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ATMOSPHERIC CO_2, SOIL-N AVAILABILITY, AND ALLOCATION OF BIOMASS AND NITROGEN BY *POPULUS TREMULOIDES*

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Abstract. Our ability to predict whether elevated atmospheric CO_2 will alter the cycling of C and N in terrestrial ecosystems requires understanding a complex set of feedback mechanisms initiated by changes in C and N acquisition by plants and the degree to which changes in resource acquisition (C and N) alter plant growth and allocation. To gain further insight into these dynamics, we grew six genotypes of *Populus tremuloides* Michx. that differ in autumnal senescence (early vs. late) under experimental atmospheric CO_2 (35.7 and 70.7 Pa) and soil-N availability (low and high) treatments. Atmospheric CO_2 concentrations were manipulated with open-top chambers, and soil-N availability was modified in open-bottom root boxes by mixing different proportions of native A and C horizon soil. Net N mineralization rates averaged 61 ng $N \cdot g^{-1} \cdot d^{-1}$ in low-N soil and 319 ng $N \cdot g^{-1} \cdot d^{-1}$ in high-N soil. After 2.5 growing seasons, we harvested above- and belowground plant components in each chamber and determined total biomass, N concentration, N content, and the relative allocation of biomass and N to leaves, stems, and roots.

Elevated CO_2 increased total plant biomass 16% in low-N soil and 38% in high-N soil, indicating that the growth response of *P. tremuloides* to elevated CO_2 was constrained by soil-N availability. Greater growth under elevated CO_2 did not substantially alter the allocation of biomass to above- or belowground plant components. At both levels of soil-N availability, elevated CO_2 decreased the N concentration of all plant tissues. Despite declines in tissue N concentration, elevated CO_2 significantly increased whole-plant N content in high-N soil (ambient = 137 g N/chamber; elevated = 155 g N/chamber), but it did not influence whole-plant N content in low-N soil (36 g N/chamber). Our results indicate that plants in high-N soil obtained greater amounts of soil N under elevated CO_2 by producing a proportionately larger fine-root system that more thoroughly exploited the soil. The significant positive relationship between fine-root biomass and total-plant N content we observed in high-N soil further supports this contention. In low-N soil, elevated CO_2 did not increase fine-root biomass or production, and plants under ambient and elevated CO_2 obtained equivalent amounts of N from soil. In high-N soil, it appears that greater acquisition of soil N under elevated CO_2 fed forward within the plant to increase rates of C acquisition, which further enhanced plant growth response to elevated CO_2.

Key words: allocation of tree biomass; atmospheric CO_2 and soil-N availability; carbon cycling and storage in forests; global climate change, forest response; nitrogen, allocation and concentration in tissues; plant biomass; Populus tremuloides; *soil-N availability; tree response to elevated CO_2.*

INTRODUCTION

The recent, and relatively rapid, rise in atmospheric CO_2 has the potential to alter the cycling and storage of carbon (C) in terrestrial ecosystems. Understanding the response of forest ecosystems to rising atmospheric CO_2 is important, because forests cover a substantial proportion of Earth's land surface (43%), contain 40% of the C in living and dead biomass, and account for 72% of global net primary productivity (NPP; Melillo et al. 1993). Recent empirical evidence and theoretical analyses suggest that temperate forests are a globally important sink for atmospheric CO_2 (Wofsy et al. 1993, Ciais et al. 1995, Tans et al. 1995, Goulden et al. 1996). Some have suggested that current rates of C storage in temperate forests may be sufficient to moderate the anthropogenic rise in atmospheric CO_2, thus potentially slowing an increase in global temperature (Schimel

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1995, Woodwell and Mackenzie 1995). The rapid accumulation of biomass in early-successional temperate forests and the lessening of plant N limitation by atmospheric deposition may contribute to greater C sequestration by temperate forests (Peterson and Melillo 1985, Kauppi et al. 1992). However, it is uncertain whether the recent rise in atmospheric CO_2 has directly altered tree growth or ecosystem C storage (LaMarch et al. 1984, Kienast and Luxmoore 1988, Graybill and Idso 1993).

Elevated atmospheric CO_2 can substantially increase C assimilation and growth in many tree species under experimental conditions (Ceulemans and Mousseau 1994, Wullschleger et al. 1995, Curtis 1996, Curtis and Wang 1998), presenting the possibility that greater tree growth under elevated atmospheric CO_2 could further increase C storage in temperate forests. Several reviews suggest that tree growth responses to elevated CO_2 can be substantial, but vary widely among species, genotypes, and experimental conditions (0% to 290%, Ceulemans and Mousseau 1994, Ceulemans et al. 1995, McGuire et al. 1995, Curtis and Wang 1998). Greater C assimilation and plant growth under elevated CO_2 are accompanied by substantial declines in leaf N concentration (McGuire et al. 1995, Cotrufo et al. 1998, Curtis and Wang 1998), and it has been argued that plants grown under elevated CO_2 allocate less N to carboxylating enzymes and more to other metabolic functions (Drake and Gonzàlez-Meler 1997). Therefore, C assimilation and growth increase under elevated CO_2, while the amount of N allocated to leaves is thought to decline. Regardless of changes in N allocation to leaves under elevated CO_2, there are functional relationships between leaf N concentration and photosynthesis that may limit plant growth response to elevated CO_2. Low soil-N availability constrains leaf N concentration, which in turn limits C assimilation and plant growth (Field and Mooney 1986). Although more C is assimilated by leaves with lower N concentrations under elevated CO_2, this relationship suggests low soil-N availability could potentially limit plant growth response to elevated CO_2. Furthermore, elevated atmospheric CO_2 could modify whole-plant N allocation if large quantities of N are allocated to plant tissues (e.g., fine roots) other than leaves as atmospheric CO_2 rises.

Changes in belowground plant growth and allocation to roots (i.e., percentage of total biomass) under elevated CO_2 have important implications for the acquisition of soil resources. Although plant growth often increases under elevated CO_2, the amount of biomass plants allocate to roots vs. shoots appears somewhat more variable. Curtis and Wang (1998) concluded biomass allocation in woody plants was relatively unaltered by elevated atmospheric CO_2. That is, growth increases under elevated CO_2 were equally partitioned above- and belowground; others have argued for small shifts in biomass allocation to roots (Ceulemans and Mousseau 1994, McGuire et al. 1995). Notwithstanding these contrasting views, it is well understood that biomass allocation in woody plants varies during the growing season (Pregitzer et al. 1990, Horwath et al. 1994), during ontogeny, and with soil-resource availability (Waring and Pitman 1985, Pregitzer et al. 1995). Biomass allocation also is under genetic control and varies among genotypes, especially in fast-growing trees (Radoglou and Jarvis 1990, Ceulemans et al. 1995, Ceulemans and Isebrands 1996). The observation that elevated CO_2 could increase root allocation, while greater soil-N availability could decrease the allocation of biomass to roots (McGuire et al. 1995), suggests that both atmospheric CO_2 and soil-N availability could modify patterns of biomass allocation.

We have observed that *Populus tremuloides* Michx. grown under elevated CO_2 assimilated more C and produced more fine roots than plants grown under ambient CO_2, a response that was dampened by low soil-N availability (Curtis et al. 2000, Pregitzer et al. 2000). In this paper, we describe how elevated atmospheric CO_2 and soil-N availability influence growth and allocation in *P. tremuloides.* We predicted that plant biomass would increase under elevated atmospheric CO_2, but low soil-N availability would constrain this response. We further hypothesized that elevated CO_2 should shift the allocation of N from leaves to fine roots, a response that would enable plants to more effectively forage for limiting soil resources (i.e., N). Our experiment included six genotypes of *P. tremuloides,* which differ in autumnal leaf senescence, to explore genotypic variation in growth and allocation of biomass and N in response to atmospheric CO_2 and soil-N availability.

Methods

Biomass harvest

Our experiment was conducted at the University of Michigan Biological Station (45°34′ N, 84°40′ W), near Pellston, Michigan, USA. We investigated the influence of atmospheric CO_2 and soil-N availability on *Populus tremuloides* using a randomized complete-block design with factorial atmospheric CO_2 (35.7 and 70.7 Pa) and soil-N availability (low and high) treatments. Our experiment consisted of five blocks, each containing the four atmospheric-CO_2–soil-N-availability treatment combinations. Soil-N availability was modified in open-bottom roots boxes (10.9 m^2 × 0.4 m deep) by mixing different proportions of native A horizon and C horizon soil. High-N-availability soil was 100% A horizon, and low-N-availability soil was 20% A horizon and 80% C horizon. A horizon material was excavated from a Typic Haplorthod (Kalsaska series) and the C horizon material was collected from an Entic Haplorthod (Rubicon series), both commonly occurring forest soils in northern Lower Michigan. Differences in organic matter (low N = 3559 mg C/kg; high N =

12489 mg C/kg) resulted in net N mineralization of 61 ng $N \cdot g^{-1} \cdot d^{-1}$ in low-N soil and 319 ng $N \cdot g^{-1} \cdot d^{-1}$ in high-N soil (see Zak et al. [2000] for details). Mean growing-season rates of net N mineralization in Lake States forests, estimated by isotope dilution and incubation techniques, range from 50 ng $N \cdot g^{-1} \cdot d^{-1}$ in xeric oak-dominated forests on outwash sands to 1000 ng $N \cdot g^{-1} \cdot d^{-1}$ in mesic sugar maple-dominated forests on finer-textured glacial moraines (calculated from Pastor et al. 1984, Zak et al. 1989, Zak and Pregitzer 1990, Holmes and Zak 1999). *Populus tremuloides* commonly establishes across this range of soil conditions following harvest, fire, or other stand-destroying disturbance. Nitrogen mineralization rates in our experiment fall well within the range that this species encounters under field conditions. A complete summary of soil physical, chemical, and biological properties is presented in Curtis et al. (2000) and Zak et al. (2000).

In early spring 1994, open-top chambers (2.3 m in diameter, 3 m in height) were placed over the 20 open-bottom root boxes in order to control atmospheric CO_2 over the duration of our experiment. Further details regarding our CO_2-exposure system and its performance can be found in Curtis et al. (2000).

On 4 June 1994 we planted two softwood cuttings of six *P. tremuloides* Michx. genotypes into each root box. Softwood cuttings were propagated from roots of locally occurring genotypes that differed in autumnal leaf senescence; three genotypes senesce in early autumn and three senesce in late autumn. Rooted cuttings were graded for size prior to planting; height averaged 17.3 ± 0.45 cm (mean ± 1 SE) and the number of leaves averaged 12.3 ± 0.33 leaves/plant. Leaf litter produced following the 1994 and 1995 growing seasons fell on the soil surface, where it resided during the remaining portion of our experiment. Additional details regarding plant growth conditions can be found in Curtis et al. (2000).

After 2.5 growing seasons (7 June 1994 to 8 July 1996), we destructively harvested above- and belowground tree biomass. One week prior to harvest, we collected 12 soil cores (10 cm in diameter, 45 cm deep) from each open-bottom root box to determine the biomass and N concentration of fine roots (see Pregitzer et al. [2000] for details). At harvest, the largest trees were ~3.5 m tall and had basal stem diameters of 3–4 cm. Aboveground components were harvested by cutting each stem at the root collar. Each tree canopy was divided into three portions, and we immediately determined the fresh mass of leaves in the top, middle, and bottom canopy positions. We then composited all leaves and determined leaf area on a subsample of known mass using a LI-COR LI-3000 leaf-area meter (LI-COR, Lincoln, Nebraska). After the leaves were harvested, we located terminal bud scars, and harvested branch and stem portions produced during the 1994, 1995, and 1996 growing seasons; the fresh mass of each was immediately determined. Approximately 5% of the fresh mass of the leaves, and the branch and stem fractions, were removed and oven-dried at 70°C.

After all aboveground biomass was removed from a chamber, the open-bottom root box was disassembled, and root systems were freed from the sandy soils by hydro-excavation. To accomplish this task, we used a fire hose (50-mm diameter) to wash the contents of each root box and underlying soil into an adjacent 1.5-m-deep trench. This approach allowed us to recover the intact coarse root (>1 mm diameter) system of each tree, while imposing little damage to the outer bark (D. R. Zak, *personal observation*). Root systems were separated from one another by hand, and all roots <1 mm in diameter were removed. The remaining coarse-root systems were weighed and 5% of the fresh mass of each was oven-dried at 70°C. Our destructive harvest was completed on 8 August 1996 ~4 wk after it began.

Oven-dried leaf, branch, stem, and root tissues from each tree were ground to a fine powder using a Tecator Cyclotec 1093 sample mill (Perstorp Analytical, Silver Springs, Maryland, USA) and their N concentration was determined with a CE Elantech NC 2500 elemental analyzer (Elantech, Lakewood, New Jersey, USA). The biomass and N content of leaves, stems, coarse roots, fine roots, and very fine roots was expressed on a chamber basis (grams per chamber); the relative allocation (percentage of total) of biomass and N to leaves, stem, and roots also was summarized on a chamber basis. To evaluate genotypic responses to atmospheric CO_2 and soil-N availability, we compiled the biomass and N content of leaves, stems, and coarse roots on an individual-tree basis. However, we could not include fine and very fine roots in this analysis, because these biomass components were estimated on a chamber basis, not on an individual-tree basis.

Statistical analyses

We analyzed total-plant biomass using an analysis of variance (ANOVA) for a fixed effects, randomized block design with two factorial treatments: atmospheric CO_2 and soil-N availability. Elevated CO_2 can accelerate plant ontogeny so that differences in biomass allocation, N allocation, and N concentration between ambient- and elevated-CO_2-grown plants can be explained by differences in plant size (Bazzaz et al. 1993, Coleman et al. 1993, Gebauer et al. 1996). We used total-plant biomass as a covariate to remove the potentially confounding effect of plant size in our analysis of biomass allocation, N allocation, and tissue N concentration. Biomass data expressed on an individual-tree basis were analyzed using a complete-block, split-plot design with two factorial treatments. In this analysis, atmospheric CO_2–soil-N-availability treatment combinations are split by genotype (fixed effect). We also used an analysis of covariance to remove the influence of plant size on our individual-tree-based anal-

TABLE 1. Harvest biomass (kg/chamber) of *Populus tremuloides* plants after 2.5 growing seasons under experimental atmospheric-CO_2 and soil-N-availability treatments.

Plant components†	Interaction means (n = 5)				Main-effect means (n = 10)					
	Low soil N		High soil N		Soil N			CO_2		
	Ambient CO_2	Elevated CO_2	Ambient CO_2	Elevated CO_2	Low	High	Change‡ (%)	Ambient	Elevated	Change‡ (%)
Leaves [**]	1.01[a] (0.043)	1.12[a] (0.144)	2.51[b] (0.104)	3.44[c] (0.092)	1.07 (0.104)	2.98 (0.239)	178**	1.76 (0.255)	2.28 (0.395)	30**
Stems [**]	1.75[a] (0.166)	1.93[a] (0.245)	6.70[b] (0.269)	8.96[c] (0.572)	1.84 (0.202)	7.83 (0.680)	326**	4.22 (0.838)	5.44 (1.208)	29**
Roots§										
Coarse (diameter > 1.0 mm) [**]	1.54[a] (0.144)	1.92[a] (0.236)	3.57[b] (0.099)	5.07[c] (0.286)	1.73 (0.205)	4.32 (0.409)	149**	2.55 (0.347)	3.50 (0.553)	37**
Fine (diameter 0.5–1.0 mm) [**]	0.07 (0.007)	0.08 (0.011)	0.16 (0.003)	0.20 (0.012)	0.08 (0.009)	0.18 (0.012)	137**	0.12 (0.015)	0.14 (0.021)	20*
Very fine (diameter < 0.5 mm) [**]	0.24[a] (0.011)	0.28[a] (0.035)	0.57[b] (0.038)	0.94[c] (0.046)	0.26 (0.026)	0.75 (0.097)	194**	0.40 (0.058)	0.61 (0.114)	52**
Biomass										
Total aboveground [**]	2.76[a] (0.207)	3.05[a] (0.387)	9.20[b] (0.307)	12.40[c] (0.602)	2.91 (0.301)	10.80 (0.878)	272**	5.98 (1.088)	7.72 (1.595)	29**
Total belowground [**]	1.85[a] (0.156)	2.28[a] (0.244)	4.29[b] (0.102)	6.21[c] (0.298)	2.06 (0.218)	5.25 (0.498)	154**	3.07 (0.417)	4.24 (0.680)	38**
Total [**]	4.61[a] (0.355)	5.33[a] (0.619)	13.50[b] (0.374)	18.61[c] (0.882)	4.97 (0.505)	16.05 (1.3640)	223**	9.05 (1.501)	11.97 (2.271)	32**

Notes: Data are means with 1 SE in parentheses. Within rows, interaction means with the same lowercase superscript letter are not significantly different at $P \leq 0.05$.

* $P \leq 0.05$; ** $P \leq 0.01$; NS = not significant.

† Significance of N × CO_2 interaction is given in brackets.

‡ Percentage change is calculated as the second mean relative to the first. For example, the change in total biomass from low to high N = 100(16.05 − 4.97)/4.97 = 223%.

§ Fine-root and very-fine-root biomass were calculated from Pregitzer et al. (2000).

ysis of biomass allocation, N allocation, and tissue N concentration. Main effect and interaction means were compared using a protected Fishers' least-significance-difference test. Linear and nonlinear regression analyses were used to explore the relationships between biomass components (i.e., fine-root biomass and leaf area). Statistical significance was accepted at $\alpha = 0.05$; all statistical analyses were performed using SYSTAT (Wilkinson 1990).

RESULTS

Plant biomass

Atmospheric CO_2 and soil-N availability interacted to influence the leaf, stem, root, and total biomass of *Populus tremuloides,* wherein elevated CO_2 produced a much greater increase in high-N-availability soil, than in low-N-availability soil (Table 1: interaction means). Elevated CO_2 increased total-plant biomass by 16% in low-N soil and by 38% in high-N soil; the increase in low-N soil was not statistically significant. Of all biomass components, coarse roots displayed the largest relative increase (24%) to elevated CO_2 in low-N soil, whereas the biomass of very fine roots displayed the largest response (65% increase) to elevated CO_2 in high-N soil (Pregitzer et al. 2000; Table 1: interaction means).

Atmospheric CO_2 and soil-N availability were significant main effects in the chamber-level analysis of plant biomass (i.e., kilograms per chamber); both substantially increased the total, leaf, stem, and root biomass of *P. tremuloides.* Total biomass increased by 223% from low- to high-N-availability soil, whereas elevated CO_2 increased total plant biomass by 32% relative to plants grown under ambient CO_2 (Table 1: main-effect means). Stem biomass was most responsive to soil-N availability and exhibited a 326% increase from low- to high-N-availability soil. This differs substantially from the growth response of *P. tremuloides* to atmospheric CO_2, in which the biomass of very fine roots exhibited the largest increase to elevated CO_2 (52% Table 1: CO_2 main effect).

On an individual-tree basis, we observed a significant interaction between genotype and soil-N availability, in which the increase in leaf, stem, coarse-root, and total biomass from low- to high-N-availability soil was greatest for late-senescing clones (Fig. 1A). In contrast, the biomass of early- and late-senescing genotypes responded in a similar manner to atmospheric CO_2 (Fig. 1B), so that there was no significant genotype × atmospheric-CO_2 interaction.

Plant N concentration and content

Atmospheric CO_2 and soil-N availability did not interact to influence tissue N concentrations of leaves, stems, and roots (in milligrams of N per kilogram of

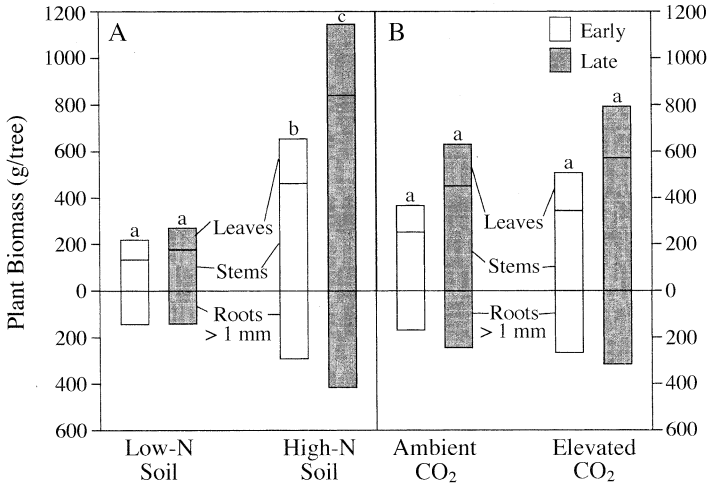

FIG. 1. The influence of (A) soil-N availability and (B) atmospheric-CO_2 concentration on the biomass of leaves, stem, and coarse roots in early- and late-senescing *Populus tremuloides* genotypes. Soil-N availability caused a disproportionate increase in the N capital of late-senescing genotypes, but atmospheric CO_2 increased the biomass of early- and late-senescing genotypes in a similar manner. Fine roots and very fine roots were not included in this analysis, because these plant components were determined on a chamber basis, and not on an individual-tree basis. Bars with the same lowercase letter (total biomass) are not significantly different at $\alpha = 0.05$.

dry mass [mg N/kg]; Table 2: interaction means). Although atmospheric CO_2 and soil-N availability were significant as main effects in our analysis, they had opposing influences on the N concentration of plant tissues. As one would expect, the N concentration of leaves, stem, and root increased from low- to high-N-availability soil (Table 2: soil N main effect). However, elevated atmospheric CO_2 consistently decreased the N concentration of all plant tissues, with the largest declines (−17% to −22%) occurring in leaves, coarse roots, and very fine roots (Table 2: CO_2 main effect). These reductions resulted in an 18% decline in whole-plant N concentration. Total biomass was not a significant covariate in any chamber-level analyses of tissue N concentration, indicating that reductions in N concentration under elevated CO_2 cannot be attributed to differences in plant size. Consistent with this analysis, we found no CO_2 × N-availability interaction on an

TABLE 2. Nitrogen (mg N/kg) of *Populus tremuloides* plant tissues grown under atmospheric-CO_2 and soil-N-availability treatments.

Plant components‡	Interaction means (n = 5)				Main-effect means (n = 10)					
	Low soil N		High soil N		Soil N			CO_2		
	Ambient CO_2	Elevated CO_2	Ambient CO_2	Elevated CO_2	Low	High	Change (%)	Ambient	Elevated	Change (%)
Leaves [NS]	17 024 (421)	13 839 (325)	23 520 (585)	19 886 (532)	15 432 (830)	21 703 (1 006)	41**	20 272 (1 605)	16 863 (1 485)	−17**
Stems [NS]	4 222 (267)	3 893 (284)	4 954 (164)	4 598 (316)	4 057 (271)	4 776 (252)	18**	4 588 (271)	4 245 (328)	−7†
Roots§										
Coarse (diameter > 1.0 mm) [NS]	4 001 (356)	4 296 (585)	9 038 (448)	5 852 (486)	4 148 (462)	7 445 (871)	79**	6 519 (1 247)	5 074 (626)	−22**
Fine (diameter 0.5–1.0 mm) [NS]	7 582 (142)	7 632 (222)	9 598 (619)	8 730 (262)	7 607 (176)	9 164 (492)	20**	8 590 (636)	8 181 (346)	−5[NS]
Very fine (diameter < 0.5 mm) [NS]	19 318	16 724	20 783	16 001	18 021 (611)	18 392 (1 127)	2[NS]	20 050 (345)	16 362 (170)	−18*
Biomass										
Total aboveground [*]	8 980[a] (480)	7 564[a] (292)	10 025[b] (404)	8 877[b] (513)	8 272 (501)	9 451 (521)	14*	9 502 (486)	8 220 (501)	−13*
Total belowground [*]	6 119[a] (342)	5 941[a] (685)	10 618[b] (318)	7 480[c] (453)	6 030 (512)	9 049 (827)	50**	8 368 (1 105)	6 710 (657)	−20*
Total [*]	7 841[a] (355)	6 876[a] (451)	10 216[b] (247)	8 411[c] (465)	7 358 (455)	9 313 (551)	26**	9 026 (630)	7 643 (563)	−18*

Notes: Total aboveground and belowground N tissue concentration represent weighted averages based on the mass and N concentration of the component tissues. Data are means with 1 SE in parentheses. Within rows, interaction means with the same lowercase superscript letter are not significantly different at $P \leq 0.05$.

† $P \leq 0.10$, * $P \leq 0.05$; ** $P \leq 0.01$; NS = not significant.

‡ Significance of N × CO_2 interaction is indicated in brackets.

§ The concentrations of N in fine and very fine roots were calculated from Pregitzer et al. (2000).

TABLE 3. The N capital of plants (g N/chamber) growing under experimental atmospheric-CO_2 and soil-N-availability treatments.

Plant components‡	Interaction means (n = 5)				Main-effect means (n = 10)					
	Low soil N		High soil N		Soil N			CO_2		
	Ambient CO_2	Elevated CO_2	Ambient CO_2	Elevated CO_2	Low	High	Change (%)	Ambient	Elevated	Change (%)
Leaves [**]	17.2[a] (0.36)	15.6[a] (2.20)	58.9[b] (2.43)	68.4[c] (2.21)	16.4 (1.08)	63.7 (2.21)	288**	38.1 (7.05)	42.0 (8.92)	10†
Stems [**]	7.2[a] (0.35)	7.3[a] (0.70)	33.0[b] (0.91)	40.7[c] (2.22)	7.3 (0.37)	36.9 (1.70)	408**	20.1 (4.33)	24.0 (5.67)	19*
Roots§										
Coarse (diameter > 1.0 mm) [NS]	6.1 (0.99)	7.9 (1.35)	31.4 (2.58)	29.0 (1.60)	7.0 (0.84)	30.2 (1.49)	333**	18.7 (4.42)	18.4 (3.65)	−2[NS]
Fine (diameter 0.5–1.0 mm) [NS]	0.5 (0.05)	0.6 (0.07)	1.5 (0.08)	1.7 (0.14)	0.6 (0.04)	1.6 (0.08)	186**	1.0 (0.17)	1.2 (0.20)	13[NS]
Very fine (diameter < 0.5 mm) [*]	4.5[a] (0.21)	4.6[a] (0.58)	11.8[b] (0.79)	15.0[c] (0.74)	4.6 (0.29)	13.4 (0.75)	192**	8.2 (1.26)	9.8 (1.79)	20*
Biomass										
Total aboveground [**]	24.4[a] (0.68)	22.9[a] (2.86)	92.0[b] (2.91)	109.0[c] (3.73)	23.7 (1.41)	100.5 (3.62)	325**	58.2 (11.35)	66.0 (14.53)	13*
Total belowground [NS]	11.2 (1.22)	13.1 (1.73)	44.7 (2.44)	45.7 (1.59)	12.1 (1.05)	45.2 (1.38)	273**	27.9 (5.73)	29.4 (5.55)	5[NS]
Total [**]	35.6[a] (1.68)	36.0[a] (4.22)	136.7[b] (2.69)	154.8[c] (4.15)	35.8 (2.14)	145.7 (3.81)	307**	86.1 (16.92)	95.4 (19.99)	11*

Notes: Data are means with 1 SE in parentheses. Within rows, interaction means with the same lowercase superscript letter are not significantly different at $P \leq 0.05$.

† $P \leq 0.10$; * $P \leq 0.05$; ** $P \leq 0.01$; NS = not significant.

‡ Significance of N × CO_2 interaction is indicated in brackets.

§ The data for fine and very fine roots are from Pregitzer et al. (2000).

individual-tree basis, and no interaction genotype between atmospheric CO_2 or soil-N availability (data not shown); individual-tree biomass (i.e., leaf + stem + coarse roots) also was not a significant covariate in this analysis.

Although elevated atmospheric CO_2 generally lowered the N concentration of all plant tissues, total-plant N content (grams of N per chamber) at elevated CO_2 was equivalent to (low-N soil) or greater than (high-N soil) total-plant N under ambient CO_2 (Table 3: interaction means). In high-N soil, we found a significant, linear relationship between fine-root (<1.0 mm diameter) biomass and total-plant N content (g N/chamber = 46.6 (g fine root/chamber) + 23.8; $r = 0.66$; $n = 10$ observations), indicating that increases in fine-root biomass under elevated CO_2 in part contributed to greater whole-plant N content in high-N soil. We found no relationship between fine-root biomass and whole-plant N content in low-N soil, in which we observed equivalent total-plant N contents under ambient and elevated CO_2. Moreover, atmospheric CO_2 significantly increased the N content of leaves, stem, and very fine roots in high-N soil, but it did not influence the N content of these plant components in the low-N soil (Table 3: interaction means). The N content of coarse and fine roots was unaltered by the atmospheric CO_2 at both levels of soil-N availability.

Atmospheric CO_2 and soil-N availability were significant main effects in our analysis; both produced a significant increase in total-plant N, albeit of different magnitudes (Table 3). Averaged across CO_2 treatments, total-plant N in low-N soil was 35.8 g N/chamber and 145.7 g N/chamber in high-N soil, a 307% increase from low- to high-N-availability soil. On the other hand, total-plant N content increased 11% from ambient to elevated atmospheric CO_2 (Table 2: CO_2 main effect). As expected, high-N soil (main effect) substantially and significantly increased the N content of all plant components, with stem N content exhibiting the largest (408%) increase between the N-availability treatments. Changes in the N content of plant components were variable in response to atmospheric CO_2, wherein elevated CO_2 significantly increased the N content of leaves, stem, and very fine roots but did not alter the N content of coarse roots (Table 2: CO_2 main effect). Although fine-root N content increased under elevated CO_2, this 13% increase was not statistically significant. Total biomass was not a significant covariate in any analysis of plant N content, indicating that differences in plant size did not contribute to the treatment responses we observed.

Analysis of plant N content on an individual-tree basis revealed a significant genotype × soil-N availability interaction, in which late-senescing clones displayed a proportionately larger increase in leaf, stem, coarse-root, and total-plant N content than early-senescing clones (Fig. 2A). There was no genotype × atmospheric-CO_2 interaction, indicating that atmo-

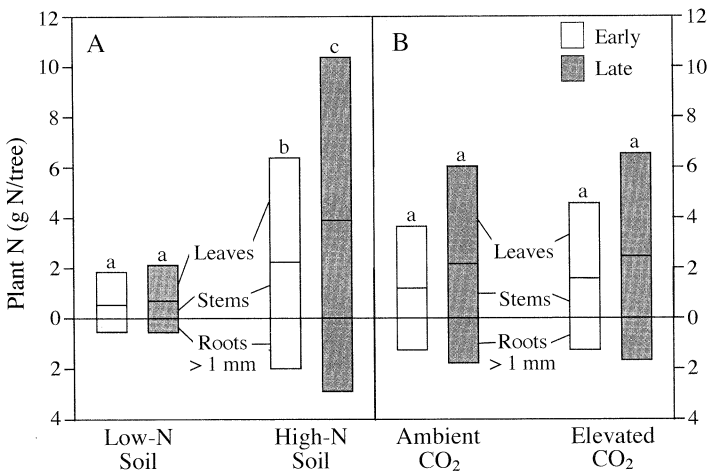

FIG. 2. The influence of (A) soil-N availability and (B) atmospheric CO_2 concentration on plant N capital for early- and late-senescing *Populus tremuloides* genotypes. The increase in N capital from low- to high-N soil was proportionately greater for late-senescing genotypes, relative to the increase in N capital for early-senescing genotypes. Atmospheric CO_2 increased the N capital of early- and late-senescing genotypes in a similar manner, leading to a nonsignificant genotype × atmospheric-CO_2 interaction. Fine and very fine roots were not included in this tree-level analysis, because these components were determined only on a chamber basis. Bars with the same lowercase letter (total-plant N) are not significantly different at $\alpha = 0.05$.

spheric CO_2 increased the N capital (leaves, stem, and coarse root) of early- and late-senescing genotypes by the same proportion (Fig. 2B); individual-tree biomass was not a significant covariate in this analysis.

Allocation of biomass and N

Atmospheric CO_2 and soil-N availability did not interact to influence allocation to leaves, stems, and roots (Table 4: interaction means). We also found that total biomass was not a significant covariate influencing the allocation of biomass to any plant component. When partitioned into total above- and belowground allocation, elevated CO_2 increased belowground biomass allocation at both levels of soil-N availability. Nevertheless, the magnitude of this response was small and was only significant in high-N soil (Table 4: interaction means). Atmospheric CO_2 and soil-N availability were significant main effects in our analysis of biomass allocation, but each had a different effect on allocation to leaves, stems, and roots. Soil-N availability significantly increased allocation to stems and decreased allocation to all other plant components (Table 4: soil-N main effect). This pattern resulted in an overall increase in aboveground allocation (58.5% at low N and 67.4% at high N) and a subsequent decline in belowground allocation from low- to high-N-availability soil. Al-

TABLE 4. Relative allocation of (%) biomass to leaves, stem, and roots under experimental atmospheric-CO_2 and soil-N-availability treatments.

	Interaction means (n = 5)				Main-effect means (n = 10)					
	Low soil N		High soil N		Soil N			CO_2		
Plant components†	Ambient CO_2	Elevated CO_2	Ambient CO_2	Elevated CO_2	Low	High	Change (%)	Ambient	Elevated	Change (%)
Leaves [NS]	22.3 (0.90)	21.0 (0.44)	18.6 (0.80)	18.6 (0.86)	21.6 0.52	18.6 0.55	−14**	20.4 0.83	19.8 0.60	−3^{NS}
Stems [NS]	37.7 (0.98)	36.0 (0.97)	49.5 (0.66)	48.0 (0.98)	36.9 0.71	48.8 0.61	32**	43.6 2.05	42.0 2.10	−4*
Roots										
Coarse (diameter > 1.0 mm) [NS]	33.3 (0.71)	36.0 (1.05)	26.5 (0.68)	27.2 (0.44)	34.6 0.74	26.8 0.40	−23**	29.9 1.23	31.6 1.55	6**
Fine (diameter 0.5–1.0 mm) [NS]	1.5 (0.16)	1.6 (0.25)	1.2 (0.05)	1.1 (0.10)	1.6 0.14	1.1 0.06	−27**	1.4 0.10	1.3 0.15	−3^{NS}
Very fine (diameter < 0.5 mm) [NS]	5.2 (0.30)	5.5 (0.93)	4.2 (0.22)	5.1 (0.29)	5.3 0.46	4.6 0.23	−13^{NS}	4.7 0.24	5.3 0.46	13^{NS}
Biomass										
Aboveground [*]	60.0^{a} (0.75)	57.0^{a} (1.21)	68.2^{b} (0.61)	66.6^{c} (0.45)	58.5 0.83	67.4 0.44	15**	64.1 1.44	61.8 1.71	−4*
Belowground [*]	40.0^{a} (0.75)	43.0^{a} (1.21)	31.8^{b} (0.61)	33.4^{c} (0.45)	41.5 0.83	32.6 0.44	−21**	35.9 1.44	38.2 1.71	6*

Notes: Values are the percentage of total biomass (means with 1 SE in parentheses) allocated to each plant component. Within rows, interaction means with the same lowercase superscript letter are not significantly different at $P \leq 0.05$.

* $P \leq 0.05$; ** $P \leq 0.01$; NS = not significant.

† Significance of N × CO_2 interaction is indicated in brackets.

TABLE 5. The percentage allocation of N to leaves, stem, and roots of *Populus tremuloides* grown under atmospheric-CO_2 and soil-N-availability treatments.

Plant components†	Interaction means (n = 5)				Main-effect means (n = 10)					
	Low soil N		High soil N		Soil N			CO_2		
	Ambient CO_2	Elevated CO_2	Ambient CO_2	Elevated CO_2	Low	High	Change (%)	Ambient	Elevated	Change (%)
Leaves [*]	48.6[a] (1.31)	43.0[b] (1.81)	43.1[b] (1.68)	44.2[ab] (1.02)	45.8 (1.41)	43.7 (0.94)	−5[NS]	45.9 (1.35)	43.6 (1.00)	−5[NS]
Stems [NS]	20.4 (0.85)	20.6 (1.29)	24.2 (0.26)	26.2 (0.86)	20.5 (0.73)	25.2 (0.54)	23**	22.3 (0.76)	23.4 (1.18)	5[NS]
Roots										
Coarse (diameter > 1.0 mm) [**]	16.8[a] (1.87)	21.5[bc] (1.51)	23.0[b] (1.78)	18.7[ac] (0.80)	19.2 (1.38)	20.8 (1.16)	9[NS]	19.9 (1.59)	20.1 (0.93)	1[NS]
Fine (diameter 0.5–1.0 mm) [NS]	1.5 (0.12)	1.7 (0.19)	1.1 (0.04)	1.1 (0.11)	1.6 (0.11)	1.1 (0.06)	−30**	1.3 (0.09)	1.4 (0.15)	9[NS]
Very fine (diameter < 0.5 mm) [NS]	12.8 (0.17)	13.1 (1.64)	8.6 (0.63)	9.8 (0.60)	13.0 (0.78)	9.2 (0.45)	−29**	10.7 (0.76)	11.4 (1.00)	7[NS]
Biomass										
Aboveground [*]	68.9[a] (2.23)	63.6[a] (2.52)	67.3[ab] (1.70)	70.4[b] (0.97)	66.3 (1.73)	68.9 (1.06)	4[NS]	68.1 (1.23)	67.0 (1.71)	−2[NS]
Belowground [*]	31.1[a] (2.23)	36.4[a] (2.52)	32.7[ab] (1.70)	29.6[b] (0.97)	33.7 (1.73)	31.1 (1.06)	−8[NS]	31.9 (1.23)	33.0 (1.71)	3[NS]

Notes: Data are means with 1 SE in parentheses. Within rows, interaction means with the same lowercase superscript letter are not significantly different at $P \leq 0.05$.

* $P \leq 0.05$; ** $P \leq 0.01$; NS = not significant.

† Significance of N × CO_2 interaction is indicated in brackets.

though atmospheric CO_2 significantly increased allocation to coarse roots and decreased allocation to stem, changes in biomass allocation with respect to atmospheric CO_2 were small (Table 3: CO_2 main effect). Overall, atmospheric CO_2 resulted in a 4% decline in aboveground allocation and a 6% increase in belowground allocation (Table 3: CO_2 main effect). Taken together, our results indicate that the growth of *P. tremuloides* changed allometrically in response to increased soil-N availability and isometrically with respect to rising atmospheric CO_2. This response could not be attributed to differences in plant development among treatments, because plant size was not a significant covariate in any analysis of biomass allocation.

In low-N soil, the allocation of N to leaves significantly declined from 48.6% at ambient atmospheric CO_2 to 43.0% at elevated CO_2, but we did not observe a similar reduction related to atmospheric CO_2 in high-N soil (Table 5: interaction means). Allocation of N to stems was not influenced by an atmospheric-CO_2–soil-N-availability interaction, nor was allocation of N to fine and very fine roots (Table 5: interaction means). Allocation of N to coarse roots in low-N soil increased from 16.8% under ambient CO_2 to 21.5% under elevated CO_2. However, in high-N soil, allocation of N to coarse roots declined from 23.0% to 18.7% in the ambient and elevated CO_2 treatments, respectively (Table 5: interaction means).

As main effects, soil-N availability significantly influenced plant N allocation, but atmospheric CO_2 had little influence on the partitioning of N within the plant. Between the low- and high-N-availability soil, we observed significant declines in the proportion of N allocated to very fine roots, fine roots, and leaves. In contrast, we observed a large increase in N allocated to stem from low- to high-N-availability soil (Table 5: soil N main effect). Allocation of N to coarse roots slightly increased from low- to high-N soil, but this increase was not significant. On the other hand, we observed no significant changes in the allocation of N to leaves, stems, and roots related to atmospheric CO_2 (Table 5: CO_2 main effect). Total-plant biomass also was not a significant covariate in any analysis of plant N allocation. In short, soil-N availability substantially altered plant N allocation, but atmospheric CO_2 did not.

DISCUSSION

Our ability to predict whether elevated atmospheric CO_2 increases, decreases, or does not alter ecosystem C-storage centers on understanding changes in the acquisition of C and soil nutrients by plants and the extent to which changes in resource acquisition alter plant growth and allocation. In our experiment, increases in plant biomass under elevated CO_2 were constrained by soil-N availability, a response consistent with that in many other woody plants (Brown 1991, Conroy et al 1992, Bazzaz and Miao 1993, Johnson et al. 1997, Kinney and Lindroth 1997, Prior et al. 1997, Johnson et al. 1998). In a 57-d experiment with *Populus tremuloides,* Kinney and Lindroth (1997) observed elevated CO_2 (65 Pa) increased total biomass by 35% in low-N soil and by 71% in high-N soil, a much larger

increase than we observed after 2.5 growing seasons. Further, they observed the growth responses of *Quercus rubra* and *Acer saccharum* to elevated CO_2 also were dependent on soil-N availability, wherein the greatest response to elevated CO_2 occurred in N-rich soil. Several studies with coniferous trees have drawn similar conclusions. Prior et al. (1997), for example, found that *Pinus palustris* exhibited virtually no growth response to elevated CO_2 (72 Pa) when soil-N availability was low, but elevated CO_2 substantially increased growth (45%) when N was in ample supply. Johnson et al. (1998) summarized a series of laboratory and field studies and concluded low soil-N availability limited the growth response of *P. ponderosa* and *P. taeda* to elevated CO_2 (70–71 Pa). Although the aforementioned studies indicate that tree growth under elevated CO_2 can be greater when soil resources are in ample supply, it will be necessary to determine the extent to which ontogenetic differences contributed to such a response. Norby et al. (1996) demonstrated that variation in plant growth response to elevated CO_2 could be attributed to ontogenetic differences in leaf-area display, regardless of variation in soil-resource availability. Nonetheless, our results indicate the greatest growth response to elevated CO_2 occurred in high-N soil, and that such a response could not be attributed to differences in plant development.

At a fundamental level, C assimilation by leaves, the accumulation of leaf area, and nutrient acquisition by fine roots and mycorrhizae control plant resource acquisition (i.e., C and N) and hence the patterns of plant growth we observed among our atmospheric-CO_2 and soil-N-availability treatments. Over the duration of our experiment, elevated atmospheric CO_2 increased leaf-level C assimilation at both levels of soil-N availability (Curtis et al. 2000). Similarly, leaf area increased under elevated CO_2 by 28% in high-N soil, but elevated CO_2 did not influence leaf area in low-N soil (Curtis et al. 2000). Although leaf-level C assimilation increased to a much smaller extent from low- to high-N soil (e.g., 22%, Curtis et al. 2000), greater C acquisition in high-N soil was facilitated by a much larger increase in leaf area (197%). Thus, greater rates of leaf-level C assimilation and leaf-area accumulation resulting from increases in atmospheric CO_2 and soil-N availability directly corresponded to differences in total biomass among our atmospheric-CO_2–soil-N-availability treatments. Moreover, the large increase in very-fine-root biomass (52%) we observed under elevated CO_2 (Table 1: CO_2 main effect), compared to the relatively smaller increases in leaf mass (30%) and area (20%; Curtis et al. 2000), suggest that fine roots are more responsive to elevated CO_2 than are leaves. This response appears to have important implications for the acquisition of soil resources under elevated CO_2.

Elevated atmospheric CO_2 enhanced the ability of *Populus tremuloides* to forage for N in our high-N soil, a contention supported in part by a substantial increase in whole-plant N content under elevated CO_2. This response did not occur in low-N soil, in which whole-plant N content was equivalent under ambient and elevated CO_2. Although the influence of elevated CO_2 on nutrient acquisition is somewhat variable among studies, others have observed that increases in whole-plant nutrient contents under elevated CO_2 were controlled by soil-nutrient availability. For example, elevated CO_2 decreased the whole-plant N content of *Eucalyptus grandis* when soil-N availability was very low, but substantially increased whole-plant N content when soil N was in ample supply (Conroy et al. 1992). Johnson et al. (1997) grew *Pinus ponderosa* over a range of soil-N availability and observed consistent increases (61%) in whole-plant N content under elevated CO_2. Others have observed equivalent or small increases in whole-plant N content under elevated CO_2, but these small increases were not statistically significant (Berntson and Bazzaz 1996, 1998). Differences in whole-plant N content among these studies, and hence the acquisition of N from soil, are undoubtedly controlled by changes in root foraging and the extent to which net N mineralization is modified by above- and belowground plant litter inputs to soil (sensu Diaz et al. 1993, Hungate et al. 1997, Berntson and Bazzaz 1998).

Several lines of evidence suggest that greater N acquisition under elevated CO_2 resulted from a more thorough exploitation of high-N soil by a larger and more productive root system with an equivalent physiological capacity to assimilate N (micromoles per gram per second). First, Rothstein et al. (2000) observed that elevated CO_2 did not alter the maximum velocity of NH_4^+ or NO_3^- uptake (i.e., V_{max}, in micromoles per gram per second) in the fine roots *Populus tremuloides* growing in our experiment. However, the maximum velocity for NH_4^+ uptake declined in high-N soil as did the affinity of the enzyme system for substrate. That is, the physiological capacity of fine roots to assimilate N declines with greater N availability, but this was not affected by elevated CO_2. Second, elevated CO_2 significantly increased the biomass and net production of fine roots in high-N soil and had no effect on the fine roots of plants grown in low-N soil (Pregitzer et al. 2000), a pattern that paralleled differences in whole-plant N content. Third, we found a significant, positive relationship between whole-plant N content and fine-root biomass in high-N soil. And finally, gross rates of N mineralization and microbial immobilization were not altered by elevated CO_2, which provided for equivalent rates of net N mineralization under conditions of ambient and elevated CO_2 (Zak et al. 2000). Taken together, plants in high-N soil further increased fine-root production under elevated CO_2 and acquired more soil N, which likely fed forward within the plant to increase leaf-level C assimilation and leaf area (Curtis et al. 2000). Additionally, the large increase in whole-

plant N content we observed from low-N to high-N soil suggests the advantage conferred through greater soil exploitation by a larger fine-root system (i.e., increased surface area) must have far surpassed the physiological reduction in ion uptake per unit of fine root (mmol NH_4^+ or $NO_3^-\cdot g^{-1}\cdot h^{-1}$).

The total biomass and N content of early- and late-senescing genotypes responded differently to soil-N availability, but both responded in the same manner to atmospheric CO_2. Late-senescing clones, which produced greater leaf area than early-senescing genotypes (Curtis et al. 2000), displayed proportionately larger increases in plant biomass and N content than early-senescing genotypes (Figs. 1 and 2) in response to soil-N availability. However, both genotypes increased growth to the same extent under elevated CO_2. *Populus* genotypes are known to vary widely in their growth response to soil-nutrient availability (Ceulemans and Isebrands 1996), and several studies have documented that growth responses to elevated CO_2 also differ among genotypes (Radoglou and Jarvis 1990, Ceulemans et al. 1995, 1996). Given the very limited number of genotypes in our study (i.e., six), it is difficult to draw conclusions about genotypic responses to atmospheric CO_2 in *Populus*. This topic clearly warrants further attention, because genotypic responses to atmospheric CO_2 will likely be an important factor controlling variability in the growth response of *P. tremuloides* forests to rising atmospheric CO_2.

While some have argued that elevated CO_2 will increase allocation to roots (McGuire et al. 1995, Rogers et al. 1996), we found little evidence to support this contention. In our study, elevated atmospheric CO_2 did not alter the allocation of biomass or N in *P. tremuloides,* and this was true in both low- and high-N soil. Moreover, total plant mass was not a significant factor influencing allocation to any biomass component, suggesting that elevated CO_2 did not alter the rate of ontogeny in *P. tremuloides*. Although the relatively small decrease in aboveground biomass allocation (−4%) and slight increase in belowground (6%) under elevated CO_2 (main effect) were statistically significant, these small changes are of little biological consequence in light of the much larger increase in plant biomass under elevated CO_2 (compare Tables 1 and 4). Radoglou and Jarvis (1990) also observed that elevated CO_2 (70 Pa) elicited no change in biomass allocation for several *Populus* genotypes, while others working with different genotypes have drawn similar conclusions (Bosac et al. 1995). Rey and Jarvis (1987) noted no shift in the biomass allocation of *Betula pendula* grown under elevated CO_2 (70 Pa). Understanding the response of biomass allocation to elevated CO_2 has important ecosystem-level implications for the cycling and storage of C and N in forest ecosystems.

We found no evidence to support the hypothesis that elevated CO_2 decreases the amount of N allocated to leaves, thereby lowering their N concentration. Moreover, declines in tissue N concentration under elevated CO_2 also cannot be attributed to differences in plant development as some have argued (Coleman et al. 1993), because total plant biomass was not a significant covariate in any analysis of tissue N concentration. McGuire et al (1995) concluded that elevated CO_2 can produce substantial reductions in leaf N concentration (−21%), but often causes much smaller reductions in the N concentration of fine roots. In a more recent synthesis, Cotrufo et al. (1998) also suggested that elevated CO_2 caused plants to increase N allocation to roots, because the N concentration of aboveground tissues (−14%) declined to a much greater extent than that of roots (−9%). Similarly, in our study, the N concentration of leaves (−17%) produced under elevated CO_2 declined to a much greater extent than did the N concentration of fine roots (−5%; Table 2: CO_2 main effect). However, the changes in N concentration we observed did not result from shifts in N allocation. In fact, elevated CO_2 did not alter the proportion of N allocated to any biomass component, a result consistent with patterns of biomass allocation. Given no shift in biomass or N allocation under elevated CO_2, declines in tissue N concentration simply result from a 32% increase in total biomass and only a 17% increase in whole-plant N content under elevated CO_2 Tables 1 and 3: (CO_2 main effect). That is, relative allocation was not altered by elevated CO_2, but increases in total biomass surpassed increases in whole-plant N content, giving rise to a decline in whole-plant-N tissue N concentration.

Atmospheric CO_2 did not substantially alter biomass allocation in *P. tremuloides,* but soil-N availability did. There was a greater amount of biomass allocated to stems in high-N soil, while allocation of biomass to all other plant components declined as N availability increased. These changes were sufficient to significantly decrease belowground allocation from 41% in low-N soil to 33% in high-N soil, a response consistent with that of many herbaceous and woody plants. Similarly, we observed greater allocation of N to stem in high-N-availability soil and a decline in N allocation to leaves, fine roots, and very fine roots, while there was no change in N allocation to coarse roots. Notwithstanding these changes, allocation of N to belowground plant components did not change from low-N (34%) to high-N soil (31%). From these results, it is clear that soil-N availability is a potent modifier of above- vs. belowground biomass allocation, but it has a much smaller influence on the allocation of N to above- vs. belowground plant components.

Summary and implications

Understanding the interaction between atmospheric CO_2 and soil-N availability on the growth and biomass allocation of *Populus tremuloides* has important im-

plications for ecosystem development and forest management. *P. tremuloides* is perhaps the most widely distributed deciduous tree species in the Northern Hemisphere and is broadly used by the forest industry in the Lake States region(USA) and Canada. Throughout the Upper Lake States (i.e., Minnesota, Wisconsin, and Michigan), this and other fast-growing, early-successional aspen (i.e., *Populus grandidentata*) occupy $\sim 4.8 \times 10^6$ ha over a range of soil conditions that our experimental N-availability treatments were designed to reflect (Smith 1986, Miles et al. 1995, Leatherberry and Spencer 1996). The majority of this land area comprises relatively young (<60 yr), even-aged stands that regenerated following clear-cut harvest (Smith 1986, Miles et al. 1995, Leatherberry and Spencer 1996). Although it is difficult to directly extrapolate from our results to *P. tremuloides* forests throughout the Lake States region, the response of young trees in our experiment is relevant to these ecosystems. A substantial proportion of the forested landscape in the Upper Lake States region is covered by young *P. tremuloides* stands that are rapidly accumulating biomass, and their response to rising atmospheric CO_2 has the potential to alter fiber production and ecosystem C storage across a large spatial extent (Alban and Perala 1992).

If trees respond in the field as they did in our experiment, then elevated atmospheric CO_2 will likely increase the rate of biomass accumulation in young, aggrading *P. tremuloides* stands. Our results indicate the extent of this increase will be governed by soil-N availability, wherein the greatest responses will likely occur on the most fertile soils. Given that total biomass increased 17% even in our low-N soil, it is also likely that elevated CO_2 will increase rates of biomass accumulation on relatively poor soils with low net N-mineralization rates. Moreover, these increases cannot be attributed to more rapid rates of tree development or ontogeny under elevated CO_2, because total plant mass was not a significant covariate in our analyses of biomass allocation. Regardless of soil-N availability, plants grew larger under elevated CO_2, not just faster, with a constant proportion of leaves, stem, and roots (i.e., no change in biomass allocation).

Greater rates of biomass accumulation under elevated CO_2 present the possibility that *P. tremuloides*-dominated forests will reach both commercial and ecological maturity over a shorter period of time. Such a response could lessen the commercial rotation age and accelerate rates of ecosystem development. However, it is unclear whether the growth response of individual trees to elevated CO_2 will be maintained as canopy closure occurs aboveground and root closure occurs belowground. Although elevated atmospheric CO_2 enabled *P. tremuloides* to accumulate more N from our high-N soil (i.e., greater whole-plant N content), it is likely that such a response will not be maintained once roots fully exploit the soil. If such a response is not maintained, it will be important to determine whether this will eventually result in a reduction in enhanced biomass accumulation under elevated CO_2 on fertile soils. It also will be important to determine if greater growth will be maintained on soils of low N availability in which plants obtain equivalent quantities of soil N under ambient and elevated CO_2. The extent to which growth responses to elevated CO_2 diminish following canopy and root closure will be an important determinant of whether elevated atmospheric CO_2 increases, decreases, or does not alter the cycling and storage of C in forest ecosystems. Achieving this understanding can only occur through longer-term experiments in which trees have fully exploited both above- and belowground resources.

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