Below-Ground Architectural and Mycorrhizal Responses to Elevated CO$_2$ in Betula alleghaniensis Populations

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Below-ground architectural and mycorrhizal responses to elevated CO_2 in *Betula alleghaniensis* populations

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Summary

1. Replicate populations of crowded, regenerating stands of *Betula alleghaniensis* were grown in ambient and elevated (700 p.p.m.) atmospheric CO_2 concentrations in monoliths of forest soil. Early in the second year the seedlings were harvested and detailed measurements of individual plant root architectural parameters and ecto-mycorrhizal colonization were made.

2. Comparing the average responses of individual plants within the populations, elevated CO_2 had no significant effects on architectural parameters that improve a plant's ability to forage for and acquire soil resources. In contrast, the intensity and magnitude of mycorrhizal colonization, and whole plant C/N ratios were significantly enhanced with elevated CO_2.

3. The allometric scaling relationship between total plant biomass and root biomass was not affected by CO_2, suggesting that relative allocation between roots and shoots was not affected. However, the allometric scaling relationships between root architectural parameters and plant biomass, and between fine root biomass and woody root biomass were significantly altered by elevated CO_2. For all of these relationships, elevated CO_2 reduced the 'size bias' of architectural components in relation to plant size within the populations; in elevated CO_2 root architectural size (e.g. root length) per unit biomass was more similar between the smallest and largest individuals within the population than was the case for ambient CO_2.

4. Overall, the results of this study suggest that the average individual seedling biomass and architectural growth responses within populations of plants exposed to elevated atmospheric CO_2 levels may be unresponsive, but that mycorrhizal responses and interactions among plants within populations may be altered significantly. These findings have important implications for how we make predictions about plant growth responses to elevated CO_2 in natural ecosystems. Significant increases in mycorrhizal infection rates and architecture–biomass allometries suggest that below-ground competitive interactions within plant populations may be reduced in elevated CO_2. Alterations in competitive interactions may lead to shifts in productivity and plant population structure.

Key-words: Allocation, allometry, C/N, competition, ectomycorrhizal fungi, seedlings

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Introduction

Terrestrial vegetation has the potential to slow global warming by acting as a long-term sink to atmospheric CO_2 (Woodwell & Mackenzie 1995). A wealth of experimental data has demonstrated that the magnitude of CO_2-stimulated increases in biomass production by plants in natural communities is mediated by the amount of available soil resources (Bazzaz 1990). In addition, several recent studies have suggested that terrestrial ecosystem growth responses to elevated CO_2 will be constrained by reduced nutrient cycling

under elevated CO_2 (Comins & McMurtrie 1993; Comins 1994; Schimel 1995; McMurtrie & Comins 1996), though it is possible that other plant or microbially mediated responses can mitigate these constraints (Zak *et al.* 1993; Berntson 1996). In order to assess the capacity of terrestrial ecosystems to respond to globally rising atmospheric CO_2 levels, it is critical that we explicitly consider the role that plant roots and associated symbionts play in regulating plant capacity for nutrient acquisition (Curtis *et al.* 1994). The below-ground responses of plants to elevated CO_2 include changes in more than just biomass

production, including changes in root architecture, mycorrhizal colonization and physiology. These changes may lead to significantly altered (usually increased) nutrient-acquiring potential (Berntson & Woodward 1992; Rogers *et al.* 1992; Berntson 1994; Norby 1994; Rogers, Runion & Krupa 1994; Berntson 1996).

Nutrient acquisition by plants is strongly dependent on root system growth, physiology (Nye & Tinker 1977; Barber 1984), whole root system architecture (Fitter 1985, 1987; Fitter *et al.* 1991; Berntson 1994) and mycorrhizal status (Yanai, Fahey & Miller 1995). On the basis of optimal allocation theory (Bloom, Chapin & Mooney 1985), increasing concentrations of CO_2 in the atmosphere represent an enhancement in above-ground resource pools. Thus it is not surprising that most characteristics of root systems involved in below-ground resource acquisition have been found to be sensitive to increasing CO_2 levels. Overall, below-ground biomass enhancement tends to be greater than above-ground enhancement (Rogers *et al.* 1994). Whole root system architecture and morphology can also be altered dramatically (Berntson & Woodward 1992; Rogers *et al.* 1992), and intensity of mycorrhizal infection is usually increased (O'Neill 1994; Ineichen, Wiemken & Wiemken 1995; O'Neill, O'Neill & Norby 1991). In addition, the input of plant-derived organic material into the soil has the potential to alter significantly nutrient cycling, microbial populations and thus nutrient availability to plants (Díaz *et al.* 1993; Zak *et al.* 1993; Berntson 1996). These below-ground responses may have significant implications for plant productivity in a future high-CO_2 world. If plants are to maintain higher NPP, their capacity to acquire potentially limiting below-ground resources needs to be increased commensurate with the increases in carbon fixation rates owing to elevated CO_2 (Norby 1994).

Most plants in natural conditions do not grow in isolation. This observation is important because there is growing evidence that the presence of neighbouring plants, be they of the same or a different species, greatly modifies plant growth responses to elevated CO_2, usually reducing it. In a review of plant–plant interactions in CO_2 studies Bazzaz & McConnaughay (1992) concluded that increasing CO_2 levels lead to altered patterns of competition between plants through indirect effects on growth and allocation and subsequent effects on resource pre-emption. These altered interactions led to an overall decline in the response of communities of interacting plants to elevated CO_2 relative to non-interacting individuals. In a companion study to the one presented here, the effect of elevated CO_2 on biomass production in *Betula alleghaniensis* Britt. was reduced from 48% to 16% owing to the presence of neighbours (Wayne & Bazzaz 1995). These results are consistent with observations of reductions in CO_2-induced growth enhancement for a variety of herbaceous species (Bazzaz & McConnaughay 1992; Bazzaz *et al.* 1995).

The purpose of this study is to provide a detailed account of the below-ground growth responses of 2-year-old birch populations in elevated CO_2. Specifically, we examined patterns of biomass accumulation and allocation, root architecture, mycorrhizal colonization and C/N ratios of the individual plants within these populations. We characterize these growth responses using two complementary approaches. First, we examined 'average' individual responses, where all the individual plants were pooled together and compared using a nested (repeated measures) analysis of variance. Second, we examined the allometric relationships between biomass, architecture and mycorrhizal infection for each replicate population in order to characterize the size-dependent variations in allocation, architecture and mycorrhizal colonization.

Materials and methods

STUDY SYSTEM

We selected Yellow Birch (*B. alleghaniensis*) as our study species for three reasons. First, Yellow Birch is a mid-successional tree of wide distribution within New England and of significant economic importance (Harlow, Harrar & White 1979; Erdmann 1990). Second, Yellow Birch often regenerates within dense monocultures of tree seedlings (Burns & Honkala 1990; Carlton 1993) and thus studying model systems may provide ecologically relevant information about the growth of this important, widespread temperate deciduous tree. Third, we have been studying regenerating model communities of the species and are accumulating an increasingly in-depth understanding of Yellow Birch growth responses to elevated CO_2. Companion studies to the one we present here include the effect of plant–plant interactions on growth responses to elevated CO_2 (Wayne & Bazzaz 1995), the effects of elevated CO_2 on plant- and soil-mediated nitrogen cycling (Berntson & Bazzaz 1997) and developing methods for characterizing competitive interactions within plant populations using distributions of resource acquisition (G. M. Berntson & P. M. Wayne, unpublished data).

EXPERIMENTAL DESIGN AND GROWTH CONDITIONS

Seeds of Yellow Birch were collected from three maternal trees in the Harvard Forest National Science Foundation Long-Term Ecological Research Site (Petersham, MA, USA). Seeds were germinated in a vermiculite:peat:sand mixture and transplanted into large growth containers ($0.45 \times 0.35 \times 0.15 \, m^3$, 24 l) when they were 2–3 cm tall and had three to four leaves. Only seedlings of equal size were transplanted. Within each growth container a total of 48 seedlings were planted. In the central portion of the growth container 24 target plants (planted in a 6×4

hexagonal array with an average distance to nearest neighbour of 5·5 cm) were used as the experimental plants, surrounded by a border of plants (one to two deep) to minimize edge effects. Each growth container is referred to as a 'population' of 24 individuals.

Twelve growth containers were prepared and placed within six separate glasshouse modules. Half of the modules were maintained at approximately ambient CO_2 (375 ± 23 p.p.m.), the other half in elevated CO_2 (700 ± 20 p.p.m.). Glasshouse modules were spatially arranged in pairs to create three blocks of paired CO_2 modules. Plants were unshaded but received approximately 70% full sun owing to glasshouse structures. Day/night temperatures were maintained at 26/19 °C with a 13-h day throughout both years of the experiment. Transitions between day/night temperatures were made over a 2-h ramped period.

At the end of the first year's growing season, temperatures and day lengths within the modules were gradually reduced to simulate autumnal conditions. Once approximately 90% of leaves had senesced (20 November 1993) the growth containers were moved into an outdoor, common garden. All senesced leaves were allowed to fall into the tubs so that the organic matter input into the soil which takes place each year in actual forest systems was simulated. At no point during the experiment were any of the tubs fertilized. When placed outside for the winter, growth containers were placed in trenches so that the soil surface within the growth containers was level with the surface of soil outside the growth containers. The following spring (12 March 1994) the growth containers were returned to the CO_2 controlled glasshouse modules when the buds began to swell but before the first new leaves were expanded.

SOIL

Soil within the growth containers was reconstructed to simulate typical profiles at the Harvard Forest, where the seeds were collected. The top 10–15 cm within each growth container was O2 forest floor material (with fine roots) collected from the Prospect Hill Tract of the National Science Foundation Harvard Forest Long Term Ecological Research site (LTER). Underlying mineral soils from this site are stony to sandy loams of the Canton Sandy Loam series (Lent & Smith 1994). Typical upper soil layers in this site are composed of a low density O2 horizon (forest floor) composed almost entirely of organic matter where virtually all fine roots are located (Lyford 1975). Average depth of the O2 layer was 7–10 cm. Forest floor material was passed through a 2-cm sieve to remove large roots, branches and rocks. Litter layers were removed prior to soil collection from the field. The lower soil type within the growth containers was a 1:1 combination of sand and mineral soil. Soil was collected, processed, and placed into the growth containers within a 72-h period.

HARVEST

After complete canopy closure in the second year (about a month after the growth containers were brought in from the common garden), plants were harvested. At the start of harvest, all plant stems were cut approximately 1 cm above the soil surface. For all the target plants, tags were attached to the remaining stem so that the roots could be identified. The roots of every target plant were carefully washed from the soil by placing the entire soil block in a tub of water, letting it soak for 1·5 h and then carefully disentangling and extracting the roots by hand. While some of the fine roots were lost during this procedure, care was taken to keep each root system as intact as possible. Entire root systems for each target plant were wrapped in a moist paper towel, placed in an airtight plastic bag (with all the air removed) and frozen prior to root morphological and mycorrhizal measurements. Above-ground plant material was separated into leaves and stems and oven dried for 96 h at 70 °C, then weighed to the nearest mg.

ROOT ARCHITECTURE AND MYCORRHIZAL ASSESSMENTS

To characterize root architecture and mycorrhizal status of each individual target plant, we made detailed measurements on subsamples of each target plant's fine roots. Fine roots were defined as those <0·5 mm in diameter which showed no clear signs of secondary growth or lignification. Woody roots (with clear secondary growth and lignification) were typically of a yellow to orange colour. We used approximately 300 individual root tips (296 ± 63), taken from three to four randomly selected locations within each root system, for root subsamples used to estimate specific root length (SRL), specific root number (SRN) and mycorrhizal colonization. For the smallest individuals examined, all the fine roots were used as the subsample. For each subsample, the number of root tips and the number of root tips with a mycorrhizal sheath were counted under a dissecting microscope. After counting, the subsample was laid out in a Petri dish with ~2 mm of water to minimize overlap of individual roots and scanned into a computer as 8-bit gray scale images at 118·1 pixels cm^{-1}. From these images total root length and average diameter of the fine root subsample were calculated using the procedures and algorithms proposed by Pan & Bolton (1991). From all of these measurements made on the fine root subsamples the following parameters were derived: per cent mycorrhizal root tips, root diameter, SRL (m g^{-1}) and SRN (number of root tips g^{-1}).

Total fine root length and number of root tips for each plant were derived by multiplying SRL and SRN by fine root mass. After taking the fine root subsamples, fine roots were separated from the woody roots

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after air drying. Similar criteria were used to separate fine roots from woody roots for air-dried samples. One of the more convenient characteristics which allowed us to separate rapidly the fine roots from the woody roots is that the fine roots would disintegrate (fall apart) when rubbed between the fingers. The lignified woody roots did not. Total root surface area (for the fine roots) was calculated by assuming roots were cylindrical and multiplying total root length by $\pi *$ diameter. Total number of mycorrhizal root tips was calculated by multiplying total number of root tips by per cent mycorrhizal root tips.

CARBON-NITROGEN MEASUREMENTS

After the plant material was dried, material from a single plant (fine roots, woody roots, stem and leaves) was pooled and ground to pass through a 40 mesh screen. Subsamples of 2–3 mg homogenized, ground plant material were analysed for carbon and nitrogen content using a Europa ANCA (Europa Instruments, UK). All C/N ratios reported herein are molar C/N ratios (moles C per mole N).

STATISTICAL ANALYSIS

All parameters measured on individual target plants (from whole plant biomass to SRL) were analysed using a nested ANOVA. Blocks were treated as fixed factors. Growth containers ('populations') were nested within the CO_2 by block interaction and the CO_2. The block and CO_2 by block interaction terms were tested with the population mean square as the denominator (Velleman 1994). These ANOVAS represented a comparison of the average response of individuals in different populations.

Allocation patterns were characterized using exponential functions of the form $y = ax^b$ (Niklas 1994). We derived these allometric functions separately for each population with log–log least-squared means type-I linear regressions. The 'coefficient' term, a, and the 'exponent' term, b, from the allometric equations were analysed using an ANOVA. This approach allowed us to compare patterns of allocation and deployment between different replicate populations. Using this approach, we studied patterns of biomass allocation (biomass vs biomass allometries) and patterns of architectural deployment (biomass vs root architectural parameters) within each population.

For all ANOVAS (nested ANOVAS with individual target plants as replicates and stand two-way ANOVAS with populations as replicates) assumptions of normality and homoscedasticity were tested using a combination of normal probability plots (Velleman 1994) and log-ANOVA tests (Sokal & Rohlf 1981). When necessary, variables were either log transformed or arcsine-square root transformed to best meet the assumptions of ANOVA.

Results

Of all the average individual-level characters we examined, the intensity (% infection) and magnitude (total number of root tips) of mycorrhizal infection were the most highly responsive to elevated CO_2, showing enhancements of 65% (Tables 1 and 2). Elevated CO_2 resulted in a significant increase in total biomass, shoot biomass, root biomass, woody root biomass, per cent mycorrhizal root tips and number of mycorrhizal root tips of individual plants (Tables 1 and 2). However, elevated CO_2 did not result in significant changes in any of the root architectural parameters we measured, including root length, number of root tips, fine root surface area, root diameter, specific root length and specific root number (but excluding number of mycorrhizal root tips). The level of enhancement in total seedling biomass with elevated CO_2 (β factor) was 1·14. We observed greater enhancements in below-ground biomass than in shoot biomass ($\Sigma = 1·17$ and 1·12, respectively). However, we found only a marginally significant increase in fine root biomass with elevated CO_2. The average β for fine root biomass was large (1·17) but the level of variation was large enough to obscure a clear statistical difference (Table 1).

The exponential functions (log–log linear functions) used to characterize bivariate allometric relationships had high adjusted r^2, with the regressions explaining between 67·4% and 98·8% of the variation in the dependent variables (Table 3, Fig. 1a–f). The allometric relationship for total biomass vs root biomass showed no significant differences in either coefficients (back-transformed log–log intercepts) or exponents (log–log slopes; Table 4, Fig. 1e–f). Thus, elevated CO_2 did not lead to changes in patterns of biomass allocation to root systems. The scaling exponent for the allometric relationship for woody root biomass vs fine root biomass was marginally increased by elevated CO_2 (Tables 3 and 4). Elevated CO_2 led to significant changes in all of the architectural variables examined (Table 4, Fig. 1a–d). In every case, either the coefficient or the exponent was significantly increased with elevated CO_2. In no case were both parameters significantly affected. For total biomass vs root length (Fig. 1a), number of root tips (Fig. 1b) and root surface area (Fig. 1c), exponents were increased. For total biomass vs number of mycorrhizal root tips (Fig. 1d), the coefficient was significantly increased with elevated CO_2.

As noted previously, elevated CO_2 led to a significant increase in the average percentage of root tips colonized by ectomycorrhizae (Tables 1 and 2). The distribution of the extent of mycorrhizal colonization within populations was also significantly affected by elevated CO_2 (Tables 3 and 4). In ambient CO_2 there were significant, positive relationships between total plant biomass and % mycorrhizal root tips in half of the replicate populations (Fig. 1g). In elevated CO_2,

Table 1. Results of nested ANOVAs for individual target plant responses. df, degrees of freedom; P, probability that samples from given groups are from same population; SS, sum of squares; B, Block; C, CO_2; T, tub. The transformation used for each dependent variable are indicated

	Trans		C	B	B × C	T	Error
		df	1	2	2	6	262
Total biomass	log	P	0·040	0·551	0·274	0·533	
		SS	0·97	0·19	0·46	0·85	43·87
Shoot biomass	log	P	0·050	0·470	0·242	0·457	
		SS	1·02	0·29	0·62	1·02	46·83
Root biomass	log	P	0·029	0·796	0·518	0·591	
		SS	1·01	0·06	0·18	0·74	42·05
Woody root biomass	log	P	0·025	0·627	0·521	0·543	
		SS	1·26	0·14	0·21	0·86	44·75
Fine root biomass	log	P	0·125	0·608	0·635	0·253	
		SS	0·70	0·24	0·22	1·33	44·30
Root length	log	P	0·136	0·200	0·675	0·355	
		SS	0·56	0·81	0·16	1·14	44·47
Root surface area	log	P	0·158	0·267	0·630	0·336	
		SS	0·51	0·65	0·20	1·17	44·54
No. root tips	log	P	0·128	0·276	0·766	0·210	
		SS	0·72	0·74	0·13	1·39	42·68
No. mycorrhizal root tips	log	P	0·000	0·009	0·248	0·504	
		SS	8·38	3·89	0·61	1·03	50·54
% mycorrhizal root tips	$\sqrt{\text{arcsin}}$	P	0·000	0·020	0·024	0·002	
		SS	4·83	1·21	1·10	0·45	5·37
Root diameter	log	P	0·500	0·103	0·682	0·000	
		SS	0·001	0·016	0·002	0·015	0·061
Specific root length	none	P	0·367	0·054	0·703	0·000	
		SS	25·3	262·0	19·9	159·4	1314·5
Specific root number	none	P	0·851	0·507	0·732	0·000	
		SS	54·1	2158·8	931·1	8491·1	53287
C/N	none	P	0·042	0·393	0·670	0·001	
		SS	5413	1797	704	4922	55440

Table 2. Average values of measured variables for each CO_2 treatment with standard errors of the mean. Also included are β factors (elevated CO_2/ambient CO_2) for each variable. β marked with an asterisk (*) when significantly >1·0 ($P<0·05$, see Table 1)

Variable	Units	Ambient CO_2		Elevated CO_2		β
		Mean	SE	Mean	SE	
Total biomass	g	2·406	±0·176	2·734	±0·160	1·14*
Shoot biomass	g	1·715	±0·128	1·924	±0·112	1·12*
Root biomass	g	0·691	±0·051	0·809	±0·049	1·17*
Woody root biomass	g	0·389	±0·029	0·458	±0·027	1·18*
Fine root biomass	g	0·302	±0·023	0·352	±0·024	1·17
Root length	m	57·238	±4·57	64·355	±4·31	1·12
Root surface area	m	3·23	±0·25	3·62	±0·24	1·12
No. root tips		17602	±1493	19562	±1295	1·11
No. mycorrhizal root tips		7229	±821	11928	±787	1·65*
% mycorrhizal tips	%	38·3	±1·40	63·1	±1·30	1·65*
Root diameter	mm	0·18	±0·001	0·179	±0·001	0·99
Specific root length	m g^{-1}	18·98	±0·25	18·42	±0·22	0·97
Specific root number	no. g^{-1}	59708	±1435	58376	±1210	0·98
C/N		60·19	±1·21	69·30	±1·38	1·15*

none of the populations showed a significant relationship between plant size and the level of mycorrhizal infection. However, there was a tendency towards negative exponents in five out of six replicate populations in elevated CO_2. Taken together, these alterations in scaling relationships between plant size and level of mycorrhizal colonization with elevated CO_2 can be summarized as greater total levels and evenness of colonization by ectomycorrhizas with elevated CO_2.

Elevated CO_2 led to a significant increase in whole plant C/N ratios (Tables 1 and 2). However, the allometric scaling of C/N to total plant biomass showed no significant differences between the two atmospheric CO_2 levels (Tables 3 and 4). There was a slight, but not quite significant, trend towards greater coefficients with elevated CO_2, which is to be expected given the overall higher C/N ratios in elevated CO_2. Disregarding CO_2 treatments, in total 10 of the 12 replicate populations showed significant, positive scaling relationships between total plant C/N and total plant biomass (Fig. 1h).

Table 3. Average parameters (exponents and coefficients, see Materials and methods for details) for allometric relationships with standard errors (SE) of the mean. Also included are average adjusted r^2 values. The units for each of the dependent and independent variables are the same as those given in Table 2

X-Variable	Y-Variable	Ambient CO_2					Elevated CO_2				
		exp.		coeff.		r^2	exp.		coeff.		r^2
Woody root biomass	Fine root biomass	0·88	±0·05	0·84	±0·04	85·2%	1·01	±0·06	0·88	±0·03	85·0%
Total biomass	Root biomass	0·94	±0·02	0·60	±0·01	96·1%	0·98	±0·02	0·59	±0·01	95·7%
Total biomass	Root length	0·89	±0·02	4·06	±0·13	89·0%	1·04	±0·04	3·82	±0·18	90·7%
Total biomass	Surface area	0·90	±0·02	1·17	±0·03	89·2%	1·04	±0·04	1·09	±0·05	90·8%
Total biomass	No. root tips	0·87	±0·02	2·42	±0·10	82·7%	0·95	±0·06	2·36	±0·11	86·7%
Total biomass	No. mycorrhizal root tips	0·99	±0·06	1·48	±0·13	81·8%	0·90	±0·08	1·93	±0·08	75·7%
Total biomass	C/N	0·14	±0·01	55·39	±1·41	41·0%	0·12	±0·04	62·22	±3·54	21·8%
Total biomass	% mycorrhizal tips	0·13	±0·06	0·34	±0·06	20·4%	−0·05	±0·03	0·63	±0·03	4·8%
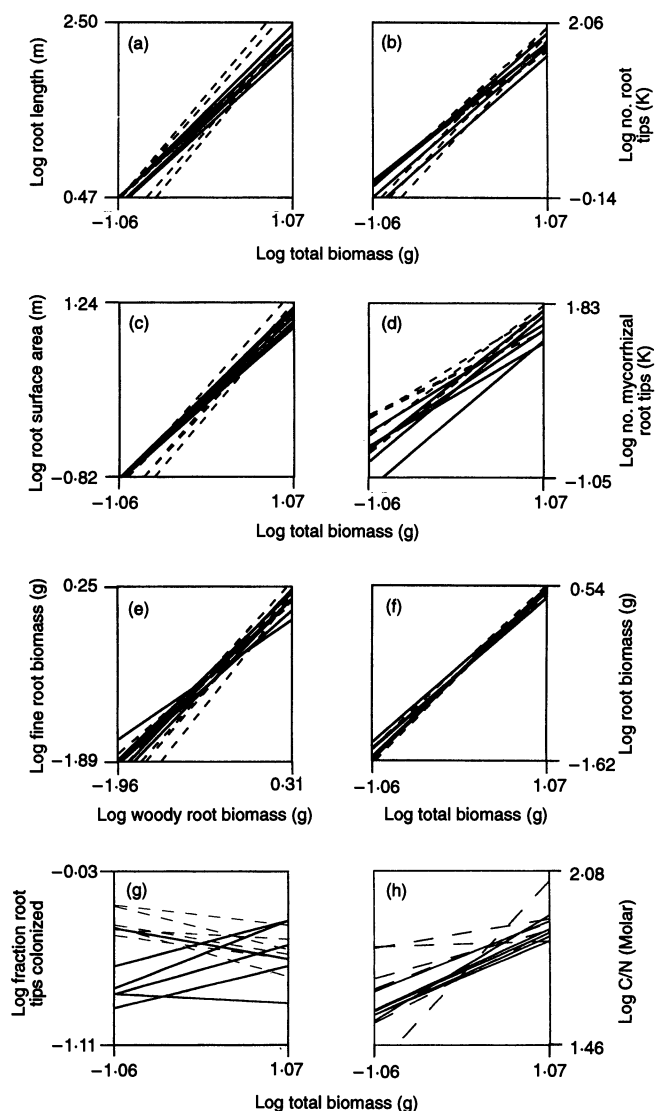
Fig. 1. Line diagrams of all the allometric scaling relationships examined. Within every plot frame, each line corresponds to the best fit regression for a single replicate population ($n = 21$–24, depending on within-population mortality rates). The solid lines are for populations maintained in ambient CO_2 levels and the dashed lines are for populations maintained in elevated CO_2 concentrations. Summaries and statistical comparisons of the parameters from these regressions are presented in Tables 3 and 4. (a) Total biomass vs total fine root length; (b) total biomass vs total number of root tips; (c) total biomass vs total fine root surface area; (d) total biomass vs total number of root tips colonized by mycorrhizae; (e) woody root biomass vs fine root biomass; (f) total biomass vs total root biomass; (g) total biomass vs fraction of root tips colonized by mycorrhizae; (h) total biomass vs total plant molar C/N ratio.

Discussion

AVERAGE INDIVIDUAL RESPONSES

In this study, elevated CO_2 resulted in greater net below-ground vs above-ground biomass enhancement in *B. alleghaniensis*. However, of the below-ground biomass component, only woody root biomass showed a significant increase. Fine root biomass showed a similar magnitude of average enhancement as woody root biomass but this enhancement was not statistically significant owing to a large variation in fine root biomass (Table 2). The lack of a significant increase in fine root biomass is contrary to observations of *Liriodendron tulipifera* and *Quercus alba* which show significant enhancements in fine root biomass in elevated CO_2 (Norby, O'Neill & Luxmoore 1986; Norby et al. 1992; Norby 1994; Norby, Wullschleger & Gunderson 1996). It is possible that the non-significant effect of elevated CO_2 on fine root biomass is not an accurate reflection of the total allocation of biomass into fine roots. Our previous work has found that elevated CO_2 not only led to significant enhancements in the gross production of fine roots but also resulted in the death of fine roots (Berntson 1996; Berntson & Bazzaz 1996). These simultaneous effects led to standing root lengths at the end of one growing season that were not significantly increased by elevated CO_2, even though gross root production had been significantly enhanced.

Similar to CO_2 effects on fine root biomass, we did not find significant alterations in fine root architecture in elevated CO_2. Root length, diameter, surface area, number of tips, specific root length (SRL, length mass^{-1}) and specific root number (SRN, number of root tips mass^{-1}) were not significantly altered by elevated CO_2. Our finding is contrary to expectations derived from other studies which have found that root architectural responses to elevated CO_2 can be very large (Kaushal, Guehl & Aussenac 1989; Berntson & Woodward 1992; Rogers et al. 1992).

In contrast, elevated CO_2 resulted in large (65%) and significant changes in the intensity (% infection) and extent (total number of infected tips) of mycorrhizal infection. Several other studies have reported

Table 4. ANOVAs of fitted parameters for allometric relationships between several variables. ANOVAs were performed on coefficients derived by fitting curves to all the individuals within a single tub. Parameters correspond to the equation: Y-Variable$= a \times (X\text{-Variable})^b$

X-variable	Y-variable	Parameter		C	B	C × B	Error
			df	1	2	2	6
Woody root biomass	Fine root biomass	b	P	0·069	0·575	0·069	
			SS	0·054	0·013	0·094	0·065
		a	P	0·430	0·476	0·358	
			SS	0·007	0·015	0·022	0·055
Total biomass	Root biomass	b	P	0·186	0·483	0·499	
			SS	0·007	0·005	0·005	0·018
		a	P	0·725	0·435	0·356	
			SS	0·000	0·003	0·003	0·008
Total biomass	Root length	b	P	0·001	0·031	0·017	
			SS	0·063	0·023	0·030	0·010
		a	P	0·217	0·061	0·059	
			SS	0·011	0·055	0·007	0·036
Total biomass	Surface area	b	P	0·001	0·060	0·021	
			SS	0·065	0·019	0·031	0·012
		a	P	0·167	0·060	0·541	
			SS	0·013	0·057	0·007	0·033
Total biomass	No. root tips	b	P	0·012	0·002	0·012	
			SS	0·021	0·076	0·033	0·010
		a	P	0·654	0·087	0·604	
			SS	0·002	0·062	0·009	0·049
Total biomass	No. mycorrhizal root tips	b	P	0·308	0·262	0·140	
			SS	0·027	0·073	0·120	0·130
		a	P	0·004	0·010	0·471	
			SS	0·212	0·214	0·017	0·060
Total biomass	C/N	b	P	0·770	0·635	0·841	
			SS	0·001	0·008	0·003	0·048
		a	P	0·135	0·349	0·697	
			SS	139·7	118·0	35·9	280·7
Total biomass	% mycorrhizal root tips	b	P	0·045	0·780	0·448	
			SS	0·097	0·008	0·028	0·090
		a	P	0·001	0·078	0·170	
			SS	0·253	0·050	0·030	0·037

that elevated CO_2 significantly increases mycorrhizal infection, especially for ectomycorrhizal species (Norby *et al.* 1987; O'Neill, Luxmoore & Norby 1987; O'Neill & Norby 1988; O'Neill *et al.* 1991; Lewis, Thomas & Strain 1992, 1994; Morgan *et al.* 1994; O'Neill 1994; Ineichen *et al.* 1995; Pérez-Soba *et al.* 1995). Ineichen *et al.* (1995) demonstrated that increased mycorrhizal infection rates for *Pinus sylvestris* under elevated CO_2 are accompanied with two-fold increases in the amount of mycorrhizal hyphae. While we did not directly quantify the amount of hyphae present within the soil, if such increases in hyphal density took place in the experiment, the altered mycorrhizal fungi density could be an important mechanism whereby *B. alleghaniensis* is able to forage through the soil more thoroughly, possibly increasing its ability to acquire below-ground resources (Yanai *et al.* 1995).

Virtually all detailed studies of below-ground non-cultivated plant responses to elevated CO_2 (see refer-

ences in introduction) have been carried out with individually grown plants or with plants grown at extremely low densities. While these studies provide valuable insight into the potential responses of plants to elevated CO_2, they are inherently limited because most plants in natural ecosystems live in close proximity to neighbours (Harper 1977). In order to understand potential growth responses to environmental change, we need to study plant responses in a natural context which includes the presence of neighbours. Plant growth responses to elevated CO_2 are dependent on the presence of neighbours (Bazzaz & Carlson 1984; Zangerl & Bazzaz 1984; Bazzaz & Garbutt 1988; Williams, Garbutt & Bazzaz 1988; Bazzaz *et al.* 1989; Reekie & Bazzaz 1989; Morse & Bazzaz 1994; Wayne & Bazzaz 1995). In general, these studies have found that increasing CO_2 levels have a smaller effect on increasing biomass production when plants are interacting with one another than when they are growing alone (Bazzaz & McConnaughay 1992; Bazzaz

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et al. 1995; Wayne & Bazzaz 1995). The small but significant increases in biomass production in populations of *B. alleghaniensis* observed in this study were not accompanied by any significant changes in average root architectural characters, only significant increases in mycorrhizal infection. This observation, if it is repeatable, is important because it suggests that even though enhancements in plant biomass and below-ground architecture may be constrained in elevated CO$_2$ atmospheres owing to the presence of neighbours, ectomycorrhizas may play a fundamentally important role in providing their host plants with the ability to maintain enhanced biomass production over long periods of time in natural communities.

ARCHITECTURAL ALLOMETRY

Even though average components of *B. alleghaniensis* root system architecture within populations were not significantly affected by elevated CO$_2$, the relationships between plant size and the various components of root architecture were significantly altered by increased CO$_2$ levels. For all measured root architectural parameters (except number of mycorrhizal root tips), elevated CO$_2$ resulted in increases in the scaling exponent with plant size (Tables 3 and 4). These increases in scaling exponents meant that they were significantly closer to 1·0 (isometric scaling) than in ambient CO$_2$ (Table 3). Put another way, elevated CO$_2$ reduced the 'size bias' of architectural components in relation to total plant size (biomass) within the populations; in elevated CO$_2$ root architectural size (e.g. root length) per unit biomass was more similar between the smallest and largest individuals within the population than was the case for elevated CO$_2$ (Fig. 2). In ambient CO$_2$, the smaller individuals tended to produce a larger architectural size per unit biomass than the larger individuals. The increase in the equality functional root size in relation to total plant biomass in elevated CO$_2$ suggests that there is an increase in the equality of foraging ability in relation to plant size in *B. alleghaniensis* populations in elevated CO$_2$.

It is possible that the increase in the architecture–biomass equality within the *B. alleghaniensis* grown at elevated CO$_2$ is a result of a reduced intensity of below-ground competitive interactions for nutrients and/or water. More intense competitive interactions in ambient CO$_2$ levels may have led to the observed greater size-bias in architecture–biomass allometries in ambient CO$_2$. It has been well established that density-dependent interactions can lead to significant alterations in above-ground plant form in relation to size, especially for height–biomass relationships (Geber 1989; Weiner, Berntson & Thomas 1990; Weiner & Thomas 1992; Weiner & Fishman 1994). There are two correlative lines of evidence to support this hypothesis.

First, elevated CO$_2$ resulted in increased population-level mycorrhizal infection rates. Several studies

have found that inter-plant mycorrhizal links can lead to inter-plant transfer of mineral nutrients and/or carbon (Chiariello, Hickman & Mooney 1982; Francis & Read 1984; Robinson 1991; Newman *et al.* 1992). If inter-plant transfer of nutrients and/or carbon were significant in our *B. alleghaniensis* populations, and if the higher levels of mycorrhizal infection under elevated CO$_2$ led to greater inter-plant transfers, then competitive interactions between adjacent plants in elevated CO$_2$ would be reduced owing to the mediating effect of inter-plant mycorrhizal connections. If the larger plants within the competing populations were supporting the subordinate members of the population owing to mycorrhizas, then we may expect a reduction in the intensity of mycorrhizal infection with larger plants. The relationship between plant size and mycorrhizal infection rates were non-significant for all six elevated CO$_2$ populations (Fig. 1g). However, there appeared to be a tendency towards decreased colonization rates with increases in plant size. This observation supports the hypothesis that inter-plant mycorrhizal links may play a role in medi-
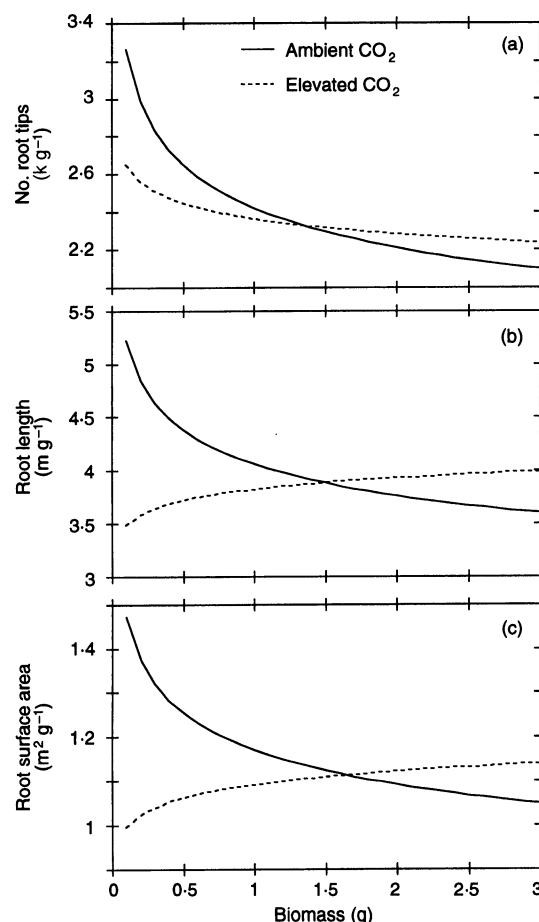
Fig. 2. Size–Bias plots of root architecture *vs* total plant biomass. The *y*-axis for each plot is the ratio of estimated architectural size (a) number of root tips; (b) root length; (c) root surface area to plant biomass. The *x*-axis is plant biomass. The curves presented are derived from the average curve parameters presented in Table 3.

ating competitive interactions in elevated CO_2. In contrast, the significant positive relationship between plant size and mycorrhizal colonization rates in half of the populations suggests that mycorrhizally mediated inter-plant transfers of resources from the dominant individuals to the subordinates would be less. The subordinate individuals simply do not have the number of mycorrhizal connections and thus have a lower chance for mycorrhizal supplies of limiting resources.

The second line of evidence suggesting that competition for below-ground resources may have been reduced under-elevated CO_2 is that size inequality within populations of *B. alleghaniensis* are reduced under elevated CO_2 (Wayne & Bazzaz 1997). For this study, the coefficient of variation (CV) for total plant biomass was 293% (standard error = 16%) in ambient CO_2 and 286% (23%) in elevated CO_2. This reduction in biomass CV was not statistically significant, but was in the direction we would expect if competitive interactions were reduced with elevated CO_2. In the absence of size-dependent mortality, one-sided competitive interactions between plants leads to increases in the level of size inequality (Weiner & Solbrig 1984; Weiner 1990). Reductions in the size inequality of plants grown in elevated CO_2, even though plants are on average larger, suggest that elevated CO_2 leads to reductions in the extent of asymmetric, one-sided competition for below-ground resources.

BIOMASS ALLOMETRY

The allometric relationships between total plant biomass and root biomass were not significantly affected by elevated CO_2. This observation is consistent with Norby *et al.*'s study of *Liriodendron tulipifera*, where they observed that patterns of below-ground allocation did not appear to be affected by elevated CO_2, but not their study of *Quercus alba*, where they observed that elevated CO_2 resulted in a marginally significant increase in the allocation of biomass below-ground for a given amount of shoot biomass (Norby 1994; Norby *et al.* 1996). In this study we found that elevated CO_2 resulted in a marginally significant alteration in the relationship between woody root biomass and fine root biomass. Similar to the architecture–biomass scaling relationships, elevated CO_2 resulted in an increase in the scaling exponent where the scaling exponent was much closer to 1·0 under elevated CO_2 than ambient CO_2. Similar to the patterns observed for the biomass–architecture relationship, this pattern suggests that the amount of fine root supported for a given amount of woody root was more even in relation to plant size for elevated CO_2 than for ambient CO_2. However, the extent of changes in size-dependent root architecture were of a much greater magnitude than changes in biomass.

This observation clearly demonstrates that in order to understand potential changes in below-ground resource acquisition potential we need to look beyond just biomass.

C/N ALLOMETRY

Reductions in plant C/N ratios have been observed in response to rising CO_2 levels in a number of studies (Bazzaz 1990). Higher C:N ratios typically lead to slower decomposition rates of plant detritus (Melillo, Aber & Muratore 1982; Aber, Melillo & McClaugherty 1990) and this has been observed to be the case for plant material produced under elevated CO_2 (Boerner & Rebbeck 1995; Cotrufo & Ineson 1995). Aside from their importance in determining potential decomposition rates in an elevated CO_2 world, C/N ratios are also indicators of nitrogen-use efficiency. Elevated C/N ratios mean that a given amount of plant biomass was produced with less nitrogen. Thus, by simply altering tissue quality, plants can achieve greater nutrient-use efficiency and thus achieve higher productivity with elevated CO_2 even when nitrogen supplies are potentially limiting. We observed that while elevated CO_2 led to significant overall increases in plant C/N ratios, elevated CO_2 did not appear to alter the relationship between C/N ratios and plant size. In both ambient CO_2 and elevated CO_2, the relationship between C/N and plant size was usually significant and positive. This observation is important because it demonstrates that for *B. alleghaniensis*, and possibly for other tree species, whole-plant C/N ratios are CO_2 as well as size dependent.

Conclusion

In this study we observed that within experimental populations of *B. alleghaniensis*, elevated CO_2 resulted in significant increases in net biomass in the second year of growth. Elevated CO_2 had no significant effects on average below-ground architectural parameters but significantly increased the intensity and magnitude of ectomycorrhizal symbiosis. The allometric scaling relationship between total plant biomass and root biomass was not affected by CO_2, suggesting that relative root-to-shoot biomass allocation was not affected. However, the allometric scaling relationships between root architectural parameters and plant biomass, and between fine root biomass and woody root biomass were significantly altered by elevated CO_2. For all of these parameters, elevated CO_2 increased the equality of architectural components in relation to plant size within the populations. Elevated CO_2 lead to significant increases in average whole plant C/N ratios, and there was evidence of increasing C/N ratios with plant size. However, elevated CO_2 did not alter the relationship between C/N ratio and plant size.

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Overall, the results of this study suggest that average individual seedling biomass and architectural growth responses within populations of plants to elevated atmospheric CO$_2$ levels may be unresponsive but that mycorrhizal responses and interactions among plants within populations may be significantly altered. These findings have important implications for how we make predictions about plant growth responses to elevated CO$_2$ in natural ecosystems. Significant increases in mycorrhizal infection rates and architecture-biomass allometries suggest that below-ground competitive interactions within plant populations may be reduced in elevated CO$_2$. Alterations in competitive interactions may lead to shifts in productivity and plant population structure.

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