Elevated CO$_2$ influences the responses of two birch species to soil moisture: implications for forest community structure

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Abstract

Increased levels of atmospheric CO$_2$ may alter the structure and composition of plant communities by affecting how species respond to their physical and biological environment. We investigated how elevated CO$_2$ influenced the response of paper birch (*Betula papyrifera* Marsh.) and yellow birch (*Betula alleghaniensis* Britt.) seedlings to variation in soil moisture. Seedlings were grown for four months on a soil moisture gradient, individually and in mixed species stands, in controlled environment facilities at ambient (375 μL L^{-1}) and elevated (700 μL L^{-1}) atmospheric CO$_2$. For both individually and competitively grown paper birch seedlings, there was a greater CO$_2$ growth enhancement for seedlings watered less frequently than for well-watered seedlings. This differential change in CO$_2$ responsiveness across the moisture gradient reduced the difference in seedling growth between high and low water levels and effectively broadened the regeneration niche of paper birch. In contrast, for yellow birch seedlings, elevated CO$_2$ only produced a significant growth enhancement at the wet end of the soil moisture gradient, and increased the size difference between seedlings at the two ends of the gradient. Gas exchange measurements showed that paper birch seedlings were more sensitive than yellow birch seedlings to declines in soil moisture, and that elevated CO$_2$ reduced this sensitivity. Additionally, elevated CO$_2$ improved survival of yellow birch seedlings growing in competition with paper birch in dry stands. Thus, elevated CO$_2$ may influence regeneration patterns of paper birch and yellow birch on sites of differing soil moisture. In the future, as atmospheric CO$_2$ levels rise, growth of paper birch seedlings and survival of yellow birch seedlings may be enhanced on xeric sites, while yellow birch may show improved growth on mesic sites.

Keywords: elevated CO$_2$, soil moisture, paper birch, yellow birch, seedling regeneration, temperate forests

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Introduction

Rising levels of atmospheric CO$_2$ will effect profound changes in the structure and function of terrestrial ecosystems (Koch & Mooney, 1996; Korner & Bazzaz, 1996). Complementary approaches have been taken to address how increased atmospheric CO$_2$ may alter ecosystem dynamics. One approach involves exposing whole ecosystems to elevated CO$_2$ levels under realistic field condi-

tions (Mooney *et al.*, 1991). These experiments integrate over many ecosystem processes and their complex interactions. Another, more mechanistic approach addresses the effect of elevated CO$_2$ on processes within ecosystems themselves, e.g. stand development, interspecific interactions, and below-ground feedbacks on productivity. In the present study, we address a mechanism by which rising levels of atmospheric CO$_2$ may influence community species composition. Specific mechanisms for future community-level changes are rarely addressed in CO$_2$

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studies. There is now clear evidence that resources may interact with one another to alter plant performance in complex ways (Chapin *et al.*, 1987; Bazzaz & Grace, 1997). By changing aspects of plant function, elevated CO_2 may influence plant responses to their physical and biological environment (Field *et al.*, 1992), i.e. species' niches (Bazzaz, 1996). These changes in resource responses may, in turn, lead to alterations in the distribution and abundance of species across their habitat range (Huston, 1994), and thus to changes in community species composition (Bazzaz *et al.*, 1985).

We address potential CO_2-induced shifts in resource responses by focusing on patterns of seedling regeneration in temperate forests in the north-eastern United States. The critical role that these aggrading forest systems currently play in the global carbon cycle makes understanding the effect of increased CO_2 concentrations on their structure and function particularly important (Wofsy *et al.*, 1993; Schimel, 1995). We consider how elevated CO_2 may alter the distribution and abundance of two relatively early successional tree species in relation to soil moisture. We focus on soil water availability for several reasons. (i) Water availability is a central factor regulating the structure of plant communities (Whittaker, 1975). (ii) There is wide variation in soil moisture availability within and between forest stands (Kleb & Wilson, 1997), and evidence that tree species do partition themselves along soil moisture gradients (Walker, 1975). (iii) Elevated CO_2 has the potential for altering plant responses to variation in soil moisture, based on well-documented effects of CO_2 concentration on stomatal conductance (Mott, 1990; Field *et al.*, 1995). The species chosen for the study were paper birch (*Betula papyrifera* Marsh.) and yellow birch (*Betula alleghaniensis* Britt.), both of which require gap formation for effective regeneration and co-occur in the field throughout much of New England (Burns & Honkala, 1990). Observations suggest that the species differ in their responses to soil moisture—mature trees of paper birch are often found on more xeric, well-drained soils, while yellow birch trees are usually associated with more mesic sites (Burns & Honkala, 1990).

Paper birch and yellow birch seedlings may regenerate in dense stands and compete with one another (Marquis, 1965). As a result of neighbour interactions, plants growing in dense stands experience a different local environment to those growing alone (Bazzaz, 1990; Goldberg, 1990; Bazzaz & McConnaughay, 1992). These changes in resource availability may affect plant responses to both soil moisture levels and atmospheric CO_2 concentrations (Groninger *et al.*, 1995; Wayne & Bazzaz, 1995; Wayne & Bazzaz, 1997). Thus, in the present study, we consider responses of both individually and competitively grown birch seedlings. Few previous studies addressing CO_2-induced changes in seedling responses to resource availability have taken this dichotomous approach.

Future increased concentrations of atmospheric CO_2 may differentially affect how paper birch and yellow birch respond to variation in soil moisture conditions. Elevated CO_2 has been shown to increase leaf-level photosynthesis and reduce stomatal conductance in many studies (Eamus & Jarvis, 1989; Woodward *et al.*, 1991), thus increasing plant water use efficiency (Eamus, 1991; Tyree & Alexander, 1993; Drake *et al.*, 1997). As a result, elevated CO_2 often improves plant water relations, especially under water stress conditions (Morse *et al.*, 1993; Jackson *et al.*, 1994; Polley *et al.*, 1996). These observations lead us to propose a hypothesis addressing the differential effects of elevated CO_2 on seedling responses to soil moisture, both for individuals and competitively grown seedlings. We hypothesize that elevated CO_2 causes a greater proportional enhancement of growth as soil moisture declines, and that there is a greater benefit for species that are associated with mesic conditions, and thus potentially more sensitive to soil moisture declines than those with xeric distributions. Therefore, we predict that, under elevated CO_2 conditions, yellow birch seedlings will improve their performance on drier soils to a greater extent than paper birch seedlings. We test our hypothesis by growing seedlings of each species individually and in mixed competitive stands under different combinations of soil moisture availability and atmospheric CO_2.

Materials and methods

Experimental design

The experiment followed a factorial design, testing the effects of soil moisture and atmospheric CO_2 concentrations on seedlings grown individually and in mixed species stands. The CO_2 treatments (375 and 700 μL L^{-1}) were replicated across three blocks and water treatments were replicated three times within each CO_2 module. Seedlings grown individually were exposed to four different water levels, resulting in 72 plants of each species (2 CO_2 levels × 3 Blocks × 4 Water levels × 3 Replicates). For the competitive mixtures, only the most extreme water treatments were used, resulting in 36 stands (2 CO_2 levels × 3 Blocks × 2 Water levels × 3 Replicates), each with 10 individuals of each species.

Experimental procedure

Seeds of paper birch (*Betula papyrifera* Marsh.) and yellow birch (*Betula alleghaniensis* Britt.) were collected in October 1994 from three parent trees of each species growing in the Prospect Hill and Tom Swamp tracts of the Harvard Forest (Petersham, MA). Seeds were air-dried and stored

at 4 °C for 18 months and then placed in 5 cm deep germination flats in mid-April 1996. Seeds were sprinkled evenly over a peat-based potting mix with added perlite and then covered with a layer of vermiculite. Based on germination trials, the paper birch seeds were set to germinate one week after those of yellow birch so that timing of emergence was synchronized. Germination flats were placed in the same glasshouse modules in which the experiment was conducted to ensure that seedlings were growing in their appropriate experimental conditions from the moment of emergence. Seedlings of both species began to emerge in the first week of May, and were transplanted into their containers two weeks later. Individuals chosen for transplantation had two true leaves and were of approximately equal size.

Seedlings to be grown individually were transplanted into 3 L square-based pots (15 × 15 × 15 cm), while those used for the competition experiment were transplanted into 15 L rectangular tubs (35 × 30 × 15 cm). Ten seedlings of each species were planted in each tub in a regular 4 × 5 criss-cross design, such that each individual was surrounded by four conspecific neighbours and four neighbours of the other species. The central three individuals of each species were the 'target' plants, while the remaining seedlings were 'edge' individuals (not included in the final harvest). The seedling density used in the experiment ($\approx$ 200 plants per m^2) is typical for birch seedlings regenerating in more open areas of temperate forests (Carlton, 1993; S. Catovsky, pers. obs.). Any seedling that died within the first two weeks following transplantation was replaced with another seedling from the germination flats.

Plants were grown at Harvard University (Cambridge, MA) in controlled environment facilities that were divided into three separate modules. In one half of each module, CO$_2$ concentration was maintained at 375 µL L^{-1} (ambient), while CO$_2$ was controlled at 700 µL L^{-1} (elevated) in the other half. The temperature in all modules was kept at 26 °C from 07.00 to 20.00 hours and at 19 °C overnight. Lighting was provided by natural sunlight filtered through the roof of the glasshouse, which reduced light levels by $\approx$ 30%. The seedlings were grown in a soil mix consisting of two parts organic forest floor material (minus litter) and one part peat-based potting soil. The forest soil was collected from the Prospect Hill tract of Harvard Forest, and was sieved and homogenized prior to thorough mixing with the potting soil. Plants were given Peter's 20–20–20 NPK water-soluble fertilizer weekly, such that the seedlings received the equivalent of 40 kg ha^{-1} y^{-1} of nitrogen to match natural rates of net nitrogen mineralization in northern hardwood forests (Aber et al., 1993).

Soil moisture was controlled experimentally by varying the frequency of watering, rather than the amount of water (Tschaplinski et al., 1993, 1995). In this way, water could penetrate the full soil profile in all treatments, and would not affect patterns of root development. Initially, plants were watered every 3, 6, 9 and 12 days (corresponding to water treatments 4, 3, 2 and 1, respectively). Watering frequency was increased mid-way through the experiment (end of July) to every 2, 4, 6 and 8 days, because the soil dried out progressively faster as the seedlings grew larger. The quantitative relationships between the watering frequencies, however, were maintained. All containers were freely draining, and field capacity was reached at each watering event by adding enough water until it began to drain from the container. Care was taken not to over-saturate the soil and create anoxic soil conditions.

Measurements

To document the effect of watering treatment, soil moisture was measured over an eight-day watering cycle in August. Every morning, a 1-cm diameter soil core was taken from one pot and one tub of each experimental watering treatment in every block. Each core was replaced with a plug of extra soil mix. Gravimetric soil moisture content (g water/g soil dry weight) was calculated from change in soil weight before and after drying for 48 h at 105 °C, and this value was then converted to volumetric moisture content using soil bulk density (0.25 g cm^{-3}) measured from noncompacted soil cores. In addition, we calculated changes in soil matric potential over the watering cycle using a soil moisture retention curve produced for O-horizon soil collected from the same stand as the experimental soil mixture (report completed by D. H. Thibault & M. I. Sheppard for K. M. Newkirk, Marine Biological Laboratory, Woods Hole, MA). The exponential curve fit for the relationship was $V = 0.294e^{-0.015\Psi}$ ($r^2 = 0.895$), where V is volumetric soil moisture content (cm^3 cm^{-3}) and Ψ is soil matric potential (kPa).

Over this eight-day watering cycle, leaf-level photosynthetic rates were measured on the same subset of individually grown plants using a Li-Cor 6200 gas exchange system (Lincoln, NE) equipped with a quarter-litre chamber. Early each morning, the plants were transferred into six glass environmental growth chambers maintained under the same light, temperature, humidity and atmospheric CO$_2$ conditions as the six modules. Three *in situ* gas exchange measurements were made on a single upper leaf per individual through the day (09.00–11.00, 12.00–14.00, 15.00–17.00 hours), and a daily average photosynthetic rate per unit leaf area was computed for each individual.

Plants were harvested in mid-September 1996, after 120 days of growth, to obtain total seedling biomass.

Isolated roots were obtained by carefully washing away the soil. For seedlings growing in competition, every individual's root system was carefully separated by hand. Plant material was dried at 70 °C for 7 days and then weighed.

Data analysis

Biomass data were analysed using four-factor analysis of variance in DataDesk® v4.2 (Odesta Corporation, Northbrook, IL), with CO_2, water level, species and block as main fixed effects, whose mean squares were tested over the residual mean square. Scheffé *post hoc* tests, corrected to give a table-wise Type I error of $P = 0.05$, were used for subsequent multiple comparisons. Block was explicitly included as a factor in the model, and we tested for CO_2-by-block interactions (Newman *et al.*, 1997). For seedlings grown in competition, the effects of the experimental treatments on mean biomass of living seedlings and seedling survival were investigated. We used a log transformation on these biomass data to comply with Anova assumptions of normality and homoscedasticity (Sokal & Rohlf, 1995). Survival data were analysed using the nonparametric Mantel–Haenszel test. We initially tested for homogeneity between blocks (no significant difference between blocks) and then combined data from all the blocks to make pairwise treatment comparisons (Sokal & Rohlf, 1995).

Soil moisture and gas exchange data were also investigated with analysis of variance, including species, water treatment, CO_2 concentration, block and day as fixed factors, and then using Scheffé *post hoc* tests for multiple comparisons between means. Soil moisture data were log-transformed to conform with Anova assumptions. In order to assess the sensitivity of photosynthesis to soil moisture, measurements of photosynthesis and conductance on plants from the two lowest water levels were grouped into bins based on soil moisture level from the day of the measurement. In this case, Bonferroni-corrected pairwise comparisons between soil moisture bins were made for each species $\times$ CO_2 combination (Sokal & Rohlf, 1995).

For individual seedling biomass, we calculated response breadth using Levins' B across four discrete water levels (Levins, 1968):

$$\text{Response breadth} = \frac{1}{\sum (p_i)^2 S}, \qquad (1)$$

where p_i is proportional biomass at each resource level (*i*) and S is number of resource levels. We used permutation tests to address if CO_2 concentration significantly influenced species' response breadth (Wilson & Lee, 1994). We randomly re-assigned CO_2 treatment labels to data

for each randomization and calculated the difference between response breadths at ambient and elevated CO_2. This randomization was repeated 1000 times for each species to provide an estimate of the distribution of differences in response breadth under the null hypothesis of no CO_2 effect. Based on this null distribution, we calculated the probability of achieving our observed differences in response breadth by chance (taken as proportion of samples whose absolute value was greater than or equal to the magnitude of the observed difference).

Results

Soil moisture changes

Varying watering frequency altered both soil moisture content and soil water availability (Table 1; Fig. 1). Watering treatments differed in both average water content/availability and the minimum moisture levels reached (Table 1). For seedlings grown individually and in mixed stands, there was a significant effect of water treatment over the eight-day watering cycle ($F_{3,367} = 164.5$ and $F_{1,76} = 93.6$, $P < 0.0001$), with average water content decreasing with decreasing frequency of watering (*post hoc*s, $P < 0.0001$). There was a distinctive pattern of variation in soil water content through the watering cycle, as evidenced by a significant water by date interaction in both pots and stands ($F_{24,367} = 26.4$ and $F_{8,76} = 10.8$, $P < 0.0001$). Watering events are clearly visible for each treatment (Fig. 1). Species and CO_2 concentration had no effect on pot soil moisture changes ($F_{1,367} = 3.3$ and $F_{1,76} = 0.1$, $P > 0.05$). However, CO_2 level did influence water content in the mixed stands ($F_{1,76} = 4.4$, $P < 0.05$), with stands grown in elevated CO_2 maintaining higher soil moisture contents than those in ambient CO_2.

Growth of seedlings without competition

For individually grown seedlings, paper birch grew marginally larger than yellow birch ($F_{1,113} = 3.6$, $P = 0.06$). Watering frequency significantly influenced the growth of individual seedlings through the growing season ($F_{3,113} = 48.4$, $P < 0.0001$; Fig. 2). Seedlings grown under water treatments 1 and 2 were significantly smaller than treatments 3 and 4 (*post hoc*s, $P < 0.0001$). CO_2 concentration also significantly influenced total biomass of individual seedlings, increasing growth by 47% on average ($F_{1,113} = 77.1$, $P < 0.0001$). There were no significant higher-order interactions between species, water and CO_2 level ($P > 0.1$). However, *post hoc* comparisons revealed that elevated CO_2 changed seedling responses to the soil moisture gradient in species-specific ways (Fig. 2). Paper birch seedlings showed significant effects of elevated CO_2

Table 1 Average and minimum values of volumetric soil moisture content and soil matric potential for experimental watering treatments

Array type	Water/CO_2 level[†]	Water content (cm^3 cm^{-3})		Matric potential[‡] (kPa)	
		Average	Minimum	Average	Minimum
Individual	1	0.176	0.091	34.4	78.4
	2	0.210	0.103	22.5	70.4
	3	0.244	0.171	12.5	36.3
	4	0.290	0.249	1.0	11.0
Stand	1, A	0.197	0.104	26.7	69.6
	1, E	0.207	0.104	23.6	69.5
	4, A	0.251	0.229	10.6	16.7
	4, E	0.276	0.245	4.2	12.2

[†]For individuals, watering treatments from dry (1) to wet (4) are shown, with species and CO_2 level combined. For stands, ambient (A) and elevated (E) CO_2 effects are shown separately.
[‡]Derived from soil moisture retention curve (see text).

in all water treatments, but the magnitude of enhancement was strongly dependent on water level, declining with increasing watering frequency. In contrast, yellow birch seedlings only showed a significant enhancement in elevated CO_2 when watered more frequently (treatments 3 and 4, $P < 0.05$), even though the absolute magnitude of enhancement did not change across the gradient. For paper birch, this differential CO_2 responsiveness reduced the growth increase between treatments 1 and 4 from 155% to 42%, and caused a marginally significant increase in response breadth (permutation test, $P < 0.1$). For yellow birch, elevated CO_2 augmented the growth increase between treatments 1 and 4 from 76% to 84%, but produced no significant change in response breadth ($P > 0.1$).

*Leaf-level photosynthesis for individually grown seedlings*

Treatment effects on seedling growth were paralleled to some extent by changes in *in situ* leaf-level photosynthetic rates (Fig. 3). Paper birch seedlings had higher rates of CO_2 fixation than those of yellow birch over the eight-day watering cycle ($F_{1,364} = 23.1$, $P < 0.0001$). For both species, rates of photosynthesis were dependent on frequency of watering ($F_{3,364} = 101.5$, $P < 0.0001$), with seedlings watered less frequently showing higher rates than those watered more frequently (*post hocs*, $P < 0.0001$). Plants grown at elevated CO_2 had significantly higher *in situ* photosynthetic rates than those in ambient CO_2 (*post hocs*, $P < 0.05$), except for the most frequently watered yellow birch seedlings (Fig. 3). There was no significant three–way interaction between species, water and CO_2 concentration ($F_{3,364} = 1.55$, $P > 0.1$), but the magnitude of CO_2 enhancement differed across water treatments for the species (Fig. 3). There was greater photosynthetic

enhancement for paper birch seedlings in low water treatments (1 and 2) than for more frequently watered seedlings (3 and 4). For yellow birch, photosynthetic enhancement was more consistent across water levels, except for low enhancement in water level 4.

For water treatments that experienced wide variation in soil moisture levels (1 and 2), the response of leaf-level photosynthesis to atmospheric CO_2 concentration varied through the watering cycle (Fig. 4). For both species, both photosynthesis and conductance showed little sensitivity to the variation in soil moisture levels experienced through the watering cycle. In ambient CO_2, however, paper birch photosynthesis declined significantly between $0.1 – 0.2$ cm^3 cm^{-3} and $0 – 0.1$ cm^3 cm^{-3} volumetric soil moisture content (Bonferroni-corrected pairwise comparison, $P < 0.05$), while there was no significant change in yellow birch photosynthesis across the watering cycle ($P > 0.05$). In elevated CO_2, there was no decline in paper birch photosynthesis in response to decreased soil moisture levels ($P > 0.05$). Stomatal conductance showed similar trends to photosynthesis, but none of the changes were significant ($P > 0.05$).

Seedling growth and survival in mixed competitive stands

When seedlings of each species were grown together in competition, paper birch seedlings were significantly larger than yellow birch seedlings and formed the stand canopy (species effect, $F_{1,179} = 128.2$, $P < 0.0001$). The species responded in different ways to soil moisture (species × water interaction, $F_{1,179} = 12.7$, $P < 0.001$; Fig. 5), with paper birch seedlings showing a significant increase in growth with increased frequency of watering (*post hocs*, $P < 0.0001$), while no such change was observed for yellow birch seedlings (*post hocs*, $P > 0.1$). As for

(a) Individually grown seedlings

(b) Competitively grown seedlings
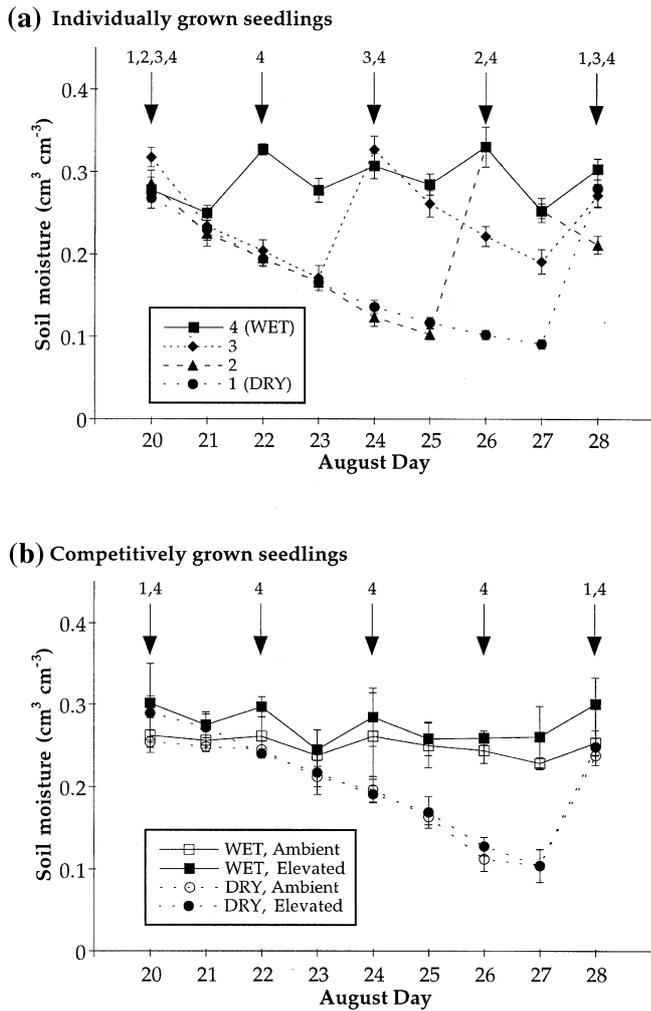
Fig. 1 Volumetric soil moisture changes over an eight-day watering cycle in August for seedlings grown individually (a) and in mixed competitive stands (b). For individual seedlings, changes for the four water treatments are shown, with species and CO_2 level combined. For stands, water and CO_2 treatments are shown. Each point represents a mean of 12 pots (individuals) or 3 stands, with error bars showing ± 1 SE of the mean. Arrows mark watering events, with the treatments applied at that time shown above each arrow.

seedlings grown individually, elevated CO_2 increased growth of seedlings in competition ($F_{1,179}$ = 10.7, $P < 0.01$), with a mean increase of 25%. Additionally, elevated CO_2 altered the way seedlings of each species responded to soil moisture (species × water × CO_2 interaction, $F_{1,179}$ = 4.1, $P < 0.05$). The increase in growth that accompanied the increase in watering frequency was much smaller for paper birch seedlings grown in elevated CO_2 than for those in ambient CO_2 (56% vs. 110% increase). In contrast, as watering frequency increased, there was a much greater increase in biomass of yellow birch seedlings in elevated than ambient CO_2 (27% vs. 1.5% increase). These changes in species' responses to

(a) Paper birch
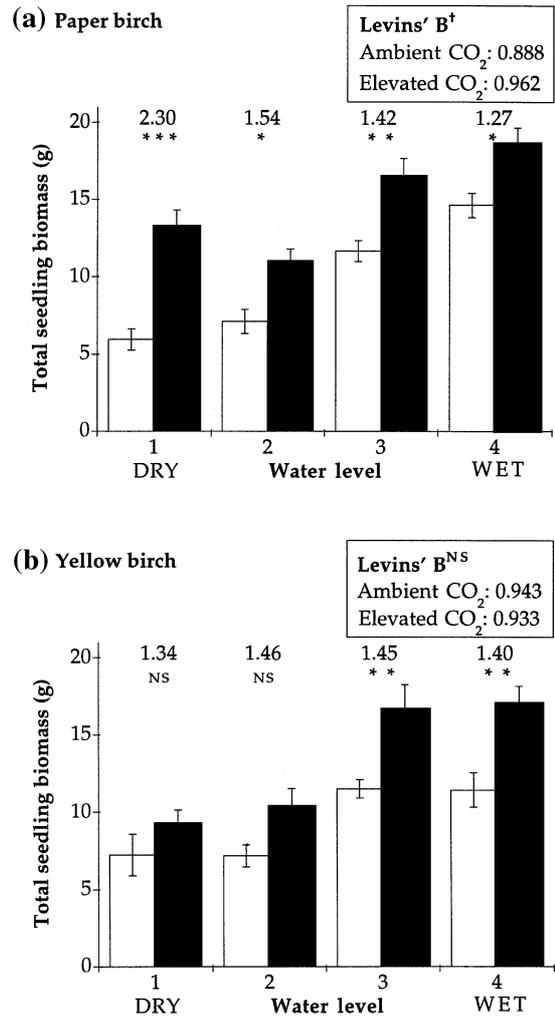
(b) Yellow birch

Fig. 2 Total biomass of paper birch (a) and yellow birch (b) seedlings grown individually in ambient (375 μL L^{-1}, □) or elevated (700 μL L^{-1}, ■) CO_2, and in one of four experimental watering treatments (see Fig. 1a). Column height is proportional to mean total biomass of 6–9 seedlings per treatment, and error bars represent ± 1 SE of the mean. CO_2 enhancement ratios (biomass at 700 μL L^{-1}/375 μL L^{-1}) and their significance (Scheffe *post hoc* comparisons; [NS] $P > 0.1$, † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) are shown above each column pair. Response breadth at each CO_2 level, calculated as Levin's B (Levins 1968), is included for each species, with significance of the CO_2 effect shown with the same symbols as enhancement ratio (permutation test).

water availability arose because CO_2 responsiveness depended on soil moisture levels (Fig. 5). Paper birch seedlings only showed a significant growth enhancement in elevated CO_2 at low soil moisture levels (*post hocs*, $P < 0.05$), while there was only a significant CO_2 effect on yellow birch seedling growth in well watered stands (*post hocs*, $P < 0.01$).

Seedling survival in mixed stands was influenced by experimental treatments (Fig. 6). Paper birch seedlings

had high survival when grown in competition, regardless of watering frequency or CO$_2$ concentration, while yellow birch seedlings showed considerable mortality, especially in stands watered infrequently. In these dry stands, elevated CO$_2$ significantly improved yellow birch survival (Mantel–Haenszel, $P < 0.01$).

Discussion

Interaction of CO$_2$ and soil moisture

We found that elevated CO$_2$ changed the way seedlings of the two birch species responded to soil moisture, both as individuals and in mixed competitive stands. Paper birch showed particularly large increases in biomass in response to elevated CO$_2$ when watered less frequently, and much smaller enhancements as watering frequency increased. This differential change in CO$_2$ responsiveness across the moisture gradient reduced the difference in seedling growth between high and low water availability and effectively broadened the regeneration niche of paper birch (*sensu* Grubb, 1977) with respect to soil moisture. In contrast, yellow birch seedlings showed significant CO$_2$ growth enhancement only at the wet end of the soil moisture gradient. For individually grown yellow birch seedlings, the magnitude of CO$_2$-induced growth enhancement did not change across the gradient, but only had a significant effect in the two treatments with higher soil moisture levels. Similarly, elevated CO$_2$ significantly increased yellow birch growth in well watered stands but not in dry stands. Much previous work on interactions between CO$_2$ and water has focused on individually grown seedlings. Results have been varied, with some studies finding a strong influence of elevated CO$_2$ on plant responses to soil moisture (Tolley & Strain, 1984; Miao *et al.*, 1992) and others observing little interaction between CO$_2$ and water (Tschaplinski *et al.*, 1993; Samuelson & Seiler, 1994). Unlike our results, stand-level studies have found little evidence for CO$_2$–water interactions (Bazzaz & Carlson, 1984; Groninger *et al.*, 1995; Groninger *et al.*, 1996).

There has been an ongoing debate in the literature about potential 'pot binding' in CO$_2$ experiments (Thomas & Strain, 1991; Kerstiens & Hawes, 1994; McConnaughay *et al.*, 1996). In the present study, it is unlikely that seedlings were 'pot-limited'. The enhancements observed in elevated CO$_2$ for these species were well within the published range for plants in general (Ceulemans & Mousseau, 1994; Wullschleger *et al.*, 1995), and for birch species in particular (Rochefort & Bazzaz, 1992; Bazzaz & Miao, 1993; Pettersson *et al.*, 1993; Wayne & Bazzaz, 1995; Berntson & Bazzaz, 1998). Seedlings were fertilized to match natural nitrogen mineralization rates observed in temperate forests (Aber *et al.*, 1993), and nutrient
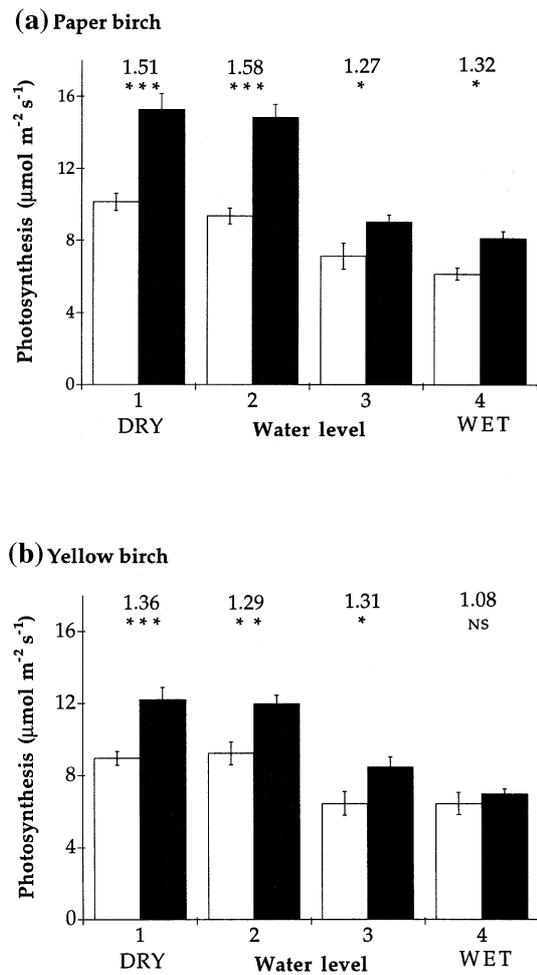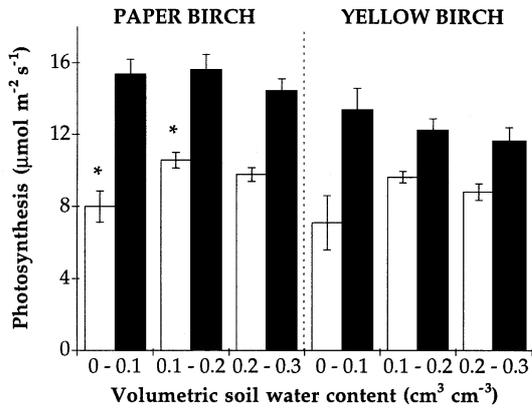

Fig. 3 *In situ* leaf-level photosynthetic rates of paper birch (a) and yellow birch (b) seedlings growing individually in ambient (375 µL L^{-1}, □) or elevated (700 µL L^{-1}, ■) CO$_2$, and in one of four experimental watering treatments (see Fig. 1a). Column height is proportional to the mean daily photosynthetic rate averaged over the eight-day watering cycle (8 measurements per mean), and error bars represent ± 1 SE of the mean. CO$_2$ enhancement ratios (photosynthesis at 700 µL L^{-1}/375 µL L^{-1}) and their significance (Scheffe *post hoc* comparisons; [NS] $P > 0.1$, † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) are shown above each column pair.

availability rather than pot size often determines the degree of 'pot binding' (McConnaughay *et al.*, 1993, 1996).

We observed remarkable convergence between the growth responses of individuals and seedlings in stands. Plants in competition often experience a very different local environment from those grown individually (Bazzaz, 1996), and so it is perhaps surprising that we saw parallels between individual- and stand-level responses (Wayne & Bazzaz, 1995). This is particularly striking for yellow birch seedlings, which were usually subordinate to paper birch in stands and thus experienced
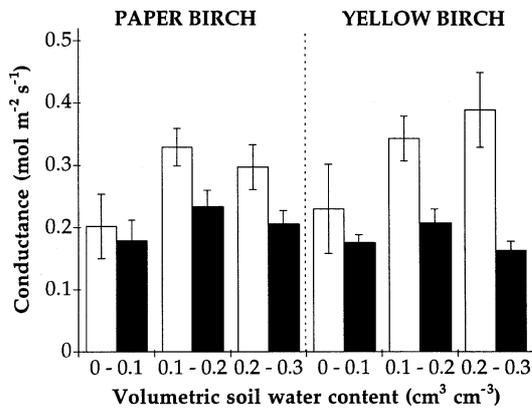
(a) Photosynthesis

(b) Conductance

Fig. 4 Sensitivity of *in situ* leaf-level photosynthetic rates (a) and stomatal conductance (b) to volumetric soil water content for paper birch (left) and yellow birch (right) seedlings growing individually in ambient (375 μL L^{-1}, □) or elevated (700 μL L^{-1}, ■) CO_2. Only measurements on seedlings in the two least frequently watered treatments were included (1 and 2, Fig. 1a). Column height is proportional to mean daily photosynthetic rate averaged for all measurements over the eight-day watering cycle that fell within that soil moisture interval (7–28 measurements per mean), and error bars represent ± 1 SE of the mean. Starred columns (*) are significantly different from one another at the 5% probability level, based on Bonferroni-corrected pairwise comparisons **within** a species and CO_2 level only.

much lower light levels than individually grown seedlings (Wayne & Bazzaz, 1997).

We began by predicting that both birch species would show larger CO_2 growth enhancements at the drier end of the gradient, and that yellow birch (species with the more mesic distribution) would benefit more from improved water use efficiency in elevated CO_2. In fact, we found that paper birch (the more xeric species) showed a stronger CO_2 enhancement at the dry end of the water

(a) Paper birch
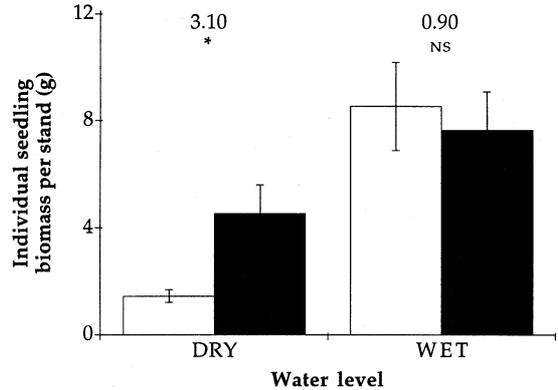
(b) Yellow birch

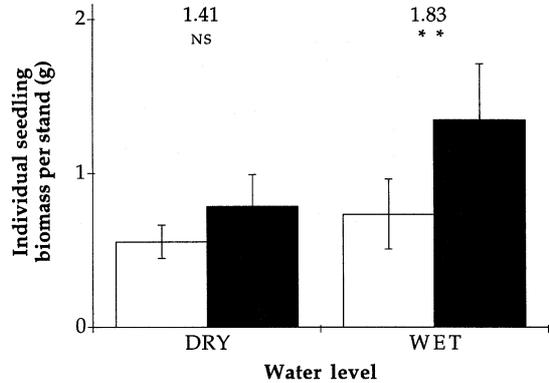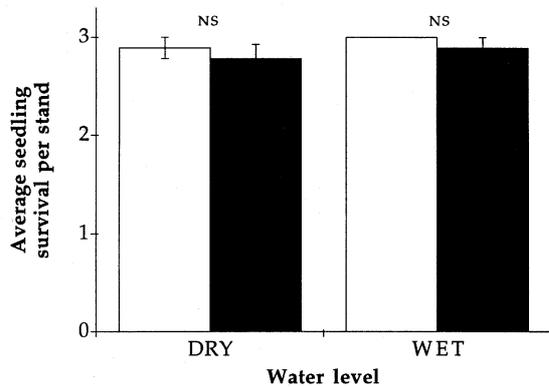
Fig. 5 Mean individual biomass of paper birch (a) and yellow birch (b) seedlings grown in mixed species competitive stands in ambient (375 μL L^{-1}, □) or elevated (700 μL L^{-1}, ■) CO_2, and in one of two experimental watering treatments (see Fig. 1b). Column height is proportional to mean of average individual biomass of living 'target' seedlings in every stand (9 measurements per mean), and error bars represent ± 1 SE of the mean. CO_2 enhancement ratios (biomass at 700 μL L^{-1}/ 375 μL L^{-1}) and their significance (Scheffe *post hoc* comparisons; [NS] $P > 0.1$, † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) are shown above each column pair.

gradient, while the growth enhancement for yellow birch was only significant in well watered plants. Why did we find a disparity between our predictions and results? The classification of these species as 'xeric' and 'mesic' may be an oversimplification. We found that, under ambient CO_2 conditions, the species did not differ from one another in their responses to soil moisture when grown individually, and in stands they responded to soil moisture in the opposite way to what we predicted. In addition, observations in the field suggest that seedlings of these species do not partition the soil moisture gradient
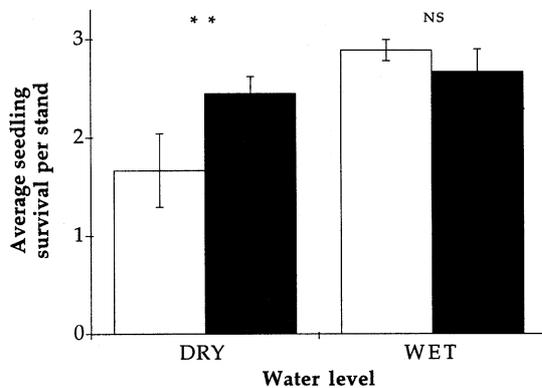
(a) Paper birch

(b) Yellow birch

Fig. 6 Stand-level survival of paper birch (a) and yellow birch (b) seedlings grown in mixed species competitive stands in ambient (375 μL L^{-1}, □) or elevated (700 μL L^{-1}, ■) CO$_2$, and in one of two experimental watering treatments (Fig. 1b). Column height is proportional to mean of average number of 'target' seedlings surviving per stand (9 measurements per mean), and error bars represent ± 1 SE of the mean. The significance of any CO$_2$ effect is shown above each column pair (Mantel–Haenszel; NS $P > 0.1$, † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

as clearly as the mature trees do (S. Catovsky, unpubl. data).

Seedling growth responses do not necessarily predict a species' demographic dynamics in the field, as they only describe one aspect of the life-cycle (Bazzaz, 1996; Pacala *et al.*, 1996). For example, in a previous study, seedlings of a species expected to be most sensitive to low water availability (*Acer saccharum*) showed, in fact, the smallest growth reduction in response to drought stress (Tschaplinski *et al.*, 1995). Our results from mixed species stands suggest that we should consider both physiological (growth) and demographic (survival) parameters to predict population- and community-level responses to rising levels of atmospheric CO$_2$. We found

that yellow birch seedlings showed different growth and survival responses to CO$_2$ and water availability. Elevated CO$_2$ significantly increased yellow birch growth only in well watered stands, while survival was improved only in dry stands. Most CO$_2$ studies focus on seedling growth responses, while demographic consequences of rising CO$_2$ levels have not been adequately addressed to date. Variations in seedling population parameters will ultimately drive future community-level changes (Bazzaz, 1993). It is particularly important to consider survival along with growth when addressing seedling responses to soil moisture availability, as drought stress commonly excludes species from sites through its effect on seedling mortality. For example, Polley *et al.* (1996) found that elevated CO$_2$ improved survival of droughted *Prosopis glandulosa* seedlings and predicted that the species may expand its distribution to drier sites in the future.

Basis for differences in species' responses

Paper birch and yellow birch differ in their responses to the availability of resources, including light (Wayne & Bazzaz, 1993) and nitrogen (Crabtree & Bazzaz, 1993; Berntson & Bazzaz, 1998). Paper birch normally appears earlier in succession than yellow birch, and often shows greater responsiveness to resource availability (Bazzaz, 1996; Carlton & Bazzaz, 1998). We found that photosynthesis of paper birch seedlings was more sensitive to decreasing soil moisture levels than for yellow birch seedlings. Elevated CO$_2$ alleviated the reduction in paper birch photosynthesis as soil moisture levels declined, and led to a larger photosynthetic enhancement for seedlings watered less frequently. In contrast, for yellow birch seedlings, CO$_2$ enhancement of photosynthesis was more consistent across water levels. Tolley & Strain (1985) found similar differential species sensitivity to CO$_2$ and water availability. They observed that, in contrast to *Pinus taeda*, *Liquidambar styraciflua* seedlings grown in elevated CO$_2$ did not undergo dramatic declines in photosynthesis as a result of water stress while those in ambient CO$_2$ did. For paper birch, photosynthetic responses to soil moisture were likely mediated by variation in stomatal conductance. There was some evidence that stomatal sensitivity to declining soil moisture was reduced in elevated CO$_2$, but the trends were not significant. Further work is needed to elucidate the physiological mechanisms underlying the observed responses.

Implications for forest community structure

Although our study was restricted to one growing season, early seedling performance has been previously demonstrated to be a good indicator of future community composition (Grubb, 1977; Bazzaz, 1996). The importance

of these early stages of regeneration are due to the pre-emptive nature of plant competition (Schwinning & Weiner, 1998) and the initial high seedling turnover in tree populations (Peet & Christensen, 1987). Thus, by affecting how seedlings respond to variation in resource availability, elevated CO_2 may influence the distribution and abundance of species across their habitat range. We found that elevated CO_2 caused paper birch to improve its performance in dry treatments to a greater extent than in well watered ones, both as individually grown seedlings and in mixed competitive stands. These changes effectively increased the breadth of the regeneration niche of paper birch and may allow this species to maintain a stronger dominance on dry sites in the future. In contrast, the responsiveness of yellow birch seedling growth to elevated CO_2 was greater on well watered soils. Our results suggest that regeneration of paper birch may be significantly improved on more xeric sites, while yellow birch seedlings may improve their performance on relatively moist soil patches in forests. These patterns may reinforce current distributions of mature trees of these species in relation to soil moisture. Other studies have similarly found that species respond most strongly to elevated CO_2 under the conditions in which they are most commonly found in the field, for water (Miao *et al.*, 1992; Groninger *et al.*, 1995; Tschaplinski *et al.*, 1995), light (Kubiske & Pregitzer, 1996; Kubiske & Pregitzer, 1997; Roden *et al.*, 1997) and nutrients (Bazzaz & Miao, 1993).

In addition, we identified seedling survival as another component of population responses to elevated CO_2 that may be important in determining species' dynamics in the future. We found that elevated CO_2 significantly improved survival of yellow birch seedlings in stands watered infrequently. Higher mortality on dry sites may be currently excluding yellow birch seedlings from regenerating on such sites, and improved survival due to elevated CO_2 may permit longer persistence of yellow birch seedlings on such sites in the future.

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References

Aber JD, Magill A, Boone R, Melillo JM, Steudler P, Bowden R (1993) Plant and soil responses to chronic nitrogen additions at the Harvard Forest, Massachusetts. *Ecological Applications*, **3**, 156–166.

Bazzaz FA (1990) Plant–plant interactions in successional environments. In: *Perspectives in Plant Competition* (eds Grace JB, Tilman GD), pp. 239–263. Academic Press, San Diego, CA.

Bazzaz FA (1993) Scaling in biological systems: population and community perspectives. In: *Scaling Physiological Processes: Leaf to Globe* (eds Ehleringer J, Field CB), pp. 233–254. Academic Press, San Diego, CA.

Bazzaz FA (1996) *Plants in Changing Environments: Linking Physiological, Population, and Community Ecology*. Cambridge University Press, Cambridge.

Bazzaz FA, Carlson RW (1984) The response of plants to elevated CO_2: I. Competition among an assemblage of annuals at two levels of soil moisture. *Oecologia (Berlin)*, **62** 196–198.

Bazzaz FA, Garbutt K, Williams WE (1985) Effect of increased atmospheric carbon dioxide concentration on plant communities. In: *Direct Effects of Increasing Carbon Dioxide on Vegetation* (eds Strain BR, Cure JD), pp. 155–170. United States Department of Energy, Washington, DC.

Bazzaz FA, Grace J (eds) (1997) *Plant Resource Allocation*. Academic Press, San Diego, CA.

Bazzaz FA, McConnaughay KDM (1992) Plant–plant interactions in elevated CO_2 environments. *Australian Journal of Botany*, **40**, 547–563.

Bazzaz FA, Miao SL (1993) Successional status, seed size, and responses of tree seedlings to CO_2, light, and nutrients. *Ecology*, **74**, 104–112.

Berntson GM, Bazzaz FA (1998) Regenerating temperate forest mesocosms in elevated CO_2: belowground growth and nitrogen cycling. *Oecologia*, **113**, 115–125.

Burns RM, Honkala BH (eds) (1990) *Silvics of North America: Volume 2. Hardwoods*. United States Department of Agriculture, Washington, DC.

Carlton GC (1993) *Effects of microsite environment on tree regeneration following disturbance*. PhD Thesis, Harvard University, Cambridge, MA.

Carlton GC, Bazzaz FA (1998) Regeneration of three sympatric birch species on experimental hurricane blowdown microsites. *Ecological Monographs*, **68**, 99–120.

Ceulemans R, Mousseau M (1994) Effects of elevated atmospheric CO_2 on woody plants. *New Phytologist*, **127**, 425–446.

Chapin FS III, Bloom AJ, Field CB, Waring RH (1987) Plant responses to multiple environmental factors. *Bioscience*, **37**, 49–57.

Crabtree RC, Bazzaz FA (1993) Seedling response of four birch species to simulated nitrogen deposition: ammonium vs. nitrate. *Ecological Applications*, **3**, 315–321.

Drake BG, Gonzalez-Meler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO_2? *Annual Review of Plant Physiology and Plant Molecular Biology*, **48**, 609–639.

Eamus D (1991) The interaction of rising CO_2 and temperatures with water use efficiency. *Plant, Cell and Environment*, **14**, 843–852.

Eamus D, Jarvis PG (1989) The direct effects of increase in the global atmospheric CO_2 concentration on natural and commercial temperate trees and forests. *Advances in Ecological Research*, **19**, 1–55.

Field CB, Chapin FS III, Matson PA, Mooney HA (1992) Responses of terrestrial ecosystems to the changing atmosphere: a resource-based approach. *Annual Review of Ecology and Systematics*, **23**, 201–235.

Field CB, Jackson RB, Mooney HA (1995) Stomatal responses to increased CO$_2$: implications from the plant to the global scale. *Plant, Cell and Environment*, **18**, 1214–1225.

Goldberg DE (1990) Components of resource competition in plant communities. In: *Perspectives on Plant Competition* (eds Grace JB, Tilman D), pp. 27–49. Academic Press, San Diego, CA.

Groninger JW, Seiler JR, Zedaker SM, Berrang PC (1995) Effects of elevated CO$_2$, water stress, and nitrogen level on competitive interactions of simulated loblolly pine and sweetgum stands. *Canadian Journal of Forest Research*, **25**, 1077–1083.

Groninger JW, Seiler JR, Zedaker SM, Berrang PC (1996) Effects of CO$_2$ concentration and water availability on growth and gas exchange in greenhouse-grown miniature stands of loblolly pine and red maple. *Functional Ecology*, **10**, 708–716.

Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, **52**, 107–145.

Huston MA (1994) *Biological Diversity*. Cambridge University Press, Cambridge.

Jackson RB, Sala OE, Field CB, Mooney HA (1994) CO$_2$ alters water use, carbon gain, and yield for the dominant species in a natural grassland. *Oecologia*, **98**, 257–262.

Kerstiens G, Hawes CV (1994) Response of growth and carbon allocation to elevated CO$_2$ in young cherry (*Prunus avium* L.) saplings in relation to root environment. *New Phytologist*, **128**, 607–617.

Kleb HR, Wilson SD (1997) Vegetation effects on soil resource heterogeneity in prairie and forest. *American Naturalist*, **150**, 283–298.

Koch GW, Mooney HA (eds) (1996) *Carbon Dioxide and Terrestrial Ecosystems*. Academic Press, San Diego, CA.

Körner Ch, Bazzaz FA (eds) (1996) *Carbon Dioxide, Populations, and Communities*. Academic Press, San Diego, CA.

Kubiske ME, Pregitzer KS (1996) Effects of elevated CO$_2$ and light availability on the photosynthetic light response of trees of contrasting shade tolerance. *Tree Physiology*, **16**, 351–358.

Kubiske ME, Pregitzer KS (1997) Ecophysiological responses to simulated canopy gaps of two tree species of contrasting shade tolerance in elevated CO$_2$. *Functional Ecology*, **11**, 24–32.

Levins R (1968) *Evolution in Changing Environments*. Princeton University Press, Princeton, NJ.

Marquis DA (1965) Regeneration of birch and associated hardwoods after patch cutting. *U. S. Forest Service Research Paper*, **NE-32**, 1–13.

McConnaughay KDM, Berntson GM, Bazzaz FA (1993) Limitations to CO$_2$-induced growth enhancement in pot studies. *Oecologia*, **94**, 550–557.

McConnaughay KDM, Nicotra AB, Bazzaz FA (1996) Rooting volume, nutrient availability, and CO$_2$-induced growth enhancements in temperate forest tree seedlings. *Ecological Applications*, **6**, 619–627.

Miao SL, Wayne PM, Bazzaz FA (1992) Elevated CO$_2$ differentially alters the responses of cooccurring birch and maple seedlings to a moisture gradient. *Oecologia*, **90**, 300–304.

Mooney HA, Drake BG, Luxmoore RJ, Oechel WC, Pitelka LF (1991) Predicting ecosystem responses to elevated CO$_2$ concentrations. *Bioscience*, **41**, 96–104.

Morse SR, Wayne P, Miao SL, Bazzaz FA (1993) Elevated CO$_2$ and drought alter tissue water relations of birch (*Betula populifolia* Marsh.) seedlings. *Oecologia*, **95**, 599–602.

Mott KA (1990) Sensing of atmospheric CO$_2$ by plants. *Plant, Cell and Environment*, **13**, 731–737.

Newman JA, Bergelson J, Grafen A (1997) Blocking factors and hypothesis tests in ecology: is your statistics text wrong? *Ecology*, **78**, 1312–1320.

Pacala SW, Canham CD, Saponara J, Silander JA Jr, Kobe RK, Ribbens E (1996) Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs*, **66**, 1–43.

Peet RK, Christensen NL (1987) Competition and tree death. *Bioscience*, **37**, 586–595.

Pettersson R, McDonald AJS, Stadenberg I (1993) Response of small birch plants (*Betula pendula* Roth.) to elevated CO$_2$ and nutrient supply. *Plant, Cell and Environment*, **16**, 1115–1121.

Polley HW, Johnson HB, Mayeux HS, Tischler CR, Brown DA (1996) Carbon dioxide enrichment improves growth, water relations and survival of droughted honey mesquite (*Prosopis glandulosa*) seedlings. *Tree Physiology*, **16**, 817–823.

Rochefort L, Bazzaz FA (1992) Growth response to elevated CO$_2$ in seedlings of four co-occurring birch species. *Canadian Journal of Forest Research*, **22**, 1583–1587.

Roden JS, Wiggins DJ, Ball MC (1997) Photosynthesis and growth of two rain forest species in simulated gaps under elevated CO$_2$. *Ecology*, **78**, 385–393.

Samuelson LJ, Seiler JR (1994) Red spruce seedling gas exchange in response to elevated CO$_2$, water stress, and soil fertility. *Canadian Journal of Forest Research*, **24**, 954–959.

Schimel DS (1995) Terrestrial ecosystems and the carbon cycle. *Global Change Biology*, **1**, 77–91.

Schwinning S, Weiner J (1998) Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia*, **113**, 447–455.

Sokal RR, Rohlf FJ (1995) *Biometry*, 3rd edn. W. H. Freeman, New York, NY.

Thomas RB, Strain BR (1991) Root restriction as a factor in photosynthetic acclimation of cotton seedlings grown in elevated carbon dioxide. *Plant Physiology*, **96**, 627–634.

Tolley LC, Strain BR (1984) Effects of CO$_2$ enrichment and water stress on growth of *Liquidambar styraciflua* and *Pinus taeda* seedlings. *Canadian Journal of Botany*, **62**, 2135–2139.

Tolley LC, Strain BR (1985) Effects of CO$_2$ enrichment and water stress on gas exchange of *Liquidambar styraciflua* and *Pinus taeda* seedlings grown under different irradiance levels. *Oecologia (Berlin)*, **65**, 166–172.

Tschaplinski TJ, Norby RJ, Wullschleger SD (1993) Responses of loblolly pine seedlings to elevated CO$_2$ and fluctuating water supply. *Tree Physiology*, **13**, 283–296.

Tschaplinski TJ, Stewart DB, Hanson PJ, Norby RJ (1995) Interactions between drought and elevated CO$_2$ on growth and gas exchange of seedlings of three deciduous tree species. *New Phytologist*, **129**, 63–71.

Tyree MT, Alexander JD (1993) Plant water relations and the effects of elevated CO_2: a review and suggestions for future research. *Vegetatio*, **104/105**, 47–62.

Walker BH (1975) Vegetation – site relationships in the Harvard Forest. *Vegetatio*, **29**, 169–178.

Wayne PM, Bazzaz FA (1993) Morning vs afternoon sun patches in experimental forest gaps: consequences of temporal incongruency of resources to birch regeneration. *Oecologia*, **94**, 235–243.

Wayne PM, Bazzaz FA (1995) Seedling density modifies the growth responses of yellow birch maternal families to elevated carbon dioxide. *Global Change Biology*, **1**, 315–324.

Wayne PM, Bazzaz FA (1997) Light acquisition and growth by competing individuals in CO_2-enriched atmospheres: consequences for size structure in regenerating birch stands. *Journal of Ecology*, **85**, 29–42.

Whittaker RH (1975) *Communities and Ecosystems*, 2nd edn. MacMillan, New York.

Wilson JB, Lee WG (1994) Niche overlap of congeners: a test using plant altitudinal distribution. *Oikos*, **69**, 469–475.

Wofsy SC, Goulden ML, Munger JW, *et al.* (1993) Net exchange of CO_2 in a mid-latitude forest. *Science*, **260**, 1314–1317.

Woodward FI, Thompson GB, McKee IF (1991) The effects of elevated concentrations of carbon dioxide on individual plants, populations, communities and ecosystems. *Annals of Botany*, **67**, S23–S38.

Wullschleger SD, Post WM, King AW (1995) On the potential for a CO_2 fertilization effect in forests: estimates of the biotic growth factor based on 58 controlled-exposure studies. In: *Biotic Feedbacks in the Global Climatic System: Will the Warming Feed the Warming?* (eds Woodwell GM, Mackenzie FT), pp. 86–107. Oxford University Press, New York.