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## SEEDLING RESPONSE OF FOUR BIRCH SPECIES TO SIMULATED NITROGEN DEPOSITION: AMMONIUM VS. NITRATE<sup>1</sup>

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**Abstract.** Chronic nitrogen deposition has the potential to alter seedling shade tolerance and growth in the temperate forests of northeastern United States, by affecting both the form and the quantity of available nitrogen. Simulated deposition treatments were applied to seedlings of four birch species that co-occur at Harvard Forest (*Betula lenta*, *B. alleghaniensis*, *B. populifolia*, and *B. papyrifera*). Seedlings were individually potted in forest soil, and grown under light treatments representative of forest understory and treefall gap light levels. In a split-plot design, N was applied at 25 and 50 kg·ha<sup>-1</sup>·yr<sup>-1</sup>, as either nitrate, ammonium nitrate, or ammonium, within each light environment. While *B. populifolia* and *B. papyrifera*, and *B. lenta* all showed increased biomass allocation to leaves with increased N, only *B. lenta* showed a significant growth response to the type of N added, and this response was conditional on rate of N application and light environment. At low light, nitrate-fed *B. lenta* grew best, and also at low rate of supply, nitrate treatments out-performed ammonium treatments. Greater growth under these conditions is probably the result of higher biomass allocation to leaves, and greater specific leaf area, which increased the leaf area ratio, and improved the capacity for carbon gain. Under N deposition regimes that increase soil nitrate availability, the differences in response of *B. lenta* and *B. alleghaniensis* to nitrate at low light may potentially lead to changes in the species composition of the seedling communities in the understory. When a treefall occurs, a different species mix of seedlings will be released, with potential consequences for sapling and tree species mix.

**Key words:** ammonium; birch; nitrate; shade tolerance.

### INTRODUCTION

The temperate forest ecosystems of northeastern USA are typically nitrogen limited (Aber et al. 1989, 1991). However, many of these forests are currently receiving N from the atmosphere as wet and dry deposition. Chronically high rates of N deposition may affect both stand species composition and productivity since each is known to vary with soil nitrogen availability (Spurr and Barnes 1964, Safford and Czapowskyj 1986, Aber et al. 1989). In highly polluted areas, N wet deposition rates alone may be as high as 25 kg·ha<sup>-1</sup>·yr<sup>-1</sup> (Smith 1990, Tomlinson 1990) and when dry deposition rates are added, the total rate is probably doubled (Lovett and Lindberg 1990). A severe N deposition rate of 50 kg·ha<sup>-1</sup>·yr<sup>-1</sup> would represent a substantial addition to a system such as Harvard Forest, which has a net N mineralization rate of 80–100 kg·ha<sup>-1</sup>·yr<sup>-1</sup> in a mixed hardwood stand (Melillo 1981).

The form of N in the deposition may differentially affect plants, since nitrate and ammonium are different nutritional substrates (Haynes 1986, Kirkby 1969).

Overall, N deposition is largely nitrate, as wet deposition is typically at least half nitrate, and dry deposition is predominantly nitric acid (Lovett and Lindberg 1990). In N-limited forests such as Harvard Forest, the soils typically have low rates of net nitrification (Melillo 1981), hence plants encounter little nitrate. It is therefore possible that nitrate-rich nitrogen deposition may be altering the relative availability of nitrate and ammonium to plants in the short term. In the long term, if chronic N deposition causes N saturation in these ecosystems, the soils will supply greater amounts of nitrate to plants, as substrate limitation of nitrification will be removed as predicted by Aber et al. (1989), and found by McNulty et al. (1991). Whether plant growth will increase under these circumstances may also depend on the extent to which accompanying soil acidification affects root function.

Tree seedling growth responses to changes in nutrition may also interact with the light environment (Bazzaz et al. 1990, Tamm 1991) leading to changes in seedling shade tolerance. Plants in low light "N saturate" at lower N supply rates than plants in high light (Ingstad and McDonald 1989). The effects of chronic N deposition may therefore be different in low light understory and high light gap environments. The form of N available may also interact with the light environment, independent of the quantity of N available.

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At high light levels, nitrate and ammonium assimilation may have similar costs to growth, but under shaded conditions, nitrate reduction may compete with carbon fixation for energy and reducing power, giving nitrate use a higher cost to growth than ammonium (Gutschick 1981, Smirnov and Stewart 1985). Hence growth of seedlings may respond differently to different ammonium : nitrate ratios in low light environments, but show no differences at high light. Both quantity and form of N available may therefore interact with the light environment and change seedling shade tolerance, in terms of growth and survivorship in the shade (Darrall and Wareing 1981, Horsley 1988, Tamm 1991), potentially projecting forward into stands of different composition.

To investigate the potential impact of N deposition of different quantities and nitrate : ammonium compositions on forest regeneration at Harvard Forest, we chose four co-occurring birches, i.e., black, yellow, gray, and white birch (*Betula lenta* L., *B. alleghaniensis* Britton, *B. populifolia* Marsh., and *B. papyrifera* Marsh.). Birch species were chosen because their seedlings have a range of shade tolerances useful for the examination of shade tolerance interaction with N deposition. They are also relatively fast growing, making short-term experimental manipulations feasible. Gray and white birch are both relatively shade intolerant, regenerating primarily in cleared areas. In contrast, black and yellow birch are more shade tolerant, forming short-lived seedling banks in the understory as well as regenerating in treefall gaps directly from seed (Fowells 1965, Spurr and Barnes 1964). Seedlings were individually potted in forest soil and grown in shadehouses simulating understory and gap light environments, to examine effects of simulated deposition on seedling performance. Although N deposition to leaves may also affect plant performance, we chose to focus on the effect of deposition to soil, as this is likely to be the major pathway for uptake.

#### METHODS

Seed of black, yellow, gray, and white birch were collected in October 1988 from a minimum of eight parent trees per species at Harvard Forest, Petersham, Massachusetts, USA. Within each species, seeds were pooled, to generate a seed mix more representative of a population. Seed mixes were germinated in a glasshouse in March 1989, and seedlings transplanted individually to pots outside in late May 1989. White birch transplanted poorly, and was replanted 2 wk later from the same seedling pool. Each 15 cm diameter pot contained 1 L of sieved forest soil collected from the organic soil layer under a stand containing *Quercus rubra*, *Acer rubrum*, *Acer saccharum*, *Betula lenta*, and *B. papyrifolia* at Harvard Forest. Soil was extracted from a single area, and sieved through a 1-cm mesh to remove large roots and homogenize the mix.

In a clearing at Harvard Forest, three blocks of paired shadehouses were constructed. Within each block, ran-

domly assigned shade treatments were created using neutral density shade cloth transmitting 8 and 70% of incident radiation, to simulate total daily irradiance in understory and large treefall gap, respectively (Sipe 1990). Since it was anticipated that the species would grow at different rates, the species were laid out in subplots within shadehouse to avoid interspecific competition for light. Species were assigned the same subplot position in all shadehouses. Within each subplot, seedlings of similar height were set out in a diffuse evenly spaced pattern to minimize intraspecific shading. Three N form treatments were applied as either ammonium sulfate, ammonium nitrate, or potassium nitrate, at one of two rates of nitrogen addition, 25 kg·ha<sup>-1</sup>·yr<sup>-1</sup> and 50 kg·ha<sup>-1</sup>·yr<sup>-1</sup>. Treatments were applied weekly in 50-mL aliquots, scaling application rate to the projected area of the pot, and assuming that a year's deposition is utilized over a 6-mo period. Pots received N at 1.89 mg/wk and 3.78 mg/wk in the 25 and 50 kg·ha<sup>-1</sup>·yr<sup>-1</sup> treatments, respectively. Each pot was contained within a shallow tub to catch flow-through and retain nutrients. Plants were watered to field capacity daily. For each species, each light × form × rate treatment had 18 replicates, 6 in each block. To minimize the effect of environmental variation within subplot, N treatments were laid out such that there was one replicate per row in each of six rows of six pots.

Plants were harvested in the 1st wk of September, and height, basal diameter, and total leaf area scored directly. Leaves and stems were severed, and the entire root system washed out carefully for each plant. Leaf, stem, and root material were dried at 60°C for a week, before dry biomass was measured to assess performance in the different treatments. To examine allocational patterns, leaf mass ratio (LWR) was calculated as leaf biomass/total plant biomass, and similarly stem mass ratio (SWR) as stem biomass/total plant biomass. Leaf area ratio (LAR) was calculated as total leaf area/total plant biomass, and specific leaf area (SLA) as total leaf area/leaf biomass.

#### Statistical analysis

Since the layout of species in the subplots was identical in each shadehouse, each species was analyzed separately, as the requirement of subplot randomization for an analysis of variance using all species could not be met. Analysis of variance tests were performed in Datadesk 3.0 (Odesta Corporation, Northbrook, Illinois, USA) using a split-plot model, with light as the main plot factor, tested over the light × block interaction term, and nitrogen rate and form effects as subplot terms 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, basal diameter, and total leaf area. Root-to-shoot biomass ratio was normalized by an arcsine transformation. The transformed parameters and residuals ob-

TABLE 1. Mean square values from ANOVA of black birch (*Betula lenta*) seedling response to simulated N deposition in three different forms at two application rates, when grown at two different light levels.

Response character‡	Source of variation									
	Light level	Block	Rate	B × L	Form	L × F	L × R	R × F	L × R × F	Error
df	1	2	1	2	2	2	1	2	2	173
Total plant biomass	12.9*	0.007	0.014	0.156	0.011	0.512**	0.053	0.205†	0.038	0.087
Height	85.06	0.022	0.012	13.79	4.05	55.15**	8.003	42.76*	2.62	9.63
Basal diameter	2.72*	0.096	0.004	0.161	0.023	0.135*	0.012	0.108†	0.041	0.041
Root : shoot	0.32*	0.016	0.11*	0.009	0.049*	0.017	0.0003	0.003	0.021	0.016
Total leaf area	220 188*	6689	11 820	8603	3976	34 882*	0.14	26 115*	1824	7726
LWR	0.00195	0.012†	0.032†	0.0065	0.028**	0.0148*	0.008	0.0056	0.0049	0.004
SWR	0.0558*	0.0035	0.0035	0.0014	0.0074*	0.0058*	0.006†	0.003	0.0008	0.0018
SLA	2115**	10.46**	0.029	3.93†	9.64**	7.26**	4.54†	16.99***	5.05*	1.454
LAR	691 698**	8018**	9355*	4951*	18 996***	14 321**	10 373**	7503**	5464**	1481

\*\*\*  $P < .001$ , \*\* $P < 0.01$ , \* $P < .05$ , † $P < .10$ .

‡ LWR = leaf mass ratio (leaf biomass/total plant biomass); SWR = stem mass ratio (stem biomass/total plant biomass); LAR = leaf area ratio (total leaf area/total plant biomass); SLA = specific leaf area (total leaf area/leaf biomass).

tained from the models were all judged to be normally distributed. Scheffé-Box tests indicated that the variances of residuals were homogenous (Sokal and Rohlf 1981).

The analysis suggested several a posteriori hypotheses. To examine the effect of adding nitrate vs. ammonium at different light levels (light × form interaction) on LAR in black birch, and the effect of N form on SLA in white birch, linear contrasts with one degree of freedom were performed using the General Linear Models (GLM) procedure in SAS (Joyner 1985). A posteriori multiple comparisons of least squares means were also carried out in GLM, and significance values corrected by the number of comparisons made. Marginally significant results, where  $P < .10$ , are reported here, where the biology is suggestive.

RESULTS

As analysis was done species by species, results will be presented by species, except for the finding that all species had significantly greater biomass at high light.

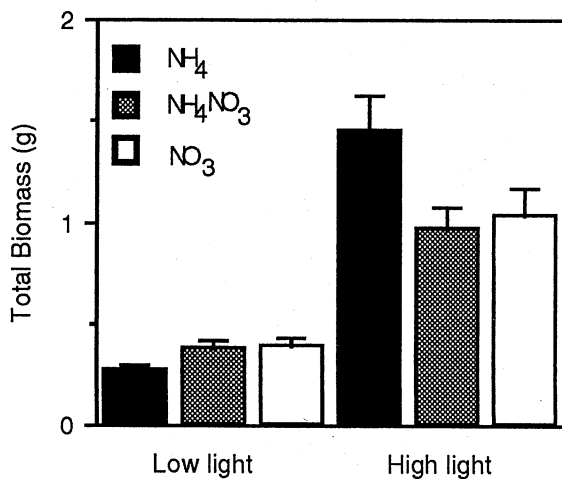


FIG. 1. Black birch (*Betula lenta*) total biomass response to form of N addition at two light levels, means adjusted for effect of block and rate. Data show means and 1 se.

N form effects on black birch growth were conditional on light and on rate of N application for total biomass, height, and basal diameter. ANOVA results for black birch are summarized in Table 1. Total biomass (Fig. 1) and height both showed a significant light × form interaction. Although none of the means differ significantly within light level, there was a trend showing that at low light the nitrate-fed plants had greater biomass, and vice versa at high light. At low light, both ammonium nitrate and nitrate-treated plants were significantly taller than ammonium-fed plants ( $P < .05$ ). Form also interacted with rate of N application, significantly affecting height (Fig. 2), and marginally affecting total biomass ( $.05 < P < .10$ ). Plants fed nitrate at the low rate grew significantly taller than ammonium-treated plants ( $P < .05$ ), with taller plants having greater biomass.

Biomass allocation patterns in black birch responded directly to both rate (Table 2) and form of N application, with ammonium-fed plants allocating signifi-

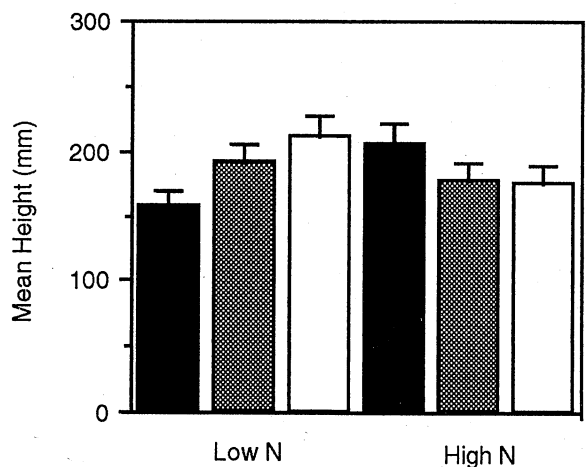


FIG. 2. Black birch height response to form of N addition at two rates of N addition, means adjusted for effect of block and light. Data show means and 1 se. Shading as shown in Fig. 1.

TABLE 2. All species responses to rate of simulated N deposition shown by least squares means, adjusted for block, light, and N form effects, and shown  $\pm 1$  SE. Significant differences within species and character at  $P < .05$  shown by different superscript letters.

Species	Rate	Response character				
		Total biomass (g)	Height (mm)	Root : shoot	LWR	LAR
Black	Low	0.606 $\pm$ 0.043 <sup>a</sup>	185.3 $\pm$ 8.8 <sup>a</sup>	0.398 $\pm$ 0.013 <sup>a</sup>	0.429 $\pm$ 0.009 <sup>a</sup>	165 $\pm$ 4 <sup>a</sup>
	High	0.631 $\pm$ 0.044 <sup>a</sup>	185.8 $\pm$ 8.6 <sup>a</sup>	0.351 $\pm$ 0.013 <sup>b</sup>	0.455 $\pm$ 0.007 <sup>b</sup>	179 $\pm$ 4 <sup>b</sup>
Gray	Low	1.101 $\pm$ 0.063 <sup>a</sup>	240.8 $\pm$ 7.2 <sup>a</sup>	0.376 $\pm$ 0.013 <sup>a</sup>	0.431 $\pm$ 0.009 <sup>a</sup>	180 $\pm$ 5 <sup>a</sup>
	High	0.993 $\pm$ 0.057 <sup>a</sup>	239.5 $\pm$ 7.2 <sup>a</sup>	0.358 $\pm$ 0.014 <sup>a</sup>	0.45 $\pm$ 0.01 <sup>b</sup>	192 $\pm$ 5 <sup>a</sup>
White	Low	0.520 $\pm$ 0.040 <sup>a</sup>	108.6 $\pm$ 5.5 <sup>a</sup>	0.360 $\pm$ 0.011 <sup>a</sup>	0.445 $\pm$ 0.007 <sup>a</sup>	129 $\pm$ 5 <sup>a</sup>
	High	0.531 $\pm$ 0.039 <sup>a</sup>	115.6 $\pm$ 5.3 <sup>a</sup>	0.331 $\pm$ 0.011 <sup>a</sup>	0.476 $\pm$ 0.007 <sup>b</sup>	139 $\pm$ 4 <sup>a</sup>
Yellow	Low	0.485 $\pm$ 0.046 <sup>a</sup>	107.6 $\pm$ 7.8 <sup>a</sup>	0.406 $\pm$ 0.017 <sup>a</sup>	0.432 $\pm$ 0.011 <sup>a</sup>	136 $\pm$ 6 <sup>a</sup>
	High	0.464 $\pm$ 0.041 <sup>a</sup>	101.9 $\pm$ 6.9 <sup>a</sup>	0.383 $\pm$ 0.015 <sup>a</sup>	0.450 $\pm$ 0.010 <sup>a</sup>	138 $\pm$ 6 <sup>a</sup>

cantly more biomass to roots ( $P < .05$ ) than ammonium nitrate plants and marginally more than nitrate-fed plants. Leaf biomass allocation patterns showed strong light  $\times$  form interactions (Table 3). Under low light conditions, plants receiving any nitrate allocated significantly more biomass to leaves than ammonium-fed plants. Similarly, at low rate of N application, across both light levels, ammonium-fed plants allocated significantly less biomass to leaves than plants treated with nitrate (Table 4). Within-leaf allocation of biomass, shown by SLA, was very plastic, responding to light, form, light  $\times$  form, and rate  $\times$  form. Plants receiving any nitrate had greater SLA under both low light and low N conditions, which in combination with greater allocation to leaves gave these plants significantly higher LAR (Tables 3 and 4). The effect of form on LAR was due to the difference between plants that received any nitrate at all vs. seedlings fed ammonium only, as shown by linear contrast of plants receiving any nitrate vs. no nitrate (1 degree of freedom,  $F = 10.1$ ,  $P = .0018$ , explains 99% of variance).

White birch grew poorly in the soil from the organic horizon used in this experiment. Mortality reduced the total number of white birch to 182 out of 216. The surviving plants were highly variable in size, so only strong effects were detectable. Nitrogen treatments had no significant effect on seedling growth in terms of total biomass, height, or basal diameter. As in black birch, white birch increased biomass allocation to leaves and decreased allocation to roots with increased N (Table 2). Form of addition had a marginally significant effect on SLA ( $F = 2.68$ ,  $P = .07$ ). A linear contrast between

plants receiving ammonium vs. any nitrate revealed that plants receiving any nitrate had greater SLA (99% of variance explained).

Gray birch also allocated significantly more biomass to leaves at higher N supply (Table 2). Height showed a significant rate  $\times$  form interaction ( $F = 4.98$ ,  $P = .01$ ), with the ammonium nitrate fed plants marginally taller than nitrate-fed plants at low rate, and the reverse at high rate.

Yellow birch showed no significant response to any of the N treatments (Table 2) except a significantly higher allocation to roots in ammonium nitrate treatments. No significant changes in total biomass, basal diameter, or height accompanied this shift in allocation.

## DISCUSSION

For Harvard Forest soils, the simulated deposition rates used in this experiment represent a massive increase in atmospheric N inputs, from 10 kg  $\cdot$  ha<sup>-1</sup>  $\cdot$  yr<sup>-1</sup>, the current level of deposition (W. Munger, unpublished data) to 25–50 kg  $\cdot$  ha<sup>-1</sup>  $\cdot$  yr<sup>-1</sup>, representing moderate to severe deposition rates in polluted North American forests. Compared with conventional fertilizer rates, which fall in the range of 100 to 400 kg  $\cdot$  ha<sup>-1</sup>  $\cdot$  yr<sup>-1</sup> N (e.g., Safford and Czapowskyj 1986), these input rates are relatively small, but clearly affected seedling behavior. Although total biomass, basal diameter, and height did not respond to increased N, for three out of four species grown in the soil from Harvard Forest, biomass allocation to leaves increased

TABLE 3. Biomass allocation in black birch in response to simulated N deposition. Figures are means adjusted for rate and block, and shown  $\pm 1$  SE. Comparisons made within light level, significant differences at  $P < .05$  shown by different superscript letters.

Light level	N form	LWR (g/g)	SLA (cm <sup>2</sup> /g)	LAR (cm <sup>2</sup> /g)
8% full daylight	NH <sub>4</sub> <sup>+</sup>	0.405 $\pm$ 0.011 <sup>a</sup>	484 $\pm$ 8.56 <sup>a</sup>	199 $\pm$ 6.8 <sup>a</sup>
	NH <sub>4</sub> NO <sub>3</sub>	0.464 $\pm$ 0.12 <sup>b</sup>	514 $\pm$ 8.96 <sup>b</sup>	240 $\pm$ 7.0 <sup>b</sup>
	NO <sub>3</sub> <sup>-</sup>	0.469 $\pm$ 0.012 <sup>b</sup>	545 $\pm$ 9.13 <sup>c</sup>	262 $\pm$ 7.2 <sup>b</sup>
70% full daylight	NH <sub>4</sub> <sup>+</sup>	0.433 $\pm$ 0.011 <sup>a</sup>	256 $\pm$ 8.55 <sup>a</sup>	111 $\pm$ 6.8 <sup>a</sup>
	NH <sub>4</sub> NO <sub>3</sub>	0.434 $\pm$ 0.011 <sup>a</sup>	240 $\pm$ 8.85 <sup>a</sup>	105 $\pm$ 7.1 <sup>a</sup>
	NO <sub>3</sub> <sup>-</sup>	0.451 $\pm$ 0.011 <sup>a</sup>	261 $\pm$ 8.74 <sup>a</sup>	118 $\pm$ 6.9 <sup>a</sup>

TABLE 4. Black birch biomass allocation responses to different forms of N at different rates of application. Comparisons made within rate, significant differences at  $P < .05$  shown by different letters.

N level	N form	LWR (g/g)	SLA (cm <sup>2</sup> /g)	LAR (cm <sup>2</sup> /g)
25 kg·ha <sup>-1</sup> ·yr <sup>-1</sup>	NH <sub>4</sub> <sup>+</sup>	0.398 ± 0.011 <sup>a</sup>	345 ± 8.55 <sup>a</sup>	135 ± 6.8 <sup>a</sup>
	NH <sub>4</sub> NO <sub>3</sub>	0.434 ± 0.012 <sup>ab</sup>	387 ± 9.15 <sup>b</sup>	172 ± 7.2 <sup>b</sup>
	NO <sub>3</sub> <sup>-</sup>	0.457 ± 0.012 <sup>b</sup>	412 ± 8.99 <sup>b</sup>	189 ± 7.1 <sup>b</sup>
50 kg·ha <sup>-1</sup> ·yr <sup>-1</sup>	NH <sub>4</sub> <sup>+</sup>	0.441 ± 0.011 <sup>a</sup>	395 ± 8.55 <sup>a</sup>	175 ± 6.8 <sup>a</sup>
	NH <sub>4</sub> NO <sub>3</sub>	0.464 ± 0.012 <sup>a</sup>	366 ± 8.7 <sup>b</sup>	172 ± 6.9 <sup>a</sup>
	NO <sub>3</sub> <sup>-</sup>	0.463 ± 0.011 <sup>a</sup>	394 ± 8.86 <sup>b</sup>	191 ± 6.9 <sup>a</sup>

in response to a 25 kg·ha<sup>-1</sup>·yr<sup>-1</sup> N increase (Table 2). This suggests that none of the seedlings were initially N limited, but that N limitation had started by the end of the experiment. Integrated over a longer time period than the duration of this experiment, such differences may lead to greater growth. Data from the 1st yr of a parallel field experiment in a forest clearing at Harvard Forest show a very similar pattern of species responses (Crabtree 1992). Gray, white, and black birch all showed significantly greater growth in a 50 kg·ha<sup>-1</sup>·yr<sup>-1</sup> nitrate treatment compared with a 0-addition control. Only gray birch showed a significant growth response to a 50 kg·ha<sup>-1</sup>·yr<sup>-1</sup> ammonium addition, and yellow birch responded to neither N treatment. This reinforces the conclusion that gray and yellow birch are relatively insensitive to N form, while black birch responds to nitrate addition.

The expectation that seedlings would grow less when given nitrate at low light due to the higher assimilatory cost of nitrate (Smirnov and Stewart 1985) was not met, in comparison with Margolis and Vézina (1988) who found that yellow birch grew significantly less when given nitrate at low light. However, in this experiment no seedling is likely to have experienced a pure nitrate supply, since the pots contained forest soil, which was actively supplying N by mineralization. Since the pH of Harvard Forest soil is typically <4, which is likely to inhibit nitrification (although see Novick et al. 1984), the treatments probably gave rise to a range of ammonium and nitrate availabilities in the soil that were still heavily skewed towards ammonium. The total range created by the simulated deposition may well have been close to the 70:30 to 50:50 ammonium: nitrate range that Horsley (1988) found optimal for yellow birch seedling growth. This may explain the lack of response to N form by yellow birch. Ingestad (1971) found that *B. verrucosa* (a relative of white and gray birch) was largely unresponsive to alterations in ammonium: nitrate ratio; this is consistent with the lack of growth response from white and gray birches.

In direct contrast, black birch seedlings grew better when given nitrate at low light, which fits with the observation of Peace and Grubb (1982), that forest understory herbs grew better on nitrate-rich soils (holding total N availability constant). Greater growth on nitrate may reflect the relative ease with which roots obtain the more mobile nitrate ion compared with am-

monium, which is less mobile in soils (Nye and Tinker 1977). Gutshick (1981) discusses the higher assimilation cost of nitrate over ammonium, but predicts that there may be "a large cost incurred from the increased root growth required to access the less mobile ammonium ion." Certainly, black birches given nitrate at low light allocated less biomass to roots, had a higher LWR, higher SLA, and therefore higher LAR, which may have led to greater light capture, potentially leading to greater growth under light-limited conditions. Similarly, at low rate of application, nitrate-fed seedlings also had significantly higher LAR, potentially leading to the greater growth observed. Differences in LAR between N form treatments disappeared as N supply rates increased, and all plants had decreased allocation to roots and increased LWR. Such changes in root: shoot ratio and LAR as N supply increases are well documented for birch (Ingestad and Lund 1979, McDonald et al. 1986). Differences in LAR between different N forms are also noted in Margolis and Vézina (1988) for yellow birch, although only at high light, where ammonium-fed plants have significantly lower LAR than plants receiving any nitrate. These plants also showed greater biomass allocation to roots when fed ammonium. Similar decreases in leafiness for ammonium-fed *Betula pendula* (another relative of white and gray birch) are suggested in Darrall and Wareing (1981), perhaps reflecting ammonium toxicity effects.

The effect of changed biomass allocation to leaves is complemented by changes in the biomass distribution within leaves, further increasing LAR. Both black and white birch show increased SLA when fed any nitrate, and the effect is more marked at low light. Changes in leaf area: mass (SLA) may be directly affected by nitrate nutrition, as nitrate may be used as osmoticum, particularly at low light (Steingröver et al. 1986), thereby allowing higher leaf elongation rates and resulting in greater SLA.

While the design of the experiment makes species comparisons a matter of inference, it is tempting to ask why the species respond differently to the different forms of nitrogen. That gray and white birches use nitrate and ammonium equally well may reflect availability of the two forms of N in the disturbed areas where these plants regenerate. Perhaps competition for nutrients is a greater issue than assimilatory costs, especially in the high light environment of these early

successional trees (Smirnov and Stewart 1985). However, the difference between black and yellow birches under low light conditions is harder to explain. Black birch seedlings are highly branched with many small leaves relative to yellow birch seedlings, which have a single stem, with fewer, larger leaves. Perhaps the many smaller leaves allow for more flexible patterns of canopy display, resulting in greater plasticity for black birch in the use of nitrate. Alternatively, black birch may also be able to respond to nitrate by initiating a greater number of leaves, as well as by increasing the SLA of emerging leaves.

In conclusion, even the addition of relatively small amounts of nitrogen may modify seedling biomass allocation patterns and potentially alter overall growth of seedlings in Harvard Forest soil. No interaction between light and N environment was found, perhaps because the seedlings were not N limited for part of the experimental duration. Form of N deposition did not affect growth in three out of four species, and for black birch, the effect of form was conditional on light environment and rate of N application. Growth differences with N form in black birch probably reflect changes in biomass allocation. Prediction of seedling behavior in the field based on results of a shadehouse study is always tentative, however this study clearly points to some interesting differences between species in potential response to N deposition. Under N deposition regimes that increase soil nitrate availability, the differences in response of black and yellow birch to nitrate at low light may potentially lead to changes in the species composition of the seedling communities in the understory. Following disturbances such as tree-falls or hurricane damage, a different species mix of seedlings will be released, with potential consequences for sapling and tree species mix.

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