

Growth responses of seven major co-occurring tree species of the northeastern United States to elevated CO₂

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We examined how elevated CO₂ affected the growth of seven co-occurring tree species: American beech (*Fagus grandifolia* Ehrh.), paper birch (*Betula papyrifera* Marsh.), black cherry (*Prunus serotina* Ehrh.), white pine (*Pinus strobus* L.), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and eastern hemlock (*Tsuga canadensis* (L.) Carr). We also tested whether the degree of shade tolerance of species and the age of seedlings affected plant responses to enhanced CO₂ levels. Seedlings that were at least 1 year old, for all species except beech, were removed while dormant from Harvard Forest, Petersham, Massachusetts. Seeds of red maple and paper birch were obtained from parent trees at Harvard Forest, and seeds of American beech were obtained from a population of beeches in Nova Scotia. Seedlings and transplants were grown in one of four plant growth chambers for 60 d (beech, paper birch, red maple, black cherry) or 100 d (white pine, hemlock, sugar maple) under CO₂ levels of 400 or 700 $\mu\text{L} \cdot \text{L}^{-1}$. Plants were then harvested for biomass and growth determinations. The results showed that the biomass of beech, paper birch, black cherry, sugar maple, and hemlock significantly increased in elevated CO₂, but the biomass of red maple and white pine only marginally increased in these conditions. Furthermore, there were large differences in the magnitude of growth enhancement by increased levels of CO₂ between species, so it seems reasonable to predict that one consequence of rising levels of CO₂ may be to increase the competitive ability of some species relative to others. Additionally, the three species exhibiting the largest increase in growth with increased CO₂ concentrations were the shade-tolerant species (i.e., beech, sugar maple, and hemlock). Thus, elevated CO₂ levels may enhance the growth of relatively shade-tolerant forest trees to a greater extent than growth of shade-intolerant trees, at least under the light and nutrient conditions of this experiment. We found no evidence to suggest that the age of tree seedlings greatly affected their response to elevated CO₂ concentrations.

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Nous avons étudié l'effet d'un enrichissement en CO₂ sur la croissance de sept espèces d'arbre qui sont associées : le hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.), le bouleau à papier (*Betula papyrifera* Marsh.), le cerisier tardif (*Prunus serotina* Ehrh.), le pin blanc (*Pinus strobus* L.), l'érable rouge (*Acer rubrum* L.), l'érable à sucre (*Acer saccharum* Marsh.) et la pruche de l'Est (*Tsuga canadensis* (L.) Carr.). Nous avons également vérifié si le degré de tolérance à l'ombre d'une espèce et l'âge des semis influençaient la réponse des plants à divers niveaux d'enrichissement en CO₂. Des semis d'au moins 1 an, de toutes les espèces à l'exception du hêtre, furent prélevés en période de dormance dans la forêt de Harvard, à Petersham au Massachusetts. Des graines d'érable rouge et de bouleau à papier furent récoltées sur des arbres dans la forêt de Harvard et des graines de hêtre à grandes feuilles provenant d'un peuplement de hêtre de la Nouvelle-Écosse furent obtenues. Les semis et les plants furent placés dans une des quatre chambres de croissance pour 60 jours, dans le cas du hêtre, du bouleau à papier, de l'érable rouge et du cerisier tardif, et 100 jours, dans le cas du pin blanc, de la pruche et de l'érable à sucre, à des concentrations de CO₂ de 400 ou 700 $\mu\text{L} \cdot \text{L}^{-1}$. Les plants ont ensuite été récoltés pour effectuer les mesures de biomasse et de croissance. Les résultats ont montré que la biomasse du hêtre, du bouleau à papier, du cerisier tardif, de l'érable à sucre et de la pruche était significativement plus élevée dans une atmosphère enrichie en CO₂, alors que la biomasse de l'érable rouge et du pin blanc n'était que légèrement plus élevée dans les mêmes conditions. De plus, les concentrations de CO₂ plus élevées ont causé des augmentations de croissance très différentes selon l'espèce, de telle sorte qu'il semble approprié de prédire qu'une des conséquences de l'augmentation du niveau de CO₂ serait d'augmenter la compétitivité de certaines espèces par rapport à d'autres. En outre, les espèces d'arbre qui ont subi la plus forte augmentation de croissance à cause des concentrations en CO₂ élevées étaient les essences d'ombre comme le hêtre, l'érable à sucre et la pruche. Par conséquent, une augmentation du niveau de CO₂ pourrait favoriser davantage la croissance des essences relativement tolérantes que celle des essences intolérantes, au moins dans les conditions de lumière et de nutrition de cette expérience. Finalement, nous n'avons obtenu aucun résultat suggérant que l'âge des semis influence de façon importante leur réponse à des concentrations plus élevées de CO₂.

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Introduction

Strong evidence from a large number of sources shows that the concentration of atmospheric CO₂ is steadily rising (e.g., Keeling 1986; Bolin et al. 1986). Presently, the con-

centration of atmospheric CO₂ is approximately 350 $\mu\text{L} \cdot \text{L}^{-1}$, and it is predicted to reach 700 $\mu\text{L} \cdot \text{L}^{-1}$ by the mid 21st century (see Conway et al. 1988). There is a consensus among scientists that these rising levels of CO₂ will have substantial direct and indirect effects on the biosphere (National Academy of Science 1988).

An area of particular concern is the effect of rising levels of atmospheric CO₂ on the structure and productivity of

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forest ecosystems. Although evidence suggests that many trees exhibit an initial stimulation in productivity as a result of exposure to CO₂ (reviewed in Sionit and Kramer 1986, Kramer and Sionit 1987, and Eamus and Jarvis 1989), it is unclear to what extent, if any, that stimulation of tree productivity can be sustained through time. One reason for this uncertainty is that different tree species can differ in the magnitude of their growth response to elevated CO₂ levels (Carlson and Bazzaz 1980; Tolley and Strain 1985). This could result in substantial changes in the structure of forest communities (see Bazzaz et al. 1985; Williams et al. 1986; Reekie and Bazzaz 1989), which, in turn, might lead to changes in ecosystem productivity. For example, Williams et al. (1986), using two deciduous tree assemblages, found that elevated levels of CO₂ did not affect the total community biomass after one growing season, but did cause substantial changes in the relative proportion of biomass that each species represented within the community. Reekie and Bazzaz (1989) observed similar patterns using an assemblage of tree seedlings from a wet tropical rain forest. Since individual species can play extremely important roles in ecosystem functioning (e.g., Vitousek et al. 1987; Vitousek and Walker 1989) and because management of forests for wood products is usually directed towards promoting the growth of only a small subset of species from any forest community (e.g., Smith 1980), a change in the relative abilities of species to grow in a forest community can have far-reaching consequences. Moreover, computer models predicting the effect of changes in both global climate and CO₂ levels on North American forests suggest that substantial changes in the species composition and productivity of these ecosystems may occur (e.g., Solomon et al. 1984; Pastor and Post 1988).

We report the responses of seven co-occurring tree species (American beech (*Fagus grandifolia* Ehrh.), paper birch (*Betula papyrifera* Marsh.), black cherry (*Prunus serotina* Ehrh.), eastern white pine (*Pinus strobus* L.), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and eastern hemlock (*Tsuga canadensis* L.) to elevated levels of CO₂. These species co-occur in forests of the north-eastern United States and span the spectrum of shade tolerance. Paper birch, black cherry, and white pine are classified as relatively shade intolerant because they usually become established in relatively large canopy gaps caused by a large-scale disturbance event, whereas beech, hemlock, and sugar maple are classified as relatively shade tolerant because they endure prolonged overstory suppression and still grow quickly after a small-scale canopy opening occurs (Fowells 1965; Bormann and Likens 1979; Spurr and Barnes 1980). Consequently, we also examined whether the degree of shade tolerance of these species was related to the magnitude or direction of their response to elevated CO₂ levels. Finally, using red maple and paper birch, we examined whether newly germinated seedlings responded differently to enriched CO₂ atmospheres than seedlings greater than 1 year old in order to understand better the role of tree ontogeny in mediating plant responses to elevated CO₂ concentrations.

Materials and methods

Plant material and growth conditions

Forest transplants

Approximately 70 seedlings per species of paper birch, black cherry, white pine, red maple, sugar maple, and eastern hemlock

that had survived at least one dormant season were removed from sites at Harvard Forest, Petersham, Massachusetts, prior to bud break, on a single day in March 1989. Sugar maples were obtained from the understory of a mixed hardwood stand composed of an overstory of sugar maple, white ash (*Fraxinus americana* L.), black cherry, and red oak (*Quercus rubra* L.). Black cherry seedlings were obtained on the edge of this stand. Paper birch seedlings were obtained in a mixed hardwood – pine stand that experienced a shelterwood cut in 1982. White pine seedlings were obtained from a relatively older pine stand interspersed with many different hardwood species. Eastern hemlock seedlings that had germinated and became established in decaying logs were obtained from an adjacent stand dominated by eastern hemlock. Red maple seedlings were obtained from the understory of red pine (*Pinus resinosa* Ait.) stand. The seedlings of all species were brought back to Cambridge, Massachusetts and immediately transplanted into 1-L pots (red maple, sugar maple, black cherry, paper birch) or 2-L plots (white pine, hemlock) in a 1:1:1 mixture of sand–perlite–peat with 2.4 g of Osmocote slow-release fertilizer (15:15:15 N–P–K) and placed in a glasshouse at 20°C with natural photoperiod.

After transplants had sprouted, all individuals from each species were measured for plant height and diameter and assigned to one of six groups. Assignments were made such that each group contained approximately the same range and variation in plant heights and diameters for a given species. Two groups were harvested immediately to attain an estimate of the initial biomass for each species and certify that our assignments had produced groups with similar variation in plant size.

Each of the other four groups was assigned to one of four plant growth chambers (Environmental Growth Chambers Inc., Chagrin Falls, Oh) and to one of two CO₂ treatments (400 or 700 $\mu\text{L} \cdot \text{L}^{-1}$). Each CO₂ treatment had two replicate blocks. The high CO₂ treatment represented the predicted values for atmospheric CO₂ concentrations 50 years hence. The low value represents ambient CO₂ conditions expected during the present decade. A 14-h photoperiod was used to represent midsummer conditions; light:dark temperatures were 27:25°C, relative humidity was $70 \pm 2\%$ (± 1 SE), and light levels at the top of the plant canopy were maintained at approximately $520 \pm 30 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (± 1 SE). The light:dark temperatures do not accurately reflect an average diurnal temperature span at Harvard Forest during July and August, but these temperatures frequently occur at this site during these months in both the understory and canopy gaps (Sipe 1990). The light regime of $520 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ for 14 h is equivalent to the average daily photon flux received by plants on the northeast side of large canopy gaps (75 m²) at Harvard Forest. However, peak light intensities are at least twice this level in both large and small (25 m²) canopy gaps, whereas peak light intensities in the understory of a hardwood stand are approximately this level (Sipe 1990). Plants from each block in each CO₂ treatment were rotated together between chambers every week to avoid problems associated with differences in environmental chambers.

First-year seedlings

Seeds of American beech were not obtainable at Harvard Forest because of a particularly poor seed crop in 1988, and the distribution of seedlings in the forest was too spotty to allow us to attain 50 or more seedlings in a given location. Consequently, we attained viable beech seeds from Nova Scotia collected by the USDA Forest Service during the fall of 1988 and then stratified in sand under cold storage at 4°C (Dr. David Houston, USDA Forest Service, Hamden, CT). Germinating seeds were brought to Cambridge, Massachusetts, on April 30, 1989, planted into 1-L pots in the soil mix described earlier, and placed into a glasshouse at 20°C with natural photoperiod and light. After seeds germinated, plants were sorted into four groups, and each group was assigned to a growth chamber as described earlier. There was very little variation in the size of seedlings at the onset of the experiment, so an initial harvest was not conducted.

Seeds of paper birch were collected from trees at Harvard Forest in October 1988. Six trees bearing heavy seed loads were felled onto a 3 × 4 m tarp, and seeds were collected and placed in plastic containers. These containers were stored at 4°C for approximately 6 months. Seeds were germinated in a 2:1 mixture of peat moss – vermiculite in peat “Jiffy Pots.” After germination, peat pots were thinned to one seedling, and planted into 1-L pots in a 1:1:1 mix of sand–perlite–peat. Plants were fertilized and then assigned into four groups and two CO₂ treatments as described earlier for older seedlings.

Red maple fruits were collected from 6 to 8 roadside trees as they ripened in May 1989 near Harvard Forest. Fruits were then imbibed in water for 48 h and germinated in a vermiculite medium. After germination, plants were transplanted into 1-L pots and assigned to treatments as described earlier.

Measurements of plant size

Seedlings of beech, black cherry, paper birch, and red maple were grown for a period of 60 d, whereas the seedlings of hemlock, white pine, and sugar maple were grown for 100 d because they grew at much slower rates. Plant height and basal diameter were measured both prior to the placement of plants in growth chambers and on the final day of growth. Plant height was measured from the soil–stem interface to the tip of the apical bud, and diameter was measured at the soil–stem interface. Leaf area was measured at the time of harvest by passing all leaves from a plant through a Li-Cor Leaf area meter (Li-Cor, Lincoln, NE). Plant height growth and diameter growth were obtained by subtracting initial plant height and diameter from final plant height and diameter, respectively. Following final height and diameter measurements, plants were separated into roots, stems, and leaves, oven-dried at 40°C for at least 48 h, and weighed.

Statistical analysis

All data were analyzed for normality, and arcsin transformations were done on root/shoot biomass data. An ANOVA was used to determine the overall significance of CO₂ treatment on parameters relating to plant size (biomass, height, diameter, root/shoot ratio), whether there was an interaction between CO₂ treatment and the identity of a species in determining plant size, and whether there were significant differences between experimental blocks. Student's *t*-tests were used to determine if CO₂ concentrations affected plant size parameters for each individual species. Three measures were employed to be certain that initial plant size did not affect the final results. First, data on the biomass of plants harvested at the onset of the experiment were analyzed with ANOVA and *t*-tests; these showed that plant biomass did not differ solely as a function of block assignment (*p* > 0.5). Second, initial heights and diameters for all plants of each species were analyzed with ANOVA and *t*-tests and showed that there were no significant differences in these parameters at the start of the experiment (*p* > 0.3). Finally, ANCOVA was used to analyze the final biomass data using initial plant height and initial diameter as covariates.

Results

Biomass

Beech, paper birch, black cherry, sugar maple, and hemlock seedlings responded to elevated CO₂ treatment with increased mean biomass in comparison with plants grown at ambient CO₂ (*p* < 0.05; *t*-test by species) (Fig. 1). The other species tended to have increased mean biomass accumulation under elevated CO₂ conditions, but this was not statistically significant (*p* > 0.1; Table 1). The largest relative increase in the biomass of plants grown in 700 μL·L⁻¹ CO₂ in comparison with those grown in 400 μL·L⁻¹ CO₂ occurred for seedlings of the shade-tolerant species (i.e., sugar maple, beech, and hemlock), but

TABLE 1. Mean (1 SE in parentheses; *n* = 10) values for a number of growth characteristics of seedlings grown for 60 d (beech, red maple, birch, cherry) or 100 d (pine, hemlock, sugar maple) under 400 or 700 ppm CO₂

	Root/shoot biomass			Height growth (cm)			Diameter growth (mm)			Final leaf area (cm ²)		
	700 ppm	400 ppm	700:400 ppm	700 ppm	400 ppm	700:400 ppm	700 ppm	400 ppm	700:400 ppm	700 ppm	400 ppm	700:400 ppm
Eastern hemlock (<i>Tsuga canadensis</i>)	0.38 (0.01)	0.36 (0.01)	1.06	1.62 (0.50)	1.40 (0.44)	1.16	3.30 (0.35)	3.28 (0.24)	1.01	661.00 (47.6)	630.39 (57.9)	1.05
American beech (<i>Fagus grandifolia</i>)	0.20 (0.02)	0.31 (0.02)	0.65**	32.75 (2.14)	21.31 (1.18)	1.53**	3.28 (0.16)	2.46 (0.23)	1.33**	348.96 (42.7)	181.78 (20.0)	1.92**
Sugar maple (<i>Acer saccharum</i>)	0.86 (0.07)	0.77 (0.07)	1.12	5.02 (2.27)	1.42 (0.15)	3.53	2.60 (0.46)	1.65 (0.31)	1.58	343.03 (69.05)	147.57 (22.54)	2.32*
Red maple (<i>Acer rubrum</i>)	0.24 (0.02)	0.21 (0.02)	1.15	55.44 (4.93)	50.68 (3.94)	1.09	3.83 (0.34)	3.47 (0.23)	1.10	1299.09 (151.1)	1394.29 (85.86)	0.93
Red maple seedling (<i>Acer rubrum</i>)	0.20 (0.01)	0.20 (0.01)	1.00	67.91 (3.52)	70.00 (2.48)	0.97	5.60 (0.13)	5.43 (0.14)	1.03	1096.18 (57.6)	1122.96 (39.2)	0.98
White pine (<i>Pinus strobus</i>)	1.08 (0.11)	0.97 (0.07)	1.11	2.53 (0.37)	2.15 (0.24)	1.18	3.34 (0.46)	3.30 (0.15)	1.01	220.05 (44.7)	255.35 (31.9)	0.86
Black cherry (<i>Prunus serotina</i>)	0.44 (0.01)	0.39 (0.03)	1.13	37.51 (2.89)	33.80 (3.00)	1.11	3.57 (0.33)	2.66 (0.22)	1.34*	1080.40 (76.2)	968.78 (53.7)	1.11
Paper birch (<i>Betula papyrifera</i>)	0.39 (0.02)	0.42 (0.02)	0.93	21.48 (2.10)	25.76 (2.24)	0.83	4.66 (0.23)	4.29 (0.15)	1.09	1470.37 (103.1)	1251.86 (99.6)	1.17
Paper birch seedling (<i>Betula papyrifera</i>)	0.41 (0.02)	0.43 (0.02)	1.05	28.23 (1.24)	31.67 (0.66)	0.89	6.86 (0.28)	6.50 (0.27)	1.05	1160.97 (37.7)	1352.36 (58.5)	0.86*

NOTE: Red maple and birch “seedlings” were used during their 1st year of growth. All other species, except beech, were at least 1 year old at the time of the experiment. Species are listed in order by decreasing shade tolerance (Fowells 1965). *, significant at *p* < 0.05 (*t*-test). **, significant at *p* < 0.01 (*t*-test).

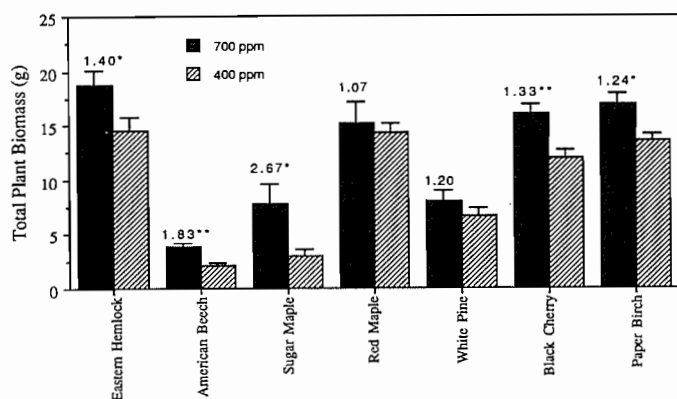


FIG. 1. Mean total plant biomass (± 1 SE; $n = 10$; *, significant at $p < 0.05$, t -test; **, significant at $p < 0.01$, t -test) for a number of tree species grown for 60 d (beech, red maple, birch, cherry) or 100 d (pine, hemlock, sugar maple) under 400 or 700 ppm CO_2 . The ratio of total biomass at 700:400 ppm CO_2 is written over each pair of bars. All seedlings, except beech, were at least 1 year old at the time of the experiment. Species are depicted from left to right in order of decreasing shade tolerance (Fowells 1965).

there was substantial variation in the growth of sugar maple (Fig. 1). ANCOVA results showed that the effect of CO_2 concentration on plant growth was not due to initial differences in seedling heights and diameters between CO_2 treatment groups (minimum $p > 0.30$). Older seedlings of paper birch showed increased biomass under elevated CO_2 conditions ($p < 0.05$; Fig. 1), whereas 1st-year seedlings showed a nonsignificant trend for increased biomass (mean ± 1 SE = 12.6 ± 0.38 g at $700 \mu\text{L} \cdot \text{L}^{-1}$ and 12.16 ± 0.4 g at $400 \mu\text{L} \cdot \text{L}^{-1}$; $p > 0.3$). In the case of red maple, neither 1st-year (mean ± 1 SE = 11.9 ± 0.69 g at $700 \mu\text{L} \cdot \text{L}^{-1}$ and 11.04 ± 0.5 g at $400 \mu\text{L} \cdot \text{L}^{-1}$, $p > 0.35$) nor older seedlings (see Fig. 1; $p > 0.25$) showed increased biomass with increasing CO_2 concentration. Root/shoot biomass allocation was reduced for American beech ($p < 0.05$) as a result of elevated CO_2 but was unaffected for all the other species (minimum $p > 0.2$; Table 1).

Height, diameter, and leaf area

The height growth of beech seedlings (1st-year) was increased in elevated CO_2 conditions, whereas the height growth of 1st-year birch seedlings decreased in these conditions ($p < 0.05$; Table 1). Older birch seedlings showed a nonsignificant trend for decreased growth with elevated CO_2 ($p > 0.10$; Table 1). All other species showed a nonsignificant trend for increased height growth with increasing CO_2 (minimum $p > 0.1$). Mean diameter growth increased for all species as a result of elevated CO_2 but increases were only significant for beech and black cherry ($p < 0.05$; Table 1). Mean plant leaf area for beech and sugar maple increased in elevated CO_2 levels, but the leaf area of 1st-year birch seedlings decreased in these conditions ($p < 0.05$; Table 1). Older birch seedlings showed a nonsignificant trend for increased leaf area ($p > 0.15$), while both 1st-year and older red maple seedlings showed a nonsignificant decrease in mean leaf area (minimum $p > 0.2$).

Discussion

We drew three major conclusions from this study. First, there were large interspecific differences in the magnitude

of growth enhancement by increased levels of CO_2 . Consequently, it seems reasonable to predict that one consequence of increasing levels of CO_2 may be to increase the competitive ability of some species relative to others, perhaps resulting in a change in forest community structure (see Carlson and Bazzaz 1980; Strain and Bazzaz 1983; Bazzaz et al. 1985; Williams et al. 1986). Second, the three species exhibiting the largest increase in growth as a function of increased CO_2 concentrations are shade tolerant (i.e., beech, sugar maple, and hemlock). Thus, it is possible that CO_2 may enhance the growth of this class of forest trees to a greater extent than the growth of shade-intolerant trees, at least in the light and nutrient conditions of this experiment. Third, although there were some differences in the response of 1st-year birch seedlings and older birch seedlings to increased levels of CO_2 we found no evidence to suggest that the age of tree seedlings greatly affected their response to increasing concentrations of CO_2 .

General responses of trees

The results reported in this study are consistent with those reported elsewhere in the literature. In this study, the mean biomass production of all species increased to some degree, albeit there were a few cases where this increase was not significant. Eamus and Jarvis (1989) reviewed the literature regarding the effect of enhanced CO_2 concentrations on tree growth and reported that in general, all the tree species that had been tested exhibited increased or no change in growth as a function of increasing CO_2 concentrations, irrespective of other environmental conditions in the experiment. Furthermore, Eamus and Jarvis (1989) concluded that under conditions of high nutrients, as was the case in this experiment, trees usually showed no change or decreased root/shoot biomass allocation as a function of increasing CO_2 levels; our results are consistent with these findings. Only beech showed a significant change in root/shoot partitioning as a function of CO_2 treatment in the present study and root/shoot biomass allocation decreased in this case.

Shade tolerance and responsiveness to CO_2

An interesting and counterintuitive result of this study was that the three species characterized as shade tolerant (beech, sugar maple, and hemlock) showed the greatest stimulation of growth by increasing CO_2 . There have been few studies that have directly examined this issue (but see Jurik et al. 1985). Williams et al. (1986) showed that hickory (intermediately shade tolerant) seedlings tended to increase their representation in an artificial seedling community relative to tulip-poplar (*Liriodendron tulipifera* L.) (shade intolerant) under conditions of elevated CO_2 conditions. Alternatively, Norby et al. (1986) and O'Neill et al. (1987) together found little difference in the growth response of white oak (*Quercus alba* L.) (shade tolerant) and tulip-poplar (shade intolerant) seedlings to elevated CO_2 levels and Eamus and Jarvis (1989), in their review of the literature, found no strong relationships between the identity of tree species and the magnitude of growth stimulation by CO_2 . However, ours is the first study that we know of to examine simultaneously such a large number of co-occurring species in one experiment.

In general, early successional, fast-growing species show the greatest plasticity to environmental conditions (see Bazzaz 1979; Chapin 1990), thereby enabling them to take

greater advantage of increased resource availability than later successional, slow-growing species. In general, shade-intolerant trees are usually classified as early successional species and have inherently fast growth rates, whereas shade-tolerant trees are considered to be late successional and generally have slower inherent growth rates than shade-intolerant species (see Spurr and Barnes 1980; Chapin 1990). Consequently, we predicted that the relatively shade-intolerant and fast-growing paper birch, red maple, white pine, and black cherry would show the strongest enhancement to the increased availability of CO₂, but this was not what we observed.

So why did the shade-tolerant, slower growing trees (i.e., beech, sugar maple, hemlock) show greater stimulation of growth by increased CO₂ than shade-intolerant trees? One explanation revolves around the light environment used in this experiment. Although the daily total photon flux was quite high (i.e., equivalent to that of a large canopy gap), the peak light intensity was relatively low (i.e., equivalent to understory conditions). Given the relatively low peak light intensities, it is likely that leaves of the shade-intolerant species exhibited an acclimation response that resulted in increased quantum yield, but decreased maximum rates of photosynthesis and a lower light saturation level than would occur for plants grown with a similar average daily photon flux but with higher peak irradiances (see Bazzaz and Carlson 1982). Consequently, it is likely that the shade-intolerant trees were not able to take full advantage of increased availability of CO₂, in terms of increased rates of carbon gain, because their rates of photosynthesis were simultaneously limited by light. Alternatively, the peak light intensities in the growth chambers were equivalent to the light saturation level for leaves of many shade-tolerant trees under a wide range of conditions (see Kramer and Kozlowski 1979; Bazzaz and Carlson 1982), so maximal rates of photosynthesis were probably not light limited. Consequently, photosynthesis was more likely to be limited by CO₂ than by light for the shade-tolerant trees, so the shade-tolerant species were probably able to take complete advantage of increasing CO₂ in terms of increased photosynthetic rates. Therefore, we hypothesize that if this experiment were conducted with similar mean daily photon fluxes but with peak light intensities greater than 1000 $\mu\text{m} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, then the shade-intolerant species would exhibit considerably greater increases in growth as a function of increased CO₂ concentrations than they did in this experiment.

First-year seedlings vs. older seedlings

Generally, it is thought that young seedlings show the most rapid and the greatest response to elevated CO₂ levels because older seedlings and saplings have large carbon reserves that may buffer plant responses to increasing CO₂ (see Sinoit and Kramer 1986; Eamus and Jarvis 1989). However, this question has rarely been examined. In the present study, 1st-year red maple seedlings and older red maple seedlings showed similar responses to CO₂ treatment but the growth of red maple seedlings from both groups was not significantly affected by CO₂ treatment. For paper birch, the biomass of older seedlings was significantly increased under elevated CO₂ concentrations, whereas the biomass of 1st-year seedlings only marginally increased in these conditions. Moreover, the height growth of 1st-year paper birch seedlings was significantly less in elevated CO₂ levels

relative to ambient CO₂ levels, whereas the height growth of older seedlings was only marginally less in elevated CO₂ environments. The trend of the effect of elevated CO₂ levels on leaf area production by birches was different for the different seedling ages but elevated CO₂ only significantly affected leaf area of 1st-year seedlings. Overall, we have no evidence to support the notion that very young seedlings show greater stimulation of growth under elevated CO₂ conditions than do older seedlings (see Table 1).

Global change and forest communities

Many authors have suggested potential scenarios for changes in the structure of forest communities as a result of changes in the global environment (e.g., Davis et al. 1986; Pastor and Post 1988; Roberts 1989). Many of these authors use models that focus solely on the effect of increasing global temperatures on forests, because historical records suggest that past temperature regimes have had a substantial effect on the composition of today's forest communities (e.g., Davis et al. 1986). For example, it was suggested that American beech may be particularly susceptible to rapid increases in global temperatures because paleoecological data from pollen records suggest that this species was particularly sensitive to changes in temperature; and, moreover, beech has large seeds, which might not be easily dispersed to cooler regions where this species might thrive (Davis et al. 1986; Roberts 1989). Additionally, Pastor and Post (1988) modelled the effect of the increasing CO₂ concentration, increasing temperature, and a changing moisture regime on North American forests and suggested that substantial changes in the composition and productivity of these forests could occur. Although models such as these can generate potentially important and interesting scenarios, they have so far not included the potentially important direct effects of elevated CO₂ levels on plant performance. For example, our results show that American beech can be one of the most responsive trees to increasing CO₂ levels in greenhouse experiments; it almost doubled its growth rate in the present study. Thus, it is quite possible that rising levels of atmospheric CO₂ might help to ameliorate some detrimental effects of rising temperature for this species, and this could ultimately result in a greater representation of beech in a community than was previously anticipated. Although this scenario awaits further testing, we feel that it is crucial to consider the direct effects of CO₂ on vegetation when proposing scenarios relating global environmental change to forest structure and productivity.

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