



**Rooting Volume, Nutrient Availability, and CO<sub>2</sub>-Induced Growth Enhancements in Temperate Forest Tree Seedlings**

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*Ecological Applications*, Volume 6, Issue 2 (May, 1996), 619-627.

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## ROOTING VOLUME, NUTRIENT AVAILABILITY, AND CO<sub>2</sub>-INDUCED GROWTH ENHANCEMENTS IN TEMPERATE FOREST TREE SEEDLINGS<sup>1</sup>

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**Abstract.** We examined growth and allocation responses to CO<sub>2</sub> enrichment for three species of co-occurring temperate forest tree seedlings grown in pots of varying rooting volumes and nutrient supply. Under both current and projected future CO<sub>2</sub> atmospheres, tree seedling growth was substantially greater with greater total nutrient supply (either due to increased nutrient addition rate or increased rooting volume) for all species. Increasing rooting volume alone, holding total nutrient supply constant, increased growth for gray and yellow birch and decreased growth for red maple. Root/shoot ratios were less and specific leaf masses were greater for plants grown in smaller pots, suggesting that the smaller pots did restrict root growth with consequences for whole-plant carbon allocation. After 12 wk of growth at light levels simulating those found in small gaps in temperate forests, each species exhibited growth, allocational and/or architectural differences due to increased CO<sub>2</sub>. Of 11 traits measured, 9 were significantly altered by CO<sub>2</sub> regime. Gray birch responded in architectural and allocational parameters only; total carbon accumulation after 12 wk of growth was not affected by CO<sub>2</sub> regime. Red maple and especially yellow birch grew larger in elevated CO<sub>2</sub>, and were less responsive in architectural and allocational parameters than gray birch. Increasing N concentration did not increase CO<sub>2</sub>-induced growth enhancements, except for increased leaf production in gray birch. In fact, CO<sub>2</sub>-induced increases in branch production were greatest at low nutrient concentration. Pot size had no effect on CO<sub>2</sub>-induced growth responses, except that CO<sub>2</sub>-induced enhancement in branch production was greater in smaller pots. With few exceptions, conditions within pots did not influence responses to elevated CO<sub>2</sub>, despite the many growth and architectural responses manifested by these tree seedlings in response to CO<sub>2</sub>, nutrient regime, and pot size.

**Key words:** *acclimation; Acer rubrum; Betula alleghaniensis; Betula populifolia; carbon dioxide; nutrient concentration; nutrients; rooting volume; temperate trees; tree seedlings.*

### INTRODUCTION

Atmospheric CO<sub>2</sub> levels are rising, and researchers generally agree that elevated CO<sub>2</sub> levels will affect plant growth and reproduction. However, there is considerable debate on the magnitude and duration of this effect. Some studies show that CO<sub>2</sub>-induced increases in photosynthetic and growth rates can be sustained over a period of years (e.g., Arp and Drake 1991, Drake and Leadley 1991, Idso and Kimball 1991). Others have shown that after an initial period of increased photosynthesis, plants exposed to elevated CO<sub>2</sub> readjust photosynthetic rates, resulting in little or no increase in growth or reproduction (reviewed in Strain and Cure 1985, Bazzaz 1990). Acclimation of photosynthesis to elevated CO<sub>2</sub> atmospheres may result from limitation of photosynthesis by other resources (light or nutrients,

for example), limited rates of phosphate regeneration, or alterations of source/sink balance within the plant (e.g., Arp 1991). Recently, the debate has focused on the apparent dichotomy between field- and non-field-based studies of CO<sub>2</sub>-induced photosynthetic and growth responses. It is argued that growing plants in small pots may restrict rooting volume and thus decrease the strength of roots as photosynthate sinks. Decreased sink strength is postulated to cause excess accumulation of photosynthate and to decrease photosynthetic rate and thus limit CO<sub>2</sub>-induced growth enhancements (Jarvis 1989, Arp 1991, Idso 1991, Thomas and Strain 1991). If this hypothesis is correct, decades of research on plant responses to increased CO<sub>2</sub> atmospheres may be compromised, and we will have to re-evaluate the potential CO<sub>2</sub>-induced growth responses of plants on a global scale (Idso 1991). Furthermore, local vegetational responses to increased CO<sub>2</sub> atmospheres may be limited where available rooting space is constrained (e.g., communities growing in areas of shallow bedrock or with extremely high root densities).

<sup>1</sup> Manuscript received 8 March 1995; revised 13 June 1995; accepted 16 June 1995.

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Most studies that have examined the relationship between rooting volume and acclimation to elevated CO<sub>2</sub> have not differentiated between the effects of restricted rooting volume and those of limited nutrient supply (McConnaughay et al. 1993a). It has been predicted, however, that CO<sub>2</sub>-induced growth enhancements for most species may be greatest at high nutrient availability (Bazzaz 1990, Mooney et al. 1991, Bazzaz and Fajer 1992). Unless total nutrient addition per pot is controlled, small rooting volumes inherently contain less nutrients than large rooting volumes. It is therefore impossible to determine whether low growth enhancement is due to limited rooting space or limited nutrient availability, either of which may be limiting under field conditions or in controlled environment studies. Recent studies that compared the effects of pot size and nutrient availability on growth enhancement due to CO<sub>2</sub> enrichment found that CO<sub>2</sub>-induced growth enhancement was either unaffected by rooting volume and nutrient availability (Samuelson and Seiler 1994) or was greater in smaller rooting volumes (Kerstiens and Hawes 1994) and/or higher nutrient regimes (McConnaughay et al. 1993a, b), depending on the species and the growth character examined. Thus, perhaps it is not root restriction per se that limits CO<sub>2</sub> responsiveness, but rather the reduced nutrient availability that may sometimes be present in smaller pots.

Studies concerning the effects of small rooting volume on acclimation to CO<sub>2</sub> enrichment have largely concentrated on herbaceous species (but see Kerstiens and Hawes 1994, Samuelson and Seiler 1994). However, acclimation to long-term exposure to increased CO<sub>2</sub> atmospheres has also been found in many tree species (Bazzaz 1990). The response of forest ecosystems to CO<sub>2</sub> rise is critical to the global carbon budget and to the interaction between the biosphere and the atmosphere (Mooney et al. 1991, Bazzaz and Fajer 1992, Wofsy et al. 1993). This study examines potential limitations to CO<sub>2</sub> responsiveness of temperate forest seedlings in growth containers. Specifically, we ask whether the CO<sub>2</sub>-induced growth responses of these temperate tree seedlings are reduced (1) in small rooting volumes, and/or (2) at lower nutrient availabilities. Throughout the paper, the term "CO<sub>2</sub> responsiveness" (sensu Hunt et al. 1991) will refer to the relative growth responses of plants grown at future predicted atmospheric CO<sub>2</sub> concentrations relative to those grown at current atmospheric CO<sub>2</sub> concentrations (i.e., 700 μL/L performance ÷ 350 μL/L performance; after Kimball 1983).

#### MATERIALS AND METHODS

Three species of common temperate forest trees were chosen for the experiment: gray birch (*Betula populifolia*), yellow birch (*Betula alleghaniensis*), and red maple (*Acer rubrum*). The species differ in successional status, with yellow birch being the most shade tolerant and gray birch being the least shade tolerant, and in CO<sub>2</sub> responsiveness, with yellow birch and red

TABLE 1. Amount of nutrient solution and total nutrients added to pots of various volumes and at two levels of nutrient addition at each fertilization. Nutrients were added weekly for 11 wk.

| Soil volume (L) | Solution volume (mL) | N, P, and K (each)* added per week (mg) |      |
|-----------------|----------------------|---|------|
|                 |                      | N1†                                     | N2   |
| 0.3             | 20.0                 | 2.54                                    | 25.4 |
| 0.7             | 46.6                 | 5.9                                     | 59   |
| 1.2             | 80.0                 | 10.2                                    | 102  |
| 3.0             | 200.0                | 25.4                                    | 254  |

\* Peter's 20-20-20 N-P-K liquid soluble fertilizer. N added as 5.61% nitrate-N, 3.96% ammonium-N, and 10.43% urea-N.

† Fertilizer addition rate of N1 solution = 0.635 g/L (≈9 mmol N, 4 mmol P, and 3.3 mmol K). Fertilizer addition rate of N2 solution = 6.35 g/L (≈90 mmol N, 40 mmol P, and 33 mmol K).

maple being more responsive to increased CO<sub>2</sub> atmospheres than gray birch (Bazzaz and Miao 1993). Seeds of the birch species were collected in October 1990 at Harvard Forest in Petersham, Massachusetts. Red maple samaras were collected from the same locale when seed drop occurred in June 1991. Seeds of all three species were germinated in flats of vermiculite under controlled greenhouse conditions in June 1991. When the first true leaves had formed, individual seedlings were transplanted into standard plastic pots of four sizes filled with 0.3, 0.7, 1.2, or 3.0 L of Cornell mix (1:1:1 sand:peat:perlite). Six randomly chosen replicate plants of each species in each of the four rooting volumes were randomly assigned to one of two nutrient-addition rates (Table 1).

The seedlings were grown in environmental growth chambers that controlled CO<sub>2</sub> level, temperature, humidity, and light. CO<sub>2</sub> levels were controlled within 20 μL/L at current (350 μL/L) or projected (700 μL/L) atmospheric CO<sub>2</sub> concentrations. There were six chambers arranged in three blocks; two replicate plants from each species × rooting volume × nutrient addition rate combination were randomly assigned to each block, for a total of 2 CO<sub>2</sub> levels × 2 nutrient addition rates × 4 rooting volumes × 3 species × 3 blocks × 2 replicates per block = 288 plants. Within each block, CO<sub>2</sub> levels were randomly assigned to the two chambers in a split-plot design. The chambers were randomized every other week (blocks were reassigned to a different pair of chambers and the low and high CO<sub>2</sub> chambers within each block were assigned randomly) to minimize chamber effects. Temperature and daylength were set to follow seasonal trends at the Harvard Forest, and were updated monthly over the growing season. Light levels in the chamber were ≈300–400 μmol·m<sup>-2</sup>·s<sup>-1</sup>, approximating a daily photosynthetic photon flux of 12.5 mol·m<sup>-2</sup>·d<sup>-1</sup> during midsummer, or that available in a small gap (Sipe 1990, Wayne and Bazzaz 1993). The pots were misted daily by hand, and humidity within the chambers was maintained at ≈50%. Smaller volume pots were placed upon overturned pots so that all

pots were at approximately the same height to ensure equivalent light conditions.

Nutrients were applied weekly in aqueous solution, in volumes scaled to the rooting volumes of each pot, at one of two nutrient addition rates (Table 1). Therefore, absolute nutrient supply varied with rooting volume and with the concentration of the nutrient solution added. This design allowed us to examine the effects of increased CO<sub>2</sub> atmospheres along two important soil resource gradients, rooting volume and nutrient availability. The nutrient additions consisted of weekly additions of 0.635 g/L (low nutrient treatment, N1) or 6.35 g/L (high nutrient treatment, N2) of Peter's 20–20–20 N-P-K liquid soluble fertilizer, N added as 5.61% nitrate-N, 3.96% ammonium-N, and 10.43% urea-N. These nutrient treatments simulated a wide range of nutrient availability seen by these species; the low nutrient addition rate approximates the nitrogen levels found in low nutrient soils at Harvard Forest (35 kg·ha<sup>-1</sup>·yr<sup>-1</sup>), and the high nutrient addition rate approximates a fertilized commercial hardwood stand (350 kg·ha<sup>-1</sup>·yr<sup>-1</sup>, estimates based on 52 weekly additions to a 15-cm (6-inch) standard pot, after Bassow et al. 1994).

Plants were harvested 12 wk after transplanting, and were separated into roots, stems, and leaves. Leaf area was measured with a leaf area meter (LI 3000, Li-Cor Incorporated, Lincoln, Nebraska). Plant parts were dried in a draught oven at 70°C for at least 1 wk before weighing. Allocational parameters were calculated as follows: leaf area ratio (LAR) = total leaf area (cm<sup>2</sup>)/total plant mass (g); specific leaf mass (SLM) = total leaf mass (g)/total leaf area (cm<sup>2</sup>); and root/shoot ratio = root mass (g)/shoot mass (g). The data were transformed when necessary to meet assumptions of normality and homoscedasticity; log-transformations were used for biomass and architectural data and arcsine transformations were used for allocational data. Data were analyzed using a split-plot analysis of variance (ANOVA) whose main effects were block, CO<sub>2</sub>, species, nutrient concentration, and rooting volume (DataDesk 3.0; Velleman 1989). All terms were tested over the residual error except for the main effect of CO<sub>2</sub>, which was tested over the main plot error term (CO<sub>2</sub> × block). To examine the effects of rooting volume independent of total nutrient supply (the physical aspects of rooting volume), we conducted a separate ANOVA using the two treatments that received the same total nutrient addition. The main effects of this model were block, CO<sub>2</sub>, species, and rooting volume. Terms were tested as above.

## RESULTS

Decreased nutrient supply, either through reduced nutrient concentration within pots or through reduced pot volume, decreased growth substantially for all species. Total mass varied over 30-fold in red maple to over 60-fold in gray birch in response to differences

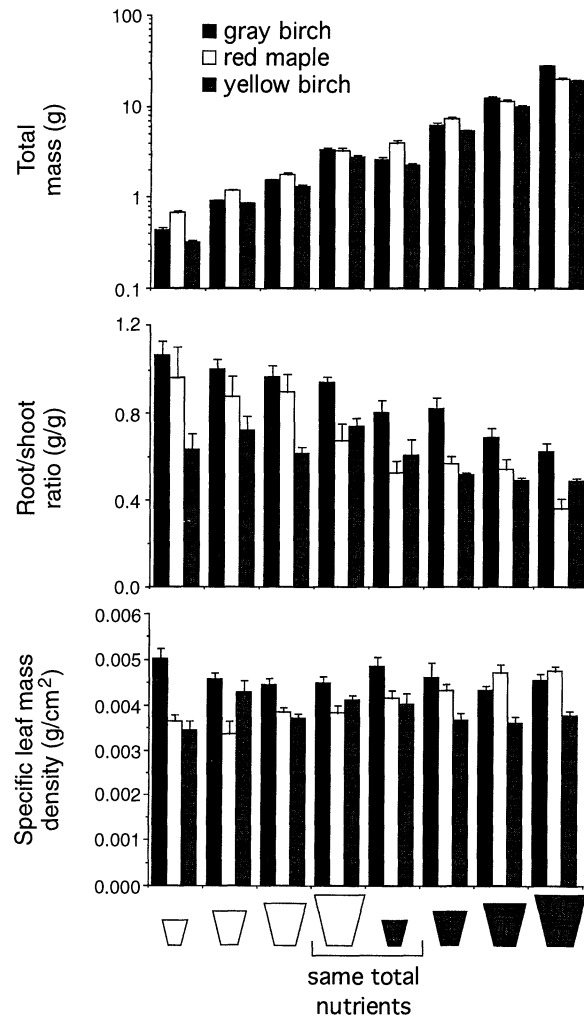


FIG. 1. Total plant dry mass, root/shoot ratios, and specific leaf masses of three temperate tree species after 12 wk of growth at current (350  $\mu$ L/L) atmospheric CO<sub>2</sub> levels as a function of pot conditions (mean  $\pm$  1 SE). The four pot sizes used were 0.3 L, 0.7 L, 1.2 L, and 3.0 L in rooting (soil) volume. Unshaded pots were fertilized at the low nutrient addition rate (0.635 g/L of Peter's 20–20–20 N-P-K liquid soluble fertilizer), shaded pots were fertilized at the high nutrient addition rate (6.35 g/L). Nutrient additions were scaled to pot volume (see Table 1 for details). Large volume, low nutrient pots and small volume, high nutrient pots had equal total nutrient contents.

in total nutrient and rooting space availability, along the gradient from small pots receiving low nutrient additions to large pots receiving high nutrient additions (Fig. 1). Decreased rooting volume independent of total nutrient supply either decreased (gray and yellow birch) or stimulated (red maple) plant growth (Fig. 1). Root/shoot ratios were less and specific leaf masses were greater for plants grown in smaller pots (Fig. 1). This suggests that (1) the range of nutrient levels and pot sizes used greatly altered plant growth rates over the 12-wk period, and that (2) the smaller pots did

TABLE 2. Effects of increased atmospheric CO<sub>2</sub> concentration on growth and allocation for temperate tree seedlings grown at small gap light levels. Arrows indicate direction of effect; significant effects ( $P < 0.05$  as determined by LSD post-hoc comparisons of adjusted means) only are shown. Effects in parentheses are significant at  $0.05 < P < 0.10$ .

|                    | Gray birch | Red maple | Yellow birch |
|--------------------|------------|-----------|--------------|
| Total mass         |            | ↑         | ↑            |
| Root mass          |            |           | ↑            |
| Leaf mass          |            | ↑         | ↑            |
| Stem mass          |            |           | ↑            |
| Branch mass*       |            | ...†      | (↑)          |
| Leaf area          | ↓          | ↑         |              |
| Number of leaves   | ↓          |           |              |
| Leaf area ratio    | ↓          |           | ↓            |
| Root:shoot ratio   | ↓          |           |              |
| Specific leaf mass | ↑          |           | ↑            |

\* Results for total branch length are similar to those for total branch mass.

† Red maple seedlings did not branch; data are not available.

restrict root growth with consequences for whole-plant carbon allocation.

After 12 wk of growth at small gap light levels, each species exhibited growth, allocational and/or architectural differences due to increased CO<sub>2</sub> (Table 2, Fig. 2). Of 11 traits measured, 9 were significantly altered by CO<sub>2</sub> regime (Table 3). Gray birch responded in architectural and allocational parameters only; total carbon accumulation did not change over the 12 wk, though it might have if growth had continued. Red maple and especially yellow birch grew larger in elevated CO<sub>2</sub>, and were less responsive in architectural and allocational parameters than gray birch (Fig. 2). Specific leaf masses for all species and branch production for the birches (red maple did not branch throughout the duration of the experiment) were greater for plants grown in elevated CO<sub>2</sub> atmospheres (Fig. 2). Leaf area ratios (LARs) were lower for birch plants exposed to high CO<sub>2</sub>; however, the mechanisms of CO<sub>2</sub>-induced LAR reduction differed between the two birch species. Increased CO<sub>2</sub> atmospheres resulted in a decline in leaf area production but no change in biomass production in gray birch (Fig. 2). Leaf area production was unaffected by CO<sub>2</sub> environment for yellow birch, but biomass production was stimulated under high CO<sub>2</sub>, resulting in decreased LAR (Fig. 2).

CO<sub>2</sub> enrichment reduced gray birch canopy sizes in terms of numbers of leaves present in the canopy but not total canopy leaf area for plants grown at the low nutrient addition rate (Table 3, Fig. 3). Rooting volume (pot size) did not alter this relationship. Although CO<sub>2</sub> enrichment reduced leaf production, branch production increased for both gray and yellow birch, but only at low nutrient addition rates (Table 3, Fig. 4). Again, rooting volume did not alter this relationship. In general, rooting volume had no effect on CO<sub>2</sub> responsiveness, except that CO<sub>2</sub>-induced reductions in gray birch

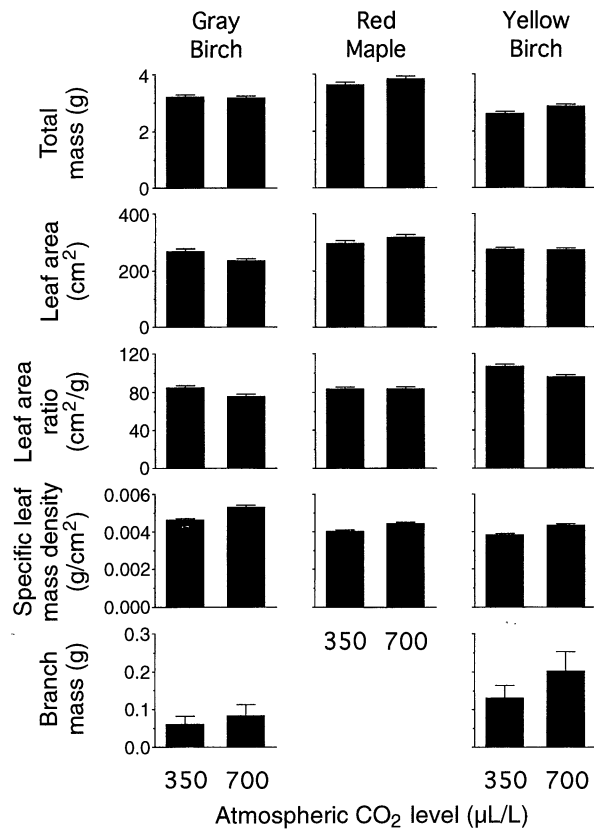


FIG. 2. Growth and allocational responses of three temperate tree species after 12 wk of growth at current (350  $\mu\text{L/L}$ ) and future predicted (700  $\mu\text{L/L}$ ) atmospheric CO<sub>2</sub> levels (mean  $\pm$  1 SE).

leaf production were less (or actually positive) and CO<sub>2</sub>-induced enhancements in branch production were greater in smaller pots (Table 3, Figs. 3 and 4). When comparing small and large pots at the same nutrient content, however, responsiveness was greater in larger pots (i.e., those with the higher nutrient addition rate). Total growth responses of yellow birch followed a non-significant trend similar to branch production responses; CO<sub>2</sub>-induced growth enhancements were greater for plants grown at low nutrient concentrations and in smaller pots (Fig. 4).

## DISCUSSION

### Responses to CO<sub>2</sub> enrichment

The CO<sub>2</sub>-induced growth enhancements found over the 12-wk period in the present study were modest (average of -1% for gray birch, 7% for red maple, and 11% for yellow birch) and somewhat lower than growth responses reported elsewhere for these (Miao et al. 1992, Bazzaz and Miao 1993, Bassow et al. 1994, but see Bazzaz et al. 1990) and other temperate tree species (reviewed in Wullschlegel et al. 1995). Other studies have reported little or no CO<sub>2</sub>-induced growth enhancement for temperate tree species (e.g., Williams et al.

TABLE 3. Results of analysis of variance on (A) growth and allocational responses of temperate tree seedlings to alterations in growing conditions within pots and atmospheric CO<sub>2</sub> concentration, and (B) CO<sub>2</sub> responsiveness under these conditions. Values are probabilities associated with split-plot analysis of variance tests of the main effects of species (*S*), atmospheric CO<sub>2</sub> concentration (*C*), nutrient addition rate (*N*), pot volume (*V*), pot volume (physical space) among pots of equal total nutrient content (*P*), and their interactions.

|   | Total mass | Root mass | Leaf mass | Stem mass | Branch mass* | Leaf area | Number of leaves | Leaf area ratio | Root/shoot ratio | Specific leaf mass |
|---|------------|-----------|-----------|-----------|--------------|-----------|------------------|-----------------|------------------|--------------------|
| A) Main effects and interactions          |            |           |           |           |              |           |                  |                 |                  |                    |
| Species ( <i>S</i> )                      | .0001      | .0001     | .0001     | .0001     | .0001        | .0001     | .0001            | .0001           | .0001            | .0001              |
| CO <sub>2</sub> ( <i>C</i> )              | NS         | NS        | NS        | NS        | NS           | NS        | NS               | NS              | NS               | NS                 |
| <i>C</i> × <i>S</i>                       | .0387      | .0138     | .0192     | NS        | NS           | .0003     | .0058            | .0064           | NS               | .0148              |
| Nutrient ( <i>N</i> )                     | .0001      | .0001     | .0001     | .0001     | .0001        | .0001     | .0001            | NS              | .0001            | .0001              |
| <i>N</i> × <i>S</i>                       | .0019      | .0001     | .0441     | .0001     | .0025        | .0001     | .0001            | .0135           | .0001            | .0001              |
| Volume ( <i>V</i> )                       | .0001      | .0001     | .0001     | .0001     | .0001        | .0001     | .0001            | NS              | .0001            | NS                 |
| <i>V</i> × <i>S</i>                       | .0001      | .0001     | .0001     | .0001     | NS           | .0001     | .0001            | .0001           | .0005            | .0001              |
| Physical space ( <i>P</i> )†              | .0100      | .0003     | .0115     | NS        | NS           | .0034     | NS               | NS              | .0074            | NS                 |
| <i>P</i> × <i>S</i> †                     | .0001      | .0041     | .0174     | .0001     | .0216        | NS        | .0413            | .0440           | NS               | NS                 |
| <i>N</i> × <i>V</i>                       | .0001      | .0148     | .0024     | .0001     | .0004        | .0033     | .0001            | NS              | NS               | NS                 |
| <i>N</i> × <i>V</i> × <i>S</i>            | .0374      | NS        | NS        | .0429     | .0081        | NS        | .0001            | NS              | NS               | .0267              |
| B) CO <sub>2</sub> responsiveness         |            |           |           |           |              |           |                  |                 |                  |                    |
| Nutrient ( <i>C</i> × <i>N</i> )          | NS         | NS        | NS        | NS        | .0448        | NS        | NS               | NS              | NS               | NS                 |
| <i>C</i> × <i>N</i> × <i>S</i>            | NS         | NS        | NS        | NS        | NS           | NS        | .0176            | NS              | NS               | NS                 |
| Volume ( <i>C</i> × <i>V</i> )            | NS         | NS        | NS        | NS        | NS           | NS        | NS               | NS              | NS               | NS                 |
| <i>C</i> × <i>V</i> × <i>S</i>            | NS         | NS        | NS        | NS        | NS           | NS        | NS               | NS              | NS               | NS                 |
| Physical space ( <i>C</i> × <i>P</i> )†   | NS         | NS        | NS        | NS        | .0187        | NS        | NS               | NS              | NS               | NS                 |
| <i>C</i> × <i>P</i> × <i>S</i> †          | NS         | NS        | NS        | NS        | NS           | NS        | NS               | NS              | NS               | NS                 |
| <i>C</i> × <i>N</i> × <i>V</i>            | NS         | NS        | NS        | NS        | NS           | NS        | NS               | NS              | NS               | NS                 |
| <i>C</i> × <i>N</i> × <i>V</i> × <i>S</i> | NS         | NS        | NS        | NS        | NS           | NS        | NS               | NS              | NS               | NS                 |
| Model <i>r</i> <sup>2</sup>               | 98.8       | 97.2      | 98.5      | 98.2      | 92.3         | 98.3      | 92.5             | 51.5            | 66.4             | 68.9               |

\* Results for total branch length are similar to those for branch mass.

† Contrast of 0.3 L and 3.0 L volume pots at equal total nutrients per pot.

1986, Bazzaz et al. 1990, Norby et al. 1992). While the relatively short duration of the experiment (12 wk) may have contributed to these modest growth responses, previous evidence does not support this. A careful perusal of the data bases published in recent reviews reveals that CO<sub>2</sub>-induced growth enhancements for trees exposed to CO<sub>2</sub> for shorter duration (12 wk or less) are 10–15% greater than those for trees exposed for longer (12 wk to 2 yr) time periods (Poorter 1993, Wullschleger et al. 1995). This suggests that short-term growth responses of trees are generally an overestimate of long-term growth stimulation. Declining stimulation in leaf level carbon gain seen after the first 6 wk of exposure to increased CO<sub>2</sub> levels (Curtis 1996), and/or reduced growth capacities of older seedlings (Poorter 1993) may contribute to the decline in growth enhancements as exposure duration increases.

Bazzaz and Miao (1993) found that CO<sub>2</sub>-induced growth enhancements were greater for these species under lower, understory light conditions. Light levels used in the present study approximated those found in a small gap (Wayne and Bazzaz 1993), considerably higher than those found in the temperate forest understory, and may have contributed to the modest growth responses seen here. Despite the modest overall growth response to increased CO<sub>2</sub>, nearly all growth, allocational, and architectural characters measured exhibited significant responses to CO<sub>2</sub> enrichment. While CO<sub>2</sub>-

induced changes in allocation and architecture may not necessarily result in increased whole-plant carbon gain in temperate trees (see also Norby et al. 1992), such changes may significantly alter canopy display, light interception, and growth within complex (multispecific) plant stands (Reekie and Bazzaz 1989, Körner and Arnone 1992).

#### *Effects of pot conditions on CO<sub>2</sub> responsiveness*

CO<sub>2</sub>-induced growth, architectural, and allocational responses of gray and yellow birch and red maple seedlings to increased CO<sub>2</sub> atmospheres were generally not influenced by nutrient availability, contrary to predictions in the literature (e.g., Bazzaz 1990, Mooney et al. 1991, Bazzaz and Fajer 1992). There were few exceptions to this trend; the number of leaves (but not leaf area) produced by low-nutrient-fed gray birch seedlings was reduced under high CO<sub>2</sub> regimes relative to seedlings grown under current CO<sub>2</sub> atmospheres, while the production of branch mass by both gray and yellow birch was increased in these same treatments (Figs. 3, 4). While it is possible that the low nutrient addition rate used in the present study was higher than those that might be considered truly stressful (plants receiving the low fertilizer application had access to a maximum of 28 mg each of N, P, and K in the smallest volume pots and nearly 280 mg in the largest pots, ignoring losses due to leaching, immobilization by mi-

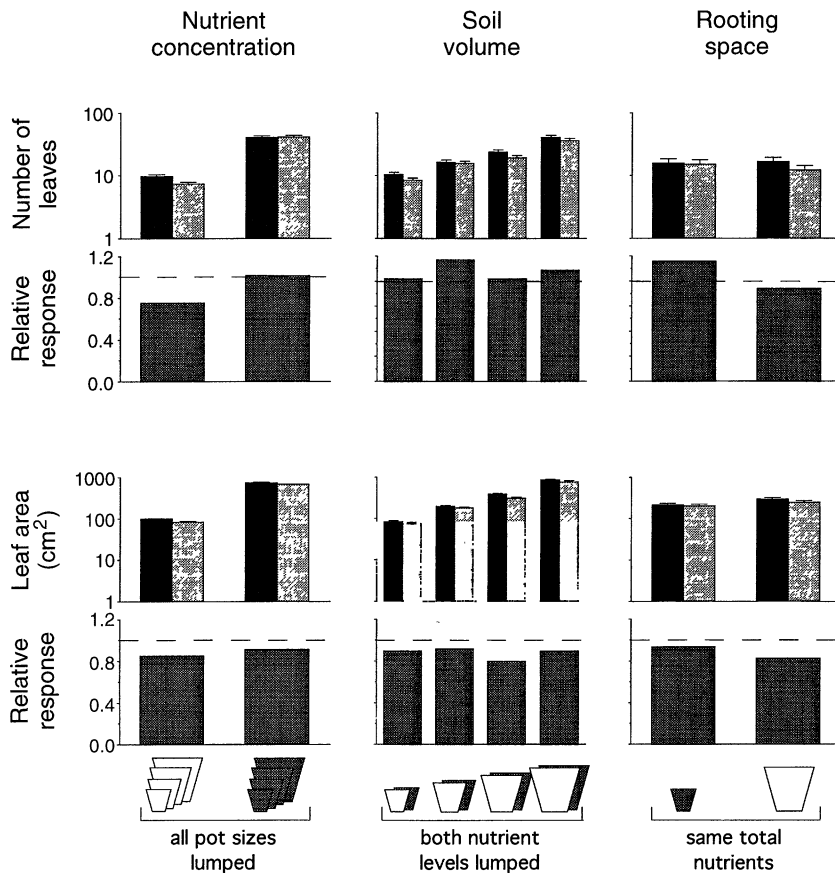


FIG. 3. Standing canopy size, in terms of number of leaves present and total canopy leaf area, of gray birch seedlings after 12 wk of growth at current ( $350 \mu\text{L/L}$ , solid bars) and future predicted ( $700 \mu\text{L/L}$ , shaded bars) atmospheric  $\text{CO}_2$  levels under various pot conditions (mean  $\pm 1$  SE), and relative responses to  $\text{CO}_2$  enrichment ( $700 \mu\text{L/L}$  performance  $\div$   $350 \mu\text{L/L}$  performance, shaded bars) under these conditions. Pot sizes and nutrient additions used as in Fig. 1. Means presented in the nutrient concentration panel are for all pot sizes lumped, means presented in the soil volume panel are for both nutrient levels lumped, means presented in the rooting space panel are only for those two treatments with equal total nutrient additions per pot (high nutrient, small volume pots and low nutrient, large volume pots; see Table 1). All means and errors have been adjusted for block and chamber effects.

crobes, etc.; cf. total plant mass of 0.5 and 3 g in small vs. large volume pots in the low nutrient treatment), it is representative of the lower range of nutrient availability in the generally nutrient-limited Harvard Forest (J. Melillo, *personal communication*). Furthermore, the nutrient addition rates used in the present study were identical to those in previous work that clearly demonstrated nutrient limitation to  $\text{CO}_2$  responsiveness in these species (Bazzaz and Miao 1993, Bassow et al. 1994). Finally, plant growth did increase by fivefold from low to high nutrient availability, independent of  $\text{CO}_2$  regime or pot size (Fig. 1), suggesting that the lower nutrient addition rate presented a substantive limitation to growth in these seedlings. Therefore, we do not feel justified in concluding that the nutrient levels used in the present study were non-limiting.

The general lack of effect of nutrient regime on  $\text{CO}_2$  responsiveness is in contrast with results from previous studies of these same species that found that  $\text{CO}_2$ -in-

duced growth enhancements were greater when nutrient availabilities were increased (Bazzaz and Miao 1993, Bassow et al. 1994), but agree with results from other temperate tree species (Norby and O'Neill 1991, Kerstiens and Hawes 1994, Samuelson and Seiler 1994). In a recent review of 73 studies, Wullschlegel et al. (1995) found no effect of nutrient limitation on  $\text{CO}_2$ -induced growth enhancements.

Similarly, although rooting volume varied 10-fold and all species exhibited large growth and allocational responses to this variation in rooting volume, there were few effects of rooting volume on  $\text{CO}_2$ -induced growth, architectural, or allocational responses. Exceptions to this trend were decreased leaf production for gray birch in large rooting volumes and increased branch production for gray and yellow birches in small rooting volumes when treatments with equal total nutrient content per pot were compared (Fig. 3). However, as these treatments necessarily altered nutrient con-

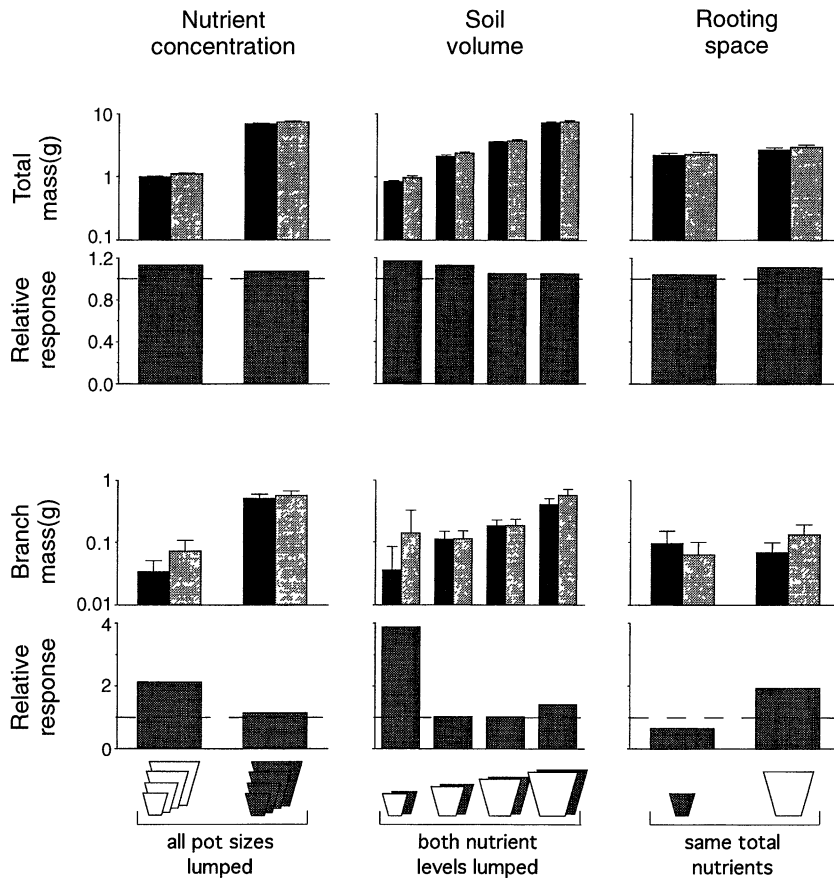


FIG. 4. Total plant dry mass and branch production of yellow birch seedlings after 12 wk of growth at current (350  $\mu\text{L/L}$ , solid bars) and future predicted (700  $\mu\text{L/L}$ , shaded bars) atmospheric CO<sub>2</sub> levels under various pot conditions (mean  $\pm$  1 SE), and relative responses to CO<sub>2</sub> enrichment (700  $\mu\text{L/L}$  performance  $\div$  350  $\mu\text{L/L}$  performance, shaded bars) under these conditions. Pot sizes and nutrient additions as in Fig. 3. All means and errors have been adjusted for block and chamber effects. Gray birch branch production responses to increased CO<sub>2</sub> atmospheres are similar to those shown here for yellow birch.

centrations per pot as rooting volumes were varied, we cannot comfortably ascribe these results to altered rooting volume per se.

We have previously reported that CO<sub>2</sub> responsiveness in an annual plant was greatest at high nutrient addition rates and in small pots (McConnaughay et al. 1993a, b). Results of the present study suggest that rooting environment has little or no effect on CO<sub>2</sub>-induced growth responses for temperate tree seedlings. Increasing nutrient concentration within pots altered CO<sub>2</sub>-induced responses in leaf (enhanced) and branch (reduced) production for gray birch, but did not alter other architectural or growth responses for this or other species examined. The only effect of pot size on CO<sub>2</sub> responsiveness in these species was greater CO<sub>2</sub>-induced enhancement in branch production in smaller pots. These results are in general agreement with recent studies that report no effect of rooting volume or nutrient availability on CO<sub>2</sub>-induced growth responses for red spruce seedlings following two growing seasons of exposure to increased CO<sub>2</sub> atmospheres (Samuelson

and Seiler 1994) or modest increases in CO<sub>2</sub>-induced growth enhancements for cherry seedlings following one growing season of exposure to increased CO<sub>2</sub> atmospheres with increasingly limited rooting volumes (Kerstiens and Hawes 1994).

The 12-wk growth period should have been sufficient for root restriction to have resulted in reduced sink strength and consequently reduced photosynthetic rates for seedlings in small pots (cf. 30 d of root restriction in cotton and CO<sub>2</sub>-induced photosynthetic responses, Thomas and Strain 1991). However, the link between root restriction and reduced photosynthetic rates remains ambiguous; most studies reporting photosynthetic depression as a result of root restriction confound the effects of limited nutrient supply and limited root volume (e.g., Herold and McNeil 1979, Robbins and Pharr 1988, Thomas and Strain 1991, Nobel et al. 1994, Rieger and Marra 1994). When root restriction was imposed in the absence of nutrient limitation, root restriction resulted in increased photosynthetic rates (Carmi et al. 1983), contrary to predictions based on



source/sink imbalance and end-product inhibition. The link between root restriction and photosynthetic acclimation to long-term exposure to CO<sub>2</sub> enrichment also remains ambiguous. Root restriction coupled with nutrient limitation has been reported to decrease CO<sub>2</sub>-induced photosynthetic enhancements (Thomas and Strain 1991, Nobel et al. 1994). However, no effects of rooting environment on CO<sub>2</sub>-induced photosynthetic responses were found when nutrient availability and root restriction were examined separately (Samuelson and Seiler 1994). Finally, a recent review of photosynthetic responses to elevated CO<sub>2</sub> atmospheres reports no effect of pot size on CO<sub>2</sub>-induced photosynthetic enhancements in open-top chamber studies (Curtis 1996). The effects of pot size in growth chamber studies could not be evaluated due to a lack of breadth of pot sizes used in these studies, confounding pot size with other growth-chamber-specific effects (e.g., low red-far red ratios, low light intensities, etc.).

Whether or not root restriction results in photosynthetic acclimation to long-term exposure to enriched CO<sub>2</sub> atmospheres, reductions in potential CO<sub>2</sub>-induced growth enhancements as a function of root restriction have not been reported. CO<sub>2</sub>-induced growth enhancements were unaffected by pot size (Samuelson and Seiler 1994) or were greater for plants in smaller pots (McConnaughay et al. 1993a, b, Kerstiens and Hawes 1994), even when photosynthetic rates were reduced (Thomas and Strain 1991, Nobel et al. 1994).

#### *Predicting plant growth in a high CO<sub>2</sub> future*

Despite the growing number of studies that report growth responses to CO<sub>2</sub> enrichment, few general patterns emerge concerning the degree of growth enhancements we can expect in a CO<sub>2</sub>-rich future. Predictions that nutrient or other environmental stresses (e.g., water stress) may reduce CO<sub>2</sub>-induced growth enhancements have not been substantiated by recent reviews of plant responses to elevated CO<sub>2</sub> (Wullschlegel et al. 1995, Curtis 1996). Similarly, predictions that restricted rooting volumes may be responsible for limited CO<sub>2</sub>-induced growth enhancements have not been demonstrated (Thomas and Strain 1991, McConnaughay et al. 1993a, b, Kerstiens and Hawes 1994, Nobel et al. 1994, Samuelson and Seiler 1994, review by Curtis 1996 and the present study). There is some evidence that CO<sub>2</sub>-induced growth responses may be limited under conditions of phosphorus deficiency (Wullschlegel et al. 1995).

Some evidence suggests that CO<sub>2</sub>-induced growth responses may be greatest for those species that have high growth capacities (e.g., crops, fast-growing species, indeterminate species) due to the continued presence of available sinks (Poorter 1993). Under this scenario, we might predict that environmental stresses will decrease CO<sub>2</sub> responses whenever the pool of active carbohydrate sinks declines. If Poorter's hypothesis that actively growing plants maintain positive growth

responses to CO<sub>2</sub> enrichment is correct, species-specific predictions of CO<sub>2</sub> responsiveness should include an assessment of overall growth potential as modified with respect to specific growth conditions that will alter that growth potential (e.g., the continued development of carbohydrate-demanding tissues, the number of available growing tips, etc.). This places a burden on understanding the potential growth dynamics for each species under a variety of potential environmental scenarios.

#### *Conclusion*

When examining the potential impact of elevated CO<sub>2</sub> on a species' ecology, it is important to consider the conditions under which the species naturally grows. In natural conditions, plants commonly face limitation by some critical resources, including rooting volume, nutrient availability, or light. These conditions will almost certainly affect overall allocational patterns, architectural display, and overall growth of temperate forest tree species, and could potentially influence seedling responses to increased levels of atmospheric CO<sub>2</sub>. The present study, however, does not support the hypothesis that restricted rooting volume necessarily results in CO<sub>2</sub> acclimation responses in temperate forest tree seedlings, and lends only weak support to the hypothesis that acclimation to CO<sub>2</sub> enrichment occurs more frequently under nutrient-limited conditions. The causes of modest to no CO<sub>2</sub>-induced growth enhancements in controlled environment studies of temperate tree seedlings remain unclear and warrant further study.

#### ACKNOWLEDGMENTS

We thank Glenn Berntson for discussions involving the design and scope of this experiment, Shili Miao for overseeing harvests and plant processing, and Susan Bassow, Saul Cunningham, Christopher Field, Richard Kobe, and anonymous reviewers for providing comments on an earlier version of this manuscript. This research was supported by the Department of Energy, grant number DE-FG02-84ER60257.

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