

Growth response to elevated CO₂ in seedlings of four co-occurring birch species

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Seedlings of four birch species were examined to evaluate the presence and extent of phylogenetic constraints on the response of species to global CO₂ change. The species differ in their habitat preferences and their successional status. Seedlings were grown for 3 months at near ambient (380 μL·L⁻¹) and double (690 μL·L⁻¹) CO₂ concentrations in glasshouses. We found the following: (i) yellow birch (*Betula alleghaniensis* Britton) was the only species whose survival differed among CO₂ treatments. Survival was slightly increased by elevated CO₂. (ii) All growth parameters considered in all four species were significantly stimulated by enriched CO₂ conditions, but the magnitude of response was different among species. The most shade-intolerant, fast-growing species (grey birch; *Betula populifolia* Marsh.) took greater advantage of the elevated CO₂ resource than the more shade-tolerant, later successional species (e.g., yellow birch). (iii) Patterns of allocation, shoot architecture, and leaf nitrogen content were affected differently by CO₂ concentrations for the different species. (iv) The presence and identity of a neighbor did not influence the magnitude or pattern of response to CO₂ in birches of a given community. Our results suggest that congeneric species might be more similar in their response to global CO₂ in comparison to unrelated species of the same ecosystem that had been studied by others, despite the fact that these closely related birch species differ in their habitat preferences and successional status.

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Les semis de quatre espèces de bouleau furent étudiés dans le but d'évaluer l'existence et l'ampleur des limitations phylogénétiques dans leur adaptation à un changement global dans la concentration de CO₂. Les espèces diffèrent par leur choix d'habitat et leur position dans la succession. Les semis furent cultivés en serre pendant 3 mois à des concentrations de CO₂ voisines (380 μL·L⁻¹) et deux fois plus élevées (690 μL·L⁻¹) que la concentration ambiante. Nous avons découvert que : (i) le bouleau jaune (*Betula alleghaniensis* Britton) est la seule espèce dont la survie variait selon les traitements. Le taux de survie était légèrement meilleur à la concentration la plus élevée de CO₂. (ii) Tous les paramètres de croissance étudiés étaient significativement rehaussés par un enrichissement en CO₂ mais l'ampleur de la réponse variait selon les espèces. L'espèce à croissance rapide et la plus intolérante à l'ombre, le bouleau gris (*Betula populifolia* Marsh.), a davantage profité d'une plus grande quantité de CO₂ que les espèces plus tolérantes, venant plus tard dans la succession, tel le bouleau jaune. (iii) Les patrons d'allocation, l'architecture des pousses et le contenu en azote des feuilles réagissaient différemment aux différentes concentrations de CO₂ selon l'espèce. (iv) La présence et l'identité d'un voisin n'a pas influencé la nature ou l'ampleur de la réponse au CO₂ chez les bouleaux d'une association donnée. Nos résultats suggèrent que la réponse d'espèces du même genre au niveau global de CO₂ pourrait être plus semblable que celle qui a été étudiée par d'autres chez les espèces de genres différents dans un même écosystème, même si les espèces de bouleau étudiées, quoique fortement reliées, diffèrent par leur choix d'habitat et leur position dans la succession.

[Traduit par la rédaction]

Introduction

Global increase of atmospheric CO₂ concentrations, due to fossil fuel consumption and deforestation, are well documented (e.g., Keeling 1986; Bolin *et al.* 1986). Presently the global mean CO₂ concentration is ~350 μL·L⁻¹ and is expected to double in the middle of the next century (Conway *et al.* 1988; Intergovernmental Panel on Climate Change 1990). Because of its central role in plant photosynthesis, elevated CO₂ concentrations influence growth and reproduction in plants (reviews by Strain and Cure 1985; Eamus and Jarvis 1989; Bazzaz 1990a). Increased growth, photosynthesis, water use, and changed reproductive output have been documented in high CO₂ environments for crop plants (e.g., Kimball 1986), trees (Eamus and Jarvis 1989), and many plants from natural ecosystems (e.g., Strain and Cure 1985; Bazzaz 1990a). Growth enhancement is especially evident

when other plant resources, particularly nutrients and light, are not limiting (e.g., Tolly and Strain 1984a, 1985b).

Work on forest ecosystems has shown that species from the same ecosystem can greatly differ in their responses to elevated CO₂. Such responses include changes in photosynthetic rate, water use, growth, and allocation. For example, seven co-occurring tree species in the mixed forest of New England showed great difference in growth enhancement at elevated CO₂ (Bazzaz *et al.* 1990). The differences among species in response to CO₂ levels are highly influenced by the availability of other resources such as light, nitrogen, and phosphorus (e.g., Brown 1991; Conroy 1990; Goudriann and de Ruiter 1983). Species differences in shade tolerance, successional status, and taxonomic affinities might also affect their response to CO₂ levels. In some ecosystems these differences in response can result in changes in competitive abilities of the species and a change in community composition (Williams *et al.* 1986; Reekie and Bazzaz 1989; Bazzaz 1990b).

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In the present study we wished to examine the response of four sympatric species within the genus *Betula* to elevated CO₂ concentrations. Although the species are closely related and all are relatively pioneer to midsuccessional, they do differ from each other in several characters (described below). Four species of North American birches that co-occur in the mixed forests of New England were used in the experiment: black birch (*Betula lenta* L.), white birch (*Betula papyrifera* Marsh.), gray birch (*Betula populifolia* Marsh.), and yellow birch (*Betula alleghaniensis* Britton). Gray birch is a pioneer light-demanding species found in large forest clearings and in large gaps. Yellow birch, while it benefits from increased light levels, grows well in small gaps (Forcier 1975) and is the most shade-tolerant species among the four species of this study. Early successional white and midsuccessional black birches are intermediate in their shade tolerance status (Spurr and Barnes 1980). We asked, (i) Do these four closely related birches differ in their magnitude and pattern of growth response to elevated CO₂? (ii) Are the patterns of biomass allocation, shoot architecture, and leaf nitrogen content differentially affected by CO₂ in the four species? (iii) Is the magnitude or pattern of response to CO₂ altered by the presence of neighboring congeneric birches? (iv) Do the identities of neighbors influence the response to CO₂ levels?

Materials and methods

Growth conditions

Seeds were collected from mature individuals (multiple parents) in the Harvard Forest, Petersham, Massachusetts. White birch seeds were collected well into Harvard Forest at least 8 km (5 miles) from the nearest stand of gray birch. Hence we assumed that the degree of hybridity was probably low. Furthermore, the morphology of the experimental seedlings differentiated easily the two species. Seeds of each birch species were broadcast in a tray (35 × 21 × 5 cm) filled with moistened vermiculite. Germination took place at ambient CO₂ level on a glasshouse bench. The seed trays were sprayed daily with a mist of distilled water. Seedlings were emerging in all trays after 12 days. The seedlings were sprayed twice with 1/16 strength Evans' modified Shive's nutrient solution (Salisbury and Ross 1985).

After 8 weeks of growth in the trays, seedlings of similar size (about 2 cm tall) were transplanted into gray PVC pipe tubes (20 cm high × 6.5 cm diameter). The tubes were filled with John Innes No. 3 soil mix (2:2:2.5 loam-peat-grit volume ratio, mixed with 2.4 kg of Vitax Q4 (5.3:7.5:10, N-P-K) and 500 g of lime (calcium carbonate)). Ten replicates for each of the four species were grown as single individuals. Additionally, gray, black, and yellow birches were grown in competitive arrays, i.e., either with a neighbor of the same species or a neighbor of another species. Neighbor treatments were also replicated 10 times each.

Black × gray birch

Black birch × yellow birch

Yellow birch × gray birch

The CO₂ controlled glasshouses were 2.4 by 3.7 m. The control system, designed by G. Thompson, had three major components: an ADC 220 infrared gas analyser to monitor the ambient treatment, a differential gas analyser (Binos) to maintain the 350 μL·L⁻¹ difference, and a Honeywell voltage sensing switch to control the incoming CO₂. The concentrations of CO₂ were controlled to provide a mean absolute difference of 350 μL·L⁻¹. The fluctuations in the ambient glasshouse were kept to 40 μL·L⁻¹ by using extractor fans. Throughout the experiment the concentrations of CO₂ were, on average, 343 μL·L⁻¹ during the day and 380 μL·L⁻¹ during the night in the ambient glasshouse and 690 μL·L⁻¹ during the day and

730 μL·L⁻¹ during the night in the elevated CO₂ glasshouse. The CO₂ in the elevated CO₂ glasshouse was blended in with a flow meter, and the control system was accurate to ±10 μL·L⁻¹. An even distribution of CO₂ was achieved by using three fanned injection points and an oscillating fan to create turbulence inside the whole glasshouse. Overheating was controlled by irrigating the glasshouse roofs with cold water. Throughout the experiment the mean temperature was 28 ± 5°C during the day and relative humidity was 73 ± 12%. Birches were watered daily as needed. Night temperature was not controlled but was always below 20°C. Photon flux density (PAR) was usually greater than 900 μmol·m⁻²·s⁻¹ except for a few cloudy days during the 1989 growing season. This design was repeated at two CO₂ levels (350 and 700 μL·L⁻¹). These CO₂ concentrations, respectively, represent present-day and predicted CO₂ levels in 50 years time (Conway *et al.* 1988). Plants were grown in these CO₂ controlled glasshouses for 3 months. To minimize the effect of any particular greenhouse module on the plant response, the plants were rotated every 3–4 days, the CO₂ levels in glasshouses were switched around, and the location of the plants was randomized. During the 1st month of growth the birches were fumigated twice with a fungicide. The Cheshunt Compound® fungicide included ammonium carbonate and copper sulfate components. Five millilitres of the compound was diluted into 570 mL of the water. After 2 months of growth in CO₂ controlled glasshouses, nutrients were supplemented with a commercial liquid feed (Phostrogen®, U.K.; N-P-K 10:10:27). The plants were fed every 2 weeks, and each tube received an equal amount of nutrient solution. Beneath each tube was a dish that caught excess nutrient solution. In this way nutrient levels were maintained equal for each experimental tube. The birches were harvested after 3 months of growth.

Measurements of tree performance

After 30 and 45 days of growth, we recorded the number of leaves and measured plant height and length of the longest leaf for each individual plant to evaluate their performance nondestructively. Plants were harvested after 90 days. If there was only one birch in the tube, the number of leaves and branches were counted, stem length was measured, and leaf area was calculated (with a leaf area meter, Delta-T Devices Ltd., Cambridge, U.K.). After drying the plant material for 3 days in an oven at 80°C, dry biomass was determined for leaves, stems plus branches, and roots. For the competitive arrays, shoot and root dry weights per individual were determined. Tissue nitrogen (Kjeldahl-N) concentrations were obtained on redried ground material passed through a No. 40 mesh screen using aluminium block digestion (Bremner 1965; Gallaher *et al.* 1976).

Statistical analysis

Survivorship data were examined using three-dimensional contingency analyses with the fixed margins model (procedure BMDP 4F, version 1987). For the measured or counted variables, we examined the residuals for normality and homogeneity of variance assumptions. Count (e.g., number of branches) and surface (leaf area) variables were modified with square root transformation to make them suitable for analyses of variance (ANOVA). Data for comparing birch species performance were analyzed with two-way ANOVA with CO₂ (350 or 700 μL·L⁻¹) and species (black, gray, yellow, or white birch) as attribute variables. The ANOVA were followed by Student–Newman–Keuls multiple comparison statistic (SNK) on adjusted means to determine which means were significantly different. The ANOVA were performed with the MANOVA statistical procedure from SPSS/PC+ advanced statistics.

Results

Survivorship

Overall percent survival of black and gray birches grown individually or in a competitive array did not differ between the two CO₂ levels. In contrast, the survival rate of the yellow birches was higher at elevated CO₂ ($G^2 = 3.53$; where

TABLE 1. Overall survivorship of the birch species grown either singularly or in competition

CO ₂ ($\mu\text{L}\cdot\text{L}^{-1}$)	Birch species	Overall survivorship		
		Survived	Died	% mortality
350	Gray	31	19	38
	Black	30	20	40
	Yellow	25	15	38
700	Gray	36	14	28
	Black	32	18	36
	Yellow	33	7	18

$G^2 = 3.84$ for $\alpha = 0.05$; Table 1). In all cases of competition, whether the competing array was conspecific or heterospecific, CO₂ did not influence survivorship of the pairs ($G^2 = 2.72, 0.08$, respectively; $P > 0.05$). On average 20% of both individuals died in the conspecific competition experiment. The identity of the neighbor did not influence the pattern of mortality in the experiment. Generally members of a competitive pair that was smaller at 20 days had a higher probability of death irrespective of its identity or the identity of its competitor. The percentage of pairs in which at least one individual died was not affected by the CO₂ level ($G^2 = 0.29$ for same species grown together; $G = 3.07$ for different species grown together; all $P > 0.05$).

Individually grown birches

After 30 days leaf number and longest leaf length of all birches grown individually at elevated CO₂ were significantly greater than those of birches grown individually at ambient CO₂ (both $P < 0.005$ ANOVA). At day 45 height was also significantly enhanced in plants grown individually at elevated CO₂ (all $P < 0.0001$). No interactive effect of CO₂ concentrations and species was detected for either assessment (all $P > 0.23$; data not presented).

One of the consistent results of this study is the strong effect of CO₂ on seedling performance (all $P < 0.001$; Tables 2 and 3). There were no significant differences among the four species in their response to elevated CO₂ (all $P > 0.09$; Table 3). Overall, root, leaf, stem, and total plant biomass were nearly double or more than double when the single birches were grown in enriched CO₂ compared with those grown in ambient CO₂ environment (Table 2 and Fig. 1). For most variables no difference in dry biomass was detected between the birch species (SNK tests all $P > 0.05$). Gray birch, which had greater total biomass, was the only exception.

Patterns of allocation, shoot architecture, and leaf nitrogen content were affected differently by CO₂ concentrations for the different species. Elevated CO₂ stimulated the production of branches and number of leaves for all birch species. Black and gray birches had more branches and leaves than yellow or white birches irrespective of CO₂ level (SNK tests all $P < 0.05$; Table 2). Leaf area nearly doubled for all birch species grown in elevated CO₂ conditions, whereas stem length was usually 1.5 times longer for the CO₂ enriched plants. The species did not show species-specific differences in leaf area or stem length. Birches grown at elevated CO₂ allocated more biomass to their roots relative to their above-ground organs than did birches grown at ambient CO₂ (Fig. 1). There were small differences among the species in the pattern of allocation. When grown at elevated CO₂, birches

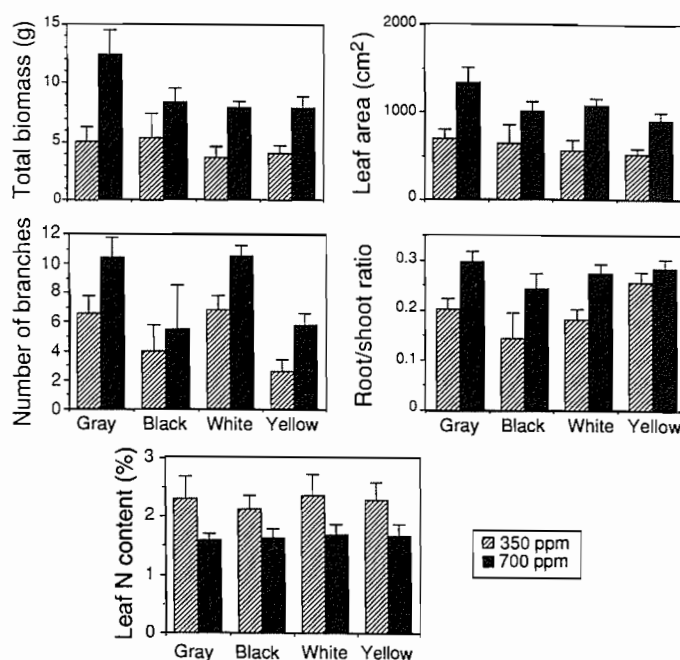


FIG. 1. Mean values (all ± 1 SE; $n = 10$) of total biomass, number of branches, total leaf area, root/shoot ratio, and nitrogen content of the singularly grown birches at 350 and 700 $\mu\text{L}\cdot\text{L}^{-1}$ CO₂ concentrations after 90 days of growth.

of all species had significantly lower nitrogen concentrations (two-way ANOVA; $F = 85.5$, $P < 0.001$). However, there were no significant differences among the four birch species in nitrogen concentration ($F = 0.94$, $P = 0.4$; Fig. 1).

Birches grown in competition

Two-way ANOVA of the total biomass per pair of birches grown in competitive arrays showed that the effect of CO₂ on the birches in competition did not vary depending on species. This result was true for both conspecific competition (CO₂ by species term, $F = 0.13$, $P = 0.9$) and heterospecific competition (CO₂ by species, $F = 0.47$, $P = 0.63$). In general, the total dry biomass per pair of birches more than doubled when grown in elevated CO₂ environment (Table 4). The weight of one birch species, relative to the total weight of both birches in the tube, was not influenced by the CO₂ level ($P = 0.98$) or by the species of the other birch ($P = 0.09$; data not presented).

Analyses of variance with arcsine transformed root/shoot ratio for the birches grown in competition (both types) showed that more biomass is allocated to the roots relative to shoots at higher CO₂ concentrations. This was also the case for the birches grown singularly.

Discussion

CO₂ and survivorship

There was greater mortality of yellow birch under ambient CO₂ conditions (340 $\mu\text{L}\cdot\text{L}^{-1}$) than under enriched CO₂ concentrations (700 $\mu\text{L}\cdot\text{L}^{-1}$) (Table 1). This may have resulted because the yellow birch seedlings grown in elevated CO₂ grew faster than those grown at ambient CO₂ (Fig. 1, Table 2). It has been shown that the concentration of CO₂ in a forest varies spatially, daily, and seasonally. Measurements of the CO₂ concentrations in a mixed deciduous forest in New

TABLE 2. Mean values (1 SE in parentheses) for number of leaves, stem length, root mass, stem mass, and leaf mass of white, black, gray, and yellow birches grown at 350 and 700 $\mu\text{L}\cdot\text{L}^{-1}$ CO_2 concentrations

Birch species	No. of leaves		Stem length (cm)		Root mass (g)		Stem mass (g)		Leaf mass (g)	
	350 $\mu\text{L}\cdot\text{L}^{-1}$	700 $\mu\text{L}\cdot\text{L}^{-1}$	350 $\mu\text{L}\cdot\text{L}^{-1}$	700 $\mu\text{L}\cdot\text{L}^{-1}$	350 $\mu\text{L}\cdot\text{L}^{-1}$	700 $\mu\text{L}\cdot\text{L}^{-1}$	350 $\mu\text{L}\cdot\text{L}^{-1}$	700 $\mu\text{L}\cdot\text{L}^{-1}$	350 $\mu\text{L}\cdot\text{L}^{-1}$	700 $\mu\text{L}\cdot\text{L}^{-1}$
Gray	45.1 (7.1)	62.6 (9.6)	37.0 (3.6)	59.8 (8.3)	0.958 (0.3)	2.922 (0.6)	1.245 (0.3)	3.875 (0.7)	2.897 (0.6)	5.646 (0.9)
White	28.8 (8.6)	31.3 (4.1)	35.0 (8.3)	54.9 (2.8)	0.874 (0.4)	1.717 (0.3)	1.466 (0.6)	2.417 (0.4)	3.017 (1.1)	4.254 (0.6)
Black	38.0 (6.0)	63.9 (4.4)	33.0 (3.4)	47.7 (1.4)	0.655 (0.2)	1.700 (0.2)	0.993 (0.3)	2.251 (0.2)	2.016 (0.4)	3.930 (0.3)
Yellow	24.5 (4.1)	43.2 (4.6)	30.5 (2.9)	46.5 (3.4)	0.871 (0.1)	1.810 (0.3)	0.861 (0.2)	2.024 (0.3)	2.298 (0.3)	3.977 (0.4)

TABLE 3. Results of a 2×4 ANOVA for the singularly grown birch design

Variables	Main effects									Residual SS
	Species			CO_2			Interaction, species by CO_2			
	SS	F	P	SS	F	P	SS	F	P	
No. of branches	15	7.4	<0.001	8	11.5	0.001	0.6	0.3	0.818	36
No. of leaves	36	7.1	<0.001	24	14.2	<0.001	4	0.8	0.476	89
Leaf area (cm^2)	175	1.5	0.234	1108	27.8	<0.001	36	0.3	0.822	2115
Stem length (cm)	860	2.6	0.060	4603	42.1	<0.001	144	0.4	0.726	5795
Root mass (g)	5	2.5	0.068	20	32.9	<0.001	2	1.4	0.264	32
Stem mass (g)	10	4.4	0.007	31	40.7	<0.001	5	2.3	0.087	40
Leaves mass (g)	14	2.5	0.070	49	25.8	<0.001	3	0.6	0.620	101
Total biomass (g)	78	3.0	0.038	288	33.4	<0.001	32	1.2	0.310	458
Root/shoot	0.04	2.6	0.062	0.08	14.6	<0.001	0.02	1.0	0.402	0.28
Root/leaves	0.07	1.6	0.207	0.31	14.6	<0.001	0.04	1.0	0.408	0.75
Root/leaf area	0.002	1.8	0.167	0.011	24.9	<0.001	0.001	0.9	0.472	0.023

NOTE: Attributes were two CO_2 levels (350 and 700 $\mu\text{L}\cdot\text{L}^{-1}$) and four birch species (white, black, gray, and yellow). The degrees of freedom for the model are consistently 3 for species, 1 for CO_2 , and 3 for the interaction terms. SS, sum of squares; F, F-ratio; P, probability of null model.

TABLE 4. Mean total biomass (g; 1 SE in parentheses; $n = 10$) for the conspecific and heterospecific pairs of birches grown at 350 and 700 $\mu\text{L}\cdot\text{L}^{-1}$ CO_2 concentrations after 90 days of growth

Birch species	350 $\mu\text{L}\cdot\text{L}^{-1}$	700 $\mu\text{L}\cdot\text{L}^{-1}$
Conspecific		
Gray	4.130 (0.770)	8.590 (1.100)
Black	1.634 (0.520)	5.200 (0.700)
Yellow	2.938 (0.820)	6.783 (1.410)
Heterospecific		
Black-gray	4.262 (0.590)	7.851 (1.000)
Black-yellow	2.217 (0.680)	6.341 (0.920)
Yellow-gray	4.844 (0.490)	8.634 (0.650)

England, where the seeds were collected, showed that the CO_2 concentration at 50 cm above the forest floor can reach values above 460 $\mu\text{L}\cdot\text{L}^{-1}$ of CO_2 during the peak growing season (Bazzaz and Williams 1991). Since most of our birch seedlings were smaller than 60 cm after 90 days of growth, it might well be that seedlings would usually experience higher levels of CO_2 in the field, at the beginning of the growth period. Our most shade-tolerant seedlings (yellow birches) exhibited the greatest response to this CO_2 limitation. This species may be naturally subjected to higher CO_2 concentration compared with the other birch species because it is more tolerant of understory conditions.

CO₂ and competitive interactions among birches

The outcome of competition among four congeneric species was not modified by CO_2 levels. The identity of the neighbor was more important for the outcome than the level of CO_2 . We have yet to see whether there will be differences in competitive outcome among these species after several growing seasons in a high CO_2 environment. However, given the differential response of the species to elevated CO_2 , it is expected that these differences will occur.

Growth responses of congeneric trees

All growth parameters considered in this study were significantly stimulated by elevated CO_2 concentrations in all four birch species (Fig. 1, Table 2). These results are generally consistent with those of many other studies (reviews in Strain and Cure 1985; Eamus and Jarvis 1989; Bazzaz 1990a). The growth of gray birch was more enhanced by elevated CO_2 than the growth of white, black, or yellow birch. Therefore, the shade-intolerant, fast-growing, early successional species (gray birch) took greater advantage of the increased resource in CO_2 than more shade-tolerant, slower growing, relatively late successional species (yellow birch). The result is in accordance with predictions about higher responsiveness of early successional species to increased resource availability (e.g., Bazzaz 1979, 1990b; Chapin 1991). This result, however, contrasts with a previous study of seven noncongeneric species for the same ecosystem, the mixed forest of New England (Bazzaz *et al.* 1990). They found that the highest relative enhancement of growth by elevated CO_2 concentrations

occurred in the shade-tolerant species. They suggest that because of the relatively low light intensity used in their experiment ($520 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), photosynthesis and growth of their shade-intolerant trees were probably limited by light. Therefore the plants were prevented from taking full advantage of increased availability in CO_2 . Our observations indicate that in a nonlimited light environment our most shade-intolerant species (gray birch) was probably able to photosynthesize most of the time at maximum rates and to take full advantage of increased availability of CO_2 . Thus gray birch had the largest carbon gain of the four species.

All growth parameters were enhanced by elevated CO_2 , and all species responded similarly to CO_2 enrichment. The ANOVA presented in Table 3 revealed that the variance for each growth parameter was mostly explained by the effect of CO_2 , whereas the variance explained by the identity of the species was relatively insignificant. Thus, despite differences among these four congeneric species in their habitat preferences, they appear to exhibit a rather narrow range of responses to changes in ambient CO_2 concentrations, in the sense that they all responded positively to an enhancement of CO_2 . Our results suggest that congeneric species might be more constrained in their response to global CO_2 in comparison with unrelated species of the same ecosystem that had been studied by others, despite the fact that these closely related birch species differ in their habitat preferences and successional status. As the light regime of this experiment ($900 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and the one of Bazzaz *et al.* (1990; $520 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) were different, we need to investigate further if closely related species are more similar in their response to CO_2 than less related species. Future experiments, where the light as well as nutrient levels would vary along with atmospheric CO_2 would help to answer the question.

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