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CO_2 enrichment accelerates successional development of an understory plant community

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Abstract

Aims

Rising concentrations of atmospheric carbon dioxide ($[CO_2]$) may influence forest successional development and species composition of understory plant communities by altering biomass production of plant species of functional groups. Here, we describe how elevated $[CO_2]$ (eCO_2) affects aboveground biomass within the understory community of a temperate deciduous forest at the Oak Ridge National Laboratory sweetgum (*Liquidambar styraciflua*) free-air carbon dioxide enrichment (FACE) facility in eastern Tennessee, USA. We asked if (i) CO_2 enrichment affected total understory biomass and (ii) whether total biomass responses could be explained by changes in understory species composition or changes in relative abundance of functional groups through time.

Materials and methods

The FACE experiment started in 1998 with three rings receiving ambient $[CO_2]$ (aCO_2) and two rings receiving eCO_2. From 2001 to 2003, we estimated species-specific, woody versus herbaceous and total aboveground biomass by harvesting four 1 × 0.5-m subplots within the established understory plant community in each FACE plot. In 2008, we estimated herbaceous biomass as previously but used allometric relationships to estimate woody biomass across two 5 × 5-m quadrats in each FACE plot.

Important findings

Across years, aboveground biomass of the understory community was on average 25% greater in eCO_2 than in aCO_2 plots. We could not detect differences in plant species composition between aCO_2 and eCO_2 treatments. However, we did observe shifts in the relative abundance of plant functional groups, which reflect important structural changes in the understory community. In 2001–03, little of the understory biomass was in woody species; herbaceous species made up 94% of the total understory biomass across $[CO_2]$ treatments. Through time, woody species increased in importance, mostly in eCO_2, and in 2008, the contribution of herbaceous species to total understory biomass was 61% in aCO_2 and only 33% in eCO_2 treatments. Our results suggest that rising atmospheric $[CO_2]$ could accelerate successional development and have longer term impact on forest dynamics.

Keywords: community composition • FACE • aboveground biomass • woody • herbaceous • sweetgum • *Microstegium vimineum* • *Lonicera japonica*

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INTRODUCTION

The concentration of atmospheric carbon dioxide ($[CO_2]$) continues to increase and is expected to double this century from pre-industrial levels (IPCC 2007). Increases in atmospheric $[CO_2]$ will have direct, as well as indirect effects on plant performance (Poorter and Navas 2003), ultimately affecting plant-competitive interactions and, hence, plant community composition. While controlled CO_2 enrichment studies have demonstrated that elevated $[CO_2]$ (eCO_2) can enhance growth

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when plants are grown in monoculture settings (Poorter and Navas 2003; Poorter *et al.* 1996), the impacts of eCO_2 on plant community dynamics remains little understood.

Plant community responses to CO_2 enrichment have generally been described in terms of changes in total aboveground production (Belote *et al.* 2004; Koch and Mooney 1996; Morgan *et al.* 2004), community composition (Belote *et al.* 2004; Körner and Bazzaz 1996; Teyssonneyre *et al.* 2002; Zavaleta *et al.* 2003b), diversity (Niklaus and Körner 2004; Zavaleta *et al.* 2003a), nitrogen fixation (Garten *et al.* 2008) and potential successional trajectories over time (Mohan *et al.* 2007; Potvin and Vasseur 1997; Vasseur and Potvin 1998). Much of the current community-level eCO_2 research has been conducted in grassland or desert systems (Dukes *et al.* 2005; Morgan *et al.* 2004; Nagel *et al.* 2004; Niklaus and Körner 2004; Smith *et al.* 2000), and research investigating the effects of eCO_2 on forests has focused on dominant overstory trees because of their importance in carbon, water and nutrient cycling (Asshoff *et al.* 2006; Field *et al.* 1997; Norby *et al.* 2002, 2005; Schulze *et al.* 2000). However, forest understory communities are increasingly recognized as sites for maintaining species diversity, habitat and ecosystem processes including regeneration of overstory trees and nutrient cycling (Gilliam and Roberts 2003). Moreover, understory communities may be particularly responsive to eCO_2 because plants growing in low irradiance of closed-canopy forests are more carbon limited than those growing in open, early-successional habitats (Hättenschwiler 2001; Kersteins 2001). Thus, more research is needed to understand how understory communities will respond to a CO_2-enriched atmosphere over longer temporal scales pertinent toward forest management and conservation (e.g. Awmack *et al.* 2006; Bandeff *et al.* 2006; Belote *et al.* 2004; Mohan *et al.* 2007).

Here, we quantify the response of an understory plant community to eCO_2 in terms of total aboveground biomass and composition over time. We conducted our research over an 8-year period (2001–08) within the understory of a sweetgum (*Liquidambar styraciflua*) forest in eastern Tennessee, USA. We predicted that total biomass of the understory plant community would increase more with eCO_2 than in ambient $[CO_2]$ (aCO_2). CO_2 enrichment can enhance the production of certain species or functional groups, while having little or no influence on other species (e.g. Belote *et al.* 2004; Mohan *et al.* 2007). Specifically, we predicted that eCO_2 favors woody species over herbaceous species as woody species can accumulate greater biomass than herbaceous species in eCO_2. Therefore, we also predicted that eCO_2 alters understory community composition.

MATERIALS AND METHODS

Site description

We conducted our research at the sweetgum free-air carbon dioxide enrichment (FACE) facility, Oak Ridge National Environmental Research Park, Oak Ridge, Tennessee, USA (35°54′N; 84°20′W) (Norby *et al.* 2002). The research site is a planted *L.styraciflua* L. monoculture established in 1988 on an old terrace of the Clinch River (elevation 230 m above sea level). The *L.styraciflua* trees were ~16 m tall in 2002 and 18 m tall in 2008, with a closed canopy (leaf area index (LAI) = 5.5) that reduced the light in the understory 70–95% during the growing seasons. The soil, classified by the Natural Resources Conservation Service (United States Department of Agriculture) as an AquicHapludult, 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), and environmental data are available at http://public.ornl.gov/face/.

Experimental design

FACE technology applies eCO_2 to natural systems with minimal effects on potential confounding factors such as light, temperature and precipitation (Hendrey *et al.* 1999). In 1998, five 25-m diameter circular experimental units (hereafter 'rings') established in the sweetgum plantation were assigned to one of two $[CO_2]$ treatments: eCO_2 (n = 2; target $[CO_2]$ = 565 p.p.m.) and aCO_2 (n = 3). Supplemental CO_2 delivered to the two eCO_2 rings via blowers was distributed by 24 vertical vent pipes spaced 3.3 m apart around the perimeter of each ring. Mean daytime $[CO_2]$ in these rings was 548, 552, 549 and 557 p.p.m. in the 2001–03 and 2008 growing seasons, respectively. Three control rings received aCO_2; mean daytime $[CO_2]$ through the sweetgum canopy in these rings ranged from 384 and 398 p.p.m. over 5-year period (Norby *et al.* 2001; Norby *et al.* 2004). At the understory, daytime $[CO_2]$ measured in aCO_2 and eCO_2 rings 474 and 577 p.p.m., respectively (R.J. Norby, unpublished data). The CO_2 treatments were initiated in April 1998 and maintained each year from April to November (i.e. growing season). Nighttime fumigation was discontinued in 2001 because it interfered with soil respiration measurements. The research site had a sparse understory community in 1997 when the FACE plots were established, but by the growing season of 2000, plant cover in the understory became continuous and codominated by two non-native invasive plant species, Nepal grass (*Microstegium vimineum* (Trin.) A. Camus) and Japanese honeysuckle (*Lonicera japonica* Thunb.) (Belote *et al.* 2004).

Sampling methods

We determined total understory aboveground biomass between September and early October in 2001–03 and in October in 2008. We clipped all plants at ground level within each of four 0.5-m^2 subplots randomly located across four sampling quadrants within each of the five FACE rings. We sorted individuals into species and oven-dried samples at 65°C for at least 48 hours and weighed samples to obtain (i) species-specific biomass, (ii) biomass of resident and transient understory components and (iii) total understory biomass. We

categorized species into the resident and the transient component of the understory based on Gilliam and Roberts (2003). Plant species were defined as resident (herbaceous layer) or transient (woody layer) based on whether species remain as part of the ground-level vegetation or are capable of growing above the ground vegetation layer, respectively. Hence, we considered grasses, herbs and vines (including woody vines such as *L.japonica*) as resident species while shrubs and tree saplings as transient species (Table S1 in online supplementary material). Hereafter, resident species will be referred to as 'herbaceous' and transient species as 'woody'.

By 2008, woody understory vegetation had increased in stature and 0.5-m^2 subplots were no longer the appropriate spatial scale to quantify woody species abundance (i.e. aboveground biomass). Therefore, in 2008, we installed two 25-m^2 (5 × 5 m) subplots in each of five FACE rings to quantify aboveground biomass of woody species. We established subplots in a stratified random manner, whereby one subplot was located at a random location within each of two randomly chosen quadrants within each FACE ring. In each subplot, we measured the height and stem diameter of all woody saplings >50 cm in height. Using previously developed allometric equations (Figure S1 in online supplementary material), we estimated aboveground biomass of all woody species within each 25-m^2 subplot. We developed allometric equations by measuring the height and diameter of woody saplings and shrubs adjacent to FACE rings and then harvesting and weighing their aboveground biomass. We developed species-specific allometric equations for six species commonly found in the experimental plots: *Acer negundo* L., *Acer rubrum* L., *Cornus florida* L., *Fraxinus pennsylvanica* Marsh., *Lindera benzoin* L. and *Prunus serotina* Ehrh. (Figure S1 in online supplementary material). We assessed the most important predictors (diameter, diameter squared, height, diameter × height, diameter squared × height) of species-specific allometric equations to determine the best single or combinations of predictors. For individuals belonging to rare species, we applied an across-species allometric equation using diameter squared × height as the predictor variables ($y = 0.255\ x^{0.57}$, $R^2 = 0.97$).

Statistical analyses

Univariate analyses.

We analyzed the response of total, herbaceous and woody species biomass by year for effect of [CO_2] treatments. We analyzed the data using a nested analysis of variance (ANOVA) model (SAS Institute (1999) SAS/STAT user's guide Version 8.0. SAS Institute, Cary, NC) to determine the main fixed effects of the [CO_2] treatment and the variability among the subplots nested within rings:

$$Y_{ijk} = \mu + \mathrm{CO}_{2i} + \mathrm{subplot}_j(\mathrm{CO}_2)_i + \in_{ijk},$$

where μ is the overall mean, CO_2 is the treatment effect, subplot is the nested subsample within each ring and $\in_{ijk}$ is the residual error associated with the measured dependent variable Y_{ijk}. We analyzed the response of the ratio of herbaceous to woody individuals using a two-way ANOVA with CO_2 and time (1998 and 2008) as fixed factors.

Residuals for all data sets were tested for normality with the Shapiro–Wilk *W*-statistic (Shapiro and Wilk 1965). Continuous and proportional data that did not meet these assumptions were log transformed or arcsine square-root transformed before analysis, respectively. Because of the low statistical power associated with the FACE design (i.e. $n = 2$ for eCO_2 plots, $n = 3$ for aCO_2 plots), we set our critical $\alpha = 0.10$ to reduce the possibility of a Type II statistical error (Filion *et al.* 1999).

Multivariate analyses.

We analyzed [CO_2] effects on plant community composition in 2001–03 and 2008, using redundancy analysis (RDA). RDA is an ordination technique designed to detect those patterns of variation in community composition that can be explained by one or more environmental variables; we used [CO_2] treatment (eCO_2 or aCO_2) as the environmental variable. The sampling design did not allow us to analyze the data as repeated measurements because subplot locations within rings were relocated each year. Therefore, RDAs were run for each year separately. Significance was tested using Monte Carlo permutation tests (999 permutations). We used permutation tests restricted for our 'nested' design: data within rings were permuted completely at random, while subplots within rings were not permuted (Lepš and Šmilauer 2003).

RESULTS

Understory biomass

Across years, total aboveground biomass of the understory community was on average 25% greater in eCO_2 plots than in aCO_2 plots (Fig. 1). In 2002 and 2003, understory biomass was significantly greater in eCO_2 plots than in aCO_2 plots; in 2001 and 2008, the difference in biomass production between eCO_2 and aCO_2 plots was not significant (Table 1).

Interestingly, initial biomass responses of the understory community to eCO_2 were driven by the herbaceous species, while later responses were driven by the woody species. Herbaceous biomass was 30% greater in eCO_2 plots than in aCO_2 plots during the early years (2001–03) but was 30% less in eCO_2 than in aCO_2 plots during the last year of our study (2008) (Table 1, Fig. 1). In contrast, biomass of woody species did not differ between eCO_2 plots and aCO_2 plots initially (comprising only 7% of total understory biomass in 2001–03). However, in 2008, woody species made up half of the total understory biomass, and woody biomass was 60% greater in eCO_2 plots than in aCO_2 plots. In 2001 and 2008, understory herbaceous biomass varied across subplots, whereas total understory and woody biomass only varied at the subplot level in 2008 (Table 1).

Community composition

Across years, eCO_2 explained only 6–14% of the total variation in understory community composition (Table 2). Except

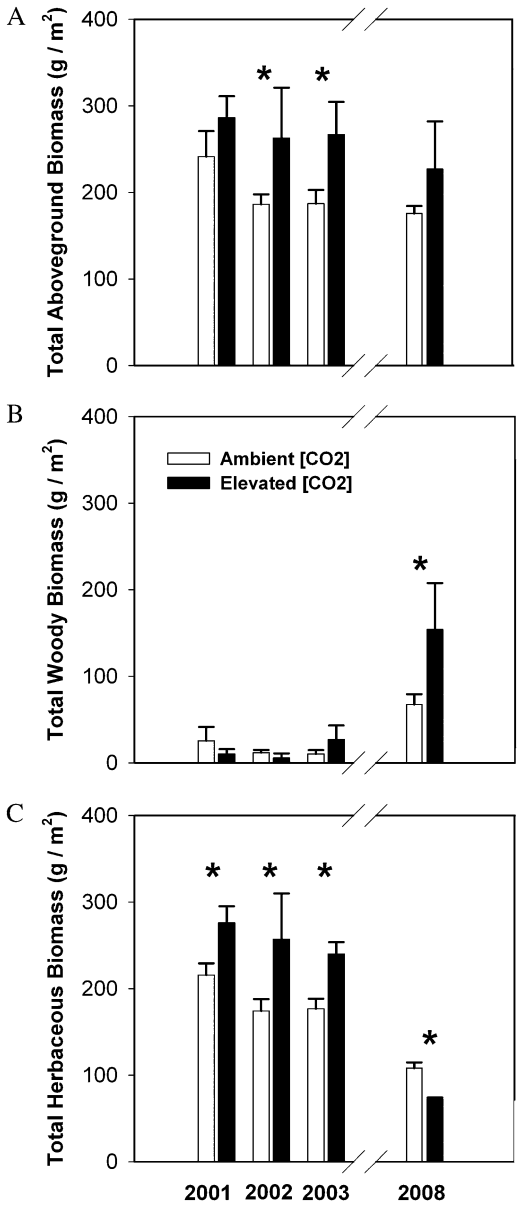

Figure 1: total aboveground biomass (A), total woody (B) and herbaceous (C) plant species biomass in eCO_2 and aCO_2 in 2001–03 and 2008. Values are mean ± standard error. Asterisks indicate significant differences ($P < 0.10$) between $[CO_2]$ treatments in each year.

for 2003, no significant eCO_2 effects on understory community composition could be detected. However, the ordination analyses show that during the early years (2001–03), abundance of *L.japonica* (a woody vine) and several other herbaceous species was generally positively associated with eCO_2 (Fig. 2). In 2008, abundance of *Liriodendron tulipifera* and *Ulmus* sp. (woody saplings) was positively associated with eCO_2, while abundance of *M.vimineum* (a C_4 grass) and *Duchesnea indica* (a forb) was negatively associated with eCO_2 (Fig. 2).

Table 1: results from nested ANOVA with $[CO_2]$ as the fixed factor and subplot as the nested factor on total, herbaceous and woody aboveground biomass in 2001–03 and in 2008

		Total understory		Total herbaceous		Total woody	
Year	Effect	*F*	*P*	*F*	*P*	*F*	*P*
2001	$[CO_2]$	2.66	0.13	8.34	**0.01**	1.26	0.28
	Subplot $[CO_2]$	2.15	0.12	3.51	**0.03**	0.64	0.70
2002	$[CO_2]$	4.60	**0.05**	6.85	**0.02**	0.52	0.48
	Subplot $[CO_2]$	0.87	0.54	0.87	0.55	0.76	0.62
2003	$[CO_2]$	6.74	**0.02**	9.22	**0.01**	0.78	0.39
	Subplot $[CO_2]$	0.67	0.67	1.81	0.18	1.32	0.32
2008	$[CO_2]$	2.81	0.14	19.73	**<0.01**	54.19	**<0.01**
	Subplot $[CO_2]$	0.37	0.71	4.92	**<0.01**	17.94	**<0.01**

Bolded *P* values are statistically significant at $\alpha = 0.10$.

Table 2: results from RDA testing the effects of $e[CO_2]$ on understory community composition

Year	% Variance explained	*F*	*P*
2001	0.14	2.86	0.20
2002	0.06	1.15	0.58
2003	0.14	2.96	**0.09**
2008	0.09	1.70	0.32

Explained variance is the sum of all canonical eigenvalues. *P* values are based on a permutation tests restricted for nested design (999 permutations). Bolded *P* values are statistically significant at $\alpha = 0.10$.

DISCUSSION

CO_2 enrichment of the sweetgum (*L.styraciflua*) forest resulted in greater aboveground biomass in the understory and accelerated the successional shift from an herbaceous-dominated community to one dominated by woody shrubs and saplings. Our data suggest that eCO_2 can stimulate successional development of understory plant communities and, thereby, influence long-term forest dynamics.

The increased dominance of woody plants in eCO_2 plots was not a consequence of earlier establishment. Based on long-term subplots established at the beginning of the FACE experiment (1998), we found no differences among plots ($P > 0.10$) in the ratio of herbaceous to woody individuals in the understory communities (Figure S2 in online supplementary material). However, once woody seedlings become established in the forest understory, they are expected to show a greater growth response to CO_2 enrichment than herbaceous plants, thereby accelerating the successional shift toward an understory plant community dominated by woody shrubs and saplings, as observed in this experiment. Given their perennial life form, woody plants have the capacity to respond to eCO_2 by successively increasing leaf area each year, as well as through increased growth

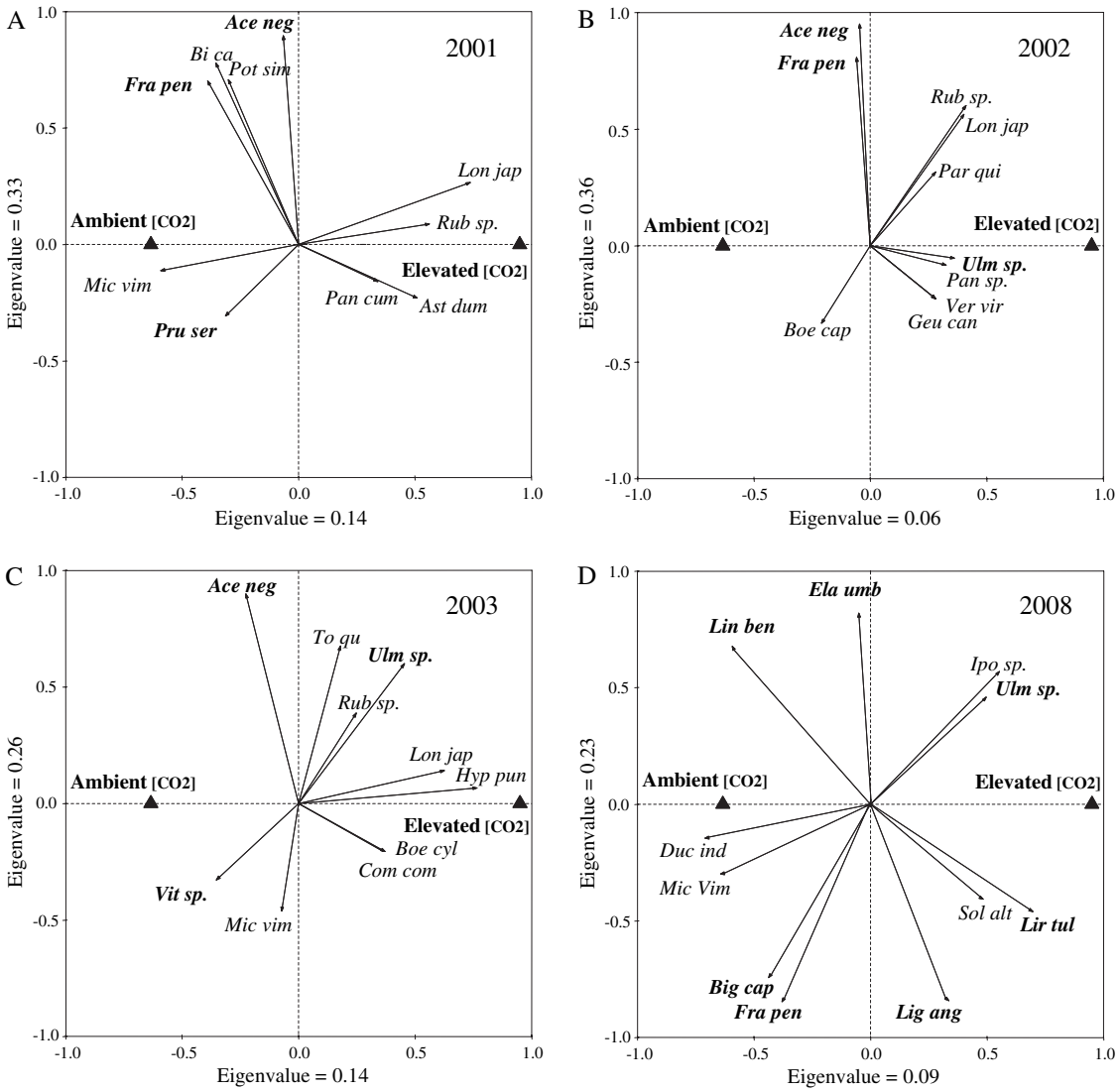

Figure 2: ordination diagrams (species-treatment biplots) of RDA for understory plant communities showing the effect of eCO_2 and aCO_2 for 2001 (A), 2002 (B), 2003 (C) and 2008 (D). Eigenvalues along the axes indicate the amount of explained variability in plant species composition. The value along the first axis is canonical (e.g. representing the [CO2] treatment); the value along the second axis is not. For clarity, only 10 plant species with the best fit range are shown. Woody species are shown in bold, whereas herbaceous species are shown in regular font. Species codes are *Ace neg*, *Acer negundo*; *Ast dum*, *Aster dumosus*; *Boe cyl*, *Boehmeria cylindrica*; *Big cap*, *Bignonia capreolata*; *Com com*, *Commelina communis*; *Duc ind*, *Duchesnea indica*; *Fra pen*, *Fraxinus pennsylvanica*; *Geu can*, *Geum canadense*; *Ipo* sp., *Ipomea* sp.; *Lin ben*, *Lindera benzoin*; *Lir tul*, *Liriodendron tulipifera*; *Lon jap*, *Lonicera japonica*; *Mic vim*, *Microstegium vimineum*; *Pan* sp., *Panicum* sp.; *Par qui*, *Parthenocissus quinquefolia*; *Pru ser*, *Prunus serotina*; *Rub* sp., *Rubus* sp.; *Sol alt*, *Solidago altissima*; *Ulm* sp., *Ulmus* sp.; *Ver vir*, *Verbesina virginica*; *Vit.* sp, *Vitis* sp.

per unit leaf area. This 'compound interest' effect during the exponential growth phase of woody plants can lead to large responses to CO_2 enrichment (Norby *et al.* 1999) that are not observed in annual plants, which do not accumulate leaf area over time. Eventually, environmental factors (e.g. light, water and nitrogen) constrain the exponential growth phase and its response to eCO_2. Increased growth of the woody component of the understory community may have reduced resources available for the herbaceous component, explaining the decline in herbaceous biomass over time, especially in eCO_2.

CO_2 enrichment may indirectly influence understory community biomass via effects on the overstory species (Norby *et al.* 2005) or by altering herbivory. In our experiment, net primary productivity (NPP) of the overstory species was 23% greater in eCO_2 than aCO_2 rings (Norby *et al.* 2005) in the first 6 years of the experiment (1998–2003), but the response of NPP to eCO_2 has subsequently declined (R.J. Norby, unpublished data). Such increases in forest NPP under eCO_2 could lead to the decline of potentially growth-limiting resources such as light, soil moisture or soil nitrogen with indirect negative effects on understory species. However, in our study,

it is unlikely that indirect effects of eCO_2 contributed to understory community responses. There were no effects of $[CO_2]$ enrichment on LAI (Norby *et al.* 2005), understory photosynthetically active radiation (Riggs *et al.* 2009) or soil moisture (Tharp and Norby 2008). Also, indirect evidence based on ^{15}N abundance indicates that N availability is declining faster under eCO_2 than under aCO_2(CT Garten, personal communication).

Increased community biomass in eCO_2 and the differential effect of eCO_2 on woody and herbaceous species was not accompanied by a clear $[CO_2]$ effect on plant species composition. Our findings contrast with several studies in which changes in productivity occurred together with changes in plant species composition (e.g. Niklaus *et al.* 2001; Reich *et al.* 2001). Perhaps, disparity between our findings and existing studies could be a function of differences in study design. In both Niklaus *et al.* (2001) and Reich *et al.* (2001), plant communities were manually constructed at the start of the experiment, whereas we did not control for initial composition, and communities were assembled by natural colonization and germination from the seed bank. Even though particular species like *L.japonica* initially dominated the understory of eCO_2 plots more so than in aCO_2 plots, there was a large variation in subordinate species within treatments. Similar to our findings, Polley *et al.* (2003), working in a grassland, and Mohan *et al.* (2007), in a forest, documented that eCO_2 accelerated successional change, leading to greater performance by later successional plant species.

CONCLUSIONS

We found that understory communities in eCO_2 plots became dominated by woody species earlier in eCO2 plots indicating more rapid development of tree regeneration layer and faster successional development of the stand. Future studies should continue to investigate effects of eCO_2 on understory community dynamics including regeneration of favored tree species. Results from this study site suggest that eCO_2 might increase biomass production of understory tree species that may influence future overstory species composition. Our findings could have implications for forest establishment and development under future climatic conditions.

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SUPPLEMENTARY MATERIAL

Supplementary Table S1 and Figures S1 and S2 are available at *Journal of Plant Ecology* online.

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Conflict of interest statement. None declared.

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