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Carbon allocation and nitrogen acquisition in a developing *Populus deltoides* plantation†

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Summary We established *Populus deltoides* Bartr. stands differing in nitrogen (N) availability and tested if: (1) N-induced carbon (C) allocation could be explained by developmental allocation controls; and (2) N uptake per unit root mass, i.e., specific N-uptake rate, increased with N availability. Closely spaced (1 × 1 m) stands were treated with 50, 100 and 200 kg N ha^{-1} $year^{-1}$ of time-release balanced fertilizer (50N, 100N and 200N) and compared with unfertilized controls (0N). Measurements were made during two complete growing seasons from May 1998 through October 1999. Repeated nondestructive measurements were carried out to determine stem height and diameter, leaf area and fine-root dynamics. In October of both years, above- and belowground biomass was harvested, including soil cores for fine-root biomass. Leaves were harvested in July 1999. Harvested tissues were analyzed for C and N content. Nondestructive stem diameter and and fine-root dynamic measurements were combined with destructive harvest data to estimate whole-tree biomass and N content at the end of the year, and to estimate specific N-uptake rates during the 1999 growing season. Shoot growth response was greater in fertilized trees than in control trees; however, the 100N and 200N treatments did not enhance growth more than the 50N treatment. Root biomass proportions decreased over time and with increasing fertilizer treatment. Fertilizer-induced changes in allocation were explained by accelerated development. Specific N-uptake rates increased during the growing season and were higher for fertilized trees than for control trees.

Keywords: belowground allocation, carbon sequestration, functional equilibrium, ontogenetic drift, phytoremediation, short rotation woody crops, specific nutrient uptake.

Introduction

Populus species are grown in short-rotation forests because of their rapid growth, easy vegetative propagation, high potential for trait manipulation through breeding, hemisphere-wide distribution and economically valuable wood and fiber (Stettler et al. 1996, Dickmann et al. 2001). *Populus* species are also used in remediation of contaminated sites (Wang et al. 1999, Isebrands and Karnosky 2001), effluent disposal (Myers et al. 1996, US Environmental Protection Agency 2000) and restoration or establishment of riparian buffers (Schultz et al. 2000).

Achieving maximum growth potential of *Populus* plantations requires effective nutrient management, with specific focus on nitrogen (N), the element that most commonly limits growth (Ericsson et al. 1992, Stanturf et al. 2001). Both optimizing poplar yields through fertilizer application and the effective use of poplar plantings for nutrient filtration, will require greater understanding of N nutrition in poplar. In controlled environments, *Populus* has a high demand for mineral nutrients (Jia and Ingestad 1984, Coleman et al. 1998), but field responses are limited by factors such as soil type and inherent growth capacity (Hansen et al. 1988, Heilman and Fu-Guang 1993). Field responses are mediated by belowground allocation, nutrient acquisition and root initiation. Therefore, it is important to consider belowground processes when evaluating responses to fertilizer amendments.

Field studies indicate that, with increasing N availability, plant biomass allocation shifts from root to shoot (Keyes and Grier 1981, Linder and Axelsson 1982, Gower et al. 1992, Beets and Whitehead 1996, Albaugh et al. 1998). The shift is especially strong in leaves and feeder-roots (Cannell 1985, Waring and Schlesinger 1985, Kozlowski and Pallardy 1997). However, there are reports that many fertilizer-induced allocation shifts are the result of either accelerated development, or extreme N stress (Gebauer et al. 1996, Gedroc et al. 1996, King et al. 1999, Retzlaff et al. 2001). Because root:shoot biomass ratios of forest trees decrease ontogenically (Ovington 1957, Reynolds and D'Antonio 1996), it is unclear whether the reduction in root:shoot ratio following fertilizer application is a direct result of increased N availability or of accelerated development resulting from better nutrition (Coleman and McConnaughay 1995). Therefore, controlling for development is critical to understanding the effects of fertilizer on biomass allocation.

Nitrogen uptake depends on both specific uptake rate (i.e.,

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uptake per unit root mass) and the amount of root surface area. Hence it may be possible to exploit trade-offs between uptake rate and root quantity to maximize productivity of *Populus* plantations. Aboveground studies of photosynthetic rate versus leaf area index (LAI) have demonstrated that the quantity, not activity, of leaves controls forest productivity in intensively managed stands (Samuelson et al. 2001). Belowground specific N uptake may increase with increasing N availability (Jones and Dighton 1993, Carlyle 1995). Therefore, it is important to estimate N uptake rates as well as the amount of acquisition surface.

We tested two hypotheses: (1) Carbon allocation in rapidly grown *Populus* stands shifts from below- to aboveground as N availability increases, and this shift is independent of stand development. (2) Fertilization increases whole-plant N uptake by increasing specific N-uptake rates. We used closely spaced plots of vegetatively propagated *Populus deltoides* Bartr. receiving a range of slow-release fertilizer treatments to test our hypotheses. Vegetative propagation limited within-plot variability. Rapid growth and treatment responses enabled us to test these hypotheses in a 2-year study.

Materials and methods

The study was conducted in Rhinelander, WI (89°25′ W, 45°38′ N) at the Hugo Sauer Nursery managed by the USDA Forest Service, North Central Research Station. The growing season of the cool continental climate averages 80 to 100 frost-free days, with a mean July temperature of 19.4 °C and a mean January temperature of –12.5 °C. The soil is a Croswell loamy-sand (Enthic Haplorthod) that developed from glacial outwash (Boelter 1993). Table 1 presents chemical and physical soil characteristics at various depths.

Plantation establishment

The study site was cultivated to a depth of 16 cm in April 1997, Roundup-Pro (Glyphosate, 5 l ha^{-1}) (Monsanto, St. Louis, MO) was applied in July, and the area was recultivated in September. In April 1998, Roundup-Pro was applied in a tank-mix with Lorox DF (Linuron, 1.1 kg ha^{-1}) (Dupont Canada, Mississauga, ON, Canada). The site was then planted with native cottonwood (*P. deltoides*) genotype D-105, which originates in southern Wisconsin and has a high growth potential. After the first growing season, D-105 ranked first in stem diameter (2.47 cm) and second in height (2.44 m) out of 60 poplar clones tested in field trials (Isebrands and Riemenschneider 1996); however, D-105 has shown susceptibility to *Melampsora* Castagne rust infection.

Table 1. Chemical and physical characteristics of pretreatment soil at three depth increments.

Depth (cm)	pH	% C	% N	C:N	% Sand	% Silt	% Clay
0–30	5.4	2.4	0.14	16.9	81.8	14.3	3.9
30–60	5.6	0.5	0.03	15.7	86.5	10.4	3.1
60–90	5.7	0.2	0.02	12.4	80.5	17.0	2.6

Greenwood cuttings (5 to 10 cm) with at least two leaves were taken from stock plants between April and September 1997. Cut basal ends were dipped in 0.1% indole-3-butyric acid, and the cuttings stuck in flats of wetted vermiculite and peat moss (3:1, v/v), and placed in a mist tent for 4 to 6 weeks. Rooted cuttings were transplanted to 0.5-l containers (Deepots, Stewe & Sons, Corvallis, OR) filled with a 1:1:2 (v/v) mix of vermiculite:sand:peat, and 0.3 g of commercial time-release fertilizer (Sierra 17,6,10; N,P,K, plus micronutrients, 3–4-month formulation, Scott, Milpitas, CA) was added per pot. The rooted cuttings were grown in the greenhouse and then moved under covered shade frames for over-wintering.

On May 1 and 2, 1998, dormant 1-year-old rooted cuttings were planted at the study site in 20-cm-deep holes at 1 × 1 m spacing. On June 4, 1998, 69 dead trees (2.2%) were replaced. The randomized complete block experimental design consisted of 16 plots with four replicate blocks, each containing four fertilizer treatments: 0, 50, 100 or 200 kg N ha^{-1} $year^{-1}$ (0N, 50N, 100N and 200N, respectively). We used commercial time-release complete fertilizer (17,6,10; N,P,K plus micronutrients) rather than a single application of soluble fertilizer, which causes spikes in nutrient availability. Fertilizer treatments were applied May 5, 1998 and April 12, 1999. Each treatment plot comprised 14 × 14 trees with a 64-tree square central measurement plot and three border rows. A 3-m alley ran between the plots; therefore, measurement plot edges were 9 m apart. Irrigation lines with 0.9-m risers ran in one direction along the alleys between blocks.

During the growing season, rainfall was supplemented with irrigation to ensure the plantation received at least 2.5 cm of water per week. We used wick applicators to apply Roundup during the growing season to eliminate weed competition. Pesticides were applied on two occasions to control lepidopteron defoliators. Lateral root exploration between plots was prevented by drawing a tractor-mounted flat disk along the alleys around each plot at midsummer and during the dormant season.

Measurements

Growth was monitored by both regular nondestructive measurements and destructive harvests. At weekly intervals throughout both growing seasons, we measured heights and diameters of four trees located at the plot center to determine seasonal growth patterns. In October 1998 and 1999, we measured heights and diameters of 64 trees per plot.

We determined biomass and production of plant parts based on representative trees harvested on three occasions. In May 1998, we harvested 30 randomly selected trees for dry mass measurements. In October 1998 and 1999, we harvested two representative trees from the middle border row of each plot for a total of eight trees per treatment. Trees, which were selected to represent the diameter range of each treatment, were separated into stem, branch and coarse root fractions, dried at 70 °C and weighed. Coarse roots (> 5 mm) were collected to a depth of 40 cm from the 1-m^2 growing space surrounding each harvested tree. We estimated tissue biomass and N content of

each tree in the measurement plot as (cf. Landsberg and Waring 1997):

$$y = bD^m \quad (1)$$

where b and m are the multiplier and exponent of the regression, respectively, y is dry mass or N content of the tissue fraction and D is ground-line diameter. We determined annual biomass and N content on a unit land area basis. We applied Equation 1 with tissue and treatment specific parameters (Appendix Table 1A) to all trees on the plot. Plot means were scaled by any mortality occurring in measurement plots (mortality was less than 0.2%). Production was calculated as the difference between initial and final biomass for each tissue.

In October 1998, we determined fine-root biomass in eight 5 × 30 cm cores per treatment plot, collected about 25 cm away from randomly selected trees. Roots were extracted from cores with a root washer (Gillison's Variety Fabrication, Benzonia, MI) and stored in 20% methanol until processed. Roots were separated from soil organic matter and divided into feeder (< 1 mm) and perennial (1 to 5 mm) size classes. Roots larger than 1 mm had secondary thickening. Over 95% of poplar roots observed in minirhizotrons are < 0.6 mm diameter (Kern et al. 2004). Roots were dried at 70 °C and weighed. We collected samples in October, when live-root biomass peaks (Coleman et al. 2000) and when we expected treatment differences to be greatest.

Monthly changes in fine-root biomass and mortality were determined from proportional changes in minirhizotron-observed live-root length (Kern et al. 2004) and biomass sampled in October 1998. To convert the minirhizotron-derived monthly root length indices to biomass, we determined the root length:mass ratio for October 1998 by dividing minirhizotron-observed root length by fine-root biomass. Monthly root biomass was calculated by dividing monthly minirhizotron root length by the root length:mass ratio. Monthly fine-root mortality was calculated by dividing minirhizotron root mortality by the root length:mass ratio. We defined fine-root production as the sum of standing crop and root mortality for each month, and annual production as the sum of all monthly production values. Fine root biomass and production for each plot were included with average plot whole-tree biomass and production, respectively. For budgets and analyses, we grouped perennial roots with the coarse-root fraction.

Monthly changes in leaf biomass were determined from proportional changes in ceptometer-derived LAI and a destructive harvest. In July 1999, we harvested two trees per plot from the middle border row to quantify LAI for eight trees per treatment. The harvested trees, which were selected to represent the stem diameter range for each treatment as described previously, were separated into 1-m height fractions. Leaves from each height fraction were dried (70 °C) and weighed. Total leaf mass was the sum of all height fractions. Leaf mass for all plot trees was estimated by Equation 1 and leaf biomass expressed on a unit ground area basis. We measured LAI monthly through the 1999 season with a ceptometer (AccuPar, Decagon, Pullman, WA). Monthly leaf mass was calculated from July leaf length:mass ratio and monthly LAI. First the leaf length:mass ratio was calculated by dividing LAI by mean plot leaf mass, both collected during the same week in early July 1999. Monthly leaf mass was calculated by dividing other monthly LAI values by this ratio. As with the root length:mass ratio, the leaf length:mass ratio allowed us to convert ceptometer-derived LAI to leaf biomass.

Nitrogen uptake

We calculated N uptake from changes in tissue nutrient content resulting from growth and concentration shifts. Tissue C and N contents of leaves harvested in July 1999 and woody tissue taken in the two October harvests were determined by the Dumas combustion method. Fine-root N and C concentrations were assumed to equal coarse root concentrations. Tissue N content of harvested trees was calculated as the product of biomass and concentration. Tissue N content for all plot trees was estimated with Equation 1, and the plot average of all tissue, including fine roots and leaves, was summed. We calculated monthly specific-N-uptake rates for the 1999 growing season by dividing the monthly change in whole-plot N content by mean fine-root biomass. Calculations were based on post-leaf-flush measurements, so all changes in tissue N content were assumed to reflect current N uptake.

Statistical analyses

We analyzed biomass, production, N concentration and content, and total N uptake based on a randomized complete block design with four treatments and four blocks. The shape of the treatment response was evaluated by orthogonal polynomial contrasts, i.e., linear or nonlinear. Means were separated by Tukey's test and differences in periodic N uptake were tested by repeated-measures analysis.

Effects of resource availability and plant development on C allocation were evaluated by calculating allometric relationships according to the model (Pearsall 1927, Ledig et al. 1970, Hunt 1978):

$$\ln y = a + k \ln x \quad (2)$$

where x and y are tissue components, a is the y intercept and the slope, and k is the allometric coefficient. If k is equal among treatments, changes in allocation are explained by development (Hunt 1978). We used analysis of covariance on log-transformed data to assess differences among treatments. Total biomass, shoot biomass or leaf production was the covariate; and shoot biomass, root biomass or fine-root production, respectively, was the dependent variable. Fertilization treatment was the class variable (Gebauer et al. 1996, King et al. 1999). If treatments alter allocation, i.e., k differs among treatments, a significant interaction among the covariate and fertilization is expected. All analyses were made with SAS software (SAS Institute, Cary, NC).

Results

Initial size and seasonal growth

At the time of planting, mean stem height was 22.4 ± 3.4 cm, mean root collar diameter was 2.5 ± 0.2 mm, mean shoot mass was 0.576 ± 0.14 g, mean root mass was 0.56 ± 0.10 g (mean ± SEM) and no coarse roots or branches were present. Height and diameter growth rates were low through mid-June of the first growing season, but reached an exponential growth phase that lasted through August (Figure 1). Rapid growth started earlier in the second growing season, but second-year growth was less than that of first-year growth, probably because of a severe infection by *Melampsora* rust in 1999.

Height and diameter

Fertilizer treatments did not increase tree height and diameter until the final measurement period in 1999 (Figures 1 and 2). The response to fertilizer application was similar in all treatments, despite a threefold difference in amount of applied N.

Tissue biomass and N fractions

Biomass and N content relationships developed from harvested trees closely followed the power function described in Equation 1. Parameters and statistics for prediction equations are presented in Appendix Table 1A.

Standing biomass

Standing biomass increased 1.8- to 2.8-fold from 1998 to 1999 (Table 2). The biomass increase was greater in fertilized trees than in control trees. In October 1998, total biomass was 9% greater in fertilized trees than in control trees; by July 1999, the difference was 24% (data not shown); and in October 1999, total biomass was 40% greater in fertilized trees than in control trees.

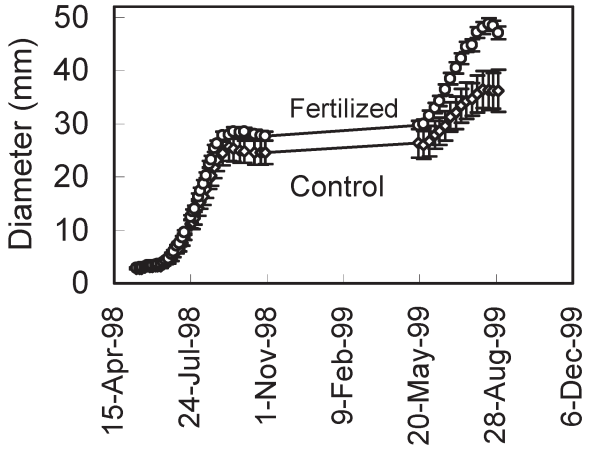

Figure 1. Weekly diameter measurements during two growing seasons for fertilized and non-fertilized cottonwood trees. Each value for the fertilized trees is the mean ± SE of 12 plots (4 trees per plot). Each value for the control trees is the mean ± SE of four plots (4 trees per plot).

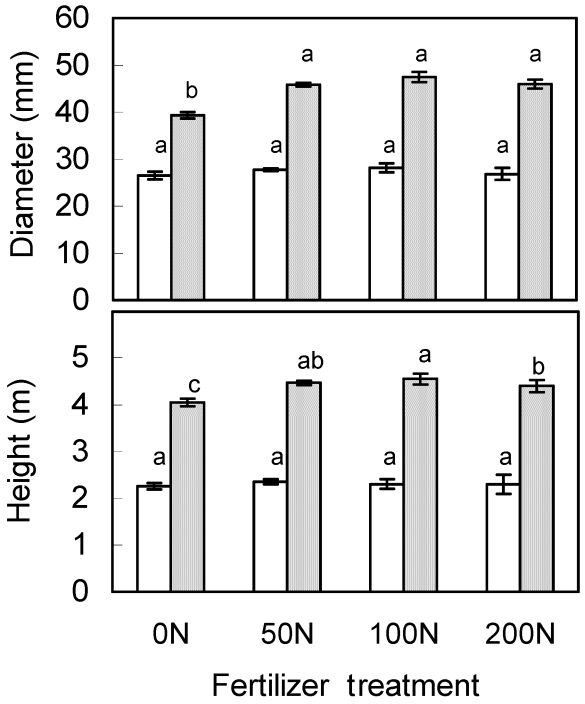

Figure 2. Cottonwood height and diameter measurements in October 1998 (open bars) and October 1999 (shaded bars). Fertilizer treatments were 0, 50, 100 or 200 kg N ha^{-1} $year^{-1}$ (0N, 50N, 100N and 200N, respectively). Each bar is the mean ± SE of four plots (64 trees per plot). Treatment bars with the same letter are not significantly different (Tukey's HSD, $\alpha = 0.05$).

Shoot biomass response to fertilizer differed from that of roots. There were highly significant fertilizer effects on total and shoot biomass in October 1999, but with all fertilizer treatments resulting in statistically similar responses. In contrast, an effect of fertilizer on root biomass could be detected only by polynomial contrast, and showed a linear increase in root biomass with increasing N availability (Table 2).

Annual production

Annual biomass production of ephemeral and perennial tissue depended on stand age, treatment and tissue type, in a manner similar to standing biomass. There were fewer treatment responses in 1998 than in 1999. Fertilizer application increased aboveground production by less than 7% in 1998 (data not shown), compared with 40% in 1999 (Table 2). In 1999, fertilizer application had a greater effect on shoot production than on root production. Root production increased linearly with increasing N availability, whereas all fertilizer treatments caused a similar increase in shoot production.

Carbon allocation

To differentiate between developmental and treatment effects on carbon allocation, we examined proportional biomass fractions. Between October 1998 and October 1999, the proportion of biomass accumulated in roots decreased from 41.7 ± 0.8 to 27.4 ± 0.7%. In 1998, there were no treatment differ-

Table 2. Dormant cottonwood standing biomass and annual production. Fertilizer treatments were 0, 50, 100 or 200 kg N ha^{-1} $year^{-1}$ (0N, 50N, 100N and 200N, respectively). Within a row, means ± SE (n = 4) followed by the same letter are not significantly different (Tukey's HSD, α = 0.05). The significance of the treatment factor is divided into polynomial contrast for linear, quadratic or lack-of-fit (LOF). Significance of analysis of variance factor is indicated by asterisks: *, P = 0.10; **, P = 0.05; ***, P = 0.01; and ns, not significant.

	0N	50N	100N	200N	Treatment	Linear	Quadratic	LOF
Final biomass (g m^{-2}) 1998								
Total shoot	210 ± 13	233 ± 5	240 ± 16	221 ± 24	ns	ns	ns	ns
Total root	154 ± 7	164 ± 8	153 ± 4	176 ± 26	ns	ns	ns	ns
Total root + shoot	363 ± 18	397 ± 10	393 ± 19	397 ± 48	ns	ns	ns	ns
Final biomass (g m^{-2}) 1999								
Branch	225 ± 9 b	343 ± 6 a	371 ± 18 a	350 ± 18 a	***	***	***	ns
Stem	493 ± 15 b	748 ± 11 a	757 ± 36 a	690 ± 33 a	***	***	***	**
Total shoot	719 ± 24 b	1091 ± 17 a	1128 ± 54 a	1041 ± 52 a	***	***	***	*
Coarse roots (> 1 mm)	241 ± 12	291 ± 10	283 ± 11	293 ± 27	ns	*	ns	ns
Fine roots (< 1 mm)	75 ± 4	86 ± 10	103 ± 11	118 ± 29	ns	*	ns	ns
Total root	315 ± 10	377 ± 8	386 ± 13	412 ± 53	ns	**	ns	ns
Total root + shoot	1034 ± 34 b	1468 ± 21 a	1514 ± 63 a	1452 ± 97 a	***	***	***	ns
Annual production (g m^{-2} $year^{-1}$) 1999								
Leaves	248 ± 21	288 ± 24	281 ± 24	238 ± 28	ns	ns	ns	ns
Branch	170 ± 6 b	279 ± 6 a	305 ± 16 a	290 ± 12 a	***	***	***	ns
Stem	340 ± 9 b	579 ± 12 a	583 ± 31 a	530 ± 21 a	***	***	***	***
Total shoot	757 ± 32 b	1146 ± 33 a	1169 ± 54 a	1058 ± 55 a	***	***	***	*
Coarse roots (> 1 mm)	121 ± 3 b	163 ± 4 a	169 ± 10 a	159 ± 5 a	***	***	***	ns
Fine roots (< 1 mm)	61 ± 5	65 ± 11	81 ± 14	94 ± 33	ns	ns	ns	ns
Total root	182 ± 5	229 ± 8	250 ± 12	253 ± 35	*	**	ns	ns
Total root + shoot	940 ± 34 b	1375 ± 32 a	1419 ± 57 a	1310 ± 85 a	***	***	***	ns

ences. By October 1999, fertilizer treatments generally decreased root proportions compared with the control (Figure 3), the response being most pronounced in the 100N treatment. Shoot and total root mass ratios in the 200N treatment did not differ from control values.

Biomass allocation to shoots increases both ontogenetically and with increased N availability (King et al. 1999, McConnaughay and Coleman 1999, Poorter and Nagel 2000); therefore, we compared the effects of fertilizer on above- and belowground biomass accumulation at the same developmental stage, i.e., plant size. Figure 4 shows individual treatment data fit to Equation 2 for various above- and belowground tissue fractions for 1998 and 1999. Individual treatments fell on the same line for all fractions, including perennial tissue (analysis of covariance interaction: $P > 0.3$), and apparent slope differences for ephemeral tissues (Figure 4C) were not significant because of the large residual error, indicating that the fertilizer-induced change in allocation (Figure 3) was associated with accelerated development and was not a direct response to fertilizer treatment.

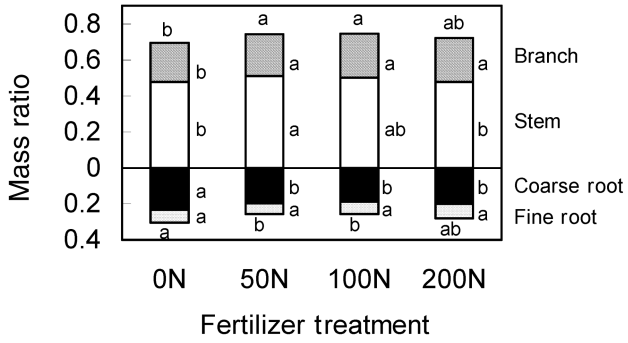

Figure 3. Mass ratios for tissues harvested in October 1999. Fertilizer treatments were 0, 50, 100 or 200 kg N ha^{-1} $year^{-1}$ (0N, 50N, 100N and 200N, respectively). Each bar is the mean of four plots (64 trees per plot). Tissue types with the same letter to the right are not significantly different (Tukey's HSD, α = 0.05). Letters above bars indicate shoot treatment differences and letters below bars indicate total root differences.

Concentrations and contents of N and C

Nitrogen and C concentrations of dormant tissue differed between years, but there were no significant treatment differences in either year. From October 1998 to October 1999, branch, root and stem N concentrations decreased. In 1998, N concentrations were 9.0 ± 0.2, 6.2 ± 0.2 and 10.3 ± 0.3 mg g^{-1} for branch, stem and root, respectively. In 1999, they were 7.5 ± 0.3, 4.0 ± 0.1 and 7.1 ± 0.3 mg g^{-1}, respectively. In 1999, small N concentration differences in stems resulted in slightly different treatment responses for N content (Table 3) than for biomass (Table 2). We observed no treatment differences in C

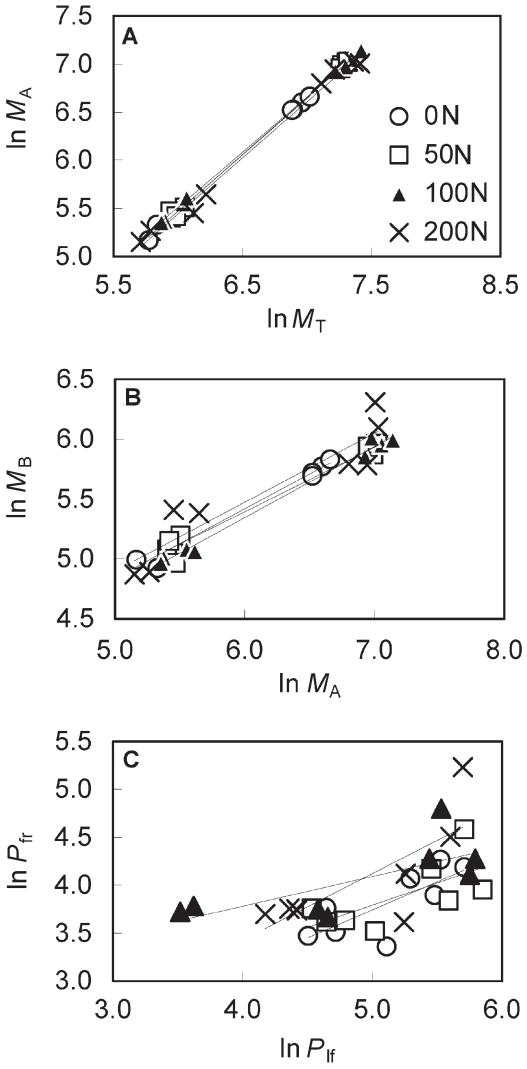

Figure 4. Allometric plots for biomass fractions fit to Equation 2. (A) Total biomass (M_T) versus aboveground biomass (M_A); (B) M_A versus belowground biomass (M_B); and (C) leaf production (P_{lf}) versus fine-root production (P_{fr}). One value is shown for each of the 16 plots in both 1998 and 1999. Fertilizer treatments were 0, 50, 100 or 200 kg N ha^{-1} $year^{-1}$ (0N, 50N, 100N and 200N, respectively).

concentration and, as a result, treatment differences in C amounts (data not shown) were identical to those shown for biomass in Table 2. As with biomass, the shoot treatment response pattern for both C and N content was nonlinear (significant quadratic polynomial, $P < 0.01$), whereas the root pattern was linear (significant linear polynomial, $P < 0.05$; nonsignificant quadratic polynomial), again suggesting a fertilizer-induced allocation response. Based on proportions, differences were apparent between years and among treatments. When data were analyzed with Equation 2, no treatment differences were observed, i.e., slopes were not significantly different among treatments, $P > 0.12$, indicating that shifts in N and C accumulation resulted from accelerated development, and not as a direct response to fertilizer treatment.

Leaf N concentration differed between years and among treatments. In 1998, mean leaf N concentration was 37 mg g^{-1} and there were no treatment differences, whereas in 1999, control leaves had significantly lower N concentration than leaves from the fertilized plots ($P < 0.001$). The N concentration of upper-canopy leaves of control trees was 40% lower in 1999 than in 1998, whereas N concentrations of upper-canopy leaves of the 50N, 100N and 200N trees were only 10, 8 and 16% lower, respectively.

Nitrogen uptake

Whole-plot N uptake differed among treatments, with fertilized trees having greater N uptake than the control trees ($P = 0.0004$). Between May 18 and August 24, 1999, N uptake was 4.2 ± 0.7, 12.5 ± 1.0, 12.1 ± 1.6 and 12.0 ± 0.8 g N m^{-2} for the 0N, 50N, 100N and 200N trees, respectively. Specific N-uptake patterns during the season reflected changes in both whole-plant biomass and the mass of fine roots. Specific N-uptake rates increased from spring to midsummer and then declined to a seasonal low by the end of August (Figure 5). Nitrogen uptake rates were always lower in control trees than in fertilized trees ($P = 0.002$), with control rates during midsummer being less than one third of those of the 50N trees.

Discussion

Trees in the 50N and 100N treatments achieved near-maximum growth potential, with growth rates exceeding region-wide rates for intensively managed hybrid poplar plantations (Isebrands and Riemenschneider 1996, Netzer et al. 2002). The 200N trees had lower growth rates than the 50N and 100N trees. Although it is possible to supply N in excess, it is unlikely that the 200N treatment was super-optimal, because 200 kg N ha^{-1} is not high compared with routine forest and agricultural fertilizer applications (Tisdale and Nelson 1975, Chappell et al. 1992). Therefore, we attribute this trend of apparent nutrient toxicity to random variation. The significant quadratic polynomial contrast among fertilizer treatments most accurately describes a saturation response rather than an optimization response.

The 100N and 200N fertilizer application rates exceeded the N demand of the trees. Based on our whole-plot N uptake data for 1999, control trees incorporated 42 kg N ha^{-1} $year^{-1}$ from native site N sources, which can be considered an estimate of the N mineralization rate at this site, although it is probably a low estimate because the poplar stand may have been unable to acquire all of the mineralized N. Trees in all fertilized plots incorporated an additional 80 kg N ha^{-1} $year^{-1}$. Trees in the 0N and 50N treatment plots retained N during the study, because N uptake in the stand equaled or exceeded the sum of mineralized and fertilized N. However, excess N was available in the 100N and 200N plots and could be a source for off-site N export. Based on these data, we predict that similar actively growing poplar stands will acquire no more than 120 kg N ha^{-1} $year^{-1}$ from the sum of native and applied N sources.

Table 3. Nitrogen content of cottonwood plots (g N m^{-2}) during dormancy. Fertilizer treatments were 0, 50, 100 or 200 kg N ha^{-1} $year^{-1}$ (0N, 50N, 100N and 200N, respectively).Within a row, means ± SE (n = 4) followed by the same letter are not significantly different (Tukey's HSD, α = 0.05). Significance of analysis of variance factor is indicated by asterisks: *, P = 0.10; **, P = 0.05; ***, P = 0.01; and ns, not significant.

	0N	50N	100N	200N	Treatment	Linear	Quadratic	LOF
October 1998								
Total shoot	1.40 ± 0.08	1.54 ± 0.03	1.58 ± 0.09	1.46 ± 0.15	ns	ns	ns	ns
Total root	1.56 ± 0.07	1.66 ± 0.08	1.55 ± 0.04	1.78 ± 0.26	ns	ns	ns	ns
Total root + shoot	2.96 ± 0.13	3.20 ± 0.09	3.13 ± 0.13	3.25 ± 0.39	ns	ns	ns	ns
October 1999								
Branch	1.49 ± 0.07 b	2.34 ± 0.04 a	2.54 ± 0.13 a	2.39 ± 0.13 a	***	***	***	ns
Stem	2.04 ± 0.04 c	2.75 ± 0.04 ab	2.92 ± 0.13 a	2.52 ± 0.11 b	***	**	***	ns
Total shoot	3.54 ± 0.11 b	5.09 ± 0.08 a	5.46 ± 0.26 a	4.91 ± 0.24 a	***	***	***	ns
Fine roots	0.54 ± 0.03	0.59 ± 0.07	0.71 ± 0.08	0.87 ± 0.22	ns	*	ns	ns
Coarse roots	1.73 ± 0.08	1.98 ± 0.07	1.95 ± 0.06	2.15 ± 0.22	ns	*	ns	ns
Total root	2.27 ± 0.06	2.57 ± 0.05	2.66 ± 0.09	3.01 ± 0.42	ns	**	ns	ns
Total root + shoot	5.80 ± 0.17 b	7.65 ± 0.11 a	8.12 ± 0.31 a	7.93 ± 0.62 a	***	***	***	ns

Carbon allocation

We observed a fertilizer-induced shift in C allocation from root to shoot (Figure 3). This finding appears consistent with the functional equilibrium hypothesis (Brouwer 1983, Poorter and Nagel 2000), which states that root growth is favored when belowground resources are limiting, and shoot growth is favored when C gain is impaired by limiting aboveground resources. Although most evidence supporting functional equilibrium has been obtained from studies of annual plants or tree seedlings (Reynolds and D'Antonio 1996, Poorter and Nagel 2000), comparable responses have been observed in forest stands. For example, Keyes and Grier (1981) showed that aboveground production of *Pseudotsuga menziesii* (Mirb.) Franco was 87% greater on a high-quality site than on a low-quality site, whereas belowground production was 49% lower. Ågren et al. (1980), by a C-budget technique, estimated that fine-root turnover decreased by 38% in fertilized *Pinus sylvestris* L. trees, whereas aboveground growth was twice that of untreated controls. Others have found similar resource-induced shifts in forest stand C allocation (Persson 1980, Gower et al. 1992, Runyon et al. 1994, Beets and Whitehead 1996, Albaugh et al. 1998). However, these reports typically compared chronologically equivalent, not developmentally equivalent, stands.

Belowground allocation in our plots decreased with stand development, with a 34% decrease between 1998 and 1999. Similar results have been reported for *Populus* and *Eucalyptus* F. J. Muell. genotypes (Scarascia-Mugnozza et al. 1997, Bernardo et al. 1998). Because the allocation shift with stand development was in the same direction as the shift in response to fertilizer addition, we investigated whether fertilizer-induced C allocation shifts were the result of stand development (King et al. 1999, McConnaughay and Coleman 1999, Poorter and Nagel 2000). Based on an allometric approach, we were unable to show differences in above- versus belowground biomass proportions between control and fertilized plants when compared at a common size (Figure 4), which appears to eliminate functional equilibrium as a factor explaining the fertilizer-induced C allocation response observed in Figure 3. King et al. (1999) reached a similar conclusion for loblolly pine stands subjected to various irrigation and fertilizer treatments.

It is important to examine ephemeral absorbing tissue and perennial support tissue separately. Evaluation of functional equilibrium with respect to ephemeral tissues is important because of their high turnover rates and the role these tissues play in resource acquisition (Cannell 1985, Poorter and Nagel 2000). Proportional increases in total stem and root mass during development are predicted on the basis of the fundamental relationships reported by Enquist and Niklas (2002), but most studies on stand-level resource-induced C allocation shifts have demonstrated differences in leaf versus fine-root production rather than in total biomass components (Persson 1980, Keyes and Grier 1981, Gower et al. 1992). Although we ob-

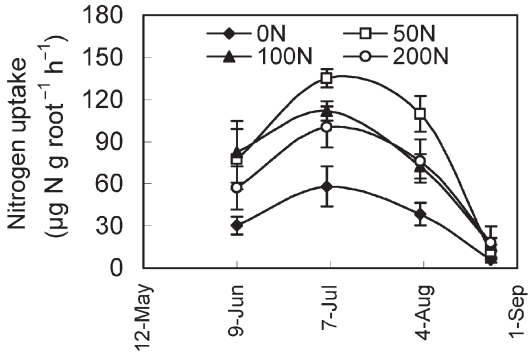

Figure 5. Specific N-uptake rates in cottonwood during four measurement periods in the 1999 growing season. Each value is the mean ± SE of four replicate plots. Fertilizer treatments were 0, 50, 100 or 200 kg N ha^{-1} $year^{-1}$ (0N, 50N, 100N and 200N, respectively).

served subtle treatment effects on fine-root production and mortality in these plots (Kern et al. 2004), we were unable to show fertilizer-induced allometric shifts in fine-root production relative to leaf production (Figure 4C), perhaps because of the high variation in our fine-root data (see also King et al. 1999). Nevertheless, there was a consistent tendency for greater fine-root production in plots containing greater total biomass ($P < 0.0001$, $r^2 = 0.56$), indicating that ephemeral tissue responses to fertilizer additions were better explained by accelerated development than by a functional equilibrium between leaves and roots. Thus, based on whole-plant allocation data and the responses of ephemeral tissue, we reject our first hypothesis that fertilizer-induced shifts in C allocation are independent of stand development.

Our results may differ from previous reports because the forest type we studied is unique. Many previous studies on belowground allocation have been with closed-canopy conifers (Persson 1980, Keyes and Grier 1981, Linder and Axelsson 1982, Gower et al. 1992, Beets and Whitehead 1996, Albaugh et al. 1998). Fine-root production differs between conifers and broadleaf trees (Coleman et al. 2000), and there may also be differences among the stages of stand development. For instance, there was little fine-root mortality in these stands relative to older poplar stands (cf. Coleman et al. 2000, Kern et al. 2004), and fine-root production increases with age in *Abies amabilis* Dougl. (Grier et al. 1981). Accordingly, fine-root turnover may respond differently to nutrient availability in young stands than in old stands.

Nitrogen uptake

Our N uptake results support the hypothesis that specific N-uptake rates increase with increasing N availability, despite parallel increases in root acquisition surface. Nitrogen uptake rates were three times higher in fertilized trees compared with control trees. The increase in N uptake rate with increasing N availability agrees with data derived from kinetic nutrient-uptake models (Yanai et al. 1995, Kelly et al. 2000) and in situ soil-core methods (Carlyle 1995). The finding that specific N-uptake rates increased with increasing N supply concomitantly with increases in fine-root biomass demonstrates that the increase in whole-plant N content resulted from increases in both acquisition surface and specific N-uptake rate. Although our data agree with measurements obtained by kinetic and in situ methods, they differ from results based on excised root assays, which show that specific N-uptake rate is negatively related to site N availability (Jones and Dighton 1993, Rothstein et al. 2000). Although excised root assays provide reproducible results from field-sampled roots, the direction of the observed response is difficult to explain. If N content increases with increased N availability and fine-root production is proportional to whole-tree biomass, it follows that uptake per unit root mass must remain constant or increase, not decline. Excised root assays are useful as indices of site N availability, but do not appear to provide accurate measures of N uptake rates.

To estimate monthly specific N-uptake rates during the growing season, we calculated changes in nutrient pools based on destructive harvests in combination with nondestructive root observations. Based on similar studies in controlled environments (Ingestad and Ågren 1988, Coleman et al. 1998), where root tissues are accurately quantified, Coleman et al. (1998) found N uptake rates for *Populus tremuloides* Michx. ranging from 8 to 252 μg g root^{-1} h^{-1}, which are comparable to our field data (6–135 μg g root^{-1} h^{-1}). Typically, field studies are reported on a whole-tree or plot basis expressed per unit land area, not a per unit root basis (Smethurst and Nambiar 1989, Carlyle 1995, Rytter 2001, Finzi et al. 2002). Nevertheless, field studies using biomass-based uptake estimates and in situ soil-core techniques agree with our results. Studies based on intact-root, excised-root and modeling methods also report specific uptake rates comparable with our rates (Rygiewicz and Bledsoe 1986, Jones and Dighton 1993, Jones et al. 1994, Rothstein et al. 1996, 2000, Högberg et al. 1998, BassiriRad et al. 1999, Kelly et al. 2000). Variations among reports may be partly explained by seasonal changes.

Generally, maximum seasonal N uptake occurs during mid-growing season when biomass production is high and the number of live fine roots has yet to reach a seasonal maximum. Silla and Escudero (2003) reported similar seasonal patterns in uptake; however, they found that peak rates occurred during the spring flush in growth, before the production decline that occured during the subsequent dry growing season. In our experiment, irrigation eliminated water stress, so production and uptake continued into summer, with peak specific N-uptake rates during midsummer. The midsummer maximum coincided with the period of most rapid whole-plant production. Specific N-uptake rates declined later in the season as root biomass, which was used to normalize uptake rates, increased relative to whole-plant production. The seasonal peak in specific N-uptake rate was pronounced in our study because peak fine-root standing crop production was delayed compared with maximum whole-plant production.

We likely overestimated N uptake because of tissue-sampling date, use of root biomass for normalizing uptake rates and assumptions about stored N. Dormant tissues store N retranslocated from leaves during autumn senescence, and contain greater N concentrations than the same tissue during the growing season (Pregitzer et al. 1990). Our biomass estimates were based on measurements of dormant tissues, which probably contained peak annual N concentrations. We assumed that fine roots (< 1 mm) are solely responsible for N uptake. However, if larger roots are also active in N uptake, our specific N-uptake values may be high. We also assumed that new tissue following initial leaf emergence acquired N only from current uptake, not from internal sources. We did not account for any accumulation or depletion of internal N storage pools. This simplifying assumption is reasonable, because total biomass increased three- to fourfold during the time we observed N uptake. Storage pools can be discounted as a possible N source because they would have been able to supply only a fraction of the N requirements during this time.

In conclusion, fertilization of poplar stands with 50 kg N ha^{-1} $year^{-1}$ increased growth over unfertilized controls, but no additional growth stimulation was observed with 100 or 200 kg N ha^{-1} $year^{-1}$ fertilizer treatments, indicating that fertilized poplar plantations acquired an additional 80 kg N ha^{-1} $year^{-1}$ compared with unfertilized plots. The lack of continued fertilizer-induced increases in growth demonstrates that N requirements were met with the addition of 50N fertilizer; however, the amount of applied N that *Populus* trees are capable of absorbing will depend on the native soil supply capacity. Nevertheless, this finding has implications when poplars are used as nutrient filters, because of the risk of exceeding uptake capacity and creating the potential for offsite N export.

Biomass allocation was affected by fertilizer treatments, but this response was dependent on developmental changes. Thus, in young poplar plantations, rather than shifting allocation with resource availability, allocation can be described with simple allometric growth models. Artificial allocation coefficients currently used in process models may be unrealistic if the patterns we observed are broadly applicable. Allocating C belowground based on development will simplify carbon stock accounting.

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Appendix

Table 1A. Parameters of allometric relationships (Equation 1) predicting biomass, nitrogen (N) and carbon (C) content (g m^{-2}) from stem diameter (mm). Each regression is significant ($P < 0.02$). The regression lines for biomass, N and C content were coincident among fertilizer treatments for all tissue fractions in 1998, and for branch fractions in 1999, but there were significant differences among treatments for coarse root and stem tissue fractions in 1999. Because treatment differences were not found in 1998 or 1999 branch fractions, the same allometric equation was used to predict branch biomass in each treatment and year.

Tissue fraction	Year of October harvest	Treatment	Biomass			N content			C content		
			m	*b*	r^2	*m*	*b*	r^2	*m*	*b*	r^2
Branch	1998		3.0	2.3E-03	0.84	2.9	3.2E-05	0.92	3.1	1.2E-03	0.84
	1999		2.7	9.1E-03	0.87	2.9	3.2E-05	0.92	2.7	4.8E-03	0.87
Coarse root	1998		2.0	1.1E-01	0.89	2.0	1.2E-03	0.86	2.1	5.3E-02	0.89
	1999	0N	1.9	2.1E-01	0.88	1.7	3.0E-03	0.74	1.9	9.6E-02	0.88
		50N	2.2	5.6E-02	0.96	2.4	1.7E-04	0.79	2.2	2.8E-02	0.96
		100N	2.5	1.8E-02	0.99	2.0	6.9E-04	0.91	2.5	8.7E-03	0.98
		200N	2.2	5.1E-02	0.97	2.9	2.8E-05	0.75	2.2	2.8E-02	0.97
Stem	1998		2.0	2.0E-01	0.94	1.6	4.1E-03	0.87	2.0	1.0E-01	0.94
	1999	0N	1.8	5.8E-01	0.85	1.3	1.9E-02	0.60	1.8	3.0E-01	0.85
		50N	2.2	1.3E-01	0.95	1.8	3.0E-03	0.81	2.2	9.2E-02	0.96
		100N	2.6	3.0E-02	1.00	2.5	1.7E-04	0.98	2.6	1.5E-02	1.00
		200N	2.5	4.3E-02	0.94	2.2	6.2E-04	0.80	2.5	2.2E-02	0.94
Leaves	1999		1.8	3.5E-01	0.96	–	–	–	1.8	1.8E-01	0.96
		0N	–	–	–	1.7	1.2E-02	0.99	–	–	–
		50N	–	–	–	1.9	8.2E-03	0.98	–	–	–
		100N	–	–	–	1.9	7.2E-03	0.96	–	–	–
		200N	–	–	–	1.8	9.8E-03	0.94	–	–	–