

LONG-TERM CO₂ ENRICHMENT OF A FOREST ECOSYSTEM: IMPLICATIONS FOR FOREST REGENERATION AND SUCCESSION

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Abstract. The composition and successional status of a forest affect carbon storage and net ecosystem productivity, yet it remains unclear whether elevated atmospheric carbon dioxide (CO₂) will impact rates and trajectories of forest succession. We examined how CO₂ enrichment (+200 μL CO₂/L air differential) affects forest succession through growth and survivorship of tree seedlings, as part of the Duke Forest free-air CO₂ enrichment (FACE) experiment in North Carolina, USA. We planted 2352 seedlings of 14 species in the low light forest understory and determined effects of elevated CO₂ on individual plant growth, survival, and total sample biomass accumulation, an integrator of plant growth and survivorship over time, for six years. We used a hierarchical Bayes framework to accommodate the uncertainty associated with the availability of light and the variability in growth among individual plants.

We found that most species did not exhibit strong responses to CO₂. *Ulmus alata* (+21%), *Quercus alba* (+9.5%), and nitrogen-fixing *Robinia pseudoacacia* (+230%) exhibited greater mean annual relative growth rates under elevated CO₂ than under ambient conditions. The effects of CO₂ were small relative to variability within populations; however, some species grew better under low light conditions when exposed to elevated CO₂ than they did under ambient conditions. These species include shade-intolerant *Liriodendron tulipifera* and *Liquidambar styraciflua*, intermediate-tolerant *Quercus velutina*, and shade-tolerant *Acer barbatum*, *A. rubrum*, *Prunus serotina*, *Ulmus alata*, and *Cercis canadensis*. Contrary to our expectation, shade-intolerant trees did not survive better with CO₂ enrichment, and population-scale responses to CO₂ were influenced by survival probabilities in low light. CO₂ enrichment did not increase rates of sample biomass accumulation for most species, but it did stimulate biomass growth of shade-tolerant taxa, particularly *Acer barbatum* and *Ulmus alata*. Our data suggest a small CO₂ fertilization effect on tree productivity, and the possibility of reduced carbon accumulation rates relative to today's forests due to changes in species composition.

Key words: Bayesian analysis; carbon dioxide (CO₂) enrichment; forest succession; global change; hierarchical Bayes.

INTRODUCTION

Understanding how successional forests respond to rising atmospheric carbon dioxide (CO₂) concentrations is critical for predicting future forest composition, diversity, and productivity. Owing to fossil fuel emissions and tropical deforestation, the current concentration of ~380 μL/L (CO₂/air) is expected to increase to 580 μL/L by the middle of this century (Prentice et al. 2001), representing the highest CO₂ level in the past 15 × 10⁶ years (Petit et al. 1999, Pearson and Palmer 2000). Concurrently, the proportion of the globe supporting successional ecosystems is increasing due to human land use and disturbance (Bazzaz 1996, Vitousek et al. 1997, Imhoff et al. 2004). Forests dominated by productive,

early successional trees are typically net carbon sinks (Goulden et al. 1996, Barford et al. 2001, Deckmyn et al. 2004, Finzi et al. 2004). Such forests exhibit maximum rates of net ecosystem productivity (NEP), representing sequestered carbon (Peet 1992, Ryan et al. 1997, 2004, Schlesinger 1997, Caspersen et al. 2000, Wardle et al. 2004). Forests of the eastern United States in particular are accumulating biomass as they recover from 19th and 20th century land clearance (Delcourt and Harris 1980, Dixon et al. 1994, Hurr et al. 2002, Foster et al. 2004), and carbon sequestration by such forests is an important component of the global carbon cycle (Ciais et al. 1995, Caspersen et al. 2000, Pacala et al. 2001, Houghton 2003, Beedlow et al. 2004, Cao et al. 2004). Although its impacts on forests are unknown, elevated CO₂ accelerated successional change toward dominance by later successional taxa in a grassland community (Polley et al. 2003). Projected feedbacks to the global carbon budget may differ if elevated CO₂ preferentially benefits early or late successional tree species, potentially impacting

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demographic patterns, probabilities of attaining canopy dominance, and future NEP levels.

The literature is equivocal regarding the relative success of successional functional groups under elevated CO₂. In glasshouse and chamber studies, high CO₂ has been observed to benefit both early (Brown and Higginbotham 1986, Hättenschwiler and Körner 1996, Hoddinott and Scott 1996) and late (Bazzaz and Miao 1993, Kubiske and Pregitzer 1996, 1997, Kinney and Lindroth 1997, Hättenschwiler and Körner 2000, Kerstiens 2001, Khurana and Singh 2004) successional forest species. Early-successional, shade-intolerant plants often have increased quantum yields and decreased light compensation points (the light level at which plants have zero net carbon assimilation and growth, and below which negative growth rates ultimately lead to death) when grown under high CO₂ conditions (Ehleringer and Björkman 1977, Chen et al. 1999), and have spread into shadier experimental microsites when given supplemental CO₂ (Hättenschwiler and Körner 1996). Early successional species are typically faster growing than late successional species (Bazzaz and Pickett 1980, Pacala et al. 1996), and species with intrinsically high growth rates under ambient CO₂ conditions often obtain greater CO₂ growth stimulation than slow-growing species (Poorter 1993, 1998, Ackerly and Bazzaz 1995). Elevated atmospheric CO₂ is a potential cause of the recent increase in growth of intrinsically fast-growing Amazonian tree species (Laurance et al. 2004).

Other studies suggest that later successional, shade-tolerant trees tend to preferentially benefit from CO₂ enrichment (Bazzaz and Miao 1993, Kubiske and Pregitzer 1996, 1997, Hättenschwiler and Körner 2000, Kerstiens 2001). Model results of Lloyd and Farquhar (1996) predict slow-growing species preferentially benefit from elevated CO₂. The overall importance of rising CO₂ for enhancing temperate forest productivity has been questioned (Caspersen et al. 2000). The potential impact of elevated CO₂ on forest regeneration and succession in the face of natural environmental variability remains unknown.

Different responses to elevated CO₂ have been observed among species within the same functional group (Bazzaz and Miao 1993, Reid and Strain 1994, Hättenschwiler and Körner 1996, 2000, Hättenschwiler 2001, Bergh et al. 2003, Polley et al. 2003, Niklaus and Körner 2004) and even among groups and individuals of the same tree species (DeLucia et al. 1994, Wayne and Bazzaz 1997, Wang et al. 2000, Mohan et al. 2004). These disparate findings may result from unrealistic resource levels and community interactions that have not been adequately reproduced in artificial experimental settings (Ackerly and Bazzaz 1995), from individualistic species responses (Hättenschwiler and Körner 2000, Belote et al. 2004), or from genetic variation within a species (Wayne and Bazzaz 1997, Wang et al. 2000, Mohan et al. 2004). Thus studies using a limited

number of trees growing under artificial conditions may be misleading. Clearly, studies are needed from intact forest understories, where CO₂ can be manipulated (Field et al. 1992, Nowak et al. 2004). Such studies must allow for the full variability in resource levels (i.e., light and CO₂) and in the populations that respond to them (Clark et al. 2003).

Here, we determine the impacts of elevated atmospheric CO₂ on the growth and survivorship of individuals and on biomass accumulation rates of temperate tree species. We initiated experiments to test how functional groups, species, and individual trees respond to elevated CO₂ in the Duke Forest free-air CO₂ enrichment (FACE) facility in North Carolina, USA. CO₂ fumigation of this intact forest provides an opportunity to examine CO₂ effects on forest understory tree dynamics and successional processes in the face of natural environmental variability, including one hurricane (which occurred before the advent of the present study), several severe winter ice storms (particularly in 2002), and a long-term drought from 1998 to 2002. Secondary succession in Duke Forest is well-documented under ambient CO₂ conditions (Oosting 1942, Keever 1950, Christensen and Peet 1981, 1984). Over 20 years in age, the experimental forest is entering the "thinning phase" during which competition for light and soil resources is intense (Christensen and Peet 1984, Peet 1992, Oren et al. 2001). Typical of forest understory environments (Canham et al. 1994, Kobe et al. 1995, Kobe and Coates 1997, Clark et al. 2003) the FACE understory is shady, with light availability in year 2000, as determined by hemispherical photography, averaging 2.8% full sunlight. Because elevated CO₂ may affect the outcome of competition for non-CO₂ resources (Bazzaz and McConnaughay 1992, Oren et al. 2001, Niklaus and Körner 2004, Nowak et al. 2004), this forest provides an ideal setting to assess potential CO₂ impacts on temperate forest successional dynamics.

METHODS

Site description and design

Forests now cover much of the southeastern United States on lands that were abandoned from agriculture early in the last century. In 1996, three ambient (~365 µL CO₂/L air) and three elevated (+200 µL/L differential, for a concentration of ~565 µL CO₂/L) plots, each 707 m² in area, were established in a 13-yr-old unmanaged loblolly pine stand at the Duke Forest FACE site, one of the few facilities to test CO₂ effects on an intact forest system (Hendrey et al. 1999). CO₂ treatments commenced September 1996. With a range extending from Delaware to Texas, *Pinus taeda* L. (loblolly pine) is one of the most common tree species in the southeastern United States, particularly on the Piedmont and Coastal Plain physiographic provinces (Martin et al. 1993). It plays a prominent role in secondary succession on abandoned land, being among the first woody species to invade (Oosting 1942, Keever

TABLE 1. The 14 tree species planted in subplots at the Duke Forest FACE experiment.

Species	Common name	Shade tolerance	No. trees per subplot	Total no. trees
<i>Acer barbatum</i>	southern sugar maple	tolerant	1	35†
<i>Acer rubrum</i>	red maple	tolerant	5	240
<i>Cercis canadensis</i>	eastern redbud	tolerant	4	192
<i>Liquidambar styraciflua</i>	sweetgum	intolerant	5	240
<i>Liriodendron tulipifera</i>	tulip poplar	intolerant	4	192
<i>Pinus schinata</i>	shortleaf pine	intolerant	3	144
<i>Pinus taeda</i>	loblolly pine	intolerant	3	144
<i>Prunus serotina</i>	black cherry	tolerant	3	144
<i>Quercus alba</i>	white oak	intermediate	3	144
<i>Quercus phellos</i>	willow oak	intolerant	3	144
<i>Quercus rubra</i>	red oak	intermediate	5	240
<i>Quercus velutina</i>	black oak	intermediate	2 or 3	109
<i>Robinia pseudoacacia</i>	black locust	intolerant	3	144
<i>Ulmus alata</i>	winged elm	tolerant	5	240

Notes: Shade tolerance classification comes from Lorimer (1983), Burns and Honkala (1990), and Harlow et al. (1991). Taxonomy follows Kartesz (1994).

† Due to a low germination rate only 35 *Acer barbatum* seedlings were planted; thus, in 13 of the 48 plots, *A. barbatum* was replaced with an individual of another species.

1950, Christensen and Peet 1981), and dense stands persist for several decades before being replaced by mixed hardwood forests (Oosting 1942, Christensen and Peet 1984). *Pinus taeda* is a major commercial species in the southeastern United States, where it dominates $\sim 11.7 \times 10^6$ hectares (Burns and Honkala 1990, Harlow et al. 1991).

The section of the Duke Forest that forms the FACE experiment was farmed a century ago, and the current plantation was established after a regenerating forest was clear cut. This forest contains a subcanopy of *Liquidambar styraciflua*, *Liriodendron tulipifera*, *Ulmus alata*, and *Acer rubrum*; these and >13 other tree species occur as seedlings and saplings in the forest (Mohan 2002). Soils are infertile Ultic Alfisols, which are widespread in the Piedmont of North Carolina (35°97' N 79°09' W).

To determine the effects of atmospheric CO₂ on understory plants during the summer of 1997 we located eight subplots (1.44 m² each) in the periphery of each of the six FACE plots (N = 48). To minimize the destructive impact of white-tailed deer (*Odocoileus virginianus*) on the understory vegetation, we surrounded the subplots with 0.9-m tall herbivore exclosures constructed from 2.54-cm wire mesh and fastened to the ground with 13-cm stainless steel ground staples (Forestry Suppliers, Jackson, Mississippi, USA). Note that during this study, mean global CO₂ rose from <360 μL/L air to ~ 380 μL/L air; but for the sake of simplicity all ambient CO₂ levels in the text and figures of this paper are denoted by 365 μL/L and elevated concentrations by 565 μL/L.

During the autumn of 1997, seeds from 14 tree species (Table 1) were obtained from several maternal trees per species and stratified at 4°C. These species typically co-occur in Piedmont forests of the southeastern United States (Martin et al. 1993). Seeds of *Prunus serotina* were scarified with sand paper and *Cercis canadensis* seeds were soaked overnight in a 10% solution of KOH. Seeds

were planted in germination trays in March 1998 and watered twice daily. They were fertilized daily for 30 days with half-strength Hoagland's fertilizer (Downs and Hellmers 1978). In April, seedlings were moved outside under filtered light conditions and planted individually into 226-cm³ "cone-tainers" (Stuewe and Sons, Corvallis, Oregon, USA) filled with Metro-Mix 200 (vermiculite, sphagnum, and perlite; The Scotts Company, Marysville, Ohio, USA), a non-nutritive planting medium. The seedlings were watered once a day with tap water and during natural precipitation events and were no longer supplied with fertilizer.

In October 1998, 49 seedlings representing the 14 tree species were planted into each of the 48 caged subplots (total number of seedlings = 2352; Table 1). For each species, subplots contained equal numbers of individuals, with the exceptions of *Acer barbatum* and *Quercus velutina* that had relatively low germination rates. Within a species, individual seedlings were randomly assigned to each subplot. Within each subplot, the location of each individual on a 7 × 7 plant grid was randomly determined. Seedlings were planted during or soon after rain events over a five-day period. To determine transplant success and initial plant size, we measured survivorship, height, and basal diameter (diameter at 5-cm height) of the seedlings two months after transplanting (December 1998) and found post-transplantation survivorship to be high (93–100% per species and CO₂ treatment). Non-planted vegetation was removed from each plot during annual weeding. Dormant season survivorship and size censuses were repeated annually through 2003.

The supplemental CO₂ source used in the elevated plots is derived from the combustion of natural gas, and contains a highly depleted δ¹³C signature of -43‰. The CO₂ concentrations in the ambient and fumigated plots are monitored down to only about 1 m from the soil surface, which was higher than the initial heights of the tree seedlings by approximately an order of magnitude.

To assess the adequacy and accuracy of the CO₂ fumigation of the understory stratum, we harvested current-year leaves of *Lonicera japonica* (Japanese honeysuckle) at ≤ 15 cm from the soil surface in each subplot in July 1997. Globally, C₃ plants are depleted in ¹³C relative to the CO₂ of the atmosphere due to photosynthetic fractionation, and have foliar $\delta^{13}\text{C}$ values around -28% (O'Leary 1988). Our ambient-plot plants exhibited a signature of -33% (Fig. 1). This depletion under Duke FACE ambient conditions exceeds the average $\delta^{13}\text{C}$ signature of C₃ plants (-28%) due to soil respiration, which releases CO₂ with a depleted $\delta^{13}\text{C}$ signature from the soil surface where these plants occurred (Andrews et al. 1999). Using the difference between the foliar $\delta^{13}\text{C}$ signatures in ambient and fumigated plots and the -8% of the ambient atmosphere in a mass-balance equation (see Appendix A for details of the equation), we calculated a CO₂ concentration of 580 $\mu\text{L/L}$ in the understory of fumigated plots. Given the low coefficients of variation of the ambient and elevated foliar $\delta^{13}\text{C}$ signatures (0.85% and 2.09%, respectively; Fig. 1), these $\delta^{13}\text{C}$ values indicate that CO₂ levels within the elevated plots were reasonably well controlled.

We used hemispherical canopy photographs obtained during uniform sky conditions (cloudy days, early morning, or late afternoon) to estimate understory light conditions at each subplot. Photos were taken in late summer during maximum canopy leaf area from a height of 1 m above each seedling plot. Images were obtained on 400-speed color slide film using a Nikon FM2 camera with a Sigma 8-mm 180° fish-eye lens and leveling tripod. Digitally scanned images were analyzed with the HemiView Canopy Analysis Software (Version 2.1, Delta-T Devices, Cambridge, UK). Photo analysis involves a user-defined threshold intensity for each photo that determines whether pixels are classified as open (sky) or obscured (canopy). The Global Site Factor (GSF) represents the proportion of full sunlight reaching the forest understory, and is used as the "light availability" term in the Bayesian analyses. The GSF combines direct and diffuse radiation but does not account for backscatter within the canopy (Rich 1989, Clark et al. 2003).

In 1998, in order to examine individual growth responses to a range of light conditions, we established four locations in the pine forest surrounding the FACE plots (two to the north and two to the south of the FACE facility) where we manually cleared 20-m diameter canopy gaps. In addition, we used a fifth 10-m diameter gap that was manually cleared in the previous year near the center of the FACE facility. In the center of each of the five gaps we positioned four 1.44-m² caged subplots along an east-west transect. In October 1998 we planted, enclosed, and monitored each subplot in the same manner as with the subplots in the FACE plots, with the exception that we had no *Acer barbatum* or *Quercus velutina* seedlings. We took

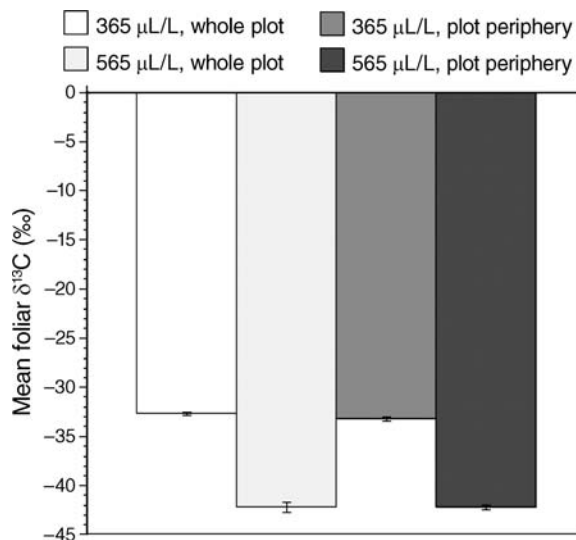


FIG. 1. Mean $\delta^{13}\text{C}$ from foliage samples of *Lonicera japonica* growing in the FACE understory. Three of the plots are maintained at ambient CO₂ concentrations (~ 365 $\mu\text{L/L}$ air), and three of the plots are maintained at elevated CO₂ concentrations (~ 565 $\mu\text{L/L}$). Within each plot, eight plants growing in the position of proposed subplots ("plot periphery") and 16 plants from random locations within each plot ("whole plot") were used to test the adequacy of the CO₂ control. Bars represent plot means ($N = 3$), and error bars denote $\pm\text{SE}$. Elevated CO₂ means (565 $\mu\text{L/L}$ air) are different from ambient CO₂ means (365 $\mu\text{L/L}$; $P < 0.004$), but there is no effect of position within each plot. The supplemental CO₂ has a $\delta^{13}\text{C}$ signature of $-43 \pm 1\%$. The depletion under ambient conditions, which exceeds the average -28% $\delta^{13}\text{C}$ signature of C₃ plants, is due to soil respiration that increases CO₂ concentrations and depletes $\delta^{13}\text{C}$ signatures at the soil surface, where these plants occurred (Andrews et al. 1999).

hemispherical photos in 1998 and 1999, but due to the inherently fast growth of these trees under the high-light conditions, we harvested all aboveground biomass from the four larger gaps in November 1999. Many of the harvested individuals produced coppice sprouts the following year, but these were not included in the present study. Individuals in the fifth smaller, darker gap had slower growth rates and were censused through autumn 2001. Data from individuals growing in the gap environments were used in the Bayesian analyses of growth vs. light and CO₂, but not in the classical growth analyses in order to focus on CO₂ effects in the forest understory.

Analysis of plant growth

The mean annual relative growth rate (RGR) of seedlings was calculated based on allometric estimates of individual plant aboveground biomass $b_{ijk,t}$ (Appendix B)

$$\text{RGR}_{ijk,t+1} = \ln b_{ijk,t+1} - \ln b_{ijk,t}$$

where b is the biomass of seedling i in subplot j of plot k in year t . Plots were then averaged to calculate the CO₂

effect on individual plant RGR ($N = 3$). For the ambient treatment

$$RGR_A = \sum_t \sum_{k \in \{A\}} \sum_j \sum_i RGR_{ijk,t}$$

where $\{A\}$ is the set of three plots subjected to the ambient treatment. A similar mean was calculated for the elevated treatment. RGR was calculated only for plants growing in the FACE plots, not on trees planted in the canopy gap environments, in order to focus on potential effects of atmospheric CO₂ for understory plant growth. We used repeated-measures multivariate analysis of variance (MANOVA) to examine CO₂ effects on mean RGR for the 12 hardwood species over the five years of growth (SAS 1990). We restricted the analyses to the first two years of growth for the pine species, because most had died by 2001 or existed in only one plot.

Our hierarchical Bayes framework allowed us to accommodate (1) the uncertainty in light available to seedlings, and (2) the random variability among seedlings within a species in how they respond to light and CO₂. The basic process model describes how plant height or biomass changes from year to year, depending on available light and atmospheric CO₂ concentration. We build on the model used by Clark et al. (2003), allowing that light availability is imprecisely known and that each plant within a given group may differ in its response (referred to as “random individual effects” within a population). The model can be viewed as a nonlinear mixed model that is hierarchical in terms of growth response to light. We allow for fixed CO₂ effects only, because each individual is subjected to only one CO₂ level, and there are only two CO₂ treatments.

Let y_{ijkt} be the annual height increment (cm/yr) or biomass increment (g/yr) of seedling i in subplot j of plot k in year t . There is a mean response μ_{ijkt} and normally distributed error ε_{ijkt}

$$y_{ijkt} = \mu_{ijkt} + \varepsilon_{ijkt}$$

The mean response is a saturating function of light availability I_{jkt}

$$\mu_{ijkt} = \mathbf{g}_{ijk} \left(\frac{I_{jkt} - I_c}{I_{jkt} + \theta} \right)$$

There is an asymptotic growth rate \mathbf{g}_{ijk} , a minimum light requirement or light compensation point for non-negative growth I_c for ambient (I_{365}) and elevated (I_{565}) CO₂ treatments, and a half-saturation constant θ that describes the light level at which growth is at half the maximum rate.

We fit models representing the four combinations of CO₂ and individual random effects, and used predictive loss (Gelfand and Ghosh 1998) as a model selection tool. The four combinations are: (A) neither CO₂ nor random individual effects, (B) random individual effects, (C) CO₂ effects, and (D) both CO₂ and random individual effects. The full model D is:

$$\begin{aligned} p[\mathbf{g}, \mathbf{I}, \mathbf{I}_{350}, \mathbf{I}_{550}, \sigma^2, \theta, \alpha, v_m | \mathbf{y}, \mathbf{I}^{(obs)}, \mathbf{c}] \\ \propto \prod_{k=1}^6 \prod_{j=1}^{m_k} \prod_{i=1}^{n_{jk}} N_{T_{ijk}}(\mathbf{y}_{ijk} | \mu_{ijk}, \sigma^2 \mathbf{I}_{T_{ijk}}) \\ \times \prod_{k=1}^6 \prod_{j=1}^m \text{Unif}(\mathbf{I}_{jk} | a_{jk}, b_{jk}) \\ \times \prod_{k=1}^6 \prod_{j=1}^{m_k} \prod_{i=1}^{n_{kj}} \text{LN}[\mathbf{g}_{ijk} | \ln(\alpha), v_m] \text{Unif}(\mathbf{I}_{350} | a_1, b_1) \\ \times \text{Unif}(\mathbf{I}_{550} | a_1, b_1) \text{Unif}(\alpha | a_\alpha, b_\alpha) \text{Unif}(\theta | a_\theta, b_\theta) \\ \times \text{IG}(\sigma^2 | a_\sigma, b_\sigma) \text{IG}(v_m | a_v, b_v) \end{aligned}$$

where $\mathbf{I}^{(obs)}$ is the observed light value from the hemispherical photo analysis and \mathbf{c} is the CO₂ concentration. For a complete description of the hierarchical Bayesian analysis, see Appendix C. For this study, we focus our attention on \mathbf{g} , the set of maximum growth rates that vary among individuals; I_c , the “light compensation point” (more precisely, the estimated light level where growth rate is zero for this model of plant growth); and θ , the light level at which growth is half of maximum. Models A and C have a single parameter \mathbf{g} for each species (because they do not contain random individual effects), and so do not include priors α and v_m . Models A and B have a single parameter value $\mathbf{I} = \mathbf{I}_{365} = \mathbf{I}_{565}$ (because CO₂ effects are not taken into account in these models). When the hierarchical model (B) and the hierarchical plus CO₂ model (D) have similar d_m values (this was the case for *Cercis* and *Pinus echinata*), we show only the parameter estimates from model D (for both of these species, models B and D had similar predictive loss, d_m , values, which were an order of magnitude less than the d_m values for models A and C).

Note that \mathbf{I}_{365} , \mathbf{I}_{565} , and θ estimates for *Pinus* species are low, in part due to the high mortality of these trees at all light levels. Pines have a disproportionately large number of observations from the first year (when they were still alive), and thus a more even distribution of light values than species that tended to die sooner at lower light levels but persisted over the six years of the study.

Survival

Effects on survival were estimated using the Cox proportional hazard model. The mortality risk for an individual in year t is the product of base hazard h_0 and covariate effects

$$h_{ijkt} = h_0 \exp(\mathbf{x}_{ijkt} \beta)$$

where h_0 is the baseline hazard, \mathbf{x}_{ijkt} is the covariate row vector of growth rate (cm/yr, used in the Bayesian analysis), light fraction I_{jt} , and CO₂ ($\log_{10}[\text{CO}_2/365]$), and β is the parameter vector.

Sample biomass

The combined effects of growth and mortality were assessed from aboveground biomass (g) of surviving

TABLE 2. Mean annual relative growth rates (RGR) of plants calculated on an individual plant basis and then averaged across plots ($N = 3$).

Species	Mean annual RGR at 365 $\mu\text{L/L}\dagger$	Mean annual RGR at 565 $\mu\text{L/L}\dagger$	Difference in mean RGR at 565 vs. 365 $\mu\text{L/L}$ (%)
<i>Acer barbatum</i>	0.5092 (0.08240)	0.5604 (0.07579)	+10.05
<i>Acer rubrum</i>	0.1513 (0.03705)	0.1772 (0.02272)	+17.14
<i>Cercis</i> sp.	0.1252 (0.1293)	0.1239 (0.1486)	-1.031
<i>Liriodendron</i> sp.	0.2525 (0.06349)	0.2322 (0.07667)	-8.062
<i>Liquidambar</i> sp.	0.2166 (0.09788)	0.2540 (0.0693)	+17.28
<i>Pinus echinata</i>	0.4210 (0.1522)	0.5351 (0.0134)	+27.13
<i>Pinus taeda</i> *	0.4376 (0.1377)	0.6351 (0.1398)	+46.75
<i>Prunus</i> sp.	0.2633 (0.1236)	0.3115 (0.1728)	+17.83
<i>Quercus alba</i> *	0.2945 (0.06996)	0.3224 (0.07369)	+9.492
<i>Q. phellos</i>	0.1162 (0.04039)	0.1525 (0.04287)	+31.19
<i>Q. rubra</i>	0.1227 (0.03752)	0.1490 (0.05117)	+21.45
<i>Q. velutina</i>	0.2307 (0.07022)	0.2388 (0.06808)	+3.516
<i>Robinia</i> sp.**	0.1879 (0.1147)	0.6200 (0.1366)	+230.0
<i>Ulmus</i> sp.*	0.1154 (0.03624)	0.1618 (0.06005)	+20.53

Notes: Terms in parentheses are standard errors. For all hardwood species the data represent means over five growing years; but due to high mortality, the analysis for *Pinus* species includes only the first two years of growth.

* $P < 0.05$; ** $P < 0.01$ for the CO₂ term in repeated-measures MANOVA.

† These columns report RGR for ambient CO₂ volume per liter of air and elevated CO₂ volume per liter of air (365 $\mu\text{L/L}$ and 565 $\mu\text{L/L}$, respectively).

sample trees, using species-specific allometric equations that relate biomass to height and basal diameter. Allometric coefficients were estimated from similarly sized plants harvested in the forest surrounding the FACE plots (Appendix B). A previous meta-analysis (Curtis and Wang 1998) and data from naturally recruited tree seedlings at this site (J. E. Mohan, unpublished data) suggest that CO₂ does not alter plant allometric relationships. "Sample biomass" B_{kt} (in grams) was defined as the aboveground biomass summed over all survivors of a species in each ambient and elevated CO₂ plot ($N = 3$), where $i =$ seedling, $j =$ subplot, $k =$ plot, and $t =$ year:

$$B_{kt} = \sum_j \sum_i b_{ijkt}.$$

We used repeated-measures multivariate analysis of variance (MANOVA) to examine sample biomass per plot over time (Sokal and Rohlf 1995). Rates of biomass accumulation were analyzed using the CO₂ \times year interaction term. We applied square-root transformation of biomass values to meet assumptions of normality and homoscedasticity (Sokal and Rohlf 1995). For species-specific repeated-measures of sample biomass, we used univariate tests of hypotheses because the number of dependent variables (six years of biomass measurements) was not less than the number of observations (six plots). In these cases, we based our interpretations on the Huynh-Feldt Epsilon correction of probabilities in ordinary F tests (Huynh and Feldt 1976, SAS 1990). Relative biomass accumulation per plot is obtained by dividing the total biomass remaining in the plot in 2003 by the initial biomass in 1998. This quotient was compared for ambient and elevated plots. We used two-sided Student's t tests to test the hypothesis

that relative accumulation was different under elevated CO₂ conditions.

RESULTS

Growth responses of individual plants to elevated atmospheric CO₂

Most trees showed little effect of CO₂ treatment on mean relative growth rate (RGR). When mean annual RGR was analyzed over the five years, individuals of only three species showed a significant response to CO₂: *Ulmus alata* (+21%), *Quercus alba* (+9.5%), and nitrogen-fixing *Robinia* (+230%; Table 2). *Pinus taeda* seedlings showed a 47% growth stimulation from elevated CO₂ during the first two years of the study, but only one seedling survived to 2002. When the effects of understory light availability and random individual plant variation are included in a hierarchical Bayesian analysis of absolute height growth, the effects of CO₂ on plant growth are small relative to variability in response within populations (Fig. 2). However, several species displayed growth benefits from elevated CO₂ (i.e., higher growth rates and decreased minimum light requirement). Among shade-intolerant taxa, *Liquidambar* and *Liriodendron* had lower light compensation points (I) for growth at elevated CO₂ (Tables 3 and 4). For *Liquidambar*, I under elevated CO₂ (I₅₆₅) was less than half that of growth under ambient CO₂ conditions (1.8% vs. 3.7% full sunlight, respectively). Beneficial effects of elevated CO₂ on the growth of *Quercus velutina*, a species of intermediate tolerance, were seen in a light compensation point at high CO₂ that was less than half of I₃₆₅ (0.22% vs. 0.47%).

Four of the five species classed as shade tolerant displayed growth benefits from elevated CO₂. *Acer barbatum* and *A. rubrum* exhibited small increases in growth, particularly at light levels less than ~30% full

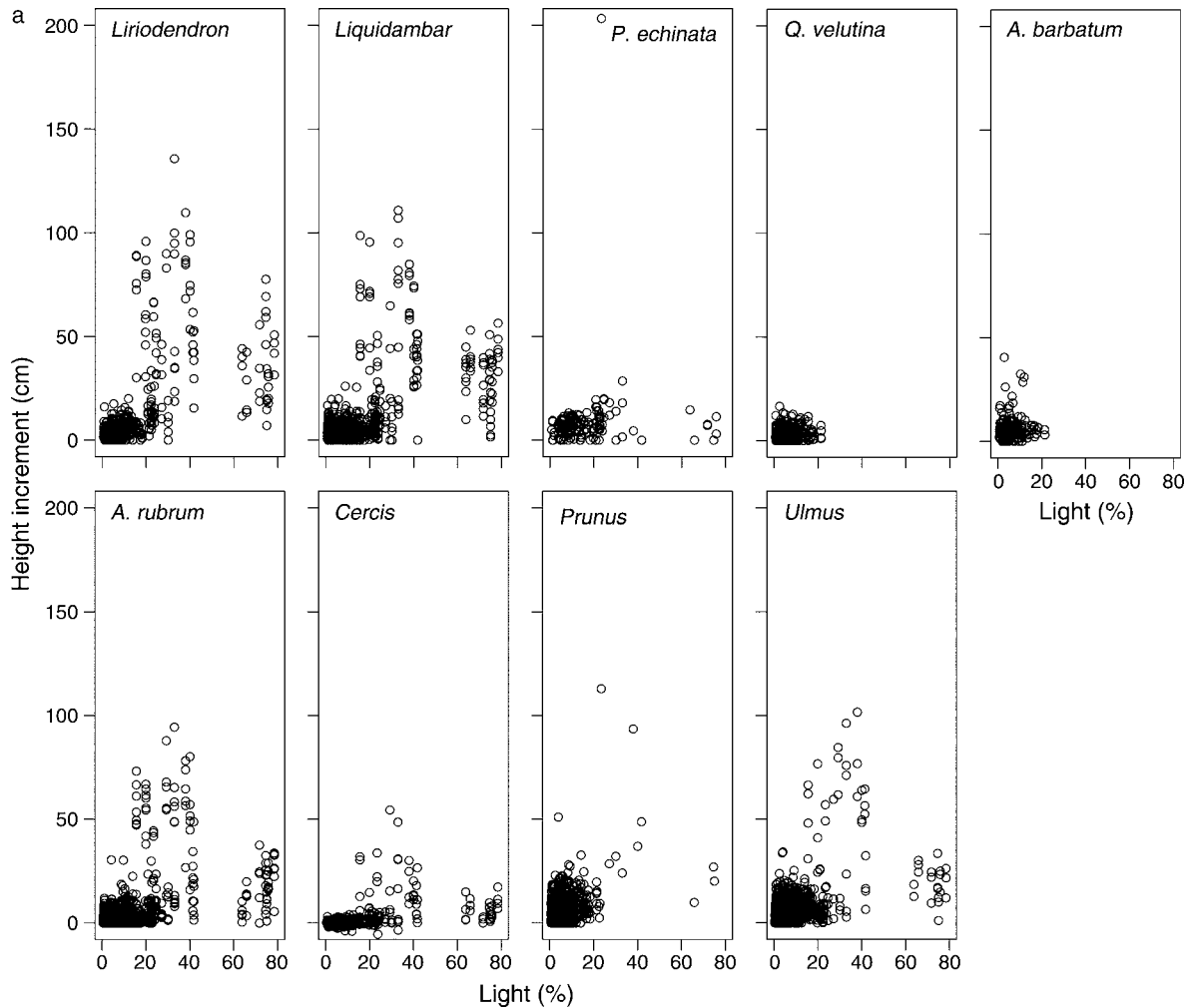


FIG. 2. Height growth increment (y -axis) vs. available light (percentage of full sunlight, x -axis) for species exhibiting individual plant growth responses to CO_2 (species that had Model C or D as the best fit in Table 3). Panel (a) depicts the growth data for individual trees and years depicted by small circles. Panel (b) shows model fits, where solid lines represent ambient CO_2 conditions and dashed lines represent elevated CO_2 . For each CO_2 treatment, there are five lines. The middle line shows the posterior median height increment. Moving outward from this central line, the next lines represent parameter uncertainty (95% credible intervals). The outermost lines include random individual effects.

sunlight (Fig. 2), and decreases in light compensation points (0.74% vs. 1.8% for *A. barbatum*, and 1.4% vs. 4.6% for *A. rubrum*; Table 3). *Prunus* had faster growth at light levels ranging from <2% to ~60% (Fig. 2), and an I_{565} that was less than half I_{365} (1.8% vs. 3.8%; Table 3). Finally, *Ulmus* grew slightly taller at elevated CO_2 under the full range of light levels (~0.10% to ~78%; Fig. 2) and had an I_{565} almost half of the I_{365} value (2.1% vs. 3.9%; Table 3). Model selections for the Bayesian analyses of aboveground plant biomass growth often did not distinguish between CO_2 levels, likely because CO_2 affected height growth of understory trees in this low light forest more than diameter growth (Table 4). When the importance of random individual variability in growth response is considered, the biggest effect of CO_2 was to reduce light compensation points of select species.

Survivorship responses to atmospheric CO_2

Overall survivorship, averaged across individuals of all species, was slightly higher under elevated CO_2 conditions (mean ambient survivorship probability in 2003 was 0.49 ± 0.01 and mean elevated survivorship probability was 0.55 ± 0.01 ; Fig. 3). Shade-intolerant taxa generally demonstrated low survivorship under both CO_2 treatments, whereas shade-tolerant trees typically had high survivorship, but the effect of CO_2 on survivorship differed by species (Fig. 4). The strongest impact of atmospheric CO_2 on survivorship probability was indirect and mediated through the CO_2 effect on growth. For most species, the growth rate in the previous year was the most important predictor of survivorship, followed by light availability (Table 5). After these factors were taken into account in a Cox

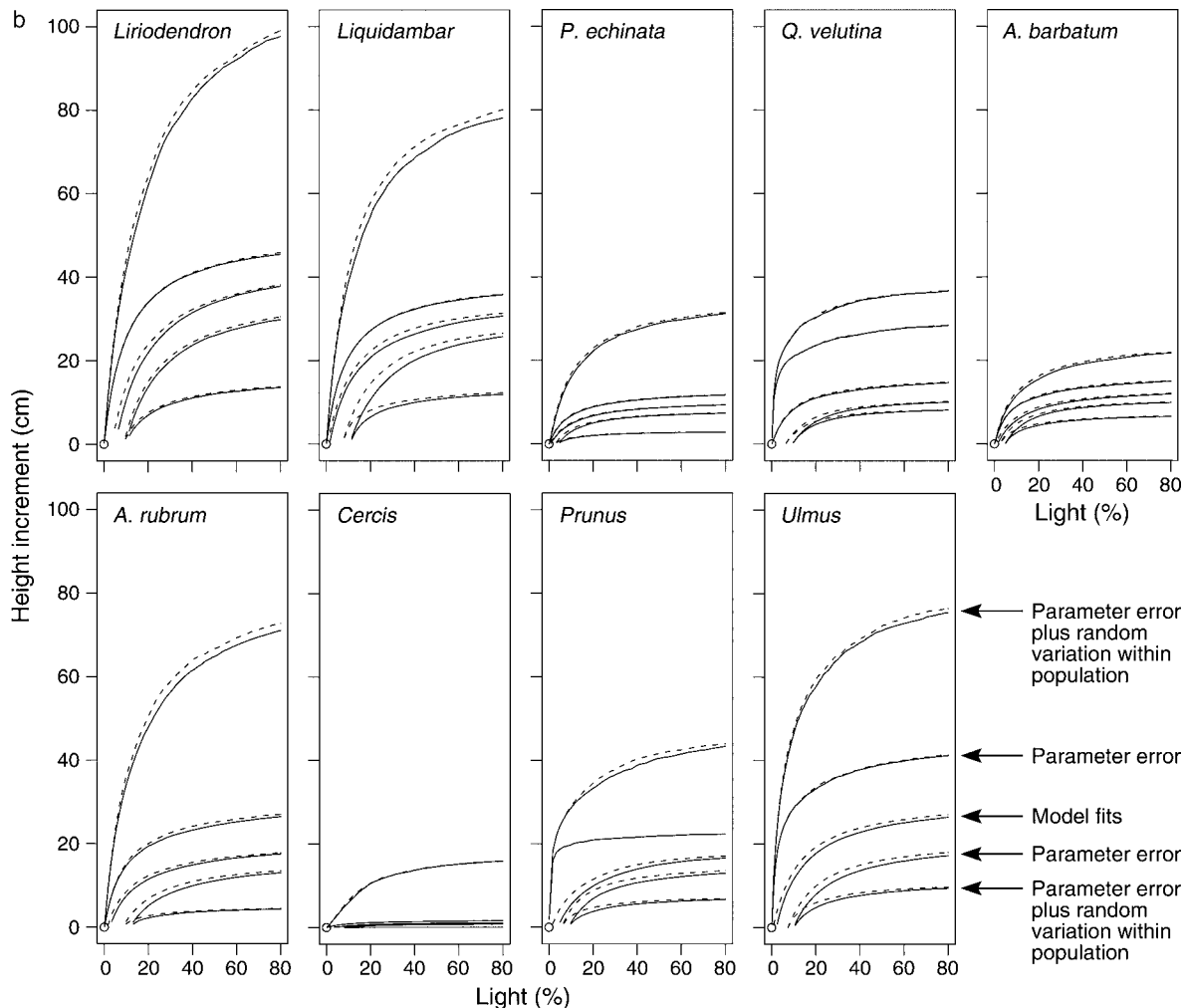


FIG. 2. Continued.

TABLE 3. Parameter estimates from the hierarchical Bayes model that best explains annual height growth increment (cm/yr) for each species.

Species	g_{max}	I_{365}	I_{565}	θ	α	v_m
<i>Acer barbatum</i> [D]	13.9 (1.86)	1.78 (1.55)	0.740 (0.782)	10.0 (2.67)	28.9 (4.92)	0.116 (0.0351)
<i>A. rubrum</i> [D]	22.0 (4.51)	4.45 (4.56)	3.06 (3.29)	10.5 (2.47)	20.30 (367)	0.688 (0.143)
<i>Cercis</i> sp. [D]	27.4 (4.71)	5.42 (4.54)	3.71 (3.38)	10.5 (1.75)	23.4 (20.9)	0.656 (0.137)
<i>Liriodendron</i> sp. [D]	45.3 (4.82)	4.78 (3.88)	4.04 (3.49)	10.5 (1.12)	32.6 (5.37)	0.340 (0.102)
<i>Liquidambar</i> sp. [D]	36.2 (2.86)	3.66 (4.09)	1.83 (2.30)	10.3 (1.16)	17.5 (4.00)	0.323 (0.0619)
<i>Pinus echinata</i> [D]	10.7 (1.51)	1.30 (1.41)	0.832 (0.972)	9.72 (2.22)	24.1 (4.74)	0.515 (0.143)
<i>P. taeda</i> [A]	14.4 (0.901)	0.479 (0.422)	...	8.4 (2.38)	48.2 (5.22)	...
<i>Prunus</i> sp. [D]	19.9 (3.02)	3.82 (3.28)	1.76 (1.91)	9.34 (4.14)	38.0 (14.6)	0.305 (0.0969)
<i>Quercus alba</i> [B]	11.0 (1.4)	7.05 (1.02)	...	8.77 (3.52)	15.8 (7.56)	0.184 (0.0428)
<i>Q. phellos</i> [A]	7.76 (0.467)	0.132 (0.105)	...	9.25 (0.943)	7.88 (0.499)	...
<i>Q. rubra</i> [B]	7.58 (0.814)	1.05 (1.31)	...	9.24 (3.18)	13.8 (4.78)	0.494 (0.0973)
<i>Q. velutina</i> [C]	9.01 (0.652)	0.466 (0.411)	0.215 (0.183)	9.67	5.62 (0.446)	...
<i>Robinia</i> sp. [B]	83.4 (10.4)	4.52 (2.02)	...	12.5 (2.87)	646 (106)	0.374 (0.160)
<i>Ulmus</i> sp. [D]	31.9 (7.31)	3.89 (3.94)	2.10 (2.59)	9.75 (3.52)	33.5 (487)	0.330 (0.102)

Notes: Values are posterior means with Bayesian standard errors in parentheses. Using predictive loss (d_m), we selected from four possible model combinations: (A) simple model containing neither CO₂ effects nor random variation between individuals, (B) hierarchical model accounting for random variation between individuals but not accounting for CO₂, (C) simple model containing CO₂ effects, and (D) hierarchical model accounting for random variation and differences between CO₂ concentrations. Designation of the best model is shown in brackets following each species name.

Explanations of parameters: θ represents the light level at which growth is half the maximum rate; α and v_m are Bayesian priors on g_{ijk} . The asymptotic growth rate (g_{ijk}) is lognormal with fixed effect α and variance (on log growth rate) v_m : $g_{ijk} \sim \text{LN}(\ln(\alpha), v_m)$.

TABLE 4. Parameter estimates from the model best explaining annual aboveground biomass growth increment (g/yr) for each species.

Species	g_{\max}	l_{365}	l_{565}	θ	α	v_m
<i>Acer barbatum</i> [B]	0.694 (0.210)	0.866% (0.875)	...	10.2% (3.07)	0.402 (0.0546)	0.877 (0.570)
<i>A. rubrum</i> [B]	1.69 (0.488)	3.01% (3.39)	...	10.5% (2.15)	0.480 (11.8)	1.31 (0.351)
<i>Cercis</i> sp. [B]	1.23 (0.356)	3.04% (2.37)	...	10.3% (1.82)	0.976 (1.06)	3.15 (0.601)
<i>Liriodendron</i> sp. [D]	3.50 (0.711)	5.65% (3.03)	4.41% (2.47)	10.6% (2.55)	1.89 (0.546)	1.53 (0.345)
<i>Liquidambar</i> sp. [D]	3.33 (0.689)	4.13% (4.31)	3.01% (3.30)	10.5% (2.20)	0.481 (2.31)	1.07 (0.256)
<i>Pinus echinata</i> [D]	0.601 (0.103)	5.43% (4.70)	3.48% (3.36)	10.2% (5.91)	8.97 (59.5)	2.05 (0.723)
<i>P. taeda</i> [B]	0.836 (0.135)	1.84% (1.37)	...	9.99% (3.16)	0.444 (0.0574)	0.482 (0.177)
<i>Prunus</i> sp. [B]	0.655 (0.224)	0.812% (0.781)	...	10.1% (2.82)	0.919 (0.0886)	1.39 (0.832)
<i>Quercus alba</i> [B]	1.44 (0.160)	0.615% (0.832)	...	9.42% (3.08)	0.664 (0.117)	0.306 (0.0748)
<i>Q. phellos</i> [A]	0.586 (0.0548)	0.331% (0.293)	...	9.39% (2.20)	0.188 (0.0114)	...
<i>Q. rubra</i> [D]	1.27 (0.168)	1.59% (1.67)	0.966% (1.09)	9.85% (3.06)	1.40 (0.150)	0.804 (0.154)
<i>Q. velutina</i> [D]	0.929 (0.143)	0.799% (0.861)	0.468% (0.511)	8.32% (3.56)	0.503 (0.0536)	0.158 (0.0978)
<i>Robinia</i> sp. [B]	19.7 (4.31)	5.47% (1.95)	...	11.5% (3.22)	143 (21.5)	1.14 (0.399)
<i>Ulmus</i> sp. [B]	1.23 (0.525)	2.45% (2.51)	...	10.5% (1.87)	0.547 (0.159)	1.40 (0.398)

Notes: Using predictive loss (d_m), we selected from four possible model combinations: (A) simple model containing neither CO₂ effects nor random variation between individuals, (B) hierarchical model accounting for random variation between individuals but not accounting for CO₂, (C) simple model containing CO₂ effects, and (D) hierarchical model accounting for random variation and differences between CO₂ concentrations. Designation of the best model is shown in brackets following each species name.

See Table 3 for explanation of parameters.

proportional hazards analysis, shade-intolerant *Liquidambar*, intermediately tolerant *Q. rubra*, and shade-tolerant *Cercis* were more likely to survive at elevated CO₂. Thus CO₂ does not appear to directly differentially benefit the survivorship of any shade tolerance group. CO₂ did not impact survivorship probabilities of the remaining species other than by affecting growth rates for the previous years, and this was particularly true for shade-tolerant taxa.

Sample biomass accumulation responses to atmospheric CO₂

Total sample biomass, which integrates plant growth rates and survivorship across members of a given species, increased over time at both ambient and elevated CO₂ conditions (Fig. 5). The rate of increase, however, was greater under high CO₂ ($P < 0.0001$ for the CO₂ ×

year interaction in a repeated-measures analysis), and elevated plots accumulated relatively more biomass by 2003 ([Biomass₂₀₀₃/Biomass₁₉₉₈] was 1.60 ± 0.05 [mean \pm SE] under ambient conditions and 2.10 ± 0.16 under elevated CO₂ conditions; $P = 0.02$). However, the rate of biomass increase and the relative amount of biomass accumulated varied among species. Most intolerant trees exhibited no effect of CO₂ on biomass accumulation (Fig. 6a). Biomass of *Pinus taeda*, a species that had very low survivorship and had completely died out of the three ambient plots by 2002, declined over time at elevated CO₂ and continued to persist in only one of the plots with elevated CO₂ by 2003. Nitrogen-fixing *Robinia pseudoacacia* had a tendency to accumulate biomass faster under elevated CO₂ ($P = 0.10$), and by 2003 had a mean biomass at high CO₂ that was eight times greater than in control plots, though the difference was not statistically significant (16 ± 8 g vs. 1.8 ± 0.7 g; $P = 0.21$). All three intermediately tolerant *Quercus* species accumulated biomass over time but none showed an overall significant effect of CO₂ on the rate of growth (Fig. 6b). After six years *Quercus rubra* had accumulated relatively more biomass when grown under high CO₂ ([Biomass₂₀₀₃/Biomass₁₉₉₈] equaled 1.52 ± 0.06 under ambient conditions and 1.87 ± 0.08 under elevated conditions; $P = 0.01$). Overall, total biomass accumulation of shade-tolerant trees showed the greatest response to CO₂ enrichment (Fig. 6c). *Acer barbatum* and *Ulmus alata* both increased sample biomass faster under elevated CO₂ ($P = 0.001$ and 0.005 , respectively; Fig. 6c) and accumulated relatively more biomass when given supplemental CO₂ (for *A. barbatum*, [Biomass₂₀₀₃/Biomass₁₉₉₈] equaled 12.2 ± 1.7 under ambient conditions and 19.9 ± 1.9 under elevated conditions [$P = 0.018$]; for *U. alata* [Biomass₂₀₀₃/Biomass₁₉₉₈] equaled 1.85 ± 0.19 under ambient conditions and 2.22 ± 0.07 under elevated conditions; $P = 0.07$).

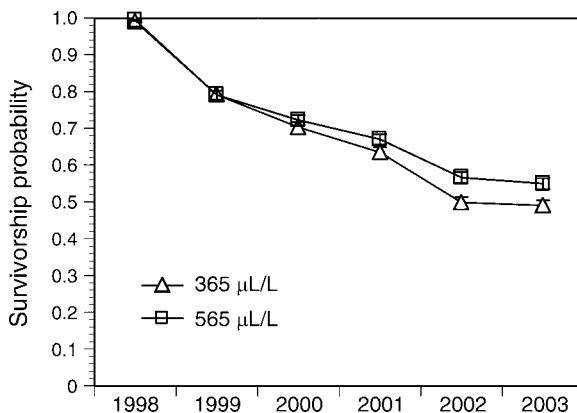


FIG. 3. Cumulative survivorship over six years averaged across individuals of all species under ambient (triangles) and elevated (squares) CO₂ treatments at FACE (canopy gap trees not included). Overall, high CO₂ plants have slightly greater survivorship. Error bars represent \pm SE.

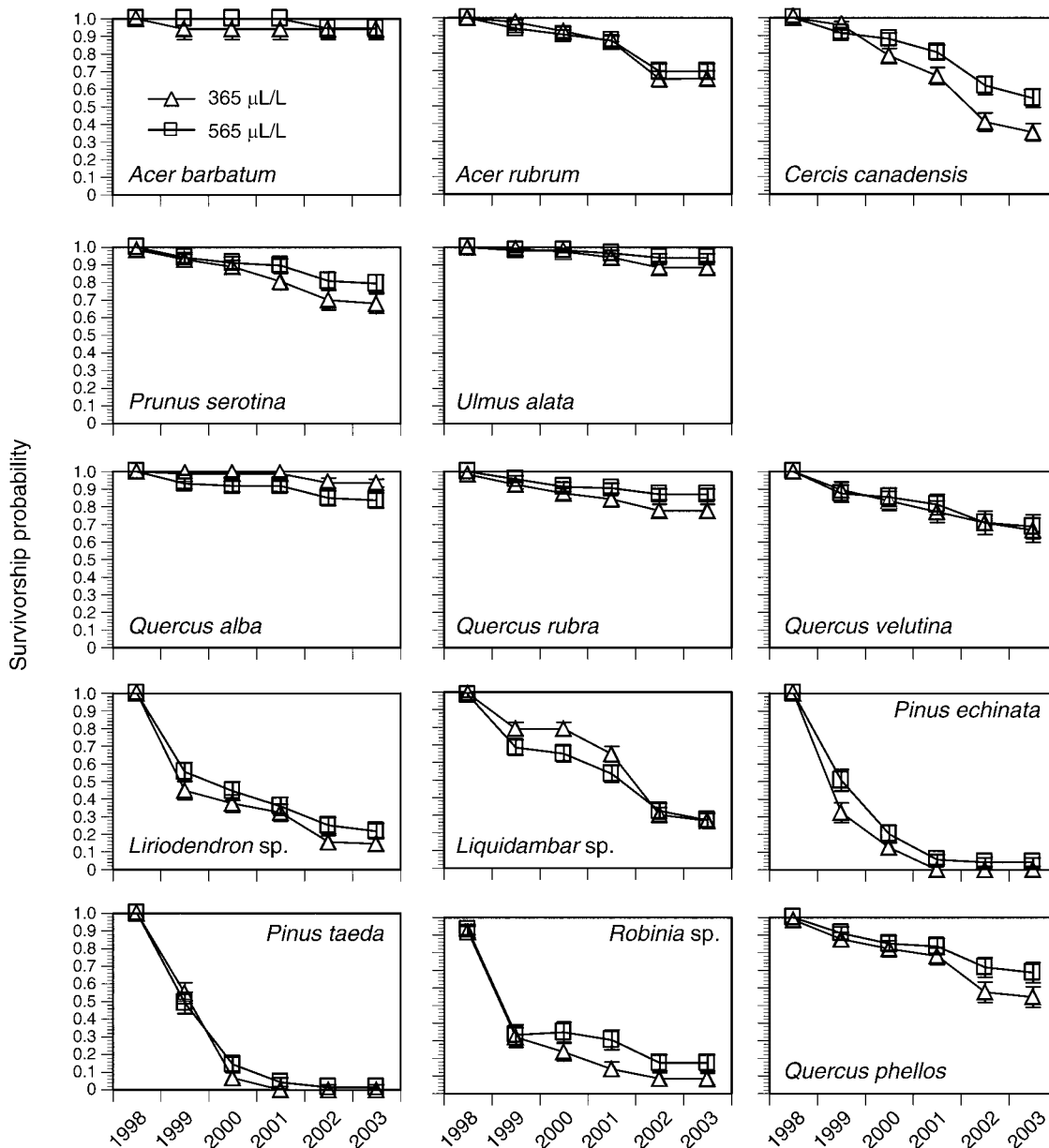


FIG. 4. Mean cumulative survivorship probabilities over six years for individual tree species growing under ambient (triangles) and elevated (squares) CO₂ treatments at FACE. Error bars represent ±SE.

DISCUSSION

This experimental analysis of forest successional response to elevated CO₂ indicates that some tree species, when given supplemental carbon, exhibit small increases in annual growth and are better able to maintain positive growth under the low light conditions typical of forest understory environments (Fig. 2, Tables 2 and 3). Such effects may accumulate over time to affect future demographic patterns of forest trees (Bazzaz 1996, Shaver et al. 2000, Nowak et al. 2004). Species-specific effects of CO₂ on the growth–light relationship may have particular relevance for future forest dynam-

ics, given that light availability explains most of the variation in the growth of temperate forest saplings (Finzi and Canham 2000). However, the effects of CO₂ enrichment on tree growth were less than reported in previous studies.

When averaged across species, trees survive better in this shady forest understory given CO₂ enrichment, but few individual taxa actually display significant effects of atmospheric CO₂ on survivorship (Fig. 4), apart from the impact of CO₂ on previous years' growth rate (Table 5; Wyckoff and Clark 2002). Six species exhibited an important indirect effect of CO₂ on survivorship

TABLE 5. Results from the Cox proportional hazards survivorship analyses.

Species	Coefficient		
	Growth	Light	CO ₂
<i>Acer barbatum</i>			
<i>A. rubrum</i>	0.412 (0.090)***		
<i>Cercis</i> sp.	0.165 (0.063)**	10.507 (3.910)**	4.611 (1.339)***
<i>Liriodendron</i> sp.	0.148 (0.042)***		
<i>Liquidambar</i> sp.	0.0933 (0.052)†	19.546 (7.173)**	9.449 (3.648)**
<i>Pinus echinata</i>		7.597 (2.980)*	
<i>P. taeda</i>		8.648 (1.620)***	
<i>Prunus</i> sp.			
<i>Quercus alba</i>			
<i>Q. phellos</i>	0.269 (0.105)*		
<i>Q. rubra</i>	0.423 (0.117)***	6.094 (3.152)†	4.774 (2.498)†
<i>Q. velutina</i>	1.300 (0.313)***	48.960 (11.100)***	
<i>Robinia</i> sp.	0.106 (0.039)**		
<i>Ulmus</i> sp.	0.226 (0.093)*		

Notes: Columns depict results of sequential term additions (growth rate in previous year, light level, and CO₂ treatment) denoting parameter estimates, with standard errors reported in parentheses. Estimates are order dependent.

† $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; cells without numbers showed no significant effect.

“indirect” referring to an effect on survivorship that is mediated through a CO₂ effect on growth) by having previous years’ growth as an important predictor of survivorship, and also exhibiting greater growth under low light conditions when exposed to supplemental CO₂. These included *Acer rubrum*, *Cercis*, *Ulmus*, *Quercus velutina*, *Liriodendron*, and *Liquidambar*. The three species with a significant direct effect of CO₂ on survivorship (i.e., *Liquidambar*, *Quercus rubra*, and *Cercis*) cross the range of shade tolerance classifications, so we see no evidence of CO₂ differentially impacting the survivorship of different successional functional groups. Further, contrary to our expectation, supplemental CO₂ did not enhance the survivorship of most of the shade-intolerant tree species, which at maturity form the most productive forest ecosystems.

When we extrapolate the results from CO₂ effects on individual plant growth and survivorship to calculate biomass accumulation rates of species, a proxy for species competitive abilities (Nowak et al. 2004), we find

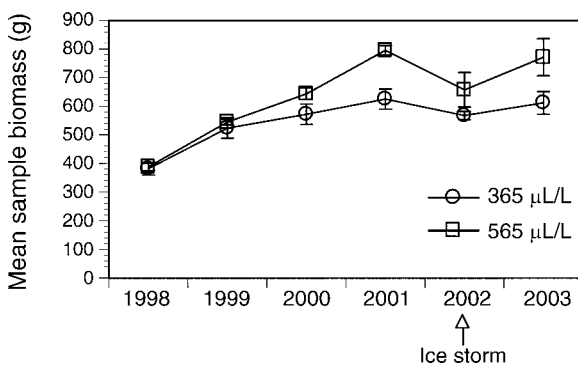


FIG. 5. Mean sample biomass (grams) over time at ambient (circles) and elevated (squares) CO₂ treatments at FACE (canopy gap trees not included; $N = 3$).

that total sample biomass accumulates faster under high CO₂ (Fig. 5). Overall, understory sample biomass was 26% larger under elevated CO₂ conditions by 2003 (771 ± 65 g [mean \pm SE] for elevated vs. 612 ± 40 g for ambient CO₂; $P = 0.10$). While understory productivity is a small component of current forest NPP (DeLucia et al. 1999), species-specific data can be used to aid forecasts of future competitive outcomes (Bolker et al. 1995, Shaver et al. 2000). Sample biomass of shade-intolerant trees is markedly unresponsive to elevated CO₂ (Fig. 6a). Although some shade-intolerant species such as *Pinus taeda* exhibit increased individual plant growth with CO₂ enrichment, this is negated by consistently low survivorship. Due to its relatively low survivorship even under elevated CO₂, it is likely that the increased sample biomass of nitrogen-fixing *Robinia* at high CO₂ is a transient response and unlikely to stimulate future forest productivity. Species of intermediate tolerance, *Quercus alba* and *Q. velutina*, do not show sample biomass responses to CO₂, although after five years *Q. rubra* accumulated relatively more sample biomass at elevated CO₂ conditions (Fig. 6b). Shade-tolerant tree species show the greatest stimulation of sample biomass from CO₂ enrichment (Fig. 6c), particularly *Acer barbatum* (southern sugar maple) and *Ulmus alata* (winged elm), subcanopy trees that are typically neither very productive nor large at maturity (Burns and Honkala 1990). The benefit of increased atmospheric CO₂ for the success of shade-tolerant tree species in a forested ecosystem supports findings of earlier work using pots and growth chambers (Bazzaz et al. 1990, Bazzaz and Miao 1993, Kubiske and Pregitzer 1996, 1997, Kinney and Lindroth 1997, Kerstiens 1998, 2001, Hättenschwiler and Körner 2000). The most responsive species in terms of sample biomass accumulation, *Acer barbatum* and *Ulmus alata*, are also two of the best survivors under ambient CO₂ conditions ($94 \pm$

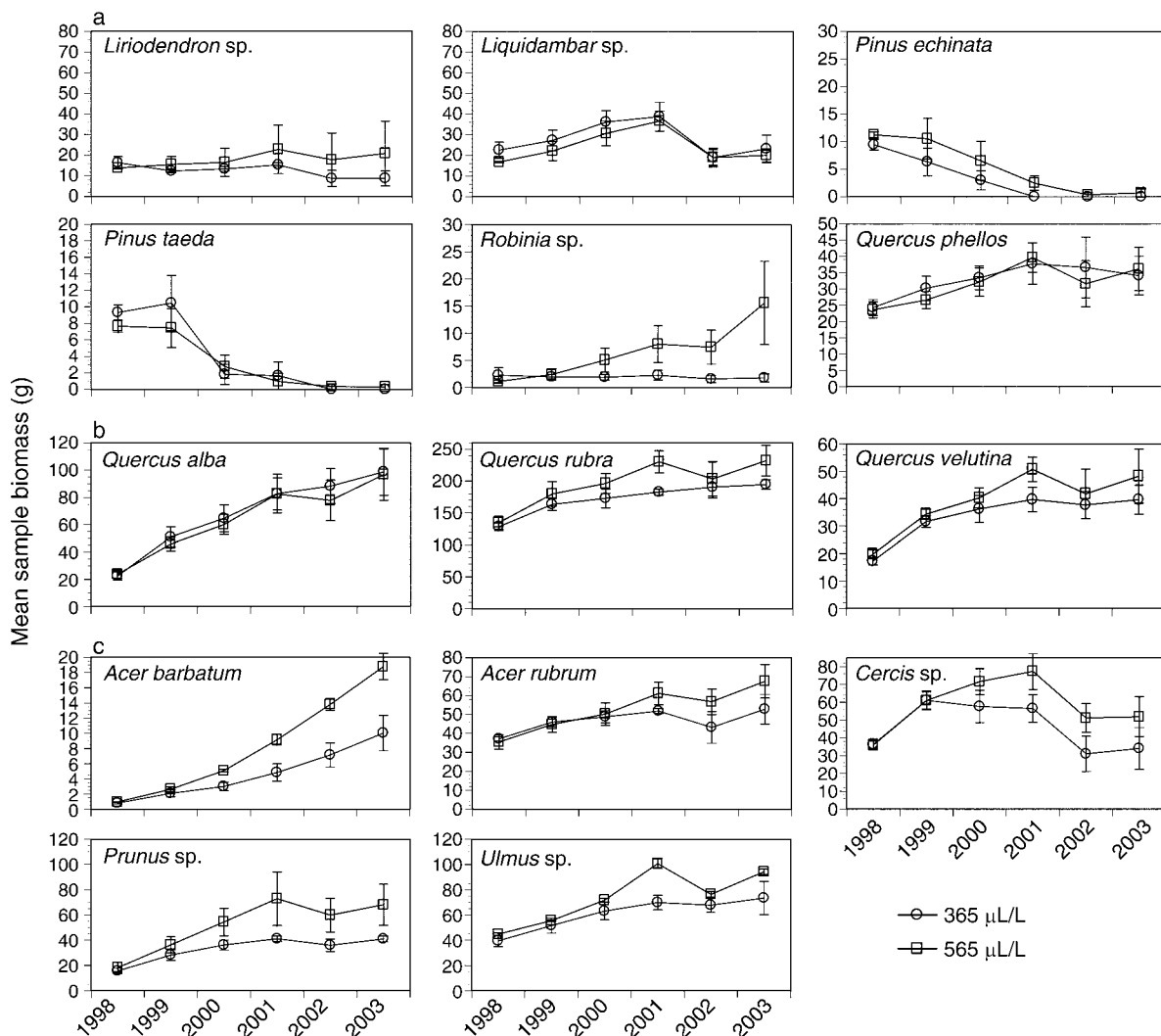


FIG. 6. Mean sample biomass over time for (a) shade-intolerant tree species, (b) intermediately tolerant tree species, and (c) shade-tolerant tree species growing at ambient (circles) and elevated (squares) CO₂ treatments at FACE (canopy gap trees not included; N = 3).

6% and 88 ± 3% surviving, respectively; Fig. 4). Although many studies examining the implications of elevated CO₂ on future community composition base conclusions solely on individual plant growth, the present study suggests that low light survivorship is an important predictor of population-scale responses to elevated CO₂.

FUTURE IMPLICATIONS

Although the relative success of juvenile trees is only one phase of forest development, individuals in the “sapling bank” typically have the greatest opportunities of attaining canopy dominance following the death of a single or several canopy trees (Pickett and White 1985). Which individuals reach the canopy is strongly influenced by juvenile growth and survival (Pacala et al. 1996, Landis and Peart 2005). Given the low survivorship of shade-intolerant tree species under both CO₂

concentrations, we have no evidence that highly productive stands dominated by such taxa will necessarily represent temperate forests of the future barring human intervention. Our data suggest that elevated CO₂ may favor recruitment of less-productive, shade-tolerant tree species, and not cause a large fertilization effect on global forest productivity. This would discount the potential for enhanced forest growth and carbon accumulation to compensate for anthropogenically derived increases in levels of atmospheric CO₂ (Idso et al. 1991, Kirschbaum 2003, Deckmyn et al. 2004). If the growth of shade-tolerant juveniles is accompanied by increased mortality of canopy trees, suggested by the faster growth (DeLucia et al. 1999) and earlier ontogenetic development (LaDeau and Clark 2001) of the *Pinus taeda* canopy at elevated CO₂ in the Duke free-air CO₂ enrichment (FACE) experiment, forest succession may accelerate. Unlike the prolonged coexistence of

early- and late-successional species observed with CO₂ enrichment of a pasture community (Potvin and Vasseur 1997), and similar to the accelerated successional change seen in a grassland ecosystem (Polley et al. 2003), we find that future competitive dynamics among temperate forest trees may be shifted toward late-successional species.

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LITERATURE CITED

- Ackerly, D. D., and F. A. Bazzaz. 1995. Plant growth and reproduction along CO₂ gradients: non-linear responses and implications for community change. *Global Change Biology* 1:199–207.
- Andrews, J. A., K. G. Harrison, R. Matamala, and W. H. Schlesinger. 1999. Separation of root respiration from total soil respiration using carbon-13 labeling during Free-Air Carbon Dioxide Enrichment (FACE). *Soil Science Society of America* 63:1429–1435.
- Barford, C. C., S. C. Wofsy, M. L. Goulden, J. W. Munger, E. H. Pyle, S. P. Urbanski, L. Hutyyra, S. R. Saleska, D. Fitzjarrald, and K. Moore. 2001. Factors controlling long- and short-term sequestration of atmospheric CO₂ in a mid-latitude forest. *Science* 294:1688–1691.
- Bazzaz, F. A. 1996. *Plants in changing environments: linking physiological, population, and community ecology*. Cambridge University Press, New York, New York, USA.
- Bazzaz, F. A., J. S. Coleman, and S. R. Morse. 1990. Growth responses of seven major co-occurring tree species of the northeastern United States to elevated CO₂. *Canadian Journal of Forest Research* 20:1479–1484.
- Bazzaz, F. A., and K. D. M. McConnaughay. 1992. Plant–plant interactions in elevated CO₂ environments. *Australian Journal of Botany* 40:547–563.
- Bazzaz, F. A., and S. L. Miao. 1993. Successional status, seed size, and responses of tree seedlings to CO₂, light, and nutrients. *Ecology* 74:104–112.
- Bazzaz, F. A., and S. T. A. Pickett. 1980. Physiological ecology of tropical succession: a comparative review. *Annual Review of Ecology and Systematics* 11:287–310.
- Beedlow, P. A., D. T. Tingey, D. L. Phillips, W. E. Hogsett, and D. M. Olszyk. 2004. Rising atmospheric CO₂ and carbon sequestration in forests. *Frontiers in Ecology and the Environment* 2:315–322.
- Belote, R. T., J. F. Weltzin, and R. J. Norby. 2004. Response of an understory plant community to elevated [CO₂] depends on differential responses of dominant invasive species and is mediated by soil water availability. *New Phytologist* 161:827–835.
- Bergh, J., M. Freeman, B. D. Sigurdsson, S. Kellomäki, K. Laitinen, S. Niinistö, H. Peltola, and S. Linder. 2003. Modeling the short-term effects of climate change on the productivity of selected tree species in Nordic countries. *Forest Ecology and Management* 183:327–340.
- Bolker, B. M., S. W. Pacala, F. A. Bazzaz, C. D. Canham, and S. A. Levin. 1995. Species diversity and ecosystem response to carbon dioxide fertilization: conclusions from a temperate forest model. *Global Change Biology* 1:373–381.
- Brown, K. R., and K. O. Higginbotham. 1986. Effects of carbon dioxide enrichment and nitrogen supply on growth of boreal trees seedlings. *Tree Physiology* 2:223–232.
- Burns, R. M., and B. H. Honkala. 1990. *Silvics of North American trees. Volume 2. Hardwoods*. U.S. Department of Agriculture, Washington, D.C., USA.
- Canham, C. D., A. C. Finzi, S. W. Pacala, and D. H. Burbank. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Resources* 24:337–349.
- Cao, M., S. D. Prince, J. Small, and S. J. Goetz. 2004. Remotely sensed interannual variations and trends in terrestrial net primary productivity 1981–2000. *Ecosystems* 7:233–242.
- Caspersen, J. P., S. W. Pacala, J. C. Jenkins, G. C. Hurtt, P. R. Moorcroft, and R. A. Birdsey. 2000. Contributions of land-use history to carbon accumulation in U.S. forests. *Science* 290:1148–1151.
- Chen, K., H. G. Hu, N. Keutgen, M. J. Janssens, and F. Lenz. 1999. Effects of NaCl salinity and CO₂ enrichment on pepino (*Solanum muricatum* Ait.): leaf photosynthetic properties and gas exchange. *Scientia Horticulturae-Amsterdam* 81:43–56.
- Christensen, N. L., and R. K. Peet. 1981. Secondary forest succession on the North Carolina piedmont. Pages 230–245 in D. C. West, H. H. Shugart, and D. B. Botkin, editors. *Forest succession: concepts and applications*. Springer-Verlag, New York, New York, USA.
- Christensen, N. L., and R. K. Peet. 1984. Convergence during secondary forest succession. *Journal of Ecology* 72:25–36.
- Ciais, P., P. P. Tans, M. Trolier, J. W. C. White, and R. J. Francey. 1995. A large northern hemisphere terrestrial CO₂ sink indicated by the ¹³C/¹²C ratio of atmospheric CO₂. *Science* 269:1098–1102.
- Clark, J. S., J. Mohan, M. Dietze, and I. Ibanez. 2003. Coexistence: how to identify trophic trade-offs. *Ecology* 84:17–31.
- Curtis, P. S., and X. Wang. 1998. A meta-analysis of elevated CO₂ effects on woody plant mass, form, and physiology. *Oecologia* 113:299–313.
- Deckmyn, G., B. Muys, J. Garcia Quijano, and R. Ceulemans. 2004. Carbon sequestration following afforestation of agricultural soils: comparing oak/beech forest to short-rotation poplar coppice combining a process and a carbon accounting model. *Global Change Biology* 10:1482–1491.
- Delcourt, H. R., and W. F. Harris. 1980. Carbon budget of the southeastern U.S. biota: analysis of historical change in trend from source to sink. *Science* 210:321–323.
- DeLucia, E. H., R. M. Callaway, and W. H. Schlesinger. 1994. Offsetting changes in biomass allocation and photosynthesis in ponderosa pine (*Pinus ponderosa*) in response to climate change. *Tree Physiology* 14:669–677.
- DeLucia, E. H., J. G. Hamilton, S. L. Naidu, R. B. Thomas, J. A. Andrews, A. Finzi, M. Lavine, R. Matamala, J. E. Mohan, G. R. Hendrey, and W. H. Schlesinger. 1999. Net carbon storage in an intact forest under experimental CO₂ enrichment. *Science* 284:1177–1179.
- Dixon, R. K., S. Brown, R. A. Houghton, A. M. Solomon, M. C. Trexler, and J. Wisniewski. 1994. Carbon pools and flux in global forest ecosystems. *Science* 263:185–190.
- Downs, R. J., and H. Hellmers. 1978. *Controlled climate and plant research*. World Meteorological Organization Technical Note Number 148. Academic Press, Geneva, Switzerland.
- Ehleringer, J., and O. Björkman. 1977. Quantum yields for CO₂ uptake in C₃ and C₄ plants. *Plant Physiology* 59:86–90.

- Field, C. B., F. S. Chapin, III, P. A. Matson, and H. A. Mooney. 1992. Responses of terrestrial ecosystems to the changing atmosphere: a resource-based approach. *Annual Review of Ecology and Systematics* 23:201–235.
- Finzi, A. C., and C. D. Canham. 2000. Sapling growth in response to light and nitrogen availability in a southern New England forest. *Forest Ecology and Management* 131:153–165.
- Finzi, A. C., E. H. DeLucia, and W. H. Schlesinger. 2004. Canopy N and P dynamics of a southeastern U.S. pine forest under elevated CO₂. *Biogeochemistry* 69:363–378.
- Foster, D. R., G. Motzkin, J. O'Keefe, E. Boose, D. Orwig, J. Fuller, and B. Hall. 2004. The environmental and human history of New England. Pages 43–100 in D. Foster and J. Aber, editors. *Forests in time: the environmental consequences of 1,000 years of change in New England*. Yale University Press, New Haven, Connecticut, USA.
- Gelfand, A. E., and S. K. Ghosh. 1998. Model choice: a minimum posterior predictive loss approach. *Biometrika* 85:1–11.
- Goulden, M. L., J. W. Munger, S. Fan, B. C. Daube, and S. C. Wofsy. 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. *Science* 271:1576–1578.
- Harlow, W. M., E. S. Harrar, J. W. Hardin, and F. M. White. 1991. *Textbook of dendrology*. Seventh edition. McGraw-Hill, New York, New York, USA.
- Hättenschwiler, S. 2001. Tree seedling growth in natural deep shade: functional traits related to interspecific variation in response to elevated CO₂. *Oecologia* 129:31–42.
- Hättenschwiler, S., and C. Körner. 1996. Effects of elevated CO₂ and increased nitrogen deposition on photosynthesis and growth of understory plants in spruce model ecosystems. *Oecologia* 106:172–180.
- Hättenschwiler, S., and C. Körner. 2000. Tree seedlings responses to in situ CO₂-enrichment differ among species and depend on understory light availability. *Global Change Biology* 6:213–226.
- Hendrey, G. R., D. S. Ellsworth, K. F. Lewin, and J. Nagy. 1999. A free-air CO₂ enrichment system for exposing tall forest vegetation to elevated atmospheric CO₂. *Global Change Biology* 5:293–309.
- Hodinnott, J., and R. Scott. 1996. The influence of light quality and carbon dioxide enrichment in the growth and physiology of seedlings of three conifer species. I. Growth responses. *Canadian Journal of Botany* 74:383–390.
- Houghton, R. A. 2003. Why are estimates of the terrestrial carbon balance so different? *Global Change Biology* 9:500–509.
- Hurr, G. C., S. W. Pacala, P. R. Moorecroft, J. Caspersen, E. Shevliakova, R. A. Houghton, and B. Moore III. 2002. Projecting the future of the U.S. carbon sink. *Proceedings of the National Academy of Sciences (USA)* 99:1389–1394.
- Huynh, H., and L. S. Feldt. 1976. Estimation of the box correction for degrees of freedom from sample data in the randomized block and split plot designs. *Journal of Educational Statistics* 1:69–82.
- Idso, S. B., B. A. Kimball, and S. G. Allen. 1991. CO₂ enrichment of sour orange trees: two and a half years into a long-term experiment. *Plant, Cell and Environment* 14:351–353.
- Imhoff, M. L., L. Bounoua, T. H. Ricketts, C. Loucks, R. Harriss, and W. T. Lawrence. 2004. Global patterns in human consumption of net primary production. *Nature* 429:870–873.
- Kartesz, J. T. 1994. *A synonymized checklist of the vascular flora of the United States, Canada, and Greenland*. Timber Press, Portland, Oregon, USA.
- Keever, C. 1950. Causes of succession on old fields of the piedmont, North Carolina. *Ecological Monographs* 20:231–250.
- Kerstiens, G. 1998. Shade-tolerance as a predictor of responses to elevated CO₂ in trees. *Physiologia Plantarum* 102:472–480.
- Kerstiens, G. 2001. Meta-analysis of the interaction between shade-tolerance, light environment and growth response of woody species to elevated CO₂. *Acta Oecologia* 22:61–69.
- Khurana, E., and J. S. Singh. 2004. Response of five dry tropical tree seedlings to elevated CO₂: impact of seed size and successional status. *New Forests* 27:139–157.
- Kinney, K. K., and R. L. Lindroth. 1997. Responses of three deciduous tree species to atmospheric CO₂ and soil NO₃⁻ availability. *Canadian Journal of Forest Resources* 27:1–10.
- Kirschbaum, M. 2003. Can trees buy time? An assessment of the role of vegetation sinks as part of the global carbon cycle. *Climatic Change* 58:47–71.
- Kobe, R. K., and K. D. Coates. 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. *Canadian Journal of Forest Resources* 27:227–236.
- Kobe, R. K., S. W. Pacala, J. A. Silander, Jr., and C. D. Canham. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications* 5:517–532.
- Kubiske, M. E., and K. S. Pregitzer. 1996. Effects of elevated CO₂ and light availability on the photosynthetic light response of trees of contrasting shade tolerance. *Tree Physiology* 16:351–358.
- Kubiske, M. E., and K. S. Pregitzer. 1997. Ecophysiological responses to simulated canopy gaps of two tree species of contrasting shade tolerance in elevated CO₂. *Functional Ecology* 11:24–32.
- LaDeau, S. L., and J. S. Clark. 2001. Rising CO₂ levels and the fecundity of forest trees. *Science* 292:95–98.
- Landis, R. M., and D. R. Peart. 2005. Early performance predicts canopy attainment across life histories in subalpine forest trees. *Ecology* 86:63–72.
- Laurance, W. F., A. A. Oliveira, S. G. Laurance, R. Condit, H. E. M. Nascimento, A. C. Sanchez-Thorin, T. E. Lovejoy, A. Andrade, S. D'Angelo, and C. Dick. 2004. Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature* 428:171–175.
- Lloyd, J., and G. D. Farquhar. 1996. Responses to elevated atmospheric CO₂ concentrations and their interaction with soil nutrient status. I. General principles and forest ecosystems. *Functional Ecology* 10:4–32.
- Lorimer, C. G. 1983. A test of the accuracy of shade-tolerance classifications based on physiognomic and reproductive traits. *Canadian Journal of Botany* 61:1595–1598.
- Martin, W. H., S. G. Boyce, and A. C. Echternacht. 1993. *Biodiversity of the southeastern United States: upland terrestrial communities*. John Wiley and Sons, New York, New York, USA.
- Mohan, J. E. 2002. *Atmospheric carbon dioxide effects on temperate forests: implications for plant evolution, forest succession, and nutrient turnover*. Dissertation. Department of Biology, Duke University, Durham, North Carolina, USA.
- Mohan, J. E., J. S. Clark, and W. H. Schlesinger. 2004. Genetic variation in germination, growth and survivorship of red maple in response to subambient through elevated atmospheric CO₂. *Global Change Biology* 10:233–247.
- Niklaus, P. A., and Ch. Körner. 2004. Synthesis of a six-year study of calcareous grassland responses to in situ CO₂ enrichment. *Ecological Monographs* 74:491–511.
- Nowak, R. S., D. S. Ellsworth, and S. D. Smith. 2004. Functional responses of plants to elevated atmospheric CO₂ – do photosynthetic and productivity data from FACE experiments support early predictions? *New Phytologist* 162:253–280.
- O'Leary, M. H. 1988. Carbon isotopes in photosynthesis. *BioScience* 38:328–336.
- Oosting, H. J. 1942. *An ecological analysis of the plant communities of Piedmont, North Carolina*. *American Midland Naturalist* 28:1–126.

- Oren, R., D. S. Ellsworth, K. H. Johnsen, N. Phillips, B. E. Ewers, C. Maier, K. V. R. Schafer, H. McCarthy, G. Hendrey, S. G. McNulty, and G. G. Katul. 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere. *Science* 411:469–472.
- Pacala, S. W., C. D. Canham, J. Soaponara, J. A. Silander, Jr., R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs* 66:1–43.
- Pacala, S. W., et al. 2001. Consistent land- and atmosphere-based U.S. carbon sink estimates. *Science* 292:2316–2320.
- Pearson, P. N., and M. R. Palmer. 2000. Atmospheric carbon dioxide concentrations over the past 60 million years. *Nature* 406:695–699.
- Peet, R. K. 1992. Community structure and ecosystem function. Pages 103–151 in D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. *Plant succession: theory and prediction*. Chapman and Hall, London, UK.
- Petit, J. R., et al. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* 399:429–438.
- Pickett, S. T. A., and P. S. White. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, New York, USA.
- Polley, H. W., H. B. Johnson, and J. D. Derner. 2003. Increasing CO₂ from subambient to superambient concentrations alters species composition and increases above-ground biomass in a C₃/C₄ grassland. *New Phytologist* 160: 319–327.
- Poorter, H. 1993. Interspecific variation in the growth responses of plants to an elevated ambient CO₂ concentration. *Vegetatio* 104/105:77–97.
- Poorter, H. 1998. Do slow-growing species and nutrient-stressed plants respond relatively strongly to elevated CO₂? *Global Change Biology* 4:693–697.
- Potvin, C., and L. Vasseur. 1997. Long-term CO₂ enrichment of a pasture community: species richness, dominance, and succession. *Ecology* 78:666–677.
- Prentice, I. C., G. D. Farquhar, M. J. R. Fasham, M. L. Goulden, M. Heimann, V. J. Jaramillo, H. S. Khashgi, C. LeQuéré, R. J. Scholes, and D. W. R. Wallace. 2001. The carbon cycle and atmospheric carbon dioxide. Pages 204–237 in J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, and C. A. Johnson, editors. *Climate change 2001: the scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Reid, C. D., and B. R. Strain. 1994. Effects of CO₂ enrichment on whole-plant carbon budget of seedlings of *Fagus grandifolia* and *Acer saccharum* in low irradiance. *Oecologia* 98:31–39.
- Rich, P. M. 1989. *A manual for analysis of hemispherical canopy photography*. Publication LA-11733-M. Los Alamos National Laboratory, Los Alamos, New Mexico, USA.
- Ryan, M. G., D. Binkley, and J. H. Fownes. 1997. Age-related decline in forest productivity: pattern and process. *Advances in Ecological Research* 27:214–262.
- Ryan, M. G., D. Binkley, J. H. Fownes, C. P. Giardina, and R. S. Senock. 2004. An experimental test of the causes of forest growth decline with stand age. *Ecological Monographs* 74:393–414.
- SAS. 1990. *User's Guide: statistics*. Version 6. Fourth edition. SAS Institute, Cary, North Carolina, USA.
- Schlesinger, W. H. 1997. *Biogeochemistry: an analysis of global change*. Second edition. Academic press, San Diego, California, USA.
- Shaver, G. R., J. Canadell, F. S. Chapin, III, J. Gurevitch, J. Harte, G. Henry, P. Ineson, S. Jonasson, J. Melillo, L. Pitelka, and L. Rustad. 2000. Global warming and terrestrial ecosystems: a conceptual framework for analysis. *BioScience* 50:871–882.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*. W. H. Freeman, New York, New York, USA.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of earth's ecosystems. *Science* 277:494–499.
- Wang, X., P. S. Curtis, K. S. Pregitzer, and D. R. Zak. 2000. Genotypic variation in physiological and growth responses of *Populus tremuloides* to elevated atmospheric CO₂ concentrations. *Tree Physiology* 20:1019–1028.
- Wardle, D. A., L. R. Walker, and R. D. Bardett. 2004. Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science* 305:509–513.
- Wayne, P. M., and F. A. Bazzaz. 1997. Light acquisition and growth by competing individuals in CO₂ enriched atmospheres: consequences for size structure in regenerating birch stands. *Journal of Ecology* 85:29–42.
- Wyckoff, P. H., and J. S. Clark. 2002. The relationship between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. *Journal of Ecology* 90: 604–615.

APPENDIX A

Mass balance equation calculating the CO₂ concentration in the understory of elevated plots at the Duke Forest FACE experiment (*Ecological Archives* A017-044-A1).

APPENDIX B

Allometric equations developed for species of the FACE site for aboveground biomass (*Ecological Archives* A017-044-A2).

APPENDIX C

Hierarchical Bayesian analysis of plant growth at variable light levels at ambient and elevated atmospheric CO₂ at the Duke University FACE experiment (*Ecological Archives* A017-044-A3).