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# Light acquisition and growth by competing individuals in CO<sub>2</sub>-enriched atmospheres: consequences for size structure in regenerating birch stands

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## Summary

**1** To investigate how CO<sub>2</sub>-enriched atmospheres may influence plant competition and stand size structure in regenerating forests, experimental populations comprised of three maternal families of yellow birch (*Betula alleghaniensis* Britt.) were grown in both ambient (350 µL L<sup>-1</sup>) and elevated (700 µL L<sup>-1</sup>) CO<sub>2</sub> concentrations in a controlled environment facility. Individual seedling growth, light acquisition, and stand size structure were monitored throughout the first year of growth.

**2** Elevated CO<sub>2</sub> increased average seedling biomass in stands by 14%, a value much lower than the average enhancement reported elsewhere for individually grown yellow birch seedlings. Maternal families within stands differed significantly in their growth responsiveness to elevated CO<sub>2</sub>, ranging from +51% to -16%. As a result, CO<sub>2</sub> altered the genetic identity of dominants in regenerating stands.

**3** Seedling size inequalities were generally lower in CO<sub>2</sub>-enriched environments, a result that contrasts with other studies that have reported increased size inequality with increased productivity in resource-rich environments. Distribution modifying functions relating initial seedling size and subsequent growth suggest that there was a relatively smaller advantage to being larger in elevated vs. ambient CO<sub>2</sub> environments. Together, these results suggest that competition in CO<sub>2</sub>-enriched environments was less size-asymmetric.

**4** Differences in stand size structure between CO<sub>2</sub> treatments were related to competition for light. Empirical measures of seedling light acquisition per unit biomass suggest competition for light was less size-asymmetric in CO<sub>2</sub>-enriched environments. Decreased size-asymmetric competition for light was attributable both to differences in the CO<sub>2</sub>-use efficiency of high-light canopy dominants vs. low-light canopy subordinates, and to CO<sub>2</sub>-induced differences in plant allometry.

**5** This study highlights the importance of stand-level competition studies in global change research, and more generally, the value of studies that combine phenomenological descriptions of stand development with physiological mechanisms of competition.

*Keywords:* *Betula alleghaniensis*, forest regeneration, global change, resource competition, size hierarchies

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## Introduction

Understanding how forest ecosystems will respond to rising CO<sub>2</sub> levels is critical, both because forests play an important role in the global carbon cycle (Wofsy *et al.* 1993; Ciais *et al.* 1995; Tans *et al.* 1995), and because CO<sub>2</sub> fertilization may necessitate changes in current silvicultural management programs (Sandenburg *et al.* 1987; Graham *et al.* 1990, Bazzaz *et al.* 1996). To date, research on the impacts of global

change on forests has relied on comparative physiological and developmental studies of individually grown tree seedlings and saplings (see reviews by Norby 1989; Eamus & Jarvis 1989; Bazzaz 1990; Ceulemans & Mousseau 1994; Wullschleger *et al.* 1995). However, in nature, tree seedlings and saplings rarely establish and grow in isolation. In a previous study, we demonstrated that density-dependent interactions in regenerating yellow birch stands resulted in a 33% lower stimulation by CO<sub>2</sub> of stand-level

productivity relative to the responses of individually grown trees (Wayne & Bazzaz 1995; Bazzaz *et al.* 1995). In this paper, we explore how CO<sub>2</sub>-induced growth enhancements may influence plant competition for light, and the consequences of these interactions for size structure and genetic composition of 1-year-old stands.

As stands develop, populations generally display a great degree of size variability or inequality, such that a few individuals often contribute disproportionately to the net productivity of the whole community (Koyama & Kira 1956; Harper 1977). Size variability often appears early in stand development, and is attributable to some combination of variation in seed size (Naylor 1980; Howell 1981), emergence time (Black & Wilkinson 1963; Stanton 1985), early growth rate (Koyama & Kira 1956; Turner & Rabinowitz 1983), and fine-scale environmental heterogeneity (Harterink & Bazzaz 1984; Fowler 1988). However, as plants begin to interact, the magnitude of inter-individual size inequality, often referred to as size hierarchy, increases unless there is much mortality of suppressed individuals. It is generally believed that the exacerbation of initial size inequalities is due to size-asymmetric or one-sided competition, where larger individuals have a disproportionate effect on smaller individuals, or obtain a disproportionate share of resources relative to their size (Begon 1984; Weiner 1990). More specifically, increases in size inequalities during stand development are believed to result from asymmetric competition for light (Ford & Diggle 1981; Weiner 1986; Weiner & Thomas 1986; Schmitt *et al.* 1987; Jurik 1991).

Whereas a number of studies have demonstrated that elevated CO<sub>2</sub> can influence the average competitive performance of individuals in single-species (e.g. du Cloux *et al.* 1987; Overdieck 1993) and mixed-species populations (e.g. Reekie & Bazzaz 1989; Chiariello & Field 1996), few studies have investigated the evolutionary and ecological consequences of CO<sub>2</sub>-induced changes in size structure (but see Morse & Bazzaz 1994). For gap-filling forest species, it is often the case that only one or two fast-growing dominant saplings successfully replace fallen canopy trees (e.g. Alvarez-Buylla & Martinez-Ramos 1992). As size and canopy stature are related to reproductive success, CO<sub>2</sub>-induced changes in plant relative sizes and dominance hierarchies could have significant consequences for patterns of natural selection (Bazzaz *et al.* 1995; Thomas & Jasienski 1996). CO<sub>2</sub>-induced changes in size structure may also have significant silvicultural implications. For example, the management of many forest species is for saw logs (i.e. nonpulpwood species). Different stocking and management practices may be needed depending on whether CO<sub>2</sub>-induced biomass increases are distributed relatively equally among all individuals, or disproportionately distributed among a few large and many small individuals (Sandenburg *et al.* 1987).

We hypothesize three alternative scenarios regard-

ing the effects of elevated CO<sub>2</sub> on stand development and plant-plant interactions. Scenario 1 predicts that by stimulating productivity, elevated CO<sub>2</sub> may accelerate rates of stand development, but not fundamentally alter the nature of competitive interactions between plants. If this were the case we would expect to observe greater inequality between individuals in elevated CO<sub>2</sub> environments at any given point in time; however, relationships between measures of seedling inequality and total stand biomass would not differ with CO<sub>2</sub> level. Scenario 2 predicts that CO<sub>2</sub>-stimulated productivity would both increase rates of stand development and also exacerbate the intensity of asymmetric competition, specifically by increasing competition for light (Bazzaz & McConaughay 1992). If this scenario occurred, we would expect not only greater size inequalities at elevated CO<sub>2</sub> at any given time, but also more positive relationships between measures of stand biomass and size inequality in high CO<sub>2</sub> treatments. A third potential scenario is based on the repeatedly observed phenomenon that CO<sub>2</sub>-induced growth enhancements of individually grown plants are greater at relatively lower light levels (Gifford 1977; Wheeler *et al.* 1991; Bazzaz & Miao 1992; Bassow 1995). Thus, in closed-canopy stands, it is possible that light-limited subordinate seedlings would be more stimulated by elevated CO<sub>2</sub> atmospheres than light-saturated dominants. If this were true, we would expect greater proportional CO<sub>2</sub>-enhancements in subordinate vs. dominant seedlings, less size-asymmetric competition for light, and thus a lower degree of overall seedling inequality per unit stand biomass in elevated vs. ambient CO<sub>2</sub> treatments.

This study investigates how elevated CO<sub>2</sub> influences the development of size hierarchies in regenerating stands composed of three co-occurring maternal families of yellow birch (*Betula alleghaniensis* Britt.), and the nature of competition for light that underlies stand development. Our experiment specifically addresses the following questions: (1) Does elevated CO<sub>2</sub> alter the magnitude of size inequalities in regenerating birch stands?; (2) If size hierarchies are altered, are differences simply due to differential rates of stand development, or are trajectories of stand development altered?; (3) To what extent does asymmetric competition for light drive the formation of size hierarchies in birch stands, and how does elevated CO<sub>2</sub> alter competition for light?; (4) Are seedlings' positions within size hierarchies correlated with their maternal family identity?

## Materials and methods

### SEED COLLECTION AND CONTROLLED-ENVIRONMENT GROWTH CONDITIONS

Seeds of yellow birch (*Betula alleghaniensis* Britt.) were collected from three mother trees within a 100 m<sup>2</sup> area in a mixed-species hardwood stand in the Har-

vard Forest, Petersham MA, USA, during the fall of 1992. Catkins were air-dried for 2 weeks, and then stored in a coldroom using the protocol of Brinkman (1974). On April 21 1993, seeds of each maternal family were sown into horticultural trays with 5.0 cm deep  $\times$  2.5 cm diameter cells filled with a 1:1:1 mixture of forest soil, sand, and peat. Trays were located in glasshouse modules set at either low ( $350 \mu\text{L L}^{-1}$ ) or high ( $700 \mu\text{L L}^{-1}$ ) atmospheric  $\text{CO}_2$  concentrations, and with day/night temperature regimes of 26/21°C. Seedlings of all maternal families in both  $\text{CO}_2$  treatments began emerging on 3 May. On June 20, when all seedlings had at least one true leaf, a total of 288 seedlings of uniform size (representing the median) of each maternal family in each  $\text{CO}_2$  level were selected. Seedlings from these cohorts were randomly allocated to one of 18 22.5-L growth containers (48.0 cm  $\times$  38.0 cm  $\times$  16.0 cm), each containing a total of 48 transplants (16 per maternal family). Seedlings in these stands were arranged in a regular hexagonal design such that seedlings of any given maternal family were surrounded by equal numbers of all three families. The 48 plants per container were at a density of  $265 \text{ m}^{-2}$ , a density commonly observed for regenerating birch in the field (Carlton 1993). To minimize edge effects, only the 24 centrally located plants in each container were used for measurements.

All growth containers were filled with a depth of 8.0 cm of mineral soil covered by 7.0 cm of sieved and mixed organic soil. The organic soil was collected at the Harvard Forest by taking the organic forest floor material (without litter) from an understorey site where the forest floor depth averaged  $\approx 10$  cm. Soils at this site are primarily Gloucester stony loam derived from granitic glacial till. Resulting growth container soil profiles were similar to those at the Harvard Forest which are often quite shallow (Lyford *et al.* 1963). Throughout the growing season, seedlings were watered as needed, and no supplementary nutrients were added. Seedlings received unmodified glasshouse light, which is about 70% of ambient.

A total of 36 mixed-family stands were equally distributed across six  $\text{CO}_2$ -controlled glasshouse modules (6 per module). The six modules were arranged as three pairs of ambient ( $350 \mu\text{L L}^{-1}$ ) and elevated ( $700 \mu\text{L L}^{-1}$ )  $\text{CO}_2$  modules, with each pair representing a block.  $\text{CO}_2$  treatments within each block were randomly designated. The six stands within each module were allocated to one of three harvests (2 per harvest). Within each module, the locations of growth containers were randomly rearranged every two weeks.

#### SEEDLING GROWTH

Seedlings in both  $\text{CO}_2$  treatments were harvested at three points throughout the growing season; 1 July (H1), 4 August (H2), and 15 September (H3). At each

harvest, shoot height, total leaf area, leaf number, leaf lengths, branch number, and main stem basal diameter were recorded. To facilitate root harvesting, growth containers were submerged in standing water for  $\approx 1.5$  h, and roots were then carefully disentangled and separated underwater. Plants were oven dried at  $70^\circ\text{C}$  for 1 week and then weighed.

At H1, nondestructive measurements of the lengths and heights of all canopy leaves, shoot height, and basal diameter were also recorded on plants in a subset of randomly chosen stands ( $n = 12$ ) to be harvested at the end of the season. These measures were repeated at H2 on a randomly chosen subset (50%) of the same plants. These nondestructive measurements were used, in conjunction with H1 and H2 destructive harvest data, to estimate standing biomass using allometric equations. Model I linear regressions were used to describe the relationship between leaf length and the square root of leaf area, after first determining that in no cases were quadratic terms (polynomial regressions) significant. Separate regressions were fitted for each  $\text{CO}_2$  treatment, maternal family and harvest. At H2, separate regressions were also fitted for main stem vs. branch leaves.

To estimate seedling biomass from nondestructive measurements, multiple regression analyses were initially used to determine the relationships between total leaf area, height, and basal diameter with total biomass using destructive H1 and H2 data. In all cases, leaf area was overwhelmingly the best predictor of total biomass; including seedling height and basal diameter in multiple regression models did not explain significantly more variance. Therefore, linear and polynomial regressions were used to estimate the allometric relationship between square root total leaf area and  $\ln$  (total biomass) at H1, and  $\ln$  (total leaf area) and  $\ln$  (total biomass) at H2. As with leaf area estimates, separate allometric equations were fitted for each  $\text{CO}_2$  level, maternal family and harvest.

#### MEASURES OF SEEDLING SIZE INEQUALITIES AND SIZE-ASYMMETRIC INTERACTIONS

Size (total biomass, height and leaf area) variability at each harvest was quantified for each stand separately using the coefficient of variation (%CV), which has been shown to be highly correlated with the Gini coefficient of size inequality (Weiner & Solbrig 1984; Weiner 1990). Inferences about the symmetry of plant competitive interactions were also made by fitting distribution modifying functions (DMFs), relating initial seedling biomass to subsequent growth increments (Westoby 1982; Weiner 1990). DMFs were fitted using model II regression (Sokal & Rohlf 1981). Model II regression was also used to characterize the relationships between seedling biomass and seedling light interception, and between seedling biomass and seedling light interception per unit biomass. The latter relationship provides a visual depiction of the mag-

nitude of size-asymmetric competition for light (Berntson 1996).

#### STAND LIGHT ATTENUATION AND SEEDLING COMPETITION FOR LIGHT

Light attenuation in stands developing in both high and low CO<sub>2</sub> was measured on representative clear days (7 July and 1 August) shortly after H1 and H2 measurements. Canopies on 7 July in both CO<sub>2</sub> treatments had not fully closed ( $LAI = 0.53$  and  $0.78$  for 350 and 700 treatments, respectively); by 1 August, they had fully closed and become much deeper ( $LAI = 5.2$  and  $4.64$  for 350 and 700 treatments, respectively). To estimate light attenuation curves, an array of 5 (7 July) or 6 (1 August) small ( $0.25 \text{ cm}^2$ ) gallium arsenide photo diodes were arranged at 2.5-cm intervals along a straight piece of plastic coated wire and attached to a Licor 1000 data logger. To avoid self shading, the radial orientations of individual diodes were slightly offset. Beginning at noon, arrays of sensors were placed vertically into two stands per CO<sub>2</sub> treatment in each of the three blocks. Within a stand, sensor arrays were consistently placed in the southern portions of the canopies of 12 randomly chosen individual seedlings per stand (four per maternal family). Arrays were located at a consistent proportional distance from seedlings' main stems, equaling one half the maximum canopy radius. The 12 measures of light at each height in each stand were averaged, and these average values were used to construct an average light attenuation curve for each stand. Light attenuation curves were then combined with seedling leaf area profiles (i.e. leaf area per unit stem height), to estimate whole-seedling light interception. Individual leaf light levels at any given height were interpolated from attenuation curves, assuming linear fits between *PAR* values measured at each height. Values of *PAR* at a given leaf height were then multiplied by leaf area, and whole plant light interception was estimated by summing up *PAR* interception by all leaves. Estimates of seedling total light interception were used both to calculate inequalities between seedlings in light interception, and to explore the relationship between seedling size and resource capture, i.e. the size-symmetric nature of competition for light.

#### DIURNAL PROFILES OF CO<sub>2</sub> AVAILABILITY WITHIN AND ABOVE STAND CANOPIES

Due to soil respiration and CO<sub>2</sub> uptake by photosynthesizing plants, CO<sub>2</sub> availability within enclosed canopies may differ from bulk CO<sub>2</sub> concentration of well-mixed air above canopies. To determine if dominant and subordinate seedlings within stands experienced different diurnal patterns of CO<sub>2</sub> availability, we measured CO<sub>2</sub> profiles in two ambient and two elevated CO<sub>2</sub> stands over a 72-h period (July 30-Aug.

1). Canopies at this time were well established ( $LAI = 5.2$  and  $4.64$  for 350 and 700 treatments, respectively). Profiles were measured using a modification of the CO<sub>2</sub> sampling system developed by Voss & Bazzaz (1994), that simultaneously measures CO<sub>2</sub> concentrations at several locations. Bev-A-line coated plastic tubes were mounted within each stand at 3 heights: near the soil surface (5.0 cm), mid-canopy (35.0 cm), and above the canopy (65.0 cm). Gases were sampled and collected 5 times per hour, with each sampling time being less than 4 s. CO<sub>2</sub> concentrations were measured using a LiCor 6262 IRGA.

#### STATISTICAL ANALYSES

The effects of CO<sub>2</sub>, maternal family identity, and their interactions on mean seedling performance were tested using ANOVA. The effect of CO<sub>2</sub> was tested against the block  $\times$  CO<sub>2</sub> variance. The variance due to error was used as the *F* ratio denominator for all other terms. Variance due to growth containers within a block was pooled with the error term.

Coefficients of variation (CV) for total biomass, height and total leaf area were estimated for each stand separately, and differences in CV between high and low CO<sub>2</sub> treatment and through time were analysed using ANOVA. The effect of CO<sub>2</sub> was tested against the block  $\times$  CO<sub>2</sub> variance and the effect of time was tested against the block  $\times$  time variance. The interactive effect of CO<sub>2</sub>  $\times$  time was tested against the 3 way interaction between block  $\times$  CO<sub>2</sub>  $\times$  time.

## Results

#### SEEDLING GROWTH

Overall stand productivity responses to CO<sub>2</sub> varied through time, and families within stands differed in their average CO<sub>2</sub>-induced growth responses (Table 1). Early in the season (H1), CO<sub>2</sub> stimulated whole-stand productivity by an average of 54%, with individual family growth responses ranging between 37% and 82% (CO<sub>2</sub>  $P = 0.025$ ; CO<sub>2</sub>  $\times$  Family  $P = 0.022$ ). By the end of the season, overall CO<sub>2</sub> enhancements declined to only 14%, but differences between families in CO<sub>2</sub>-responsiveness became greater, ranging from +51% to -16% (CO<sub>2</sub>  $\times$  Family  $P = 0.005$ ). Across all harvests and CO<sub>2</sub> treatments, families differed significantly from one another with respect to average size (Table 1).

Average seedling height growth responses to elevated CO<sub>2</sub> paralleled biomass responses, with early season CO<sub>2</sub>-induced enhancements being relatively large (42%; CO<sub>2</sub>  $P = 0.0391$ ); however, differences between families in average height growth responses to CO<sub>2</sub> were smaller than biomass responses and not significant (Table 1). By the end of the season, overall height growth responses to CO<sub>2</sub> declined to 16%, but

**Table 1** Average biomass, leaf area, and height growth responses of three maternal families of yellow birch to ambient and elevated CO<sub>2</sub> atmospheres during the first year of stand development. Values represent means pooled from all populations and blocks ± 1 standard error

Character CO <sub>2</sub> Treatment	Maternal Family G			Maternal Family W			Maternal Family Y			CO <sub>2</sub> × Family
	350 µL L <sup>-1</sup>	700 µL L <sup>-1</sup>	350 µL L <sup>-1</sup>	700 µL L <sup>-1</sup>	350 µL L <sup>-1</sup>	700 µL L <sup>-1</sup>	350 µL L <sup>-1</sup>	700 µL L <sup>-1</sup>	CO <sub>2</sub> × Family	
<b>Total Biomass (g)</b>										
Harvest 1	0.102 ± 0.007	0.186 ± 0.009	0.086 ± 0.005	0.127 ± 0.008	0.134 ± 0.01	0.184 ± 0.011	0.134 ± 0.01	0.184 ± 0.011	*	***
Harvest 2	1.11 ± 0.120	1.430 ± 0.130	0.950 ± 0.060	1.26 ± 0.080	1.600 ± 0.10	1.560 ± 0.100	1.600 ± 0.10	1.560 ± 0.100		***
Harvest 3	1.708 ± 0.207	2.577 ± 0.278	1.445 ± 0.149	1.885 ± 0.183	2.819 ± 0.213	2.374 ± 0.165	2.819 ± 0.213	2.374 ± 0.165		***
<b>Total Leaf Area (cm<sup>2</sup>)</b>										
Harvest 1	19.03 ± 1.53	32.69 ± 1.71	15.39 ± 1.01	22.5 ± 1.54	25.96 ± 2.05	33.2 ± 2.14	25.96 ± 2.05	33.2 ± 2.14	**	***
Harvest 2	182.79 ± 15.77	175.95 ± 13.38	158.62 ± 8.50	154.3 ± 8.78	255.42 ± 13.65	198.9 ± 10.32	255.42 ± 13.65	198.9 ± 10.32		***
Harvest 3	156.6 ± 16.80	179.20 ± 18.90	121.60 ± 10.80	135.9 ± 11.80	266.10 ± 18.90	209.2 ± 13.00	266.10 ± 18.90	209.2 ± 13.00		***
<b>Shoot Height (cm)</b>										
Harvest 1	3.84 ± 0.20	6.11 ± 0.27	3.98 ± 0.14	5.47 ± 0.29	5.40 ± 0.29	6.95 ± 0.36	5.40 ± 0.29	6.95 ± 0.36	*	***
Harvest 2	23.62 ± 1.60	26.98 ± 1.22	25.28 ± 1.06	27.71 ± 1.19	32.02 ± 1.23	30.50 ± 0.98	32.02 ± 1.23	30.50 ± 0.98		***
Harvest 3	25.00 ± 1.83	30.85 ± 1.44	25.93 ± 1.66	28.24 ± 1.53	35.42 ± 1.79	41.44 ± 1.66	35.42 ± 1.79	41.44 ± 1.66		***

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$  (significance probabilities resulting from a two-way ANOVA).

differences between families in CO<sub>2</sub>-responsiveness became greater, ranging from 9% to 23% (CO<sub>2</sub> × family  $P = 0.041$ ). As with biomass, across all harvests and CO<sub>2</sub> treatments, families differed significantly in average height growth (Table 1).

As expected, stand leaf area growth responses to CO<sub>2</sub> early in the season were quite similar to biomass responses, with an average CO<sub>2</sub>-induced growth enhancement of 48.6%, and individual family responses ranging from 28% to 72% (CO<sub>2</sub>  $P = 0.01$ ; CO<sub>2</sub> × Family  $P = 0.071$ ). However, by the end of the season, leaf area responses to CO<sub>2</sub> differed from biomass and height responses, with elevated CO<sub>2</sub> treatments exhibiting an average of 25% less standing leaf area than low CO<sub>2</sub>, though some maternal families within stands did show higher average values in high CO<sub>2</sub> (CO<sub>2</sub>  $P = 0.8151$ ; CO<sub>2</sub> × Family  $P = 0.016$ ). As with biomass and height, families differed in their average standing leaf area throughout the growing season (Table 1).

#### MATERNAL FAMILY IDENTITY OF STAND DOMINANTS

The maternal family identities of end-of-season stand dominants were also influenced by CO<sub>2</sub>. In low CO<sub>2</sub>, maternal family Y dominated in all stands with respect to height, and in 5 of 6 stands with respect to leaf area and total biomass. In high CO<sub>2</sub> stands, individuals of family G dominated in the majority of stands, being largest in 4 of 6 stands with respect to leaf area and total biomass, and in 3 of 6 stands with respect to height. While the identity of single dominant individuals in low CO<sub>2</sub> paralleled average family responses (e.g. family Y exhibited the largest average individuals), in high CO<sub>2</sub>, the identity of 'winners' based on dominant individuals often differed from 'winners' based on average family performance.

#### SEEDLING SIZE INEQUALITIES

Seedling size inequalities (coefficient of variation, CV) increased significantly through time when based on either total biomass (ANOVA Time effect,  $P = 0.019$ ) or total standing leaf area (ANOVA Time effect,  $P = 0.015$ ). However, inequalities in seedling height, particularly in high CO<sub>2</sub> environments, exhibited no significant change through time (Fig. 1). Increases in size inequality through time were generally correlated with total stand biomass (Fig. 1 insets). Regressions of total standing biomass vs. CV in seedling biomass were highly significant for both CO<sub>2</sub> levels ( $P = 0.0013$  and  $0.0006$ , for low and high CO<sub>2</sub> treatments, respectively). Similar patterns were observed when stand biomass was regressed on CV for seedling standing leaf area ( $P = 0.0962$  and  $0.0082$ ), but not for stand biomass vs. CV seedling height ( $P = 0.12$  and  $0.64$ ).

Despite greater standing biomass throughout the

season in high CO<sub>2</sub> treatments, size inequalities in high CO<sub>2</sub> stands were not significantly greater than in low CO<sub>2</sub> (Fig. 1). In fact, for all measures of seedling size (biomass, height and leaf area), low CO<sub>2</sub> stands exhibited consistently greater size inequalities than high CO<sub>2</sub> stands, particularly later in the season, although none of the effects were significant. For height, this difference was nearly significant (ANOVA CO<sub>2</sub> effect  $P = 0.093$ ). Slopes of regressions relating total standing biomass and size inequality were also consistently higher for the low CO<sub>2</sub> treatment, but differences between slopes were not statistically significant (Fig. 1).

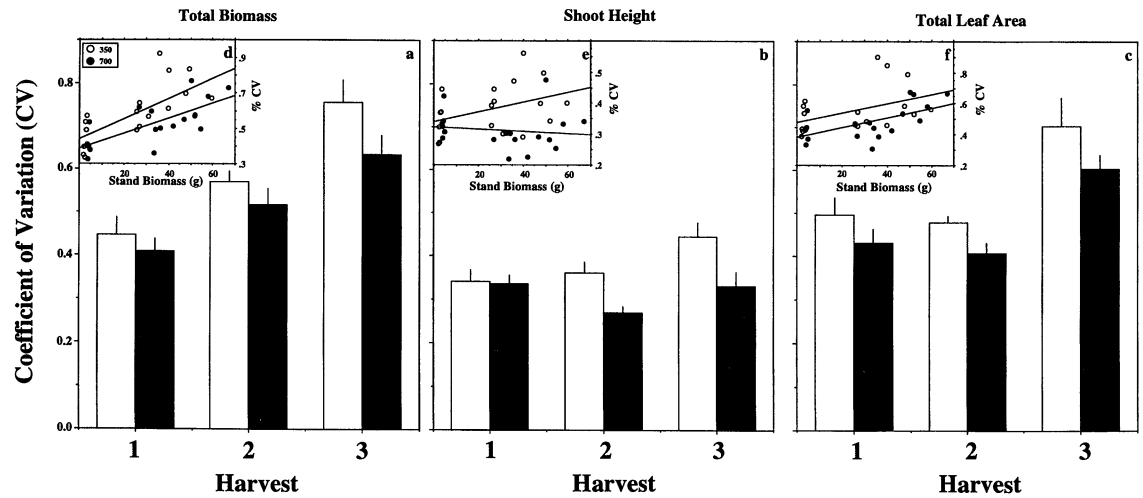
Histograms of seedling biomass distributions near the end of the growing season (H3) in both CO<sub>2</sub> treatments were highly skewed, with the majority of individuals in stands occurring within small size classes (Fig. 2). Comparisons of size distributions in high and low CO<sub>2</sub> treatments suggest that the lower size inequality (CV) in high CO<sub>2</sub> stands was mainly due to shifts in the proportion of individuals from the smaller to the intermediate, but not the largest, size classes. As there was virtually no seedling mortality throughout the growing season (total mortality: 3 of 864), shifts in frequency distributions were not attributable to self-thinning.

#### INITIAL SEEDLING SIZE VS. SUBSEQUENT GROWTH: DISTRIBUTION MODIFYING FUNCTIONS

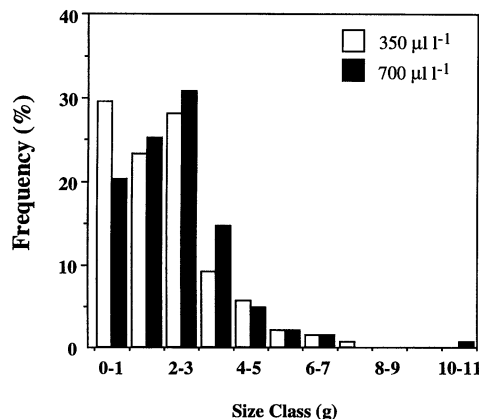
Allometric relationships between leaf length and leaf area, and between seedling total leaf area and biomass at H1 and H2 were all highly significant and are presented in Tables 2 and 3. Model II regressions relating estimated initial seedling biomass and total subsequent biomass growth between H1–H3 (DMFs) were highly significant ( $P < 0.0001$ ; Fig. 3), and slopes were significantly lower in high than in low CO<sub>2</sub> treatments ( $P < 0.05$ ). Intercepts for low- and high-CO<sub>2</sub> DMFs were also significantly different from zero ( $P < 0.0001$ ). The occurrence of both significantly positive slopes and significantly negative intercepts in DMFs has been used to infer size-asymmetric competitive interactions (Westoby 1982; Weiner 1990). The significantly lower slope of the high CO<sub>2</sub> DMF parallels the results of stand size inequality (CV), suggesting that being relatively larger in stands early in the season confers less of an advantage in high CO<sub>2</sub> than in low CO<sub>2</sub>.

#### LIGHT AVAILABILITY, SEEDLING GROWTH, AND COMPETITION FOR LIGHT

Patterns of light attenuation at the time of H1 and H2 in low and high CO<sub>2</sub> stands are shown in Fig. 4. Curves represent values averaged across all blocks ( $n = 72$  per canopy height per CO<sub>2</sub> treatment). Attenuation curves at H1 reveal slightly, but not sig-



**Fig. 1** Average stand-level coefficient of variation (CV) for yellow birch seedlings based on various measures of size: (a) total biomass (g), (b) height (cm), and (c) total standing leaf area (cm<sup>2</sup>). Open and shaded bars represent ambient (350  $\mu\text{L L}^{-1}$ ) and elevated (700  $\mu\text{L L}^{-1}$ ) CO<sub>2</sub> concentrations, respectively. Error bars represent  $\pm 1$  standard error. Insets in the upper left corner of each panel show the relationship between total stand biomass and CV in seedling (d) biomass, (e) height, and (f) leaf area. See text for results of linear regressions.



**Fig. 2** Histogram of size (g) distributions for competitively grown yellow birch seedlings after one season of growth in ambient (350  $\mu\text{L L}^{-1}$ , open bars) and elevated (700  $\mu\text{L L}^{-1}$ , shaded bars) CO<sub>2</sub> concentrations. Frequencies represent values pooled from all maternal families, populations, and blocks at the final harvest (H3).

nificantly lower light availability in the lower regions of high vs. low CO<sub>2</sub> canopies, most likely due to the greater leaf area in high CO<sub>2</sub> stands at this time. By H2, values near the bottom of the canopies in the two CO<sub>2</sub> treatments became more similar.

Combining light attenuation curves with non-destructively measured leaf area profiles provided estimates of whole plant light interception. At H1, high CO<sub>2</sub> plants intercepted nearly 6% more PAR than low CO<sub>2</sub> treatments (mean  $\pm$  1 SE for low and high CO<sub>2</sub>: 2031  $\pm$  93 and 2143  $\pm$  102  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively), paralleling the direction, but not the magnitude of differences in leaf area. CV in whole plant light interception at H1 was slightly, but not significantly lower in low vs. high CO<sub>2</sub> (0.367  $\pm$  0.24 vs. 0.413  $\pm$  0.52). At H2, high CO<sub>2</sub> plants still intercepted more light, on average, than low CO<sub>2</sub> plants (37266  $\pm$  3534 vs. 42926  $\pm$  4256), but the direction of

inequality in resource capture reversed, with slightly, but not significantly greater inequality among individuals in low vs. high CO<sub>2</sub> (0.837  $\pm$  0.103 vs. 0.759  $\pm$  0.104).

Model II regressions reveal that slopes relating seedling biomass to PAR interception ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) were all significantly different from zero (Fig. 5a–d; Table 4b). The same data presented as plots of seedling mass vs. PAR interception per unit mass more clearly illustrate the size-symmetric nature of competition for light (Fig. 5e–h). At H1, being larger did not result in seedlings intercepting a disproportionately greater amount of light, i.e. competition was relatively size-symmetric and there was no positive size bias to light acquisition (Fig. 5e,f). In contrast, at H2, when canopies were much denser, being larger resulted in significantly greater light capture per unit size, i.e. competition was size-asymmetric (Fig. 5g,h). Furthermore, slopes relating seedling size to light intercepted per unit size were significantly steeper in low vs. high CO<sub>2</sub> treatments ( $P < 0.01$ ), suggesting that asymmetric competition for light was greater in low CO<sub>2</sub> stands (Table 4).

#### CO<sub>2</sub> AVAILABILITY WITHIN AND ABOVE CANOPIES

Diurnal patterns of CO<sub>2</sub> concentrations measured above and within birch canopies in both low and high CO<sub>2</sub> treatments revealed no significant gradients in CO<sub>2</sub> availability. Twenty-four hour means in CO<sub>2</sub> in concentrations above canopies, within canopies, and near the soil surface in ambient CO<sub>2</sub>-grown stands were 384.2  $\pm$  2.9, 384.4  $\pm$  2.9 and 384.9  $\pm$  3.4, respectively. Concentrations in elevated CO<sub>2</sub> stands above, within and below canopies were 704.2  $\pm$  1.5, 714  $\pm$  12.6 and 707.3  $\pm$  1.7, respectively. Maximum



**Table 2** Model I regression equations and significance probabilities for allometric relationships between leaf length and leaf area for three maternal families of yellow birch grown in both ambient and elevated CO<sub>2</sub> environments

CO <sub>2</sub> Level	Maternal family	Regression equation	R <sup>2</sup>	P-value
<b>Harvest 1</b>				
main stem leaves				
350 µL L <sup>-1</sup>	G	$y = 0.619x + 0.120$	0.927	0.0001
350 µL L <sup>-1</sup>	W	$y = 0.585x + 0.161$	0.937	0.0001
350 µL L <sup>-1</sup>	Y	$y = 0.593x + 0.177$	0.941	0.0001
700 µL L <sup>-1</sup>	G	$y = 0.619x + 0.110$	0.943	0.0001
700 µL L <sup>-1</sup>	W	$y = 0.605x + 0.097$	0.924	0.0001
700 µL L <sup>-1</sup>	Y	$y = 0.604x + 0.176$	0.933	0.0001
<b>Harvest 2</b>				
main stem leaves				
350 µL L <sup>-1</sup>	G	$y = 0.584x + 0.188$	0.966	0.0001
350 µL L <sup>-1</sup>	W	$y = 0.570x + 0.274$	0.939	0.0001
350 µL L <sup>-1</sup>	Y	$y = 0.591x + 0.202$	0.970	0.0001
700 µL L <sup>-1</sup>	G	$y = 0.616x - 0.054$	0.958	0.0001
700 µL L <sup>-1</sup>	W	$y = 0.575x + 0.136$	0.931	0.0001
700 µL L <sup>-1</sup>	Y	$y = 0.579x + 0.257$	0.959	0.0001
branch leaves				
350 µL L <sup>-1</sup>	All	$y = 0.545x + 0.169$	0.911	0.0001
700 µL L <sup>-1</sup>	All	$y = 0.612x + 0.183$	0.913	0.0001

**Table 3** Model I regression equations and significance probabilities for allometric relationships between seedling total leaf area and total biomass for three maternal families of yellow birch grown in both ambient and elevated CO<sub>2</sub> environments

CO <sub>2</sub> Level	Maternal family	Regression equation	R <sup>2</sup>	P
<b>Harvest 1</b>				
350 µL L <sup>-1</sup>	G	$y = -0.032x^2 + 0.653x - 4.534$	0.913	0.0001
350 µL L <sup>-1</sup>	W	$y = 0.422x - 4.144$	0.860	0.0001
350 µL L <sup>-1</sup>	Y	$y = -0.043x^2 + 0.798x - 4.950$	0.941	0.0001
700 µL L <sup>-1</sup>	G	$y = 0.305x - 3.448$	0.926	0.0001
700 µL L <sup>-1</sup>	W	$y = -0.026x^2 + 0.618x - 4.416$	0.919	0.0001
700 µL L <sup>-1</sup>	Y	$y = -0.021x^2 + 0.565x - 4.253$	0.944	0.0001
<b>Harvest 2</b>				
350 µL L <sup>-1</sup>	G	$y = 1.282x - 6.648$	0.966	0.0001
350 µL L <sup>-1</sup>	W	$y = 1.278x - 6.585$	0.937	0.0001
350 µL L <sup>-1</sup>	Y	$y = 0.591x^2 + 7.875x - 24.987$	0.922	0.0001
700 µL L <sup>-1</sup>	G	$y = 1.219x - 5.982$	0.930	0.0001
700 µL L <sup>-1</sup>	W	$y = 1.288x - 6.299$	0.959	0.0001
700 µL L <sup>-1</sup>	Y	$y = 1.239x - 6.154$	0.879	0.0001

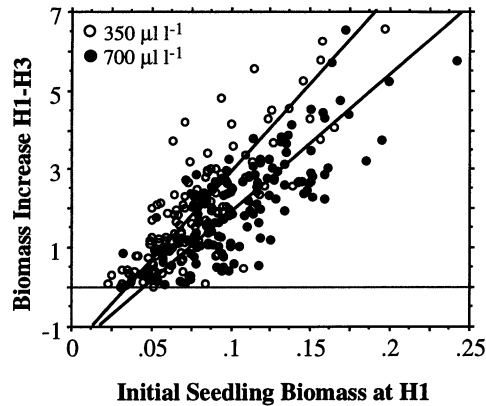
differences in CO<sub>2</sub> concentrations above and within canopies rarely exceeded 10 p.p.m., and these larger gradients only occurred during nonphotosynthetic hours.

## Discussion

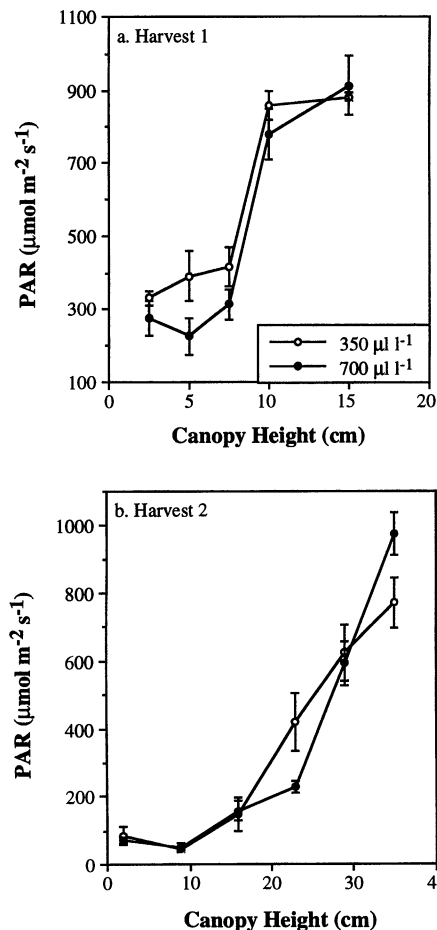
### THE EFFECTS OF CO<sub>2</sub>-ENRICHED ATMOSPHERES ON SIZE INEQUALITIES AND STAND STRUCTURE

At the outset of this study, we proposed three alternative scenarios regarding the potential effects of elevated CO<sub>2</sub> on plant competition and stand development. Neither scenario 1 nor 2 were supported by

our data for yellow birch. While size inequalities (CV) did increase through time with stand biomass, CVs were not higher in high CO<sub>2</sub> treatments despite their significantly greater biomass. This pattern was true whether measures of size inequality were compared at any point in time, or with respect to stand biomass. This finding contradicts results from most other studies which have reported increased competition and rates of density-dependent mortality with increased productivity in resource-rich environments (Bazzaz & Harper 1976; Grime 1979; Weiner 1985; but see Morris & Myerscough 1984). Rather, our results best support scenario 3. Despite significantly greater productivity throughout the growing season, all measures of seedling size (biomass, leaf area, height) inequality



**Fig. 3** Distribution modifying function showing the relationship between initial seedling size (g) at harvest 1 and biomass increases between harvest 1 and harvest 3 for plants raised in ambient ( $350 \mu\text{L L}^{-1}$ , open symbols) and elevated ( $700 \mu\text{L L}^{-1}$ , closed symbols)  $\text{CO}_2$  concentrations. Model II linear regression equations are  $y = 44.05x - 1.54$  ( $R^2 = 0.67$ ) and  $y = 35.29x - 1.59$  ( $R^2 = 0.63$ ) for ambient and elevated  $\text{CO}_2$  treatments, respectively.

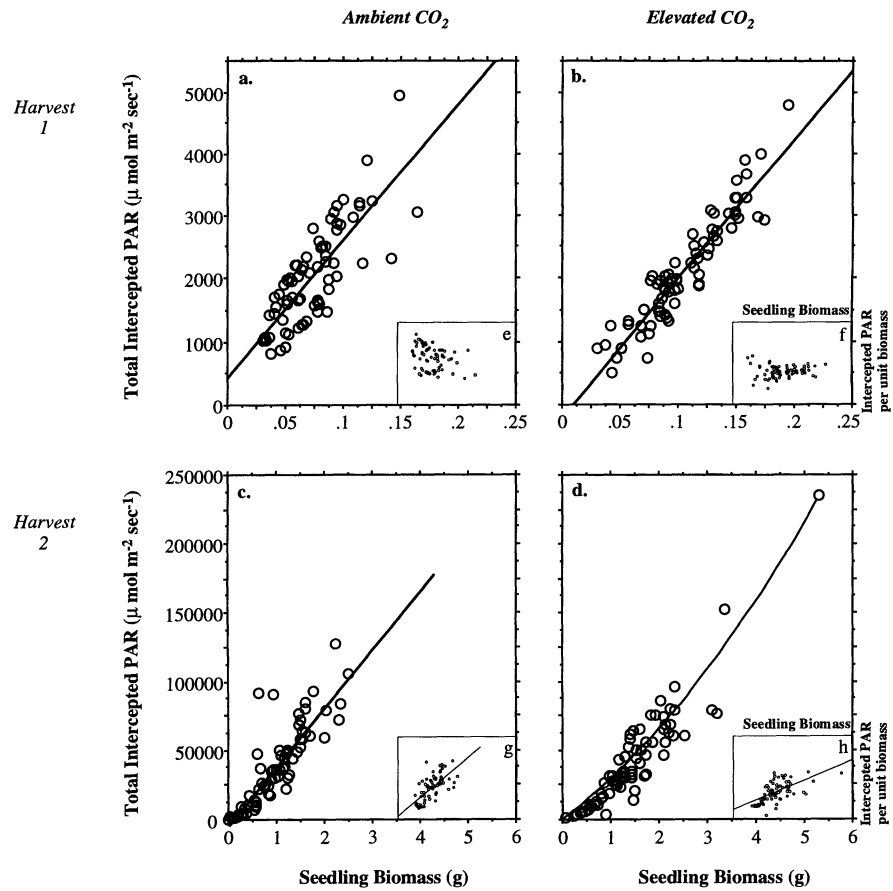


**Fig. 4** Light attenuation curves for stands of yellow birch raised in ambient (open symbols) and elevated (closed symbols)  $\text{CO}_2$  concentrations at (a) harvest 1 and, (b) harvest 2. Symbols represent mean  $\text{PAR}$  values ( $n = 72$ ) at each canopy height. Error bars represent  $\pm 1$  standard error.

were slightly, but consistently lower in  $\text{CO}_2$ -enriched environments (Fig. 1). The lower slopes relating stand biomass to both CV in biomass and CV in height in high  $\text{CO}_2$  treatments add further support to this conclusion, and demonstrate that differences in inequality were not simply a result of  $\text{CO}_2$ -induced changes in rates of stand development (Fig. 1). Though some of these results were not statistically significant, the patterns were consistent across various measures and indices of size inequality and asymmetric competition (also see below).

In this study, a number of factors can be largely excluded as having contributed to size inequality. First, seedlings were transplanted into growth containers filled with forest soil that was first homogenized, and then carefully layered into profiles with special effort given to minimizing variation within or between growth containers. Developing stands were then maintained in controlled environment glasshouses with well-mixed atmospheres and relatively homogenous light availability. Thus, environmental heterogeneity was probably not a large factor underlying initial seedling size differences. Secondly, there was virtually no seedling mortality ( $n = 3$  of 864) across the whole season, so neither self-thinning nor density-independent mortality were important factors influencing size variability. Finally, at the start of the experiment, seedlings were carefully chosen from a much larger cohort to minimize differences in age, and within maternal families, to differ very little with respect to size. Yet despite these efforts, our results reveal substantial size inequalities at H1, well before canopies had completely closed (and presumably before seedlings interacted). Some of this variability was clearly due to differences in average initial seedling sizes of the three maternal families. At H1, the largest maternal family, Y, was an average of 56% and 45% larger than the smallest family, W, in low and high  $\text{CO}_2$  environments, respectively. These values are similar to average differences in seedling sizes between families of individually grown plants of approximately the same age (unpublished data). Thus early size inequalities, and differences in equality between  $\text{CO}_2$  treatments were probably not due to competitive plant interactions, but most likely reflect variations between and within maternal families in seed size and/or initial growth rate.

However, following H1, increases in seedling size inequalities through time, and increasing differences in size inequalities between  $\text{CO}_2$  treatments, appear to result from size-asymmetric competitive interactions among plants. The significantly negative intercepts and positive slopes of DMFs relating initial seedling size and subsequent growth, suggest that larger plants grew disproportionately more than smaller plants, i.e. interactions were size-asymmetric (Westoby 1982; Weiner 1990). Furthermore, the significantly lower slope of the high  $\text{CO}_2$  DMF suggests that there was less of a disadvantage to being a relatively small sub-



**Fig. 5** Relationships between seedling biomass (g) and whole seedling *PAR* interception for competitively grown yellow birch individuals in ambient ( $350 \mu\text{L L}^{-1}$ ) and elevated ( $700 \mu\text{L L}^{-1}$ ) CO<sub>2</sub> concentrations, at harvest 1 (panels a, b) and harvest 2 (panels c, d). Insets within each panel (e–h) showing the relationships between seedling size and seedling light capture per unit size ( $\mu\text{mol m}^{-2} \text{s}^{-1} \text{g}^{-1}$ ) serve as a graphical presentation of the magnitude of size-asymmetric competition for light. Details regarding fitted Model II regressions are provided in the text and in Table 4.

**Table 4** Model II regression equations and significance probabilities for relationships between seedling total biomass and seedling total *PAR* interception  $\alpha$ , and between seedling biomass and *PAR* interception per unit biomass

CO <sub>2</sub> Level	Regression equation	R <sup>2</sup>	Slope SE	P
Seedling biomass vs. <i>PAR</i> interception				
Harvest 1				
350 $\mu\text{L L}^{-1}$	$y = 27505x + 26.0$	0.64	1980	0.0001
700 $\mu\text{L L}^{-1}$	$y = 23852x - 375.6$	0.87	1023	0.0001
Harvest 2				
350 $\mu\text{L L}^{-1}$	$y = 47173x - 10835.5$	0.88	2007	0.0001
700 $\mu\text{L L}^{-1}$	$y = 43081x - 20307.7$	0.85	1967	0.0001
Seedling biomass vs. <i>PAR</i> interception per unit biomass				
Harvest 1				
350 $\mu\text{L L}^{-1}$	$y = -234419x + 45799$	0.11	26483	0.0051
700 $\mu\text{L L}^{-1}$	$y = 97604x + 9878$	0.01	11617	NS
Harvest 2				
350 $\mu\text{L L}^{-1}$	$y = 20005x + 11231$	0.47	1798	0.0001
700 $\mu\text{L L}^{-1}$	$y = 11673x + 8878$	0.34	1130	0.0001

ordinate in high vs. low CO<sub>2</sub> environments (Fig. 3). This DMF result parallels later season measures in size inequality (CV).

#### ELEVATED CO<sub>2</sub> ALTERS COMPETITION FOR LIGHT

It has been hypothesized that competition for light, which originates from a single direction, is preemptable, and leads to size-asymmetric competition. Larger plants progressively intercept greater quantities of light per unit size than do smaller ones, eventually suppressing small individuals (Ford & Diggle 1981; Weiner & Thomas 1986). In contrast, competition for less directional, or more diffusible resources (e.g. soil nutrients and water), may be less preemptable and thus more accessible to all individuals in proportion to their size, thereby leading to size-symmetric competition (Weiner 1986, 1990). While some studies that have experimentally separated root vs. shoot competition provide circumstantial evidence to support the above theory (Weiner 1986), very few studies have empirically quantified resource capture of competing individuals varying in size, and related resource competition, to overall relative performance (but see Jurik 1991; Berntson 1996).

Differences in light attenuation by canopy strata, and in the utilization of intercepted light by dominant vs. subordinate plants, underlie the patterns in DMFs and size hierarchies that we observed in low and high CO<sub>2</sub> environments. Patterns of light interception in relation to seedling size before canopies closed (H1) suggest that competition for light was size-symmetric. Plots of seedling mass vs. light capture per gram total biomass showed no positive relationship (Fig. 5e,f). However, once canopies closed, competition for light became more size-asymmetric. Slopes of seedling mass vs. light capture per unit mass at H2 were positive. Furthermore, as with DMFs, these slopes were markedly less steep in high vs. low CO<sub>2</sub> treatments, suggesting that light competition was less size-asymmetric in CO<sub>2</sub>-enriched atmospheres (Fig. 5g,h). Reduced size-asymmetric competition for light in CO<sub>2</sub>-enriched atmospheres probably results from CO<sub>2</sub>-induced shifts in seedling developmental patterns. Birch seedlings developing in high CO<sub>2</sub> stands had significantly lower leaf area per unit biomass (i.e. leaf area ratios, LAR) than seedlings developing in low CO<sub>2</sub> (Wayne & Bazzaz 1995). The lower LARs in high CO<sub>2</sub> thus allowed more light penetration through canopies per unit biomass. This result helps explain both why light attenuation curves were so similar at H2 (Fig. 4b) despite substantial differences in standing biomass, and also why CO<sub>2</sub> modified seedling size-uptake relationships for light.

Differences in the way that dominant vs. subordinate seedlings in low and high CO<sub>2</sub> atmospheres utilized the light they received may further explain

patterns of stand development. Two independent studies in our laboratory with yellow birch have reported  $\approx 50\%$  (Bazzaz & Miao 1992) and 10% (Bassow 1995) greater CO<sub>2</sub>-induced growth enhancement of individually grown seedlings raised under partial neutral shade cloth (30% transmission) vs. full light. Greater CO<sub>2</sub>-responsiveness at low light was also found in five other hardwood species which co-occur with yellow birch (Bazzaz & Miao 1992), but this pattern has not been observed for some southern hardwood or coniferous species (Tolley & Strain 1984). Some herbaceous species also exhibit greater CO<sub>2</sub>-induced growth enhancements at lower light levels (e.g. Ford & Thorne 1967; Gifford 1977; Wheeler *et al.* 1991; Rufty *et al.* 1994; but see Hopen & Ries 1962; Sionit *et al.* 1982).

Studies with yellow birch suggest that at least some component of greater CO<sub>2</sub> growth responsiveness in low light may be related to patterns of leaf-level photosynthesis. CO<sub>2</sub>-induced photosynthetic enhancements of individually grown seedlings were substantially higher in low (138%) vs. high light (5%) environments, paralleling growth responses (Bassow 1995). While mechanisms of photosynthetic acclimation to CO<sub>2</sub> and light were not explored in this study, evidence from other species suggests that acclimatory responses may be mediated by the phenomenon of end-product inhibition (Arp 1991; Farrar & Williams 1991; Stitt 1991), where photoassimilates build up, and exceed the capacity of plants to either transport (e.g. phloem loading constraints; Körner *et al.* 1995), store or utilize them (Sasek *et al.* 1985). It is conceivable that in high CO<sub>2</sub> stands, dominant plants growing in high light would rapidly accumulate carbohydrates, and thus experience feedback inhibition to a greater extent than subordinates in low light. In contrast, end-product inhibition would not be as severe in ambient CO<sub>2</sub> atmospheres, and thus the differential between high light dominants and low light subordinates would not be as great. Thus, competitively subordinate seedlings, experiencing the lower light levels in the understory of developing stands, may have exhibited greater proportional growth responses to elevated CO<sub>2</sub> relative to dominants exposed to high light. This scenario is supported by frequency distributions of seedling sizes which show that CO<sub>2</sub>-induced increases in stand biomass were mainly due to seedlings from the smallest size classes shifting into more intermediate size classes, with very few changes in the magnitude or numbers of individuals in the larger size classes (Fig. 2).

#### INTRASPECIFIC VARIATION IN COMPETITIVE PERFORMANCE IN ELEVATED CO<sub>2</sub> ENVIRONMENTS

In contrast to numerous studies investigating the evolutionary responses of plants to a wide range of

anthropogenic stresses including heavy metals (Antonovics *et al.* 1971), atmospheric pollutants (e.g. SO<sub>2</sub>, NO<sub>2</sub>, O<sub>3</sub>; Bell *et al.* 1991), and herbicides (LeBaron & Gressel 1982), surprisingly little is known about heritable variation in CO<sub>2</sub>-responsiveness (Curtis *et al.* 1994; Thomas & Jasienski 1996). Consequently, it is unclear to what extent rising CO<sub>2</sub> can act as an important agent of selection within natural plant populations (Taylor & Pitelka 1992; Geber & Dawson 1993). In this study, any attempt to address microevolutionary processes must clearly be done qualitatively, and with great caution. First, this study investigated a small number of half-sib maternal families, not true cloned genotypes. However, since the three maternal families were all collected from an open, high light site, from parents located within 100 m of one another on the same soil type, it is unlikely that differences in maternal environments greatly influenced the small-seeded birch progeny. Second, the growth results of this study encompass only a small phase of the entire life cycle of these long-lived trees. Nevertheless, the most intense mortality occurs in the early stages of trees' life cycles, and therefore these stages may represent times with the greatest potential for natural selection (Harper 1977). Furthermore, for pioneer species, rapid early growth is often correlated with a saplings' ability to fill canopy gaps and reproduce successfully (Alvarez-Buylla & Martínez-Ramos 1992). For these reasons, despite this study's limitations, we use these data to identify potential evolutionary consequences of competition and rising CO<sub>2</sub> concentrations on regenerating forest tree populations.

Maternal families of yellow birch differed significantly in their competitive performance, independent of whether competitive performance was assessed by mean family performance, or by the identity of single dominant individuals within each replicate population. This result parallels other studies that have demonstrated that dominance hierarchies in competitive stands may have a genetic basis (e.g. Shaw 1986; Miller & Schemske 1990; Thomas & Bazzaz 1993). However, maternal families that dominated at high CO<sub>2</sub> differed from those which dominated at ambient CO<sub>2</sub> (indicated by the significant CO<sub>2</sub> × family interaction), suggesting that rising CO<sub>2</sub> has the potential to act as a selective agent, and alter the genetic composition of regenerating tree populations. In a companion study (Wayne & Bazzaz 1995), we reported that competitive dominants in high CO<sub>2</sub> environments were not necessarily members of families displaying the highest potential CO<sub>2</sub>-growth-responsiveness (i.e. CO<sub>2</sub>-responsiveness in the absence of competition). Thus while CO<sub>2</sub> may exert selective pressure on regenerating forest stands, it appears that selection in crowded populations would be unlikely to result in the evolution of increased stand-level CO<sub>2</sub> responsiveness. Similar conclusions regarding the effects of density-dependent competition on selection for CO<sub>2</sub>-responsiveness were drawn

in a recent study with the annual herb *Abutilon theophrasti* (Bazzaz *et al.* 1995).

## Conclusions

Two novel conclusions emerge from the present work. First, we found that CO<sub>2</sub> alters stand size structures, specifically by decreasing the size differential between canopy dominants and subordinates. If these CO<sub>2</sub>-induced changes in stand size structure persist beyond the regeneration stage, they could significantly impact the long-term carbon sink potential of forest ecosystems. A number of recently developed individual-based models conclude that the magnitude of variation in tree sizes within stands can be as important, if not more so, than mean species' responses for predicting long-term forest composition and productivity (Hara *et al.* 1991; Koyama 1993; Smith 1995; Bolker *et al.* (1995)). Thus, understanding how CO<sub>2</sub> alters size variability, in addition to overall average growth enhancements, may be critical to parameterizing forest global change models. Additionally, CO<sub>2</sub>-induced alterations of size distributions in forest stands may require changes in silvicultural management, such as sowing density and thinning practices.

The second novel result emerging from this study is that in regenerating yellow birch stands, elevated CO<sub>2</sub> alters the nature of plant competition, particularly for light. Mechanisms underlying this response appear to include both developmental effects of CO<sub>2</sub> on plant architecture, as well as interactive effects of light and CO<sub>2</sub> availability on photosynthesis and growth. These kinds of results are extremely useful for developing process-based, mechanistic models of stand development (e.g. Reynolds *et al.* 1993; Jarvis & Dewar 1993; Shugart *et al.* 1992; Pacala *et al.* 1993), as they may be more generalizable to other species and through time, than pure phenomenological models.

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