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Contrasting below- and aboveground responses of two deciduous trees to patchy nitrate availability

VIT GLOSER,[1–3] KATHERINE LIBERA[1] and COLIN M. ORIANS[1]

[1] *Department of Biology, Tufts University, Medford, MA 02155, USA*

[2] *Present address: Department of Plant Physiology and Anatomy, Masaryk University, Kotlarska 2, 611 37 Brno, Czech Republic*

[3] *Corresponding author (vitgloser@sci.muni.cz)*

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Summary We investigated how patchy nitrate availability influences growth and functioning of plant roots and generates, through vascular constraints on long-distance transport, aboveground heterogeneity in plant growth and chemistry. We examined two broadleaf tree species, *Acer rubrum* L. and *Betula papyrifera* Marsh. Plants were grown either in a split-root setup where a single root received full nutrient supply and the rest of the root system received all nutrients except nitrogen (patchy treatment), or in a single pot with full nutrient supply (homogeneous treatment). In both species, fine roots proliferated in the nitrogen patch, but *B. papyrifera* produced twice as much fine root biomass in response to patchy nitrate availability as did *A. rubrum*. There was no difference between treatments in nitrogen uptake rate in either species. In general, specific water uptake was higher in *A. rubrum* than in *B. papyrifera*, especially in the nitrogen-rich side pot. When nitrate availability was patchy, nitrate reductase activity in roots and leaves was unaffected in either species. In *A. rubrum*, but not in *B. papyrifera*, patchy nitrate supply resulted in aboveground heterogeneity, with leaves above the N-fertilized roots being larger and having a higher relative chlorophyll concentration than those inserted in the opposite quater of the stem.

Keywords: aboveground heterogeneity, Acer rubrum, Betula papyrifera, nitrate reductase activity, nitrate uptake, water uptake.

Introduction

Soil nutrient availability varies in both space and time and at scales relevant to individual plants (Lechowicz and Bell 1991, Jackson and Caldwell 1993, Stark 1994, Robertson and Gross 1994). In response to nutrient-rich patches, roots may proliferate, increase their specific nutrient uptake rate or live longer (Stegmann et al. 1988, Jackson et al. 1990, Pregitzer et al. 1993, Caldwell 1994, Robinson 1994, van Vuuren et al. 1996, Hodge 2004). Herbaceous plants that show increased root proliferation in response to nutrient-rich patches usually show no increase in specific nutrient uptake rate (Robinson and van Vuuren 1998, Hodge 2004). When the specific nutrient uptake rate increases, it often reflects increased nutrient demand and activity of enzymes associated with nutrient assimilation, such as nitrate reductase (Larsson 1994, Gao et al. 1996). Hodge (2004) argues that root proliferation is greater in species with inherently high growth rates and that, despite lower specific nitrate uptake rates, these species outcompete slower-growing species for resourses from long-lived nutrient patches (see also Hodge et al. 1999, Robinson et al. 1999). Limited evidence suggests that fast-growing woody species exhibit greater root proliferation than slow-growing species (George et al. 1997, van Vuuren et al. 2003). For example, *Betula populifolia* Marsh. shows greater root proliferation in nutrient-rich patches than slower growing *Acer rubrum* L. (van Vuuren et al. 2003). Whether slower growing woody species have higher specific nutrient uptake rates, as is the case among herbaceous species, is unknown.

Nutrients, once assimilated, are transported to below- and aboveground tissues. Vascular constraints on the delivery of soil resources from roots to leaves are common (Marschner 1995, Orians et al. 2004) and can influence the effect of patchy resource availability on plant development (Orians et al. 2005*a*). In tomato, leaves above roots in nutrient-rich patches accumulate more nitrogen, grow larger and produce lower concentrations of secondary chemicals than leaves on the opposite side of the stem (Orians et al. 2002, Zanne et al. 2006*a*). Few studies have examined the consequences of sectoriality—vascular constraints on long-distance transport—on tree performance. Sectoriality in vascular transport in trees varies among species (Orians et al. 2004, 2005*a*, 2005*b*, Ellmore et al. 2006, Zanne et al. 2006*b*). For example, *Quercus* is about 10 times more sectored than *Acer* and 50 times more sectored than *Betula* (Ellmore et al. 2006). Variation in sectoriality, as estimated by the relative permeability of solutes in tangential transport in branch segments (Orians et al. 2005*b*, Zanne et al. 2006*b*), has been shown to explain differences in delivery of isotopically labeled nitrogen from roots to shoots (Orians et al. 2004), but whether restricted transport generates differences in aboveground traits of trees is unknown.

The goal of this study was to examine how patchy availability of nitrate influences below- and aboveground traits in

A. rubrum and *Betula papyrifera* Marsh. To examine belowground effects related to N uptake and assimilation, we quantified the effects of localized nitrogen availability on fine root biomass, specific nitrate uptake rate (SNUR), total nitrate uptake rate (TNUR) and nitrate reductase activity (NRA) in roots and leaves. We also investigated specific water uptake rate (SWUR), because nitrate is highly mobile in soils and nitrate availability can be affected by water transport in roots (Radin et al. 1989, Clarkson et al. 2000, Gloser et al. 2007). To examine aboveground effects, we quantified leaf production, spatial patterns of leaf morphology (leaf area) and foliar chemistry (relative chlorophyll concentration). Root proliferation in nutrient-rich soil patches is greater in *B. papyrifera* than in *A. rubrum* (van Vuuren et al. 2003), but whether nitrogen alone generates this effect is unknown. We hypothesized that patchy nitrogen availability would cause greater proliferation in *B. papyrifera* but greater upregulation of specific nitrate uptake and specific nitrate reductase activity (in roots) in *A. rubrum*. Because of differences between *A. rubrum* and *B. papyrifera* in sectoriality (Orians et al. 2004, Ellmore et al. 2006), we predicted that patchy nitrate availability would result in greater aboveground heterogeneity in *A. rubrum* (a sectored species) than in *B. papyrifera* (an integrated species).

We focused on soil nitrogen (in the form of nitrate) heterogeneity for three reasons. First, nitrogen limits plant growth in many ecosystems. Second, nitrate is an important nitrogen source in forest soils (Attwill and Adams 1993) and broadleaf species usually have a high capacity for nitrate reduction in both roots and shoots (Downs et al. 1993, Black et al. 2002). Third, nitrogen is readily recycled and moved throughout the plant. Therefore, if nitrogen generates heterogeneity in growth and development, other less mobile elements might be expected to cause similar, if not greater, effects.

Materials and methods

Species

Bare-root 2-year-old saplings of *A. rubrum* (red maple) and *B. papyrifera* (paper birch) were purchased from a local nursery and planted in soil-less medium. Both species invade early successional habitats in northeastern U.S. forests: *B. papyrifera* is often found in rocky nutrient-poor soils, whereas *A. rubrum* is found in a diversity of habitats.

Plant cultivation

Trees were grown for 65 days with a patchy or homogeneous supply of nitrate, and then transferred to a hydroponic system while maintaining patchy versus homogeneous nitrate treatments (see below). After the initial 65 days, we measured treatment differences in leaf chlorophyll content and the physiological responses of roots when grown hydroponically. Final biomass measurements were taken at the end of the study.

During the initial 65 days, plants were cultivated in a greenhouse in a 16-h photoperiod with supplemental light (metal-halide lamps) with a minimum irradiance at leaf height of 400 μmol m^{-2} s^{-1} PAR, and a mean day/night temperature of 26/16 °C. Plants were grown in 6-l pots containing an inorganic substrate (quartz sand and zeolite (klinoptiolite) chips in a 1:1 (v/v) ratio) to allow root separation from substrate without damaging the roots (Bledsoe and Orians 2006). Plants in the patchy treatment were grown in a split-root setup—one longer lateral root was placed separately in a smaller pot (2 l) beside the main pot. The lateral root was directed over the side wall of the main pot to the side pot, and the upper rims of the touching pots were covered with duct tape to prevent abrasion. Both pots were filled with substrate to the top, so that only a small portion of the side root was exposed to the air. In split-root cultivation, only the pot with the lateral root received a complete nutrient solution, i.e., including nitrogen. The main pot received a nutrient solution without nitrogen. Plants in the homogeneous treatment were grown in a single pot with a complete nutrient solution to avoid heterogeneity associated with rapid root growth into competition-free-space (side pot) (Bledsoe and Orians 2006).

Nutrients were supplied every other day in 100 ml of modified Hoagland nutrient solution either with nitrogen (380 μM KH_2PO_4, 540 μM $MgSO_4$, 4 μM $MnSO_4$, 1.7 μM $ZnSO_4$, 0.3 μM $CuSO_4$, 40 μM H_3BO_3, 0.5 μM Na_2MoO_4 and 81 μM FeNa-EDTA, and nitrate as 1.2 mM $Ca(NO_3)_2$ and 1.6 mM KNO_3) or without nitrogen ($CaCl_2$ and K_2SO_4 were substituted for $Ca(NO_3)_2$ and KNO_3). The location of nitrate addition depended on the treatment. On alternate days plants were watered with deionized water.

After 65 days of cultivation, six plants from each treatment were randomly selected and transferred to a hydroponic system. We placed each pot in a container of deionized water and carefully separated the roots from the substrate. The main and side roots of plants in the patchy treatment were placed in 750- and 250-ml rectangular plastic flasks, respectively, whereas the entire root systems of plants in the homogeneous treatment were placed in 750-ml flasks. Flasks were taped together and equipped with a short wooden pole to support the plant stem. Plants were allowed to acclimate for 24 h before nitrate and water uptake rates were measured. When grown hydroponically, the nutrient solution contained: 603 μM $Ca(NO_3)_2$, 795 μM KNO_3, 190 μM KH_2PO_4, 270 μM $MgSO_4$, 2 μM $MnSO_4$, 0.85 μM $ZnSO_4$, 0.15 μM $CuSO_4$, 20 μM H_3BO_3, 0.25 μM Na_2MoO_4 and 40.5 μM FeNa-EDTA in the homogeneous treatment and side root compartment of patchy treatment. In the main root compartment of the patchy treatment, $CaCl_2$ and K_2SO_4 were substituted for $Ca(NO_3)$ and KNO_3. The nutrient solution, which was continuously aerated and mixed, was replaced immediately before the start of the uptake measurements. The initial nitrate concentration (2 mM) was never depleted more than 20% during the experiment.

Plant traits

At Day 65, six plants from each treatment were randomly selected for measurement of nitrate and water uptake rates and relative chlorophyll concentration. Plants were then analyzed for NRA in roots and leaves and total nitrate reductase capacity (NRC) and leaf area and plant biomass (roots and leaves) determined.

Nitrate and water uptake measurements

We kept plants in a 16-h photoperiod at 700 μmol m^{-2} s^{-1} PAR and 26 °C during all nitrate and water uptake measurements. Net nitrate uptake rates were estimated along with plant transpiration based on depletion of nitrate from nutrient solution with nitrate as the sole source of nitrogen. Nitrate concentration in the nutrient solution was measured at the start and end of the uptake period with a flow-through nitrate ion-selective electrode (detectIon NO_3^-, NICO Scientific, PA). We quantified water uptake by measuring the decrease in mass of the nutrient solution over time (4 h) corrected for evaporation due to aeration.

Aboveground leaf traits

On each shoot, we examined two groups of leaves. Those inserted on a quarter of the stem above and adjacent to the lateral root in the nitrogen-rich patch (adjacent orthostichy), and those inserted on the opposite quarter of the stem (opposite orthostichy). For plants in the homogeneous treatments, leaves on the opposite sides of the stems were randomly assigned to adjacent and opposite orthostichies.

We estimated relative chlorophyll concentration in leaves with a CCM 200 chlorophyll meter (Opti-Sciences, Tyngsboro, MA) before transferring the plants to the hydroponic system. We took the mean of two to six chlorophyll measurements per leaf, depending on leaf size.

At harvest, the position of each leaf on the stem was noted, and its area measured with a laser area meter CI-203 (CID, Camas, WA). Measurements were made on 3–6 leaves in each group.

Nitrate reductase activity

A subsample of leaves and roots was prepared for determination of NRA, and the remaining tissue was dried at 80 °C for 48 h and weighed. Nitrate reductase activity in leaves and fine roots was measured with an in vivo assay (Black et al. 2002). Four subsamples of leaf discs (~100 mg) or finely chopped roots (~200 mg) were combined with 5 ml of assay buffer (200 mol m^{-3} KNO_3 and 5% propanol in 100 mol m^{-3} potassium phosphate buffer, pH 7.5) in 20-ml glass vials. The vials were closed and placed in the dark at 25 °C on a shaker. Two replicate reaction vials for each sample were removed from the shaker after 10 and 90 min and placed in boiling water for 15 min. The vials were cooled to room temperature and aliquots of assay buffer were collected and stored at –20 °C. To determine nitrite concentration, 500 ml of 1% sulfanilamide in 3000 mol m^{-3} HCl and 500 ml of 0.02% *N*-naphthyl-ethylene-diamine hydrochloride in water were added to the thawed samples and kept in the dark at room temperature. After 20 min, the absorbance at 540 nm was measured. Enzyme activity was calculated by comparing the amount of nitrite produced after a 90-min incubation with that detected after 10 min (Black et al. 2002). We took the mean of two replicates and expressed NRA as μmol nitrite produced g_{DM}^{-1} (fine roots or leaves) h^{-1}. Recalculation of fresh mass to dry mass was based on separate reference samples from the same plant. Total nitrate reductase capacity was calculated by multiplying NRA by the dry mass of the corresponding tissue (leaves or fine roots).

Statistics

Treatment effects were evaluated by two-way analysis of variance with species as a random effect. The normality of residuals and homogeneity of variances were checked and data were log transformed before calculation to ensure normality. The multiple comparison of means was based on the method of LSD contrasts. Treatment and species effects were compared by the Wilcoxon matched pair test.

Results

Total biomass

Total leaf biomass differed between species ($F = 72.82$, $P < 0.001$; Table 1) and reflected differences in initial plant size (data not shown). Neither nitrogen treatment ($F = 0.105$, $P = 0.75$) nor species × nitrogen treatment interaction significantly ($F = 3.19$, $P = 0.089$; Table 1) affected total leaf biomass.

Fine roots were roughly 10–30% of the whole root system at the start of the experiment and exceeded 50% at harvest. The species differed in their response to patchy nitrate availability (species × nitrogen treatment interaction: $F = 15.23$, $P < 0.001$). Total fine root biomass of *A. rubrum* was unaffected by treatment (Table 1). Furthermore, fine root biomass production by *A. rubrum* was similar in the main (no nitrogen) and the side (nitrogen-rich) pot (Table 2). In contrast, total fine root biomass of *B. papyrifera* in the homogeneous treatment was barely one-third that in the patchy treatment (Table 1), with 60% of the fine root biomass of *B. papyrifera* in the nitrogen-rich side pot (Table 2).

Uptake rates

Specific NO_3^- uptake rate was higher in *A. rubrum* than in *B. papyrifera* ($Z = 2.98$, $P < 0.003$; Figure 1), and the relative differences between the homogeneous and patchy treatments was greater in *A. rubrum* than in *B. papyrifera*. Similarly, total

Table 1. Mean dry mass (SE) of leaves and all fine roots of *Acer rubrum* and *Betula papyrifera* saplings grown for 65 days with either a homogeneous or patchy nitrate supply. In the patchy treatment, the sum of root mass from the main and side pots is shown. Different letters indicate significant differences based on post-hoc LSD test of ANOVA ($P < 0.05$); $n = 6$ plants per treatment.

Species	Nitrate supply	Dry mass (g)	
		Leaves	Fine roots
A. rubrum	Homogeneous	4.25 (0.29) a	0.52 (0.06) a
	Patchy	3.83 (0.19) a	0.62 (0.08) a
B. papyrifera	Homogeneous	2.21 (0.16) b	0.45 (0.04) a
	Patchy	2.50 (0.09) b	1.21 (0.13) b

Table 2. Mean (SE) fine root dry mass and specific water uptake rate (SWUR; (g H_2O) (g root DM)$^{-1}$ h^{-1}) and relative water uptake (RWU) from each compartment by *Acer rubrum* and *Betula papyrifera* grown in a patchy nitrate supply treatment. Only roots in the side pot had access to nitrate. Relative contribution of the root mass in each compartment (% of total) was calculated as the percent of total fine root biomass of the whole plant. Different letters indicate significant differences based on a post-hoc LSD test of ANOVA ($P < 0.05$). Asterisks indicate significant differences between the main and side pots based on Wilcoxon test ($P < 0.05$); $n = 6$ replicates per species.

Species	Compartment	Fine roots		SWUR Mean (SE)	RWU % of total
		Dry mass (g)	% of total		
A. rubrum	Main pot	0.31 (0.04) a	50	11.82 (1.43)	45
	Side pot	0.31 (0.05) a	50	14.09 (1.25)*	55*
B. papyrifera	Main pot	0.49 (0.07) b	40	9.72 (1.82)	52
	Side pot	0.72 (0.07) c	60	5.67 (1.21)	48

NO_3^- uptake per plant was greater in *A. rubrum* than in *B. papyrifera* ($Z = 2.82$, $P = 0.005$; Figure 1). Total NO_3^- uptake rate was lower in the patchy treatment than in the homogeneous treatment in *A. rubrum* ($Z = 2.20$, $P = 0.028$) but not in *B. papyrifera* ($Z = 0.73$, $P = 0.46$).

In the patchy treatment, specific water uptake was higher in *A. rubrum* than in *B. papyrifera* (Table 2). In *A. rubrum*, both SWUR and relative water intake (RWU) were higher in the N-rich side pot ($Z = 1.99$, $P = 0.046$), whereas in *B. papyrifera,* SWUR and RWU were similar in the side pot and main pot.

Nitrate assimilation

Nitrate reductase activity differed between leaves and roots. In leaves, specific NRA was higher in *B. papyrifera* than in *A. rubrum* ($Z = 4.29$, $P = 0.001$; Figure 2A) but did not differ by treatment. In roots, specific NRA was higher in *A. rubrum* than in *B. papyrifera* ($Z = 3.06$, $P < 0.002$; Figure 2B) but did not differ by treatment. Although whole-plant NRC did not differ between the species, the relative differences between homogeneous and patchy treatments were greater in *A. rubrum* than in *B. papyrifera* ($Z = 1.99$, $P = 0.046$, Figure 2C).

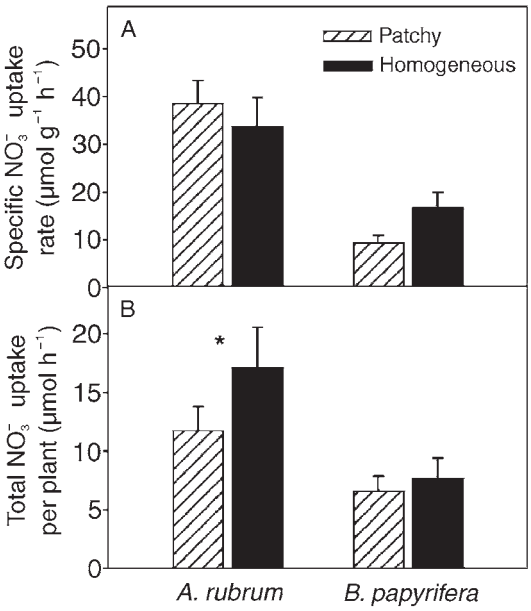

Figure 1. (A) Specific nitrate uptake rate (µmol (g root DM)$^{-1}$ h^{-1}) and (B) total uptake per plant (µmol h^{-1}) for *Acer rubrum* and *Betula papyrifera* saplings grown for 65 days with either a patchy or homogeneous nitrate supply ($n = 6$ plants per treatment per species, error bars = 2 SE). In the patchy treatment, uptake was measured only in roots with access to nitrate (in patch). An asterisk indicates significant differences between patchy and homogeneous treatments based on Wilcoxon test ($P < 0.05$).

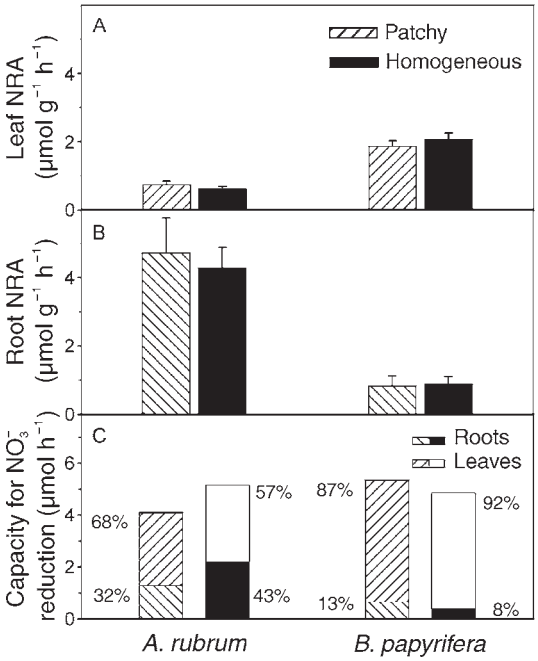

Figure 2. Mean nitrate reductase activity (NRA) in (A) leaves and (B) roots and (C) capacity for nitrate reduction in *Acer rubrum* and *Betula papyrifera* saplings grown for 65 days with either a patchy or homogeneous nitrate supply ($n = 6$ plants per treatment per species; error bars = 1 SE). In the patchy treatment, NRA was measured only in roots with access to nitrate (in patch). Numbers next to columns indicate relative contribution of roots or leaves to the capacity for nitrate reduction of the whole plant.

The relative NRA of roots differed by N treatment and species. The Wilcoxon matched pair test showed that roots (as a percentage of whole-plant capacity) of *A. rubrum* contributed only 32% in the patchy treatment but 43% in the homogeneous treatment ($Z = 2.20$, $P = 0.028$). In contrast, *B. papyrifera* roots contributed a similar percentage of the total NRA in the patchy and homogeneous treatments (13 and 8%, respectively, $Z = 0.52$; $P = 0.60$).

Aboveground heterogeneity

Belowground heterogeneity in nitrogen availability generated aboveground heterogeneity in leaf properties of *A. rubrum* but not of *B. papyrifera* (Figures 3 and 4). In *A. rubrum* grown with a patchy nitrogen supply, leaves of the adjacent orthostichy were larger than leaves of the opposite orthostichy ($F = 4.85$; $P = 0.038$, Figure 3A). As expected, there was no difference in mean leaf area between leaves on opposite sides of the stem of plants in the homogeneous treatment. Mean area per leaf in *B. papyrifera* was unaffected by the homogeneity or otherwise of the nitrogen supply ($F = 3.12$; $P = 0.80$ and $F = 2.48$; $P = 0.84$, respectively, Figure 3B).

Acer rubrum had lower relative chlorophyll concentrations in leaves of the opposite orthostichy than in leaves of the adjacent orthostichy ($F = 5.01$, $P = 0.031$), whereas there was no difference in *B. papyrifera* (Figures 4A and 4B). In both species, the mean foliar relative chlorophyll concentration was lower in the patchy treatment than in the homogeneous treatment ($F = 47.40$, $P < 0.001$), indicating that total N concentration was lower in leaves in the patchy treatment.

Discussion

Several measured traits indicate that *B. papyrifera* performed better in response to a patchy nitrate supply than *A. rubrum*. First, *B. papyrifera* exhibited greater fine-root proliferation in the nitrate-rich patch than *A. rubrum*. Second, although nitrate uptake per plant was similar in *B. papyrifera* with both a patchy and a homogeneous nitrate supply, uptake by *A. rubrum* was lower in the patchy treatment because of less root proliferation. Third, nitrate reduction capacity of roots of *A. rubrum* was reduced when nitrate availability was patchy. *Betula papyrifera* roots, in contrast, had a similar capacity for nitrate reduction in both treatments. Finally, in *A. rubrum*, unlike *B. papyrifera*, patchy nitrate availability caused aboveground heterogeneity, with leaves of the opposite orthostichy being smaller and having less chlorophyll than leaves of the adjacent orthostichy.

Root responses

Roots of most plants proliferate in nutrient-rich patches, but with varying capacity among species (Robinson 1994, Hodge

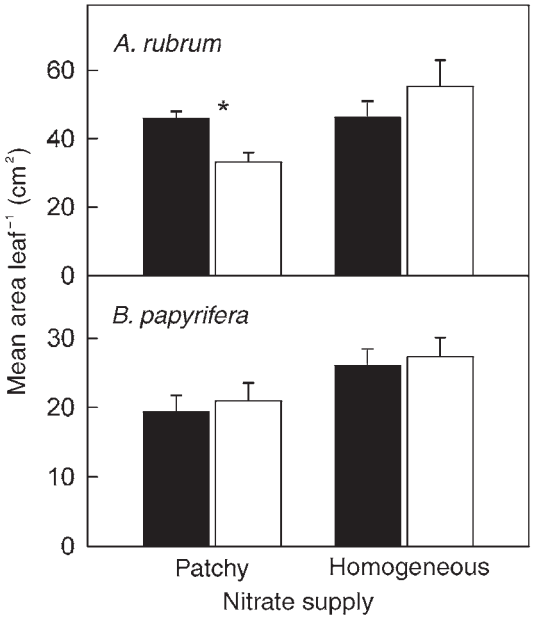

Figure 3. Mean area per leaf of *Acer rubrum* and *Betula papyrifera* saplings grown with either a patchy or homogeneous nitrate supply ($n = 6$ plants per treatment per species; 3–6 leaves per orthostichy; error bars = 1 SE). Leaves of the adjacent orthostichy (filled bars) were vertically aligned with the fertilized root in the side pot (45° around the point where the side root was attached to stem). Leaves of the opposite orthostichy (open bars) were inserted on the quarter of the stem opposite the fertilized root. An asterisk indicates a significant difference for the species between patchy and homogeneous treatments based on post-hoc LSD test of ANOVA.

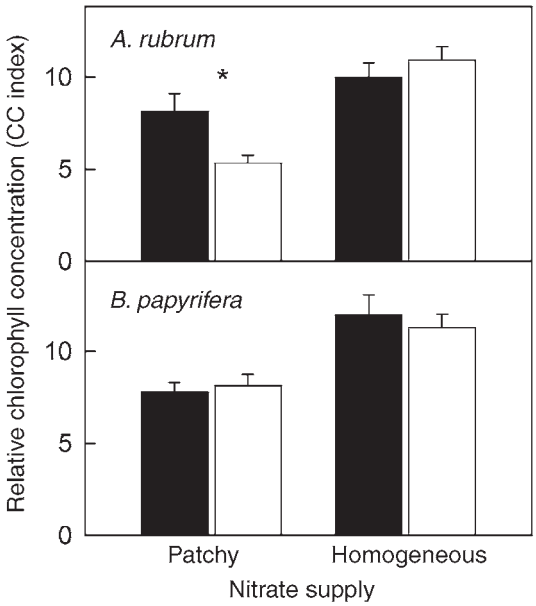

Figure 4. Mean relative chlorophyll concentration of leaves of *Acer rubrum* and *Betula papyrifera* saplings grown with either a patchy or homogeneous nitrate supply ($n = 6$ plants per treatment per species; 3–6 leaves per orthostichy; error bars = 1 SE). Leaves of the adjacent orthostichy (filled bars) were vertically aligned with the fertilized root in the side pot (45° around the point where the side root was attached to stem). Leaves of the opposite orthostichy (open bars) were inserted on the quarter of the stem opposite the fertilized root. An asterisk indicates a significant difference for each species between patchy and homogeneous treatments based on post-hoc LSD test of ANOVA.

et al. 1999, Hodge 2004). We found that, although root proliferation in the nitrate-rich patch was pronounced in both species, it was greater in *B. papyrifera* (Tables 1 and 2). The effect of inhomogeneity in nitrate supply is similar to the effect of inhomogeneity in the supply of all mineral nutrients that was reported by Robinson (1994) and van Vuuren et al. (2003).

Even in the absence of root proliferation, physiological adjustments in nitrate uptake are well known (Schenk 1996, von Wirén et al. 1997). Roots exposed to nutrient-rich patches often exhibit greater SNURs (Robinson 1994, van Vuuren et al. 1996). Hodge (2004) suggests that increases in specific uptake rates are less pronounced in species that exhibit greater proliferation. We might expect, therefore, greater up-regulation of SNUR by *A. rubrum* than by *B. papyrifera*. *Acer rubrum* had higher SNUR, but little difference between homogeneous and patchy treatments. The inherently higher SNUR in *A. rubrum* may help compensate for less root proliferation in environments where mineralization rates are high. Our measurements of SNUR, which provide a gross estimate of uptake capacities of the two species, did not reveal the mechanisms underlying these differences. Functional properties of transport systems can vary with N availability, especially in low nitrate concentrations (Rothstein et al. 2000). How these changes influence nitrate uptake by trees growing in patchy nutrient supply conditions, and how mycorrhizal associations can affect N acquisition under these conditions, are questions to be resolved.

In natural conditions, a significant portion of N can be acquired through mycorrhizal symbiosis (Smith and Read 1997) and sources of N other than nitrate are also available. We assumed that roots in our experiment were mycorrhizal, and we confirmed this in *B. papyrifera* by visual inspection. Whether mycorrhizae compensate for low root proliferation in *A. rubrum* or improve total N uptake from the patch when other forms of N are present is unknown.

Specific water uptake rate may play a role in stimulating nitrate acquisition from high-nitrate patches if increased water flow to roots enhances nitrate concentration at the root surface (Buysse et al. 1996). Our SWUR measurements suggest greater water uptake in the nitrate-rich patch by *A. rubrum* (Table 2). This effect can be mediated by lower hydraulic resistance of roots in the presence of nitrate (Radin and Boyer 1982, Clarkson et al. 2000).

Nitrogen utilization

Nitrate reduction occurred in both roots and leaves of *A. rubrum* and *B. papyrifera* but did not vary by treatment (Figure 2). In contrast, there were differences between treatments in the total capacity for nitrate reduction. In *B. papyrifera* roots, nitrate assimilation was similar in homogeneous and patchy treatments, whereas in *A. rubrum* roots, nitrate assimilation was significantly lower in the patchy treatment.

There were large differences between the studied species in the distribution of NRA. *Acer rubrum* had much higher activity in roots, whereas *B. papyrifera* had greater activity in leaves. Because the capacity of roots for nitrate assimilation and storage may be limited (Gojon et al. 1994), transport to and utilization of nitrate in leaves may enhance a plant's ability to acquire nitrogen. Moreover, the greater root proliferation of *B. papyrifera* may allow it to compensate for lower root NRA.

Hodge (2004) suggests that more competitive species will show greater root proliferation. Therefore, the higher NRA in roots of *A. rubrum* may be advantageous for rapid utilization of N-rich patches, but may be disadvantageous when species compete for longer-lived nutrient patches.

Aboveground consequences of patchy nitrogen

Suboptimal nitrogen supply can result in lower leaf growth, smaller leaves and altered chemical composition, especially concentrations of compounds involved in photosynthesis. Even when nitrogen supply is sufficient but patchy, heterogeneity in leaf growth, morphology and chemistry is expected if a species possesses a sectored vascular system (Orians and Jones 2001, Orians et al. 2005*b*). In such species, the transport of nutrients is restricted to specific vascular pathways, and certain leaves may be subject to nutrient limitation (Orians et al. 2002). In contrast, in an integrated plant, transport is unrestricted and heterogeneity in aboveground traits would not be expected.

Recent evidence suggests that *A. rubrum* is sectored whereas *B. papyrifera* is integrated (Orians et al. 2004, 2005*a*, Ellmore et al. 2006). We predicted that patchy nitrate availability would cause variation in leaf size and other variables in *A. rubrum* but not in *B. papyrifera*. As predicted, leaves of *A. rubrum* comprising the opposite orthostichy showed visible symptoms of nitrogen deficiency. They were smaller and had a lower chlorophyll content per unit area (Figures 3 and 4). However, there was no such difference in *B. papyrifera*. These results indicate that differences in sectoriality have consequences for both growth and photosynthetic capacity of woody plants.

Ecological implications

We speculate that *B. papyrifera* is more competitive than *A. rubrum* when nutrient availability is patchy for two reasons. First, *B. papyrifera* exhibits greater root proliferation in nitrate-rich patches than *A. rubrum*. Hodge et al. (1999) found that grass species with a high capacity for root proliferation are more competitive, and the same could be true for tree species. Second, patchy nitrate availability caused aboveground heterogeneity in *A. rubrum* but not in *B. papyrifera*, indicating that nutrients taken up by individual roots will be transported to the entire crown of *B. papyrifera* (see also Orians et al. 2004) whereas, in *A. rubrum*, only leaves above the nitrogen-rich patch will be fertilized and thus, if shaded by a fast-growing competitor, the photosynthetic nitrogen-use efficiency of the plant may be low. *Betula papyrifera*, in contrast, should be able to allocate resources to the branches with the most light.

These differences may affect the ability of the species to respond to localized damage. If herbivores remove leaf material above the root in a high nitrogen patch, this would limit the growth of *A. rubrum* more than that of *B. papyrifera*, because nitrogen will easily move to other parts of the crown in *B. papyrifera*. Similarly, because winter freezes can cause dieback to branches and buds (Strati et al. 2003), *B. papyrifera*, a domi-

nant species at high latitudes, should be better able to allocate soil-aquired resources to the most productive portions of the crown, wherever they may be.

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