Seedlings of Black Birch (Betula lenta L.) as Foragers for Nitrogen

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Seedlings of black birch (*Betula lenta* L.) as foragers for nitrogen

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SUMMARY

Soil nitrogen environments are highly heterogeneous, containing microsites that differ in relative and absolute ammonium and nitrate contents. We investigated whether black birch (*Betula lenta* L.) seedlings can maximize growth by foraging preferentially for a particular form of nitrogen, and whether supply rate of N and ammonium:nitrate in a patch affects preferences. Seedlings were transplanted into 5 l split pots with roots partitioned evenly, and assigned to 1 of 4 nitrogen form treatments: nitrate (NO_3^-) both sides, ammonium (NH_4^+) both sides, NH_4NO_3, 'homogeneous choice', and NO_3^- one side/NH_4^+ on the other, 'patchy choice', crossed with two rates of nitrogen supply. Use of ^{15}N-labelled nitrate revealed the proportion of seedling N from nitrate. Seedlings offered a patchy choice did not significantly out-perform seedlings in homogeneous ammonium and nitrate treatments, whereas seedlings offered a homogeneous choice did out-perform homogeneous nitrate and patchy choice treatment plants. In choice treatments, approx. 35 % of seedling N came from a nitrate source. This selectivity was unaffected by rate of nitrogen application and ammonium:nitrate ratio. That patchy choice seedlings integrated patches to achieve this ammonium:nitrate uptake suggests that black birch has a preferred balance. The seedlings offered a homogeneous choice were significantly heavier than the seedlings offered a patchy choice, perhaps reflecting an additional cost of foraging for ammonium and nitrate separately.

Keywords: *Betula lenta* (black birch), nitrogen selectivity, plasticity, heterogeneity.

INTRODUCTION

Plants forage for nitrogen in a heterogeneous soil environment, encountering microsites that differ in relative and absolute ammonium and nitrate contents. Ammonium and nitrate supply by mineralization and nitrification can vary with distance from tree trunks and identity of canopy trees, via effects on substrate availability, moisture, temperature, pH and base saturation, phosphate availability and the relative inhibition of nitrifiers (Zinke, 1962; Robertson, 1982; Nadelhoffer, Aber & Melillo, 1983; Plymale, Boerner & Logan, 1987; Lodhi & Reuss, 1988; and Boerner & Koslowsky, 1989).

Plants are known to exploit patches of higher nutrient concentration by local proliferation of roots, (Wiersum, 1958; Passioura & Wetselaar, 1972; Philipson & Coutts, 1977; St. John, Coleman & Reid, 1983; Crick & Grime, 1987; Jackson & Caldwell, 1989; Granato & Raper, 1989; Friend, Eide & Hinckley, 1990) resulting in increased growth. Differential uptake of different forms of

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nitrogen to maximize growth has been studied in aeroponics and hydroponics (Ingestad 1971; Robinson & Rorison, 1983) but remains an open issue in soil.

Studies in aeroponics, hydroponics and soil-less media with low nutrient holding capacity can only investigate part of plant foraging belowground for resources, which is preferential uptake of N forms delivered directly to the root. The use of soil with a cation exchange capacity (CEC) that alters the relative ease of encountering ammonium and nitrate, (since these have different mobilities in soil, Nye & Tinker, 1977) includes a second part of foraging, that of searching the soil volume for the resources. Root morphology, and hence nutrient access and uptake capability, are known to vary with substrate (Wiersum, 1958) and are likely to interact differently with nitrate and ammonium, due to their different mobilities in soils. For this reason, the innovative system of Campbell & Grime (1989), which uses a continuous nutrient feed system to undivided pots of sand was not used, as the sand has no CEC, and essentially acts like an hydroponics system with neutral substrate. It is an interesting question whether the birches in Ingestad (1971) would have

used similar ratios of ammonium to nitrate, if they had had to search a soil volume for the nitrogen, rather than having it delivered directly to the roots.

Given that nitrate and ammonium represent very different nitrogen sources for plants, with multiple consequences for plant growth and performance (Pate, 1980; Kirkby, 1981; Haynes, 1986; Marschner, 1986), patches of differing ammonium to nitrate ratio may represent very different nitrogen substrates to a plant. Can plants selectively exploit the form of nitrogen that gives the greatest growth?

The answer is likely to be dependent upon the experimental conditions imposed, since plant nitrate usage is known to vary with light environment, temperature, pH, ammonium and nitrate concentrations, and plant N status (Deane-Drummond, 1990; Marschner, 1986; Smart & Bloom, 1988). For example, rape plants' selectivity against nitrate is relaxed when plants are N deficient (Macduff & Wild, 1989). Because ammonium and nitrate uptake interact (Marschner, 1986), roots may respond differently to an even distribution of ammonium nitrate in soil than to two patches relatively high in ammonium and nitrate respectively, but with the same total N content. This raises the possibility that plants with roots in a patch of ammonium and a patch of nitrate may take up different proportions of the ions than plants with roots in a homogeneous ammonium nitrate patch containing the same total N, but distributed differently. Can plants integrate spatially heterogeneous patches of nitrate and ammonium to maximize growth?

Two previous studies have shown that black birch (*Betula lenta* L.) seedlings grew better with a nitrate supplement to forest soils supplying largely ammonium which suggests that black birch may prefer a mixture of ammonium and nitrate for optimal growth (Crabtree, 1992), unlike *B. verrucosa*, which shows less clear preference for an ammonium:nitrate mix (Ingestad, 1971). For black birch, it seems possible that seedlings might be capable of searching out a balanced mixture of ammonium and nitrate if offered the choice, thereby increasing seedling growth. This study used split pots and soil to investigate whether *B. lenta* (black birch) seedlings could maximize growth by foraging preferentially for a particular form of nitrogen, and whether supply rate of N and ratio of ammonium to nitrate in a patch affected preferences. Use of an ^{15}N label on nitrate supplied to the plants allowed determination of the source of seedling N in treatments where seedlings were offered a choice of ammonium and nitrate.

MATERIALS AND METHODS
Plant material and treatment

Black birch seed was collected in October 1988 from eight parent trees within an area of approximately 5 square miles at Harvard Forest, Petersham, Massa-chusetts, USA. The seed was pooled to generate a seed mix more representative of a population, and germinated in the glasshouse in late March 1990. Seedlings were transplanted in mid April, and grown until late May in individual five cm diameter peat pots containing a one part sterilized peat and one part perlite soil mix. In late May, seedlings were size graded by eye, and an even-sized group of plants approximately 3 cm tall, with 3–4 leaves, chosen for transplanting into divided pots. The peat pots were then removed by peeling and all soil washed from the root ball before seedlings were transplanted into 5 l volume divided pots, with the roots partitioned evenly down either side of the divider (seedlings did not show a strong tendency to a single tap root). The pots were then randomly assigned to one of three shadehouses (blocks) and to one of four nitrogen form treatments within shadehouse, in a randomized complete block design.

Treatments within shadehouse were: (*a*) nitrate (NO_3^-) both sides of the divider, (*b*) ammonium (NH_4^+) both sides, (*c*) NH_4NO_3, a 'homogeneous choice' and (*d*) NO_3^- one side/NH_4^+ on the other, a 'patchy choice', crossed with two rates of nitrogen supply. From 10 June to 3 July, the rates were 4·97 and 9·93 mg N pot^{-1} wk^{-1}, however the seedlings grew very slowly so from 10 July to 4 September, the rates were increased to 14·9 and 29·8 mg N pot^{-1} wk^{-1}. Each rate by form treatment had 24 replicates, 8 in each of 3 blocks. The final rates are similar to the rates of mineralization in poor and rich Harvard Forest soils. Ammonium treatments were applied as ammonium sulphate, nitrate treatments as potassium nitrate. Seedlings were watered daily to field capacity.

To provide balanced nutrition for the plants, a nitrogen-free Hoagland's solution (Hoagland & Arnon, 1938) was applied 4 d after each N treatment. Quarter-strength and half-strength nitrogen-free Hoagland's solution provided a slight excess of all other plant nutrients scaled to the N content of the 14·9 and 29·8 mg N pot^{-1} wk^{-1} treatments respectively, when each pot received 126 ml of solution. Nitrogen treatments and Hoagland's solutions were not combined, as it was feared that the salt content of the Hoagland's solution might compete with the ammonium for the soil cation exchange sites, making ammonium more mobile.

Plant environment

Shadehouses with 70% transmittance spectrally neutral shadecloth were used to produce a light environment similar to that of a natural large tree-fall gap (Sipe, personal communication) which is the environment in which black birch naturally regen-erates (Burns & Honkala, 1990). Clear plastic sheeting, transmitting 88% of incident light spec-trally unchanged (Griffin Greenhouse, 0·004 ml

Monsanto 601 colourless) was stretched over pitched shadehouse roofs to intercept rainfall, and to reduce heterogeneity in seedling watering regime. Homogeneity of light environments within and between shadehouses was tested by using Diazo paper light sensors (Friend, 1961; Sullivan & Mix, 1983) calibrated against PPFD measured by a Li-Cor sensor (D. Ackerley, personal communication). Starting 9/8/90, eight Diazo paper light sensors per shadehouse were set out evenly in a grid for a week.

To avoid mineralization of soil mix adding to soil nutrient content and producing hybrid treatments, plants were potted in a 1:1:1 mixture of turface, sand and perlite. Addition of turface, a 2:1 clay, is important because it provides the cation exchange capacity needed for the element of foraging involved in the treatments, that assume different mobility of the two forms of nitrogen. Nitrification inhibitors were not used to inhibit nitrification of ammonium, as they are not 100% effective, and are known to affect plant behaviour (D. Allen, personal communication).

Soil pH was measured for all treatments except the NH_4/NO_3 split pots on soil taken at final harvest of the plants (the two sides of the pot are equivalent to the homogeneous nitrate and ammonium treatments). Soil from top, middle and base of pot was well mixed prior to taking a 10 g wet sample for addition to 25 ml de-ionized water, swirling and testing pH.

Direct measurement of treatment effects on ammonium and nitrate pools within pots was not possible during the experiment due to space constraints. To examine the movement of ammonium and nitrate through the pots over the course of a typical week, a pot experiment simulating the nutrient and watering regimes used in 1990 was run for a month in a glasshouse, starting 13 January 1992, under temperature conditions similar to summer diurnal temperatures at Harvard Forest, day 29 °C, night 22 °C. Soil was mixed as before, using the same suppliers as in 1990, and ammonium nitrate, potassium nitrate, and ammonium sulphate treatments applied as before, at 14·9 and 29·8 mg N pot^{-1} wk^{-1}. The pots were randomly assigned to positions on a bench, and fertilized with N treatments on Mondays, followed by Hoagland's N-free solutions on Fridays. On the days when no nutrients were applied, pots were watered to field capacity. On 4 February a set of four replicate pots per treatment were sampled to assess ammonium and nitrate pools following the fourth fertilizer application and one pot watering. Four days later, a second set were sampled prior to the application of the Hoagland's solutions. A final sampling was made on a third set on 10 February for low rate of application only, to assess the state of the N pools immediately before what would have been the fifth fertilizer application. Sampling entailed coring the pot with a tube of 5 cm

internal diameter, then extruding the soil core using a plunger to obtain three 5 cm long cores, representing the bottom, middle and top thirds of the pot's soil. Within each of these segments, soil was mixed to remove any residual stratification, and 35 g wet soil sample set to extract in 100 ml 1·0 M KCl solution on a shaker for 1 h. Gravimetric soil water content was assessed on a separate sample for each third, so that nitrate and ammonium content of the soil could be expressed on a dry mass basis rather than a wet mass basis, since the soil water content increased down the pot. Nitrate and ammonium were assayed colorimetrically (Keeney & Nelson, 1982).

Plant N preferences and growth

Plant preference for a particular form of nitrogen was examined using a 245‰ ^{15}N enrichment of the nitrate nitrogen applied to NH_4NO_3 and NO_3/NH_4 pots. Dry foliar samples from the final harvest were ground to powder in liquid nitrogen, weighed and sealed with copper and cupric oxide reagents under high vacuum. Sealed samples were combusted at 875 °C for 3 h, which transformed all nitrogen to dinitrogen gas, trapped in the sealed tube. These samples were analyzed by mass spectrophotometer using the system described in McCarthy & Nevins (1986). Sampling precision was ±0·005 atom%, < 2‰, which represents approximately a 5% error. Sample enrichment was corrected for the background abundance of ^{15}N, taken as 0·3663 atom% ^{15}N.

To examine seedling growth responses to treatments, plants were harvested on 10 and 11 September 1990. Seedling height, number of leaves and branches and leaf area were scored at time of harvest. Stems were severed at the soil surface, and leaf and stem biomass separated and dried at 60 °C for 4 d before weighing. Root systems were washed out intact, dried and weighed separately for each side of the pot for all treatments. By harvesting the two halves of the pots separately for all treatments, the homogeneous pots provide a control against which the distribution of biomass between patches in the patchy treatment were compared, to examine whether there was significantly greater root biomass in a particular patch type.

Statistical analysis

Analysis of variance tests were performed for final harvest variables in Datadesk 3·0 (Odesta Corporation) using a randomized block model, with block as a random factor, and rate and form tested over the residual (error) variance. In all cases, type III sums of squares were used. Log transformation was used to normalize total biomass, and a square-root transformation was used for height. Root to shoot biomass ratio was normalized by an arcsine square-

Table 1. *Analysis of variance for total N in cores and N in top third of core*

Variable	Source	d.f.	Sum of squares	F ratio	P
Total N/core	Rate	1	2627·9	52·8	0·000
	Form	2	7454·7	74·9	0·000
	Rate × form	2	2819·7	28·4	0·000
	Harvest	2	266·2	2·68	0·080
	Rate × harvest	2	33·8	0·34	0·714
	Form × harvest	4	862·2	4·33	0·0049
	Error	43	2138·3		
	Total	56	24068·2		
N in top third of core	Rate	1	0·004744	0·643	0·427
	Form	2	0·5885	39·86	0·000
	Rate × form	2	0·0128	0·869	0·427
	Harvest	2	0·0092	0·623	0·541
	Rate × harvest	2	0·00249	0·168	0·845
	Form × harvest	4	0·0354	1·199	0·325
	Error	43	0·3174		
	Total	56	1·2558		

root transformation. The transformed parameters and residuals obtained from the models were normally distributed. Scheffé–Box tests indicated that the variances of residuals were homogeneous (Sokal & Rohlf, 1981). Pre-planned comparisons of seedling total biomass and height were carried out in the General linear models (GLM) procedure in Statistical Analysis System (Joyner, 1985).

Analysis of variance tests for total soil nitrogen within core and the proportion of total N present in the top third of the core were performed in Datadesk, using a three way model, with rate, form and harvest as fixed factors tested over the error variance.

RESULTS
Plant environment

Analysis of variance (Table 1) showed a highly significant effect of rate and form of N applied on the total amount of nitrogen found within a core. There were also significant interactions between rate and form and form and harvest, and a marginally significant effect of harvest. The proportion of total N found in the top third of the pot was only affected significantly by the form of N applied. The pattern of distribution of N, and degree of nitrification within cores is shown for different rate by form combinations in Figures 1 and 2. Soil water content by layer is shown in Figure 3. Soil pH at the end of the growing season was significantly higher in nitrate treated pots (Fig. 4), but differed by less than half a unit. Photon flux density showed no significant variation within or between blocks, all received a mean of 72 % of incoming PPFD at plant height within shadehouse.

N preferences

Analysis of variance for the proportion of seedling N that came from the labelled nitrate source in
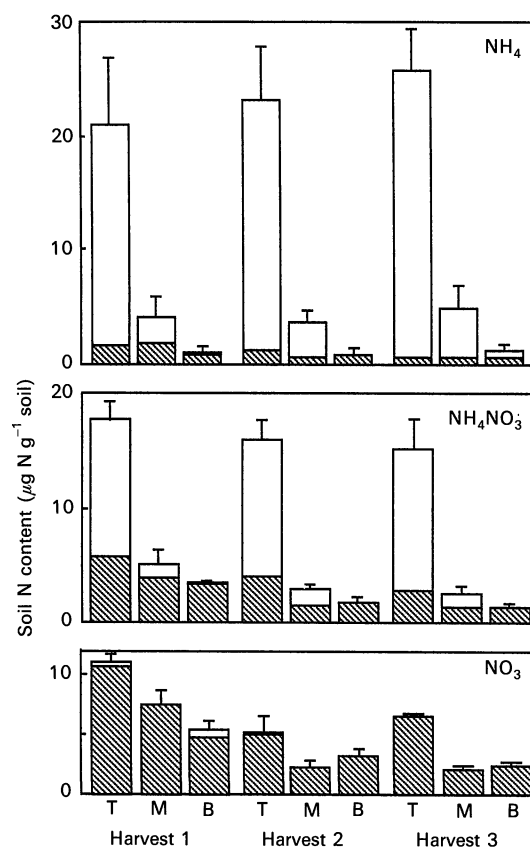

Figure 1. Distribution of ammonium (□) and nitrate (▨) within pot for low rate of application treatments. One standard error shown for total N per layer.

treatments where seedlings were offered a choice, showed no effect of rate, form or rate × form interaction. However, the weakness of the model, accounting for only 2 % of the variance (ANOVA not shown) reflects the very high variability within treatments where seedlings were offered nitrate one side of the divider, and ammonium the other, compared with a relatively narrow range of nitrate
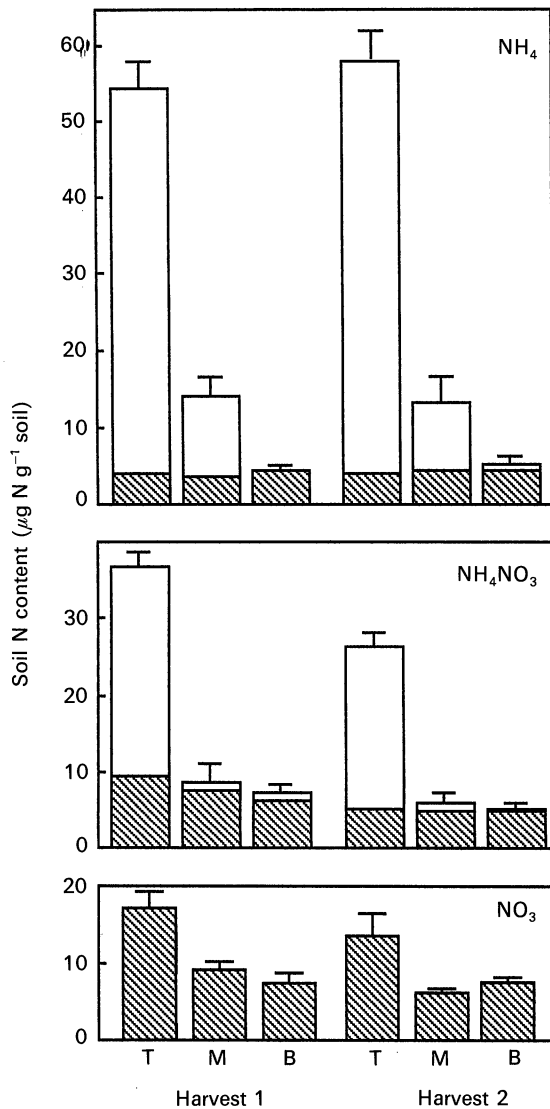
Figure 2. Distribution of ammonium (☐) and nitrate (⊠) within pot for high rate of application treatments. One standard error shown for total N per layer.
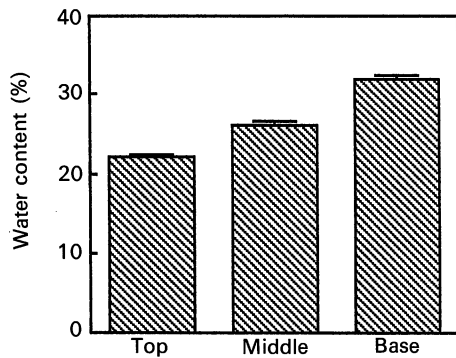

Figure 3. Mean soil water content by layer within pot, shown with one standard error.

Figure 4. Soil pH measured following plant harvest. Shown with one standard error, significant differences between treatments are shown by different letters.

Table 2. *Source of seedling N and pattern of root biomass distribution for seedlings offered a choice of ammonium and nitrate*

Treatment	Mean NO_3^- usage (%)	Root biomass allocation in pots
Low rate		
NH_4^+/NO_3^-	37.0 ± 2.5	0.55 ± 0.04
NH_4NO_3	35.8 ± 1.5	0.53 ± 0.04
High rate		
NH_4^+/NO_3^-	36.1 ± 3.4	0.52 ± 0.05
NH_4NO_3	33.0 ± 1.6	0.49 ± 0.04

For patchy treatments, root allocation is calculated as root biomass in nitrate patch divided by total root biomass for each plant. For homogeneous treatments, choice of side of divider for numerator was arbitrary. Values shown with one standard error. There were no significant differences between treatments.

Figure 5. Relationship between proportion of nitrate used and distribution of root biomass between patches for plants offered NO_3 and NH_4 patches. ($F = 42.1$, $P < 0.001$) $y = 7.403 + 53.66x$, $R^2 = 0.561$.

usage in the ammonium nitrate treatments (Table 2). For the patchy treatment seedlings, nitrate usage is significantly related to the proportion of root biomass allocated to the nitrate side of the pot ($P < 0.001$,
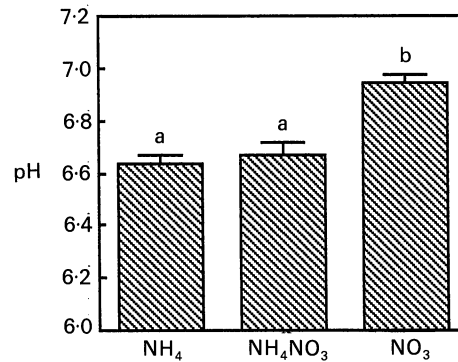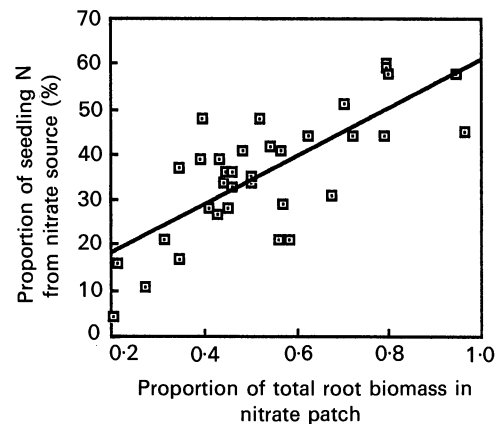
Fig. 5) whereas there is no significant relationship between proportional root allocation and nitrate usage in seedlings given ammonium nitrate through-
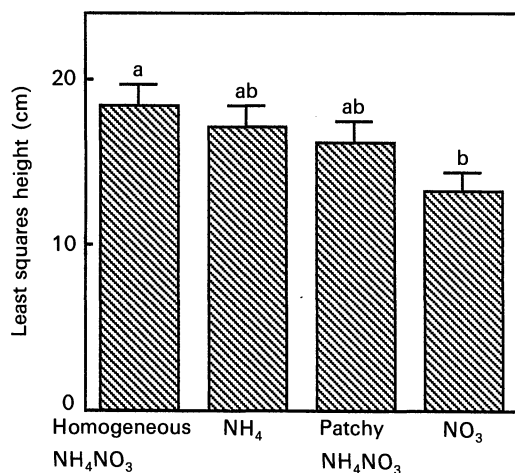
Figure 6. Least squares mean height by form of N treatment, adjusted for block, rate and rate by form effects and shown with one standard error. Letters show differences between treatments at $P < 0.05$ level.

Figure 7. Least squares mean total biomass by form of N treatment, adjusted for block, rate and rate by form effects and shown with one standard error. Letters show differences between treatments at $P < 0.05$ level.
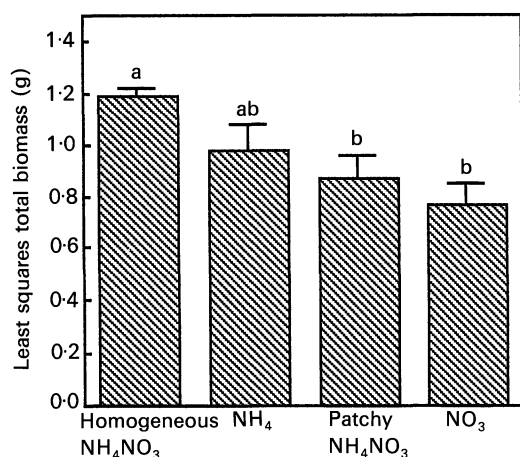
out the pot. However, at the level of treatment means there were no significant effects of treatment on pattern of root biomass allocation between halves of the pot in treatments where plants were offered a choice (Table 2).

Plant growth responses

Form of N treatment also significantly affected height and total biomass of seedlings, with nitrate fed seedlings significantly lighter than homogeneous ammonium and homogeneous choice treatments, and significantly shorter than the homogeneous choice treatment (Figs 6, 7). Seedling total biomass in the homogeneous choice treatment was significantly greater than in the patchy choice treatment. Seedlings' total leaf area followed the same pattern as for height. Seedlings were significantly

taller and had greater biomass in the high rate treatment than the low rate treatment. Root to shoot biomass allocation ratio was significantly lower in high rate than low rate of N application.

DISCUSSION

Soil N environment

Use of soil as the growing medium for the experiment led to the creation of strikingly different patch types within the pots, depending on the form of N added. To understand plant performance in this context, it is clearly important to understand how the N treatments interacted with the soil to generate the patch types the plants encountered.

As revealed by the pot experiment to simulate fertilizer effects within pots, it was not possible to set up patches of equal total N content and even distribution using nitrate and ammonium in different combinations, due to the different properties of the ions interacting with the soil medium. Although the duration of the simulation experiment was 2 wk shorter than the duration of application of modified rates during 1990, the findings from the pot study are probably representative of the types of patterns that would have been generated by fertilizer addition, since these are dependent on the cation exchange capacity of the soil. Within rate of application, the nitrogen treatments resulted in different total N quantities within the pots, since nitrate migrated through the pots but ammonium accumulated on the soil cation exchange sites.

The differential mobility of nitrate and ammonium ions also led to strikingly different patterns of N distribution within the pots. The ammonium treated pots had a concentrated patch of ammonium towards the top of the pot, that would probably have gradually extended downwards over the season, as more N was added and the CEC of the top third of the pot become saturated (compare the N content of the middle layer in low and high rates of application in the ammonium treatments; Figs 1, 2). The extent of this downward spread would likely be a function of rate of N addition. In contrast, nitrate treated pots have a more even distribution of N, producing a more diffuse patch that varied through time with the pulses of nitrate addition. The ammonium nitrate treatments were intermediate between ammonium and nitrate treatment patterns, with a patch high in ammonium at the top of the pot and a diffuse patch of nitrate throughout the pot. The pattern of transformation of added N differed for nitrate and ammonium. Little nitrate was re-mineralized to ammonium in the nitrate treatments (Figs 1, 2). The rate of nitrification of added ammonium varied with depth within the pot, with an almost complete conversion of the N that reached lower horizons, but lower rates in the middle and top of the pots. The resulting pattern was a patch of relatively pure

ammonium at the top of the pot, and a constant, much lower level of nitrate throughout the pot.

Plant growth responses and N preferences

Comparison of the performance of seedlings in pure ammonium and nitrate treatments with those in the patchy choice treatment showed that when offered a choice, seedlings selectively used a higher fraction of ammonium than nitrate, but were unable to significantly out-perform seedlings in pure treatments. In contrast, the seedlings offered the homogeneous choice significantly out-performed the pure nitrate and patchy choice treated plants, despite using the same proportion of nitrate as the patchy choice plants. The selectivity for ammonium was not affected significantly by rate of N application (Table 2), and neither was the relative performance in pure and choice treatments. In treatments where seedlings were offered a choice, approximately 35 % of seedling N came from a nitrate source.

Ammonium treatments generated a highly concentrated patch of ammonium in the top of the pot, whereas nitrate treatments generated a diffuse, lower concentration patch throughout the pot. Ammonium nitrate treatments produced an intermediate type of patch, with a concentrated ammonium patch at the top of the pot, and a diffuse, low concentration nitrate patch throughout the pot. The plant biomass trend (Fig. 7) probably reflects the N content of the top third of the pot, where seedlings started growing, and to a lesser extent the total N content of the pot. The nitrate-treated seedlings had the least N per pot, the least N in the top third of the pot, and were smallest. (The remaining nitrate was presumably leached out the pots during watering.) Ammonium-treated seedlings had access to the greatest quantity of N, and were larger. The seedlings offered a patch of ammonium and a patch of nitrate spread their roots relatively evenly between the two patch types (Table 2), encountered an intermediate quantity of N and produced intermediate biomass. Seedlings in the homogeneous ammonium nitrate treatment had a high N patch at the top of the pot like those in the ammonium treatment, but also had simultaneous access to nitrate throughout the pot. If black birch seedlings have a preferred range of ammonium:nitrate usage, then the homogeneous choice treatment allowed seedlings to forage in a relatively predictable ammonium patch for ammonium, and also encounter nitrate without additional investment. Seedlings in the patchy treatment grew additional roots in a relatively low N, pulsed nitrate environment to obtain a similar proportion of nitrate. Essentially, the homogeneous choice treatment offered 'congruent' resources, where both types of N used were supplied together, unlike the patchy treatment. A second form of resource congruity may also have contributed to the greater biomass of

seedlings in the homogeneous choice treatment, since they may also have benefitted from the nitrate lower in the pots while foraging for water which was more abundant lower in the pot (see Fig. 3).

Seedlings offered a patchy choice of ammonium and nitrate varied considerably in their distribution of biomass between patches, and used nitrate in proportion to the biomass in the nitrate patch (Fig. 5). However, per unit biomass, roots in the nitrate patch took up less N than roots in the ammonium patch. Root biomass at final harvest may not necessarily represent root biomass allocated to a patch throughout the season, and may be particularly misleading if root turnover rates differed markedly between patches, however very few dead roots were found during harvest. Still, allocation of biomass below ground is only one component of a plant's foraging ability, since the exploitation efficiency of a root system depends on how roots are deployed within the soil, and the uptake capacity of those roots (Robinson & Rorison, 1983; Fitter *et al.*, 1991). Root deployment within the soil is greatly affected by changes in specific root length (length of root per unit biomass) and by changes in topological patterns of branching and the angles at which branches depart from their parent root (Berntson & Woodward, 1992). In this experiment, plasticity of ammonium:nitrate uptake was achieved not by differential biomass allocation to different patches, but probably by changing root architecture, potentially augmented by increased uptake capacity.

Increased biomass allocation to exploit a local concentration of nutrients increases uptake of nutrients, but is only one of several alternatives to increase uptake capacity. Crick & Grime (1987) found that *Agrostis stolonifera*, a fast growing, competitive graminoid of productive habitats, responded to local enrichment by increased biomass allocation to the patch, leading to increased root proliferation, whereas *Scirpus sylvaticus*, a slower growing graminoid species of infertile habitats changed its uptake capacity without altering root growth. Robinson & Rorison (1983) found similar results from split-root studies contrasting two species of fertile habitats, *Holcus lanatus* and *Lolium perenne*, with *Deschampsia flexuosa* of infertile habitats. The range of plastic options open to a species is a function of evolutionary history, reflecting evolved strategies where growth rates and associated traits are tuned to resource availability in the environment (Grime, Crick & Rincon, 1986). Growth of additional, short-lived roots to exploit a nutrient patch may not yield equal return for the outlay for slow-growing plants of nutrient poor environments. Such species maintain a large root system continually, and make reversible physiological increases to increase uptake. For such slow-growing species, root biomass allocation and morphology may be tightly controlled genetically. Root development may also be con-

strained in faster growing species such as tomatoes (Jackson & Bloom, 1990), probably as a result of selection for root growth downwards to search for water in ancestral, dry environments.

Black birch probably falls between the two extremes discussed, as it inhabits nutrient poor forest soils, but is a relatively fast-growing member of the forest community. It is an interesting question why seedlings in the patchy treatment allocated such large quantities of biomass to the nitrate patch, when similar allocation of biomass to the ammonium patch may have greatly increased N uptake, assuming per unit biomass uptake rates were maintained. The distribution of root biomass between patches could be simply due to a trajectory already established, and the plastic options remaining being changes in architecture (display of a given quantity of root biomass) and uptake capacity. Alternatively, the roots on the ammonium side may be effectively subsidizing the growth of roots in the nitrate patch. Such a phenomenon was seen by Robinson & Rorison (1983), where the two species of fertile habitats, *Holcus lanatus* and *Lolium perenne*, continued root growth in a minus N compartment, subsidized by N taken up in a high N compartment. Several experiments show such continued root growth in low N compartments, where growth seemed more controlled by the plants' internal N status than the local N environment (Granato & Raper, 1989; Robinson & Rorison, 1983; Brouwer, 1981; Friend *et al.*, 1990). In this experiment, such a subsidy may reflect the seedlings need for the scarcer resource, nitrate, to maintain a preferred balance of ammonium:nitrate. Overall, however, caution is needed in the interpretation of these results in an ecological setting, since in nature birches are ectomycorrhizal. The mycorrhizal hyphae are likely to increase the efficiency of foraging for ammonium, but not for nitrate, since the hyphae extend short distances from the root, beyond the root depletion zone for ammonium, but not for the more mobile nitrate ion. The dedication of such quantities of root biomass in pursuit of nitrate would therefore remain an interesting finding.

In conclusion, seedlings offered a patchy choice of ammonium and nitrate selectively used a higher fraction of ammonium than nitrate, but were unable to significantly out-perform seedlings in homogeneous ammonium and nitrate treatments. Seedlings offered ammonium nitrate throughout the pot did significantly out-perform the pure nitrate and patchy choice treated plants, despite using the same proportion of ammonium:nitrate as the patchy choice plants. The selectivity for ammonium was not affected significantly by rate of N application, and neither was the relative performance in pure and choice treatments. Seedlings offered a choice of ammonium and nitrate typically obtained approx. 35% their N from the nitrate source, regardless of

how the choice was offered. That the patchy choice seedlings integrated the patches to achieve this ammonium:nitrate balance suggests that black birch has a preferred balance, despite growing well in ammonium based forest soils. The seedlings offered the choice homogeneously were significantly heavier than the seedlings offered the choice in two patches, perhaps reflecting an additional cost of foraging for ammonium and nitrate separately, or perhaps the benefit of 'congruent' resources. Greater biomass in the homogeneous choice treatment may have been the result of either or both of two types of resource congruency, either the joint supply of nitrate and ammonium at the top of the pots, or the nitrate and water lower in the pots.

REFERENCES

ABER, J. D., NADELHOFFER, K. J., STEUDLER, P. & MELILLO, J. M. (1989). Nitrogen saturation in northern forest ecosystems. *BioScience* **39**, 378–386.

BERNTSON, G. M. & WOODWARD, F. I. (1992). The root system architecture and development of *Senecio vulgaris* L. in elevated CO$_2$ and drought. *Functional Ecology* **6**, 324–333.

BOERNER, R. J. & KOSLOWSKY, S. D. (1989). Microsite variations in soil chemistry and nitrogen mineralization in a beech-maple forest. *Soil Biology and Biochemistry* **21**, 795–801.

BROUWER, R. (1981). Co-ordination of growth phenomena within a root system of intact maize plants. *Plant and Soil* **63**, 65–72.

BURNS, R. M. & HONKALA, B. H. (1990). *Silvics of North America, Volume 2, Hardwoods*. Forest Service, Washington D.C., USA.

CAMPBELL, B. D. & GRIME, J. P. (1989). A new method of exposing developing root systems to controlled patchiness in mineral nutrient supply. *Annals of Botany* **63**, 395–400.

CRABTREE, R. C. (1992). *Birch regeneration in a changing nitrogen environment*. Ph.D. Thesis, Harvard University, Cambridge, Massachusetts, USA.

CRICK, J. C. & GRIME, J. P. (1987). Morphological plasticity and mineral nutrient capture in two herbaceous species of contrasted ecology. *New Phytologist* **107**, 403–414.

DEANE-DRUMMOND, C. E. (1990). Biochemical and Biophysical Aspects of Nitrate Uptake and its Regulation. In: *Nitrogen in Higher Plants* (Ed. by Y. P. Abrol), pp. 1–37. Research Studies Press Ltd, Taunton, Somerset, England.

FITTER, A. H., STRICKLAND, T. R., HARVEY, M. L. & WILSON, G. W. (1991). Architectural analysis of plant root systems. I. Architectural correlates of exploitation efficiency. *New Phytologist* **118**, 375–382.

FRIEND, D. T. C. (1961). A simple method of measuring integrated light values in the field. *Ecology* **42**, 577–580.

FRIEND, A. L., EIDE, M. R. & HINCKLEY, T. M. (1990). Nitrogen stress alters proliferation in Douglas-fir seedlings. *Canadian Journal of Forest Research* **20**, 1524–1529.

GRANATO, T. C. & RAPER, C. D. (1989). Proliferation of maize (*Zea mays* L.) roots in response to localized supply of nitrate. *Journal of Experimental Botany* **40**, 263–275.

GRIME, J. P., CRICK, J. C. & RINCON, J. E. (1986). *The Ecological Significance of Plasticity in Plants*. Society for Experimental Biology, vol. XXXX.

HAYNES, R. J. (1986). *Mineral Nitrogen in the Plant–soil System*. Academic Press, New York.

HOAGLAND, D. R. & ARNON, D. I. (1938). *The water culture method of growing plants without soil*. University of California College Agricultural Experimental Station Circular 347. Berkeley, California, USA.

INGESTAD, T. (1971). A definition of the optimum nutrient requirements in birch seedlings II. *Physiologia Plantarum* **24**, 118–125.

JACKSON, L. E. & BLOOM, A. J. (1990). Root distribution in relation to soil nitrogen availability in field-grown tomatoes. *Plant and Soil* **128**, 115–126.

JACKSON, R. J. & CALDWELL, M. M. (1989). The timing and degree of root proliferation in fertile-soil microsites for three cold-desert perennials. *Oecologia* **81**, 149–153.

JOYNER, S. P. (Ed.) (1985). *SAS/STAT Guide for Personal Computers. Version 6 edition*. SAS Institute, Cary, North Carolina, USA.

KEENEY, D. R. & NELSON, D. W. (1982). Nitrogen-inorganic forms. In: *Methods of Soil Analysis, Part 2. Chemical and Microbiological Properties*. Madison, Wisconsin, ASA-SSSA.

KIRKBY, E. A. (1969). Ion uptake and ionic balance in plants in relation to the form of nitrogen nutrition. In *Ecological Aspects of Mineral Nutrition of Plants* (Ed. by I. H. Rorison), pp. 215–235. Blackwell Scientific Publications, Oxford.

LODHI, M. A. K. & REUSS, R. W. (1988). Variation in soil nitrifiers and leaf nitrate reductase activity of selected tree species in a forest community. *Soil Biology and Biochemistry* **20**, 939–943.

MACDUFF, J. H. & WILD, A. (1989). Interactions between root temperature and nitrogen deficiency influence preferential uptake of NH_4^+ and NO_3^- in oilseed rape. *Journal of Experimental Botany* **40**, 195–206.

MARSCHNER, H. (1986). *Mineral Nutrition of Higher Plants*. Academic Press, Harcourt Brace Jovanovich, London.

MCCARTHY, J. J. & NEVINS, J. L. (1986). Sources of nitrogen for primary production in warm-core rings 79–E and 81-D. *Limnology and Oceanography* **31**, 690–700.

NADELHOFFER, K. J., ABER, J. D. & MELILLO, J. M. (1983). Leaf litter production and soil organic matter dynamics along a N availability gradient in southern Wisconsin (USA). *Canadian Journal of Forest Research* **13**, 12–21.

NYE, P. H. & TINKER, P. B. (1977). *Solute Movement in the Soil–root System*. Blackwell Scientific Publications, Oxford.

PASSIOURA, J. B. & WETSELAAR, R. (1972). Consequences of banding nitrogen fertilizers in the soil. II. Effects on the growth of wheat roots. *Plant and Soil* **36**, 461–473.

PATE, J. S. (1980). Transport and partitioning of nitrogenous solutes. *Annual Review of Plant Physiology* **31**, 313–340.

PHILIPSON, J. J. & COUTTS, M. P. (1977). The influence of mineral nutrition on the root development of trees. *Journal of Experimental Botany* **28**, 864–871.

PLYMALE, A. E., BOERNER, R. E. J. & LOGAN, T. A. (1987). Relative N mineralization and nitrification in soils of two contrasting hardwood forests: effects of site microclimate and initial soil chemistry. *Forest Ecology and Management* **21**, 21–36.

ROBERTSON, G. P. (1982). Nitrification in forested ecosystems. *Bulletin of the Transactions of the Royal Society, London* **296**, 445–457.

ROBINSON, D. & RORISON, I. H. (1983). Relationships between root morphology and nitrogen availability in a recent theoretical model describing nitrogen uptake from soil. *Plant, Cell and Environment* **6**, 641–647.

SMART, D. S. & BLOOM, A. J. (1988). Kinetics of ammonium and nitrate uptake among wild and cultivated tomatoes. *Oecologia* **76**, 336–340.

SOKAL, R. & ROHLF, F. J. (1981). *Biometry*. W. H. Freeman, New York, New York, USA.

ST. JOHN, T. V., COLEMAN, D. C. & REID, C. P. P. (1983). Growth and spatial distribution of nutrient-absorbing organs: selective exploitation of soil heterogeneity. *Plant and Soil* **71**, 487–493.

SULLIVAN, T. J. & MIX, M. C. (1983). A simple and inexpensive method for measuring integrated light energy. *Environmental Science and Technology* **17**, 127–128.

WIERSUM, L. K. (1958). Density of root branching as affected by substrate and separate ions. *Acta Botanica Neerlandica* **7**, 174–190.

ZINKE, P. J. (1962). The pattern of influence of individual forest trees on soil properties. *Ecology* **43**, 130–133.