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## SUCCESSIONAL STATUS, SEED SIZE, AND RESPONSES OF TREE SEEDLINGS TO CO<sub>2</sub>, LIGHT, AND NUTRIENTS<sup>1</sup>

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**Abstract.** We studied how an enriched CO<sub>2</sub> atmosphere, in a fully crossed design of light and nutrients, influenced 1st-yr seedling growth in six New England deciduous forest tree species. The species, in the order of increasing shade tolerance, were gray birch (*Betula populifolia*), ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.), red oak (*Quercus rubra* L.), yellow birch (*Betula alleghaniensis* Britton), and striped maple (*Acer pensylvanicum*). Elevated CO<sub>2</sub> environments significantly stimulated the seedling growth of all six species. Generally this was more pronounced in low light. The greatest stimulation was found under the condition of low light and high nutrients. However, individual species responded differently to elevated CO<sub>2</sub> levels. Among the three early-successional species, gray birch, ash, and red maple, a significant increase in seedling growth under elevated CO<sub>2</sub> conditions was found only with high nutrients. The three late-successional species grown under elevated CO<sub>2</sub> conditions (red oak, yellow birch, and striped maple) showed a greater percentage increase in seedling growth in low light than in high light. Thus, for the early-successional species, the degree of enhancement of seedling growth by elevated CO<sub>2</sub> levels was more sensitive to nutrient levels, while in the late-successional species the enhancement was more sensitive to the level of light. Moreover, species with large seeds (e.g., red oak) exhibited a greater response to elevated CO<sub>2</sub> levels under low light than species with small seeds (e.g., gray birch).

The results emphasize the importance of plant species as well as other environmental resources in modifying the response of plants to elevated CO<sub>2</sub>. Considering the light and nutrient environment observed in forest gaps of various sizes, the results of the present experiment suggest seedling regeneration in New England deciduous forests may be altered in a future high CO<sub>2</sub> environment.

**Key words:** early- and late-successional species; elevated CO<sub>2</sub> levels; enhancement; light; nutrients; percentage increase; seedling growth.

### INTRODUCTION

Atmospheric CO<sub>2</sub> concentrations are predicted to increase to ≈700 μL/L by the mid to late 21st century (e.g., Conway et al. 1988, Fifield 1988, Hari and Arovaara 1988). While the impact of rising CO<sub>2</sub> on crops and other herbaceous plants has been intensively studied (see review in Strain and Bazzaz 1983, Kimball 1986), the direct and interactive effects of CO<sub>2</sub> and other environmental factors, such as nutrients and light, on tree species have received less attention (Eamus and Jarvis 1989, Bazzaz 1990). Experiments published so far considered either the effect of rising CO<sub>2</sub> alone (Oberbauer et al. 1985, Hollinger 1987, Reekie and Bazzaz 1989), or the interaction between CO<sub>2</sub> and a single environmental resource (e.g., Sionit et al. 1985, Tolley and Strain 1985, Conroy et al. 1986, Williams et al. 1986). In nature, several environmental resources can simultaneously limit plant growth, and plants can

benefit from various source additions to their environment (see Chapin et al. 1987). The response of plants to increased atmospheric CO<sub>2</sub> levels may largely depend on the availability of other environmental resources (Bazzaz and Fajer 1992).

An area of particular interest for global change is the effect of elevated CO<sub>2</sub> levels on the structure and productivity of forest ecosystems. If the effects of a global CO<sub>2</sub> increase at the level of ecosystems are to be predicted, a better understanding of the relationship among community members in a changed environment will be required (Mooney 1991). Tree species in a community can differ substantially in the magnitude of their growth response to elevated CO<sub>2</sub> levels (e.g., Carlson and Bazzaz 1980, Tolley and Strain 1985, Williams et al. 1986, Reekie and Bazzaz 1989, Bazzaz et al. 1990). The differential responses of tree species to increasing CO<sub>2</sub> may be related to the successional status of the species. Results from studies of this issue have been conflicting. For example, Norby et al. (1986) and O'Neill et al. (1987) found little difference in the growth

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response to elevated CO<sub>2</sub> of a shade-tolerant species, white oak (*Quercus alba* L.), and a shade-intolerant species, tulip poplar (*Liriodendron tulipifera*). However, in a study of tropical tree seedlings Oberbauer et al. (1985) found that the increase in biomass was greater for the pioneer species (*Ochroma lagopus* Swartz) in comparison with a late-successional species (*Pentaclethra macroleoba* Wild.), although both species exhibited similar patterns of photosynthesis and stomatal conductance in response to elevated CO<sub>2</sub> levels. In a study of seven co-occurring temperate tree species from the northeastern United States, Bazzaz et al. (1990) found that three late-successional species showed the greatest relative stimulation due to increased CO<sub>2</sub>. The peak light intensity (photon flux density) in their experiment was relatively low (520 μmol·m<sup>-2</sup>·s<sup>-1</sup>) and may have greatly influenced the response to elevated CO<sub>2</sub> levels.

Most of the forests of the northeastern United States are agrading ecosystems (sensu Bormann and Likens 1979), i.e., they are accumulating biomass as they recover from clearing. These forests, generally considered to be nutrient limited, are now also receiving as much as 20 kg·ha<sup>-1</sup>·yr<sup>-1</sup> of N as additional deposition impacts from atmospheric sources (Aber et al. 1989). Thus, they are potentially important to the global carbon cycle, especially as a potential sink for the "missing carbon" in the global carbon budget (Tans et al. 1990). Moreover, in trees a small increase in relative growth at the early stage can result in a large difference in size of individuals at the end of the 1st yr of growth, or even after a number of years, because of the compound interest rule. Thus, the differential effect of high CO<sub>2</sub> on seedling growth may ultimately determine forest community structure. In the present paper, we report on how an enriched CO<sub>2</sub> environment, in a fully crossed design of light and nutrients, influenced 1st-yr seedling growth. The six tree species, which co-occur at Harvard Forest, Petersham, Massachusetts, in the order of increasing shade tolerance were: gray birch (*Betula populifolia*), ash (*Fraxinus americana*), red maple (*Acer rubrum*), red oak (*Quercus rubra* L.), yellow birch (*Betula alleghaniensis* Britton), and striped maple (*Acer pensylvanicum*) (Burns and Honkala 1990). These species also represent a range of seed mass from the small gray birch to the large red oak. This design allowed us to explore the implications of the level of resource heterogeneity found in natural forest ecosystems. We focused on the following questions:

- 1) Does an elevated CO<sub>2</sub> environment enhance seedling growth of temperate deciduous tree species? If so, is the effect of an elevated CO<sub>2</sub> environment dependent on the levels of other resources important for seedling growth, such as light and nutrients?
- 2) Are the differential responses of seedling growth to elevated CO<sub>2</sub> levels in the six tree species related to their successional status, degree of shade toler-

ance, and seed mass? If so, are the responses dependent on light and nutrients?

## METHODS

### *Plant material*

First-year seedlings of the two maples and the ash were collected at the cotyledon stage from several sites at Harvard Forest, Petersham, Massachusetts, USA in early May 1990. They were brought back to Cambridge, Massachusetts and immediately transplanted into either peat "Jiffy pots" or tree tubes with vermiculite. Barely germinated or intact acorns were collected at Harvard Forest. The seedlings or acorns of red oak were immediately put into vermiculite in basins in a growth chamber at 30°/23°C (day/night). Seedlings of each species were randomly divided into two groups. One group was placed in a growth chamber with 700 μL/L CO<sub>2</sub>, and the other group was placed in a growth chamber with 350 μL/L CO<sub>2</sub>. The temperature of both chambers was 25°/23°C, and the photoperiod was 12 h.

Seeds of the two birches were collected at Harvard Forest in the fall of 1989 and germinated in May 1990 when the seedlings of the other species were collected. The seeds were divided into two groups and germinated in flats with a 4:1:0.25 mixture of vermiculite : horticultural sand : peat in 350 or 700 μL/L CO<sub>2</sub> growth chambers with the same treatment as previously mentioned.

### *Experimental design and growth conditions*

On 22 June 1990, when most of the seedlings had two true leaves, seedlings of all species were transplanted into 15 cm diameter standard plastic pots with 1.25 L of a 1:1:1 mixture of sand : perlite : peat. The pH of the soil mixture was ≈ 5.0. The transplants initially grown or germinated at 350 or 700 μL/L CO<sub>2</sub> were placed in glasshouse modules having the corresponding CO<sub>2</sub> level. The CO<sub>2</sub> concentration in both glasshouses was monitored and controlled by an infrared gas analyzer and computerized injection system. In each glasshouse, there were three benches (blocks). Each of the three benches was divided in half and the two halves were randomly assigned to two plots. One was for high light and the other was for low light. Within each plot (i.e., light treatment) two replicate seedlings were randomly assigned to one of two nutrient treatments. This resulted in 2 CO<sub>2</sub> × 2 light × 2 nutrient × 6 species × 3 block × 2 replicate, a total of 288 plants. The CO<sub>2</sub> levels and plants were rotated from one glasshouse to the other about every 3 wk, with CO<sub>2</sub> control approximately reprogrammed after each move. In the same manner, the light treatment and blocks were also rerandomized.

The elevated CO<sub>2</sub> (700 μL/L) treatment represented the predicted values for atmospheric CO<sub>2</sub> concentration 50 yr hence, whereas the low value (350 μL/L)

was the estimated ambient CO<sub>2</sub> level for the present decade. The high light treatment (natural light, supplemented by mercury vapor lamps) represented the light condition of a large gap at Harvard Forest (300 m<sup>2</sup>), whereas the low light treatment (37% of high light) was approximately equivalent to the light condition of understory (Sipe 1990). The low light treatment was obtained using neutral shade cloth frames. The shade cloth frames did not significantly affect temperature, humidity, or CO<sub>2</sub> concentrations as measured several times during the growth period. The two nutrient treatments (high and low) simulated high nutrient deposition and organic matter mineralization rates (N equivalent to 400 kg·ha<sup>-1</sup>·yr<sup>-1</sup>) and nutrient-poor forest soil at Harvard Forest (N equivalent to 40 kg·ha<sup>-1</sup>·yr<sup>-1</sup>), respectively (Aber et al. 1989). Once transplanted and assigned to the high or low nutrient treatment the plants received either 1.8 or 0.18 g of Osmocote (a slow-release fertilizer, 15:10:10 NPK plus micronutrients, 8.3% ammoniacal nitrogen, and 6.7% nitrate nitrogen, 5–6 mo formulation) per pot, respectively.

During the 1st wk, the glasshouse temperature was 27°/20°C (day/night) in natural day length. In the 2nd wk, the temperature was raised to 30°/23°C and day length extended to 15 h to approximate natural conditions. In the middle of August, the glasshouses were returned to natural light and natural day length. Temperature was gradually reduced to 6°/4°C by the end of October. At the end of October the shade cloth frames (for the low light treatment) were taken away in order to simulate the canopy opening at Harvard Forest caused by leaf fall from canopy trees. All the plants were left under these conditions until all leaves senesced.

Throughout the experiment the plants were maintained near field capacity moisture conditions. All leaves that naturally fell off or fell in response to a gentle touch were collected before the final harvest. When the leaves of most plants had fallen off (165 d after transplanting) plants were harvested, separated into roots, shoots, and leaves, and oven-dried to constant mass at 50°C.

#### *Statistical analysis*

Effects of environmental treatments, CO<sub>2</sub>, light, and nutrients, on plant growth were analyzed by analysis of variance (ANOVA). The overall model used was a four-way ANOVA in order to determine whether species responded to elevated CO<sub>2</sub> levels differently and whether the differences were dependent on the light and nutrient treatments. In the four-way ANOVA, CO<sub>2</sub>, light, nutrients, and species were treated as fixed factors, whereas the block was random and nested in the CO<sub>2</sub> treatment. The CO<sub>2</sub> effect was tested using the block variance, the light effect was tested using the block × light variance, and the remaining main effects and interactions were tested using the residual (error) variance. If a significant interaction was found, a three-

way ANOVA was carried out separately by light, nutrient, or species. When ANOVAs were run separately, the Bonferroni procedure was used to select the critical probability level to prevent Type I error. Standardized residuals of each ANOVA were examined in three ways. The probability plots and histograms of the residuals were examined to test for normality. Residuals were plotted against cell mean estimates to check for homoscedasticity. To meet the assumptions of ANOVA, data were logarithm transformed.

#### RESULTS

Of the three environmental resources studied, CO<sub>2</sub>, light, and nutrients, nutrients had the greatest effect on seedling growth. At ambient CO<sub>2</sub> levels, the total mass of seedlings grown with high nutrients was generally 2–10 times greater than that of seedlings grown with low nutrients (Fig. 1). The effects of varying light levels were related to nutrients. There was an ≈ 108% increase in total mass of seedlings grown in high light and high nutrients, and only a 15% increase in high light and low nutrients, in comparison with seedlings grown in low light and low nutrients.

Three two-way interactions between CO<sub>2</sub> and light, CO<sub>2</sub> and nutrients, and CO<sub>2</sub> and species were significant (Table 1), indicating that the stimulation of plant growth by elevated CO<sub>2</sub> levels was related to light and nutrients, and that the response to elevated CO<sub>2</sub> levels was dependent on species. For example, the enhancement of seedling growth by elevated CO<sub>2</sub> levels in all six species was generally greater for plants grown in low light than plants grown in high light, particularly under the condition of high nutrients (Figs. 1 and 2). With high nutrients, the seedling growth of all species significantly increased with elevated CO<sub>2</sub> levels (*F* of CO<sub>2</sub> main effect in a three-way ANOVA = 47.72, *P* < .002), whereas with low nutrients the significant stimulation of seedling growth by elevated CO<sub>2</sub> levels was only found in some species (*F* of interaction between CO<sub>2</sub> and species in a three-way ANOVA = 2.58, *P* < .03) (Figs. 1 and 2).

For three early-successional species, gray birch, ash, and red maple, the enhancement of seedling growth by elevated CO<sub>2</sub> levels was dependent on the nutrient treatment (*F* of interaction between CO<sub>2</sub> and nutrients in three-way ANOVAs = 7.36, 386.2, and 9.96, *P* < .0108, .0000, and .0035, respectively). A significant increase in the seedling growth in these species due to elevated CO<sub>2</sub> levels was found only with high nutrients. However, for two late-successional species, yellow birch and striped maple, the stimulation of seedling growth by elevated CO<sub>2</sub> levels was significantly related to light (*F* of interaction between CO<sub>2</sub> and light in three-way ANOVAs = 5.19 and 5.58, respectively, *P* < .022). The seedlings of the two species grown in low light exhibited a greater percentage increase due to elevated CO<sub>2</sub> than those grown in high light (Fig. 2). For red

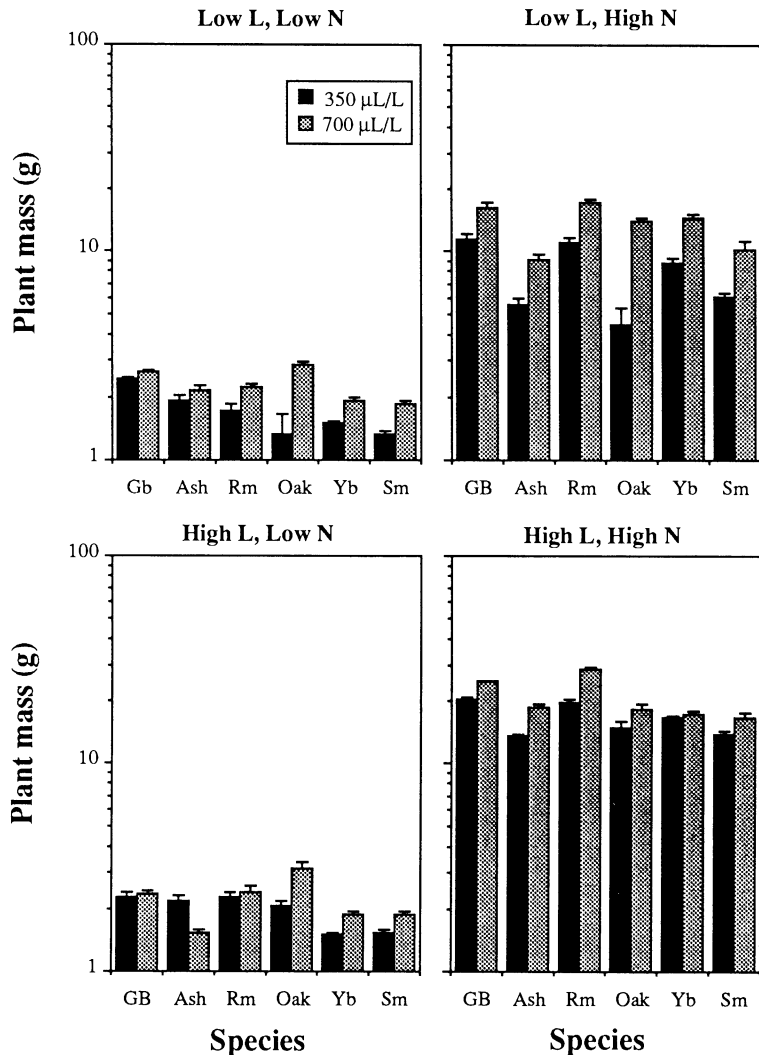


FIG. 1. Seedling growth in 165 d (mean  $\pm$  1 SE,  $n$  = 6) for six temperate tree species grown under 350 or 700  $\mu$ L/L CO<sub>2</sub> with two light (L) and two nutrient (N) treatments. Species are depicted from left to right in order of increasing shade tolerance. Gb represents gray birch; Rm, red maple; Oak, red oak; Yb, yellow birch; Sm, striped maple.

oak, the enhancement of seedling growth was greatly related to both light and nutrients ( $F$  of interaction among CO<sub>2</sub>, light, and nutrients in a three-way ANOVA = 5.79,  $P$  < .027). Moreover, with low nutrients the percentage increase of seedling growth of the three late-successional species was greater than of the three early-successional species (Fig. 2). The opposite was true when the plants were grown in high light and high nutrients, i.e., the three early-successional species exhibited a greater percentage increase of seedling growth due to elevated CO<sub>2</sub> levels in comparison with the three late-successional species. However, in low light and high nutrients, there was no difference in response to elevated CO<sub>2</sub> levels between the early- and late-successional species.

Furthermore, all species grown at ambient CO<sub>2</sub> levels showed the greatest absolute size in high light and

high nutrients (Fig. 1). The size of plants grown at ambient CO<sub>2</sub> levels, high light, and high nutrients was similar to that of the plants grown at elevated CO<sub>2</sub> levels, low light, and high nutrients. The three early-successional species exhibited a greater percentage increase due to elevated CO<sub>2</sub> levels than did the three late-successional species under high light and high nutrient condition. This might indicate that the three early-successional species had greater potential in response to elevated CO<sub>2</sub> levels in comparison with the three late-successional species.

There was a significant linear relationship between the percentage increase of seedling growth and mean seed size of species under the condition of low light (Fig. 3). Approximately 67% of the variance in the increase of growth was accounted for by mean seed size. However, under the condition of high light, there

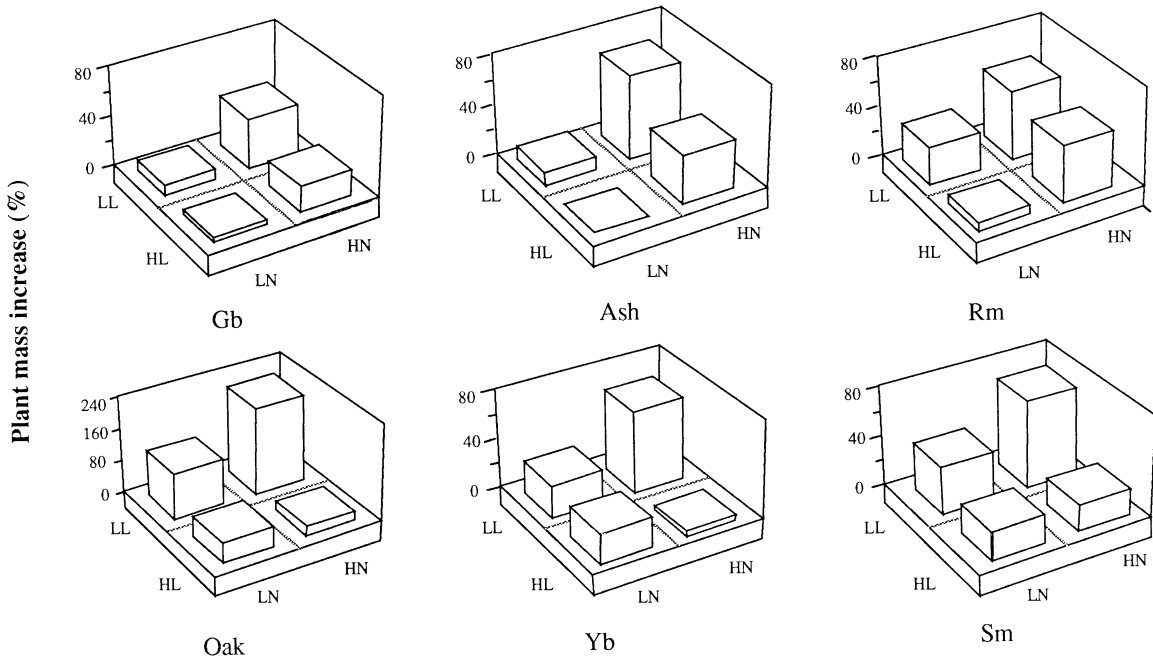


FIG. 2. Enhancement of seedling growth by elevated CO<sub>2</sub> in six temperate tree species under various light and nutrient treatments. *x* axes represent the nutrient treatment: LN, low nutrients; HN, high nutrients. *y* axes represent the light treatment: LL, low light; HL, high light. *z* axes are the ratio of total mass of plants grown at 700 μL/L CO<sub>2</sub> to that of plants grown at 350 μL/L CO<sub>2</sub>. Note that the scale of *z* axes of red oak is 3 times that of the other species. Three shade-intolerant species are in the top row and three shade-tolerant species in the bottom row.

was no relationship between the percentage increase of seedling growth and mean seed size of species (Fig. 3).

Different species exhibited different root/shoot ratios (Table 2). In general, the root/shoot ratio of all species decreased with increasing nutrients but increased with increasing light. Although a three-way interaction among CO<sub>2</sub> levels, light, and nutrients was significant (Table 1), there was no clear pattern of root/shoot ratio among species in response to elevated CO<sub>2</sub> levels (Table 2). Analysis of root biomass showed that the great-

est value was found in high light and high nutrients for gray birch, ash, red maple, and red oak, which was far greater than root biomass of these four species in the other three treatments and was greater than the root biomass of yellow birch and striped maple in high light and high nutrients (Fig. 4). In high light and high nutrients, the percentage increase of root biomass due to elevated CO<sub>2</sub> levels was greater than the percentage increase of total mass. Moreover, except for red oak there was no significant change (decline) in root/shoot

TABLE 1. Analysis of variance for seedling growth of six temperate tree species under interactive CO<sub>2</sub>, light, and nutrient conditions. \* refers to significance at *P* < .05; \*\* to significance at *P* < .01; \*\*\* to significance at *P* < .001.

Sources of variation	df	Total mass		Root/shoot ratio	
		ss	<i>F</i>	ss	<i>F</i>
CO <sub>2</sub> concentration	1	1.35	53.85***	0.04	0.52
Block	4	0.10	1.50	0.29	1.51
Light	1	1.33	30.39**	1.10	162.97***
Nutrient	1	45.47	2716.50***	3.97	83.95***
Species	5	1.46	17.47***	8.20	34.70***
CO <sub>2</sub> × light	1	0.36	8.13*	0.00	0.18
CO <sub>2</sub> × nutrient	1	0.19	11.24***	0.00	0.11
CO <sub>2</sub> × species	5	0.32	3.82**	0.22	0.94
Light × nutrient	1	0.95	56.89***	0.00	0.06
Nutrient × species	5	0.40	4.77***	0.51	2.16
Block × light	4	0.18	2.62*	0.03	0.14
CO <sub>2</sub> × light × nutrient	1	0.04	2.22	0.21	4.52*
CO <sub>2</sub> × light × species	5	0.12	1.44	0.31	1.33
CO <sub>2</sub> × nutrient × species	5	0.09	1.07	0.39	1.63
Light × nutrient × species	5	0.13	1.57	0.23	0.96
CO <sub>2</sub> × light × nutrient × species	5	0.04	0.51	0.41	1.71
Error	213	3.56		10.02	

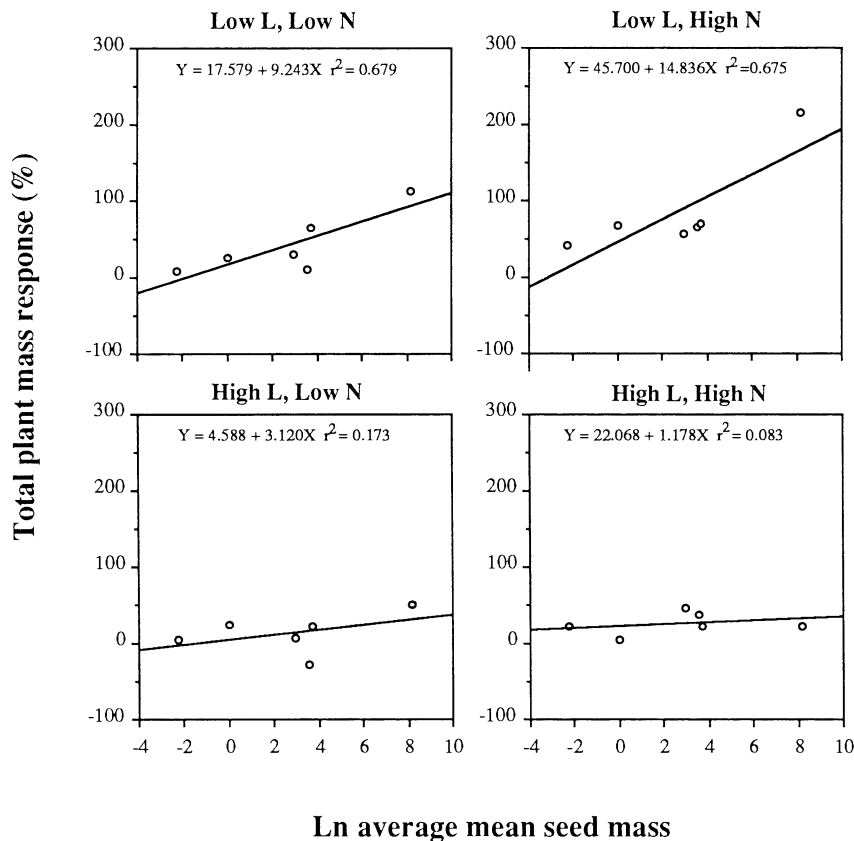


FIG. 3. Relationship between seed size and percent increase of seedling mass of six temperate tree species under various light (L) and nutrient (N) treatments.

ratio for plants grown at elevated and ambient CO<sub>2</sub> levels in high light and high nutrients (Table 2). In red oak, plants grown at elevated CO<sub>2</sub> levels significantly increased root/shoot ratio in high light and high nutrients.

#### DISCUSSION

##### *Enhancement of the response to elevated CO<sub>2</sub> is related to resource availability*

In the six species we studied, the enhancement of seedling growth by elevated CO<sub>2</sub> levels in the 1st yr was largely resource dependent: significant stimulation of seedling growth was found in some but not in all treatments. Seedlings utilized elevated CO<sub>2</sub> particularly when nutrients were plentiful. Although the stimulation of seedling growth by elevated CO<sub>2</sub> levels has been found either to increase (Williams et al. 1986) or to decrease (Sionit et al. 1982) with light intensity, the relative enhancement of seedling growth due to elevated CO<sub>2</sub> levels increased with decreasing light in the present experiment. However, the compensation of elevated CO<sub>2</sub> for low light was greater for plants grown with high nutrients than those grown with low nutrients.

There are some concerns about the ability to detect

the enhancement of plant growth by elevated CO<sub>2</sub> in small pots of glasshouse experiments. In small pots, the growth can be restricted by the lack of active sinks and by nutrient deficiency (e.g., Eamus and Jarvis 1989, Arp 1991, Hogan et al. 1991). In the present experiment, the greatest root biomass of seedlings grown in high light and high nutrients was  $\approx 6$  times greater than root biomass of seedlings grown in low nutrient treatments and 80% greater than that of seedlings grown in low light and high nutrients. Thus, plants grown in low nutrient treatments were not root bound, those grown in low light and with high nutrients were possibly less root bound, and those grown in high light and high nutrients might have been root bound. However, the least enhancement of growth was found in low nutrients rather than in high nutrients for all species grown in low light (Fig. 2). Even in the treatment of high light and high nutrients, the percentage increase of root biomass was greater than the percentage increase of total mass. Thus, our seedlings were not root bound.

That enhancement of seedling growth by elevated CO<sub>2</sub> levels decreased with increasing light availability in the present experiment may be explained by the following three points. First, in low light the capacity of light harvesting, electron transport, and the photosynthetic carbon reduction cycle to regenerate RuBP

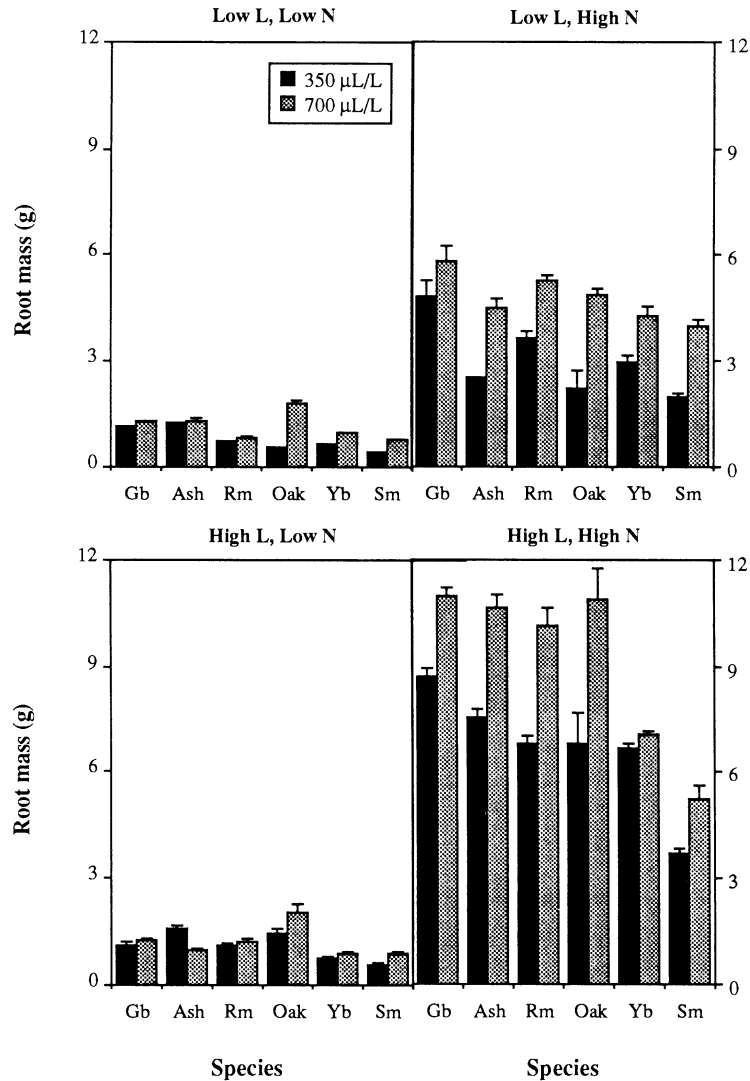


FIG. 4. Root biomass (mean and  $\pm 1$  SE,  $n = 6$ ) for six tree temperate species grown under 350 or 700  $\mu\text{L/L}$   $\text{CO}_2$  under various light (L) and nutrient (N) treatments in 165 d. Symbolism is the same as in Fig. 1.

(ribulose-1,5-bisphosphate) is generally reduced. RuBP regeneration limitation is most likely to occur in the low light environment (Sharkey 1985). It has been found that elevated  $\text{CO}_2$  compensates for the limitation on photosynthesis by RuBP regeneration in low light (Wong 1979). Since light limitation is effectively carbon limitation, it is possible that elevated  $\text{CO}_2$  would have the greater effect in low light. Second, decreased amount and activity of rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) were often observed with long-term exposure to elevated  $\text{CO}_2$  levels (e.g., Sage and Sharkey 1987). In general, rubisco limitation is most likely to occur in high light (Sharkey 1985). Thus, elevated  $\text{CO}_2$  levels would have lower effect on assimilation in high light than in low light. Third, we measured assimilation rates of the plants grown with high nutrients against a range of  $\text{CO}_2$  concentrations (S. L.

Miao and F. A. Bazzaz, *unpublished data*). We found that the initial enhancement of assimilation rates by high  $\text{CO}_2$  was greater in low light than in high light. We also observed that plants grown at high  $\text{CO}_2$  and high light started senescing earlier than plants grown at high  $\text{CO}_2$  but low light. Thus, plants grown at high  $\text{CO}_2$  and low light might have a longer period of growth time than plants grown at high  $\text{CO}_2$  but high light.

*Enhancement of elevated  $\text{CO}_2$  is related to the successional status and seed size*

One result of this study was that early- and late-successional species responded to elevated  $\text{CO}_2$  levels differently, according to the availability of light and nutrients. All conflicting results published so far with regard to responses to elevated  $\text{CO}_2$  levels between early and late-successional species were observed in



TABLE 2. Root/shoot ratio of seedlings of six temperate tree species under interactive CO<sub>2</sub>, light, and nutrient conditions (means  $1 \pm$  SE). Sample size was a total of six.

	Low light				High light			
	Low nutrient		High nutrient		Low nutrient		High nutrient	
	350 $\mu$ L/L	700 $\mu$ L/L	350 $\mu$ L/L	700 $\mu$ L/L	350 $\mu$ L/L	700 $\mu$ L/L	350 $\mu$ L/L	700 $\mu$ L/L
Gray								
birch	0.95 $\pm$ 0.01	1.00 $\pm$ 0.03	0.62 $\pm$ 0.07	0.67 $\pm$ 0.01	0.99 $\pm$ 0.02	1.08 $\pm$ 0.02	0.86 $\pm$ 0.01	0.90 $\pm$ 0.02
Ash	1.31 $\pm$ 0.06	1.33 $\pm$ 0.05	0.87 $\pm$ 0.02	1.04 $\pm$ 0.06	1.73 $\pm$ 0.09	1.26 $\pm$ 0.02	1.13 $\pm$ 0.01	1.16 $\pm$ 0.02
Red								
maple	0.85 $\pm$ 0.01	0.80 $\pm$ 0.01	0.70 $\pm$ 0.01	0.66 $\pm$ 0.01	0.95 $\pm$ 0.02	0.98 $\pm$ 0.04	0.74 $\pm$ 0.01	0.74 $\pm$ 0.01
Red Oak	1.07 $\pm$ 0.10	1.32 $\pm$ 0.05	0.88 $\pm$ 0.18	0.73 $\pm$ 0.02	1.53 $\pm$ 0.11	1.39 $\pm$ 0.07	0.89 $\pm$ 0.04	1.24 $\pm$ 0.08
Yellow								
birch	0.91 $\pm$ 0.01	0.98 $\pm$ 0.02	0.71 $\pm$ 0.00	0.62 $\pm$ 0.00	0.98 $\pm$ 0.04	0.95 $\pm$ 0.01	0.82 $\pm$ 0.01	0.83 $\pm$ 0.01
Striped								
maple	0.69 $\pm$ 0.02	0.83 $\pm$ 0.03	0.71 $\pm$ 0.01	0.72 $\pm$ 0.01	0.73 $\pm$ 0.03	0.97 $\pm$ 0.03	0.62 $\pm$ 0.01	0.69 $\pm$ 0.01

the present experiment. For example, under low nutrient condition the early-successional species exhibited a greater response to elevated CO<sub>2</sub> than the late-successional species, whereas under high light and high nutrient condition the opposite was true; under low light and high nutrient condition there was no difference between the two types of species. However, since early-successional species usually have a broader response to nutrients, moisture, and other gradients (Bazzaz 1987), and have higher growth rates than do late-successional species (see Bazzaz 1979), they may potentially have a greater ability to utilize elevated CO<sub>2</sub> than do late-successional species when other resources are available. Therefore, plant responses to CO<sub>2</sub> are not easily predictable, and depend critically on both the species and levels of other environmental resources.

The enhancement of elevated CO<sub>2</sub> levels on seedling growth was also related to seed size of species. For seedlings, resources can come from seeds and from the environments in which seedlings grow. While external environmental resources are the key to the continual growth of the plants, seed resources are particularly important for early growth of seedlings. Species with bigger seeds (such as red oak) exhibited a greater response of seedling growth to elevated CO<sub>2</sub> levels than species with smaller seeds (such as gray birch) under the low light condition (Fig. 3). The species with bigger seeds have reserves and hence might utilize more elevated CO<sub>2</sub> before root systems are fully developed and nutrient uptake insured, since the enhancement of elevated CO<sub>2</sub> levels is resource dependent.

We predict that in a nutrient-rich understory, plant-plant interaction among seedlings may be more intense in a future elevated CO<sub>2</sub> environment since the size of all species (early- and late-successional species) was significantly stimulated by elevated CO<sub>2</sub>. However, in a nutrient-rich large gap, early-successional seedlings may perform better than late-successional ones. Seedling regeneration in such a gap may be faster at elevated CO<sub>2</sub> levels than at the present time. In nutrient-poor environments, regardless of large gaps or understory,

late-successional seedlings may perform better than early-successional ones. Therefore, the regeneration in a nutrient-poor large gap or open site may be slower than at the present time. Moreover, because of the differences among species in response to various resource conditions, the geographical distribution pattern of the species may change. For example, in elevated CO<sub>2</sub> environments red oak can grow vigorously in many habitats and hence its distribution may be wider, whereas other species will be limited to specific sites.

In conclusion, the significant stimulation of seedling growth by elevated CO<sub>2</sub> levels was found in the 1st-yr seedlings of six temperate tree species. However, the enhancement was largely dependent on light, nutrients, and species; elevated CO<sub>2</sub> levels affected early- and late-successional species very differently, and this was dependent on light and nutrients. The results emphasize the importance of other environmental resources in modifying the response of plants to elevated CO<sub>2</sub>, as well as the responses of different species, and they may provide information about seedling regeneration in the northeastern deciduous forests in a future elevated-CO<sub>2</sub> world.

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