	4.1 ± 4.1	0	0	0
Allium spp.	0.5 ± 0.5	0.1 ± 0.1	0	0	0	0
Asplenium platyneuron	0.1 ± 0.1	0	0	0	0	0
Aster dumosus	0	0.5 ± 0.5	0	0	0	0
Bignonia capreolata	2.0 ± 2.0	0	0.2 ± 0.2	0	0.4 ± 0.4	0
Boehmeria cylindrica	0	0	0	0	0	4.5 ± 3.7
Carex spp.	0.1 ± 0.1	0.4 ± 0.4	0	0.2 ± 0.2	0	0
Celtus occidentalis	0	0	0	0	0.2 ± 0.2	0
Clematis virginiana	1.1 ± 1.1	0	0	0	0	0
Coenoclinum coelestinum	0	0	0	0	0	0.7 ± 0.5
Duchesnea spp.	0	0	0	0	3.2 ± 0.7	0.3 ± 0.3
Fagus grandifolia (s)	0	0	0	0	0.7 ± 0.7	0
Fraxinus spp. (s)	9.8 ± 8.5	0.3 ± 0.3	2.3 ± 2.0	1.0 ± 1.0	0.3 ± 0.3	0
Galium spp.	0	0	0	0	0.2 ± 0.1	0.7 ± 0.2
Geum canadense	1.1 ± 1.0	0.1 ± 0.1	0	1.5 ± 1.5	0	0
Hypcricum spp.	0	0	0	0	0	9.2 ± 0.8
Ipomoea spp.	0	0	0	0	0	0
Juncus tenuis	0.1 ± 0.1	0	0.3 ± 0.3	0	0	0
Juniperus virginiana (s)	0	2.0 ± 2.0	0	0	0	0.9 ± 0.9
Lespedeza cuneata	0	0.4 ± 0.4	0	0	0	0
Lobelia spp.	0	0.1 ± 0.1	0	0.2 ± 0.2	0	0
Myotosis macrosperma	0	0	0	0.1 ± 0.1	0	0
Oxalis stricta	0.1 ± 0.1	0.1 ± 0.1	0	0	0	0
Panicum spp.	0	2.6 ± 2.6	0	0.9 ± 0.9	0	0

Parthenocissus quinquefolia	0	0	0	0	1.1 ± 1.1	1.9 ± 1.6
Potentilla simplex	0.7 ± 0.6	0	0.8 ± 0.3	0.4 ± 0.3	1.7 ± 1.7	0
Prunus serotina (s)	1.8 ± 1.5	0.1 ± 0.1	0	0	0.1 ± 0.1	0
Quercus velutina (s)	0.5 ± 0.5	0	0	0	0	0
Sanicula spp.	0.2 ± 0.1	0.3 ± 0.3	0.2 ± 0.1	0.2 ± 0.2	0	0
Taraxacum officinale	0.2 ± 0.1	0	0	0	0	0
Toxicodendron quercifolia	0.2 ± 0.1	0.3 ± 0.1	0.2 ± 0.2	0.3 ± 0.3	0.2 ± 0.2	0.4 ± 0.4
Ulmus spp.	0	0.1 ± 0.1	0	0.1 ± 0.1	0	5.3 ± 4.8
Verbisina occidentalis	0	0	0	2.3 ± 2.3	0	0.8 ± 0.8
Vitis spp.	0.3 ± 0.3	0.1 ± 0.0	0	0	0.4 ± 0.4	0

Table 3. Root mass (g m^{-2}; mean ± 1 SE) at two soil depths (0-12.5 cm, 12.5-25 cm) and both depths combined (i.e., 0-25 cm), for two species types (SG = sweetgum, O = other), in two size classes (F = fine, or < 1 mm; C = coarse, or ≥ 1 mm) in FACE plots receiving ambient [CO_2] ($N = 3$) and elevated [CO_2] ($N = 2$) in 2001 through 2003.

			2001			2002			2003		
Depth (cm)	**Type**	**Size**	***P*-value**	**E**	**A**	***P*-value**	**E**	**A**	***P*-value**	**E**	**A**
0-12.5	O	F	0.53	99.6±17.1	83.7±14.3	0.88	88.5±16.5	91.6±15	0.22	18.7±1.9	12.5±3.1
		C	0.29	52.7±37.9	13.0±5.3	0.87	39.5±10.6	42.7±11.7	0.07	20.9±5.7	5.9±2.3
		C+F	0.26	152.3±45.1	96.7±14.5	0.85	128.0±20.5	134.3±20.3	0.05	39.7±5.6	18.3±3.7
	SG	F	0.47	61.0±17.5	41.8±7.0	0.13	95.7±20.7	57.9±7.1	0.44	138.1±13.7	116.9±15.2
		C	0.74	245.3±80.6	206.8±64.0	0.32	81.3±17.4	205.3±68	0.39	136.0±35.8	207±52.2
		C+F	0.64	307.1±86.7	248.6±66.3	0.47	170.6±36.9	258.8±69.9	0.60	274.1±46.2	323.9±62.5
	O+SG	F	0.39	160.6±30.8	125.5±12.5	0.48	184.2±22.3	149.5±18.3	0.35	156.8±12.5	129.3±14.8
		C	0.55	298.2±104.6	219.8±65.5	0.28	123.3±13.3	251.8±66	0.49	157.0±37.5	212.8±52.7
		C+F	0.44	456.0±112.6	345.3±68.0	0.40	303.5±29.6	400.2±66.5	0.76	313.8±47.0	342.2±62.5
12.5-30	O	F	0.43	13.6±4.1	9.1±2.9	0.14	12.9±3.1	25.0±4.5	0.44	0.2±0.2	1.6±1.2
		C	0.81	30.0±1.7	4.0±2.6	0.37	4.9±2.8	13.3±6.2	0.19	2.9±2.1	0.1±0.1
		C+F	0.61	16.6±4.9	13.1±3.8	0.12	17.9±4.0	38.4±7.3	0.56	3.2±2.2	1.6±1.3
	SG	F	0.57	26.5±3.2	43.2±21.2	0.31	20.8±5.7	13.0±3.1	0.21	44.1±6.5	28.8±5.1
		C	0.10	134.5±47	32.7±10.2	0.51	33.9±14.7	66.3±22.7	0.66	59.8±19.2	80.2±19.8
		C+F	0.24	161.0±48.9	82.5±28.9	0.63	54.7±16.5	80.4±24.8	0.79	98.7±20.1	108.9±20.3

	O+SG	F	0.66	40.0±6.3	52.3±20.3	0.65	33.7±7.5	38.1±5.0	0.27	44.3±6.5	30.4±6.0
		C	0.10	137.5±46.4	34.6±11.1	0.32	38.8±13.6	80.6±22.7	0.70	63.1±18.4	80.2±19.8
		C+F	0.21	177.6±48.0	92.7±28.3	0.32	72.5±15.9	120.2±24.7	0.82	102.3±19.3	110.6±20.6
0-30	O	F	0.43	113.1±19	92.8±13.3	0.59	90.4±18.5	116.6±15.6	0.32	19.0±1.9	14.0±3.2
		C	0.32	55.7±39.3	17.0±5.2	0.47	39.5±13.2	56.0±11.5	0.06	23.9±6.3	5.9±2.4
		C+F	0.25	168.9±46.4	109.8±13.9	0.46	129.9±25.9	172.6±17.4	0.05	42.8±6.3	20.0±4.3
	SG	F	0.95	87.4±18.9	85.0±22.3	0.19	104.5±20.9	70.9±8.6	0.34	182.2±18.4	145.7±18.8
		C	0.47	318.5±74.6	234.1±67.6	0.15	94.8±16.9	248.9±63.7	0.35	188.3±35.2	287.1±64.6
		C+F	0.61	391.3±85.7	317.4±88.0	0.27	182.6±36.0	310.9±68.3	0.52	360.5±40.8	432.8±75.4
	O+SG	F	0.62	200.6±34.1	177.8±24.5	0.90	194.9±28.9	187.6±19.7	0.32	201.1±17.3	159.7±19.5
		C	0.38	361.2±86.6	248.7±69.0	0.12	131.3±16.5	304.7±65.5	0.45	212.2±36.9	293.1±64.8
		C+F	0.53	519.6±106.2	422.6±88.1	0.16	300.1±43.7	477.0±71.3	0.65	403.3±42.3	452.8±76.1

Table 4. Mean (±1 SE) soil moisture (% VWC) in FACE plots receiving ambient [CO_2] ($N = 3$) and elevated [CO_2] ($N = 2$) in 2003.

Date	**Elevated**	**Ambient**	***P*-value**
June 11	36.7 ± 2.5	34.3 ± 2.1	0.58
July 21	33.4 ± 1.8	31.2 ± 1.5	0.41
Sept. 4	36.8 ± 2.5	34.5 ± 2.1	0.54

Table 5. Mean (± 1 SE) PPFD (μmol m^{-2} s^{-1}) in FACE plots receiving ambient [CO_2] ($N = 3$) and elevated [CO_2] ($N = 2$) in 2003.

Date	**Elevated**	**Ambient**	***P*-value**
June 23	61 ± 52	98 ± 42	0.61
July 17	77 ± 22	55 ± 18	0.49
Sept. 12	61 ± 27	59 ± 22	0.96