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Nitrogen acquisition and competitive ability of *Kalmia angustifolia* L., paper birch (*Betula papyrifera* Marsh.) and black spruce (*Picea mariana* (Mill.) B.S.P.) seedlings grown on different humus forms

R.L. Bradley[1], B.D. Titus[2] and J.W. Fyles[3]
[1]*Department of Forest Sciences, 270 - 2357 Main Mall, University of British Columbia, Vancouver, B.C., V6T 1Z4, Canada,*[*] [2]*Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, 506 West Burnside Road, Victoria, B.C., V8Z 1M5, Canada and* [3]*Department of Natural Resource Sciences, McGill University, Macdonald Campus, Ste-Anne de Bellevue, Québec, Canada, H9X 3V9*

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Abstract

Two species of boreal tree seedlings, paper birch (*Betula papyrifera* Marsh.) and black spruce (*Picea mariana* (Mill.) B.S.P.), and the ericaceous shrub *Kalmia angustifolia* L. were grown in pots with humus from a birch-dominated site and two spruce-*Kalmia* sites. Root systems interacted with humus form in controlling soil-N cycling as well as energy and nutritional deficiencies of soil microorganisms. In general, *Kalmia* seedlings affected microbial dynamics and N cycling differently than birch and spruce seedlings did. Birch and spruce seedlings reduced gross N mineralization and immobilization rates, soil mineral-N pools and the amounts of NH_4^+–N accreted on buried cation exchange resins in all three soils. Compared to birch and spruce seedlings, the growth of *Kalmia* resulted in significantly higher gross N mineralization rates, soil mineral-N pools and resin-NH_4^+ accretion in soil from the fertile birch site. Gross N immobilization rates in all soils were generally higher with *Kalmia* than with spruce or birch seedlings. All three species of seedlings acquired N from the birch site soil, whereas only *Kalmia* seedlings acquired N from the two spruce-*Kalmia* site soils. Relative to control treatments, the amount of N mineralized anaerobically increased in the birch-site soil and decreased in the poor spruce-*Kalmia* site soil with all three species of seedlings. All seedlings increased the microbial biomass in the birch-site soil. *Kalmia* humus and *Kalmia* root systems increased microbial energy-deficiency and decreased microbial nutritional deficiency compared to the other humus and seedlings used. Results are discussed in terms of each species' nutrient acquisition mechanism and its competitive ability during secondary succession.

Introduction

Patterns of vegetation change over time are of interest to both ecologists and foresters since the mechanisms responsible for natural succession have theoretical as well as practical applications. Interspecies competition as well as site characteristics influence the resource-supply trajectory and the eventual structure of the plant community (Tilman, 1985). Interspecies competition can be described as a dichotomous system of (1) each species' effects on all others and (2) the response of each species to all others. Miller and Werner (1987) found that, for each species, the magnitude of these two diametrically opposed components of competition were inversely related, leading to a hierarchy of competitive abilities within plant communities.

Temporal change in boreal forest species composition is expected to be cyclical with the reoccurence of natural disturbances such as fire. However, there are concerns that in central Newfoundland, the commonly observed invasion of some disturbed forest sites by the ericaceous shrub *Kalmia* (*Kalmia angustifolia* L.) may

[*] FAX No:+16048225744.E-mail:rbradley@unixg.ubc.ca

cause a conversion to permanent heathland. Studies have shown that neither burning nor cutting of *Kalmia* will reduce its vigorous vegetative regrowth and dominance (Mallik, 1990). Allelopathic compounds found in *Kalmia* leaves and humus have been shown to inhibit growth of commercial softwood species (Mallik, 1992). *Kalmia* can also exert non-specific antagonism by accumulating deep layers of recalcitrant soil humus in which significant amounts of organically complexed plant nutrients such as N are sequestered (Damman, 1971).

While the competitive strategies of *Kalmia* are numerous, boreal ericaceous shrubs nevertheless are vulnerable to some changes brought on by other plant species. Ericaceous plants are generally shade intolerant and canopy closure has been observed to coincide with reduced flowering and fruit production of heather (*Calluna vulgaris* (L.) Hull) (Hester, 1987; Iason and Hester, 1993) and *Kalmia* (Mallik, 1994; Titus et al., 1995). Where shading is not a factor, it has also been reported that high nutrient availability also reduces the competitive ability of some ericaceous plants (Aerts et al., 1990; Prescott et al., 1995). It is commonly accepted by foresters in Newfoundland that the ability of a dominant *Kalmia* cover to suppress softwood regeneration is inversely related to site quality. Plants that enhance soil nutrient supply may therefore reduce *Kalmia*'s competitive ability and eventually allow "*Kalmia*-sensitive" softwood species to become established. Birch (*Betula* spp.), which can follow commercially-valuable black spruce (*Picea mariana* (Mill.) B.S.P.) in some successional cycles in central Newfoundland (Meades and Moore, 1994), is one such genus reputed to outcompete swards of *Calluna* and improve heathland fertility (Hester, 1987; Miles and Young, 1980), although this effect is not universal (Dimbleby, 1953). For example, Bradley and Fyles (1996a) found that birch root systems enhanced soil nutrient cycling in mineral mull humus, but not in organic mor humus similar to that found on *Kalmia* sites.

Kalmia humus can remain in a phase of net N immobilization for extended periods of time (Damman, 1971; White et al., 1988). Results from a recent incubation study (Bradley et al., 1997) suggested that the small mineral-N pools commonly found in *Kalmia* humus may be the result of an efficient immobilization of labile-N through biochemical reactions akin to the tanning of soil protein as described by Handley (1961). More insight into *Kalmia* competitiveness could be gained by determining the effects of succession on gross soil-N process rates. A bioassay was therefore conducted with paper birch (*Betula papyrifera* Marsh.), black spruce and *Kalmia* seedlings to measure changes in gross rates of soil-N mineralization and immobilization in three central Newfoundland soils of contrasting fertility, and to compare these to plant N uptake, soil mineral-N pools and the physiological status of soil microbial communities. Our broader objective was to elucidate some of the mechanisms involved in the competitive strategies of the three species.

Materials and methods

Soils and seedlings

Soils were collected at 3 different sites (I, II and III) within a radius of 35 km of Grand Falls - Windsor (48°55′ N, 55°40′ W) in central Newfoundland in the spring of 1994. All three sites are well drained. The landscape is principally dominated by black spruce and balsam fir (*Abies balsamia* (L.) Mill.) through which stands of paper birch of a few hectares in size, as well as regenerating sites that have become dominated by *Kalmia*, frequently occur.

On Site I (hereafter referred to as the "birch site"), a mature (60–70 yr) paper birch stand had been harvested the previous winter. Sites II and III had been harvested for black spruce in the 1970s and restocked with black spruce seedlings in the early 1980s. Before harvest, Sites II and III had been classified by foresters as medium quality sites based on stand characteristics. Both of these sites were invaded by *Kalmia* between harvest and replanting. On Site II (referred to as the "rich *Kalmia* site"), twelve-year-old planted black spruce trees were commonly >2 m in height with annual leader growth attaining up to 40 cm. On Site III (the "poor *Kalmia* site"), ten-year-old planted black spruce seedlings appeared chlorotic and stunted and were usually <1 m in height. Numerous samples of both organic and mineral (0–25 cm) soil horizons were collected over a 1 ha area at each of the three sites, coarse-sieved (6 mm), bulked and brought back to a greenhouse for potting. The organic material from the birch site was black and mostly amorphous (i.e. H horizon) whereas that from each *Kalmia* site was fibrous and partly decomposed (i.e. F horizon). *Kalmia* litter appeared to be the main constituent of the humus on the two *Kalmia* sites. The coarse textured mineral soil from each site was a mixture of Ae and podzolic B hori-

zons (Agriculture Canada Expert Committee on Soil Survey, 1987).

Three composite samples of each soil horizon was collected at each site and analyzed in the laboratory for pH (soil:water = 1:2 mineral, 1:10 organic), extractable mineral N (1 N KCl) and Mehlich III extractable Ca, Mg, K and P (Mehlich, 1984). Organic samples were further analyzed for total N (micro-Kjeldahl), and were also pyrolyzed in the chemistry department of Memorial University (St. John's, Newfoundland) using a CDS Pyroprobe 120 that was interfaced to a Varian 3700 GC (Zhang, 1993). Peak areas of tannin and coumaric acid pyrolysates were recorded on a Hewlett-Packard Integrator and compared to those of pyrolyzed standards of isolated *Kalmia* tannin and pure coumaric acid. Peak areas of phenol and lignin pyrolysates were measured on a per unit sample weight basis since no standards were available.

The bioassay used (1) containerized 1 year old overwintered paper birch seedlings obtained at the onset of leaf emergence, (2) bare-root 2 year old black spruce seedlings that had been spring-seeded and fall-lifted, and (3) *Kalmia* seedlings with limited rhizome growth, collected from a natural seedbed on a disturbed sandy embankment in west-central Newfoundland.

Bioassay and resin disks

Experimental units consisted of 12 L pots (30 cm height × 22.5 cm dia.) to which were assigned one of 12 treatments comprised in a factorial array of 3 soils × (3 species + 1 control). Each treatment was replicated 5 times.

Each pot was half-filled with mineral soil which was then tamped to restore bulk density. A cation exchange resin disk was moistened with deionized water and placed horizontally over the mineral soil in the center of each pot. The disks had been prepared by enclosing 3.0 g (dry wt.) of AG^{R} 50W resin (Bio-Rad Laboratories, Richmond, CA) between two layers of nylon material that were glued to the outside faces of ABS plastic rings (9 cm dia. × 6 mm thick). Eight L of organic soil was then added to each pot and tamped to form a 15 cm thick layer.

Seedlings were washed free of soil, dried with paper towels and weighed before being planted into the organic soil layer (0–12 cm). The number of seedlings per pot varied from 12 (birch) to 2 or 3 (spruce and *Kalmia*) in order to maintain a fresh biomass range between 20 g and 30 g in each pot. Nine to fifteen additional seedlings from each species were weighed, dried at 65 °C for 72 h, digested by the micro-Kjeldhal method and analyzed for total-N. The initial plant-N content of every pot was estimated from significant ($p<0.05$) regression equations relating fresh seedling mass to total-N content (Table 1).

Table 1. Relationship between total fresh mass (TFM) and total N (TN) of seedlings at the time of planting for estimating initial N content of planted seedlings

Species	Mean fresh mass (g)	Mean total-N (mg)	Regression equation	n	R^2
Birch	1.58	5.34	TN = 4.48 (TFM) - 1.73	15	0.52
Spruce	12.69	68.33	TN = 5.78 (TFM) - 4.91	14	0.94
Kalmia	17.99	35.37	TN = 2.28 (TFM) - 5.60	9	0.60

The 60 experimental units were randomized in 5 complete blocks on a greenhouse bench and grown for 20 weeks. The temperature was allowed to vary between 8 °C and 22 °C, the relative humidity was automatically controlled to remain above 70% and a constant photoperiod of 18 hours was maintained throughout the bioassay by supplementing daylight hours with artificial light. Pots were watered to field capacity once a week. Leaves and needles that fell during the bioassay were collected and kept.

Pots were watered for the last time ten days prior to harvest at which time leaves from the birch and *Kalmia* seedlings showed no signs of senescence. Harvesting consisted of excising shoots at the soil surface and placing these in individual paper bags along with leaves and needles that had fallen during the bioassay. These were dried (65 °C) and analyzed for Kjeldahl-N. After shoot excision, root systems from each pot were carefully removed and washed free of humus particles. All underground plant material was dried, weighed and analyzed for Kjeldahl-N in the same manner as the shoots. In the case of *Kalmia*, underground growth was fine and extensive and consequently an unknown proportion of *Kalmia* fine roots may have been lost during washing.

The organic soil from each pot was placed in a separate polyethylene bag and stored at 2 °C for subsequent analyses (see below) while a subsample was dried at 105 °C to determine moisture content. The mineral soil was discarded. The resin disk from each pot was recovered, placed in an individual plastic bag and stored at 2 °C.

Gross N process rates

Gross N mineralization and immobilization rates for soil from each pot were determined immediately following harvest using the isotope dilution technique (Kirkham and Bartholomew, 1954). A subsample (ca. 15 g wet wt.) of humus was extracted in 100 mL of 2 N KCl solution and the NH_4^+–N concentration of the extract was determined colorimetrically (salicilate-nitroprusside). A duplicate set of subsamples from each pot was then weighed (10 to 50 g dry weight) and these were placed and gently tamped in either 200 mL fleakers or 500 mL mason jars. Dissolved $(^{15}NH_4^+)_2SO_4$ (99 atom % ^{15}N) was uniformly distributed through each sample by making numerous small injections with a hypodermic needle in order to obtain between 10% and 30% isotope enrichment of the initial soil NH_4^+ pool. The amount of isotope solution added ranged from 2 mL to 10 mL and thereby increased moisture in each sample by 5% to 10%. Half the duplicate samples were extracted in 2 N KCl (1:5 to 1:10 soil:extractant) after fifteen minutes, and the extracts stored at 2 °C until analyzed. The remaining samples were placed in an incubator at 22 °C for 24 hours after which they were similarly extracted. An aliquot of each KCl extract was analyzed colorimetrically for NH_4^+–N concentration. Extracts were prepared for atom % ^{15}N analysis by continuous flow mass spectrometry (CFMS) using the passive diffusion method (Brooks et al., 1989) as modified by Bradley and Fyles (1996b). The diffused samples were sent to the Stable Isotope Laboratory of the Department of Soil Science, University of Saskatchewan, for analysis.

The following equations of Kirkham and Bartholomew (1954) were used to determine gross N process rates:

$$m = \frac{M_0 - M_1}{t} \times \frac{log[(H_0 M_1)/(H_1 M_0)]}{log(M_0/M_1)}$$

$$i = \frac{M_0 - M_1}{t} \times \frac{log(H_0/H_1)}{log(M_0/M_1)}$$

where, m = gross N mineralization rate (mg g^{-1} soil d^{-1})

i = gross N immobilization rate (mg g^{-1} soil d^{-1})

M_0 = initial $^{14+15}NH_4^+$–N pool (mg g^{-1} dry soil)

M_1 = post-incubation $^{14+15}NH_4^+$–N pool (mg g^{-1} dry soil)

H_0 = initial $^{15}NH_4^+$–N pool (mg g^{-1} dry soil)

H_1 = post-incubation $^{15}NH_4^+$–N pool (mg g^{-1}dry soil)

t = time (d^{-1})

and where $M_0 \neq M_1$.

Other N measurements

The humus KCl extracts were also analyzed for NO_3^-–N concentrations (Cd reduction). Seedling N uptake over the 20 week bioassay was estimated for each pot by subtracting the estimated initial plant N content (Table 1) from the total N content of the harvested seedlings. The accretion of NH_4^+–N on cation exchange resin disks was determined by transferring the resin into 125 mL Erlenmeyer flasks for extraction in 50 mL of 1 N KCl solution and analyzing the extracts colorimetrically for NH_4^+–N. N mineralized over the course of a two week anaerobic incubation (30 °C) (Waring and Bremner, 1964) was measured on duplicate 5 g humus samples from each pot.

Soil respiration

Three respirometry measurements, namely basal respiration rate (*B*), glucose induced respiration rate (*C*) and glucose + Difco broth induced respiration rate (*CN*), were measured on duplicate samples of fresh humus (ca. 20 g dry wt.) from each pot. *B* was determined by placing each sample in a 130 mL jar, flushing the headspace with ambient air for 5 min. and then sealing the jar with an air-tight lid equipped with a rubber septum. Two hours later, an aliquot of the air in the headspace was sampled with a needle and analyzed for CO_2 concentration using a Model 5890-II GC (Hewlett-Packard, Avondale, PA). Room temperature and atmospheric pressure were noted for each sample. The ambient CO_2 concentration was then subtracted from sampled CO_2 concentrations and results were adjusted by applying Ideal Gas Laws and by centering at 22 °C using Q_{10} = 2. *C* and *CN* were determined by placing each sample in a 500 mL jar and pretreating these with either saturation amounts of ground (65 μm mesh) glucose (1 mg glucose–C g^{-1} soil) or ground

glucose + Difco nutrient broth (0.5 mg g^{-1} soil) that had been mixed with talc (250 mg total). The talc mixtures were dispersed into each soil sample using a kitchen handmixer with one beater. Each sample was then tranferred into a 130 mL jar, left uncovered for 100 minutes, flushed with ambient air for 5 minutes and sealed for 30 minutes. The CO_2 concentration in the headspace was then determined using the same GC procedure as decribed for *B*.

All three levels of soil respiration (*B*, *C* and *CN*) were reported as mg CO_2–C g^{-1} soil h^{-1}. Microbial biomass fractions and microbial physiological indices (Bradley and Fyles, 1995) were then determined for soil from each pot as follows:

$$\begin{aligned}
\text{MBe} &= \text{energy deficient microbial fraction} \\
&\quad (\text{mg } C_{mic}\ g^{-1} \text{ soil}) \\
&= 0.0815C + 0.37
\end{aligned}$$

$$\begin{aligned}
\text{MBn} &= \text{nutritionally deficient microbial fraction} \\
&\quad (\text{mg } C_{mic}\ g^{-1} \text{ soil}) \\
&= 0.0815(CN - C) + 0.37
\end{aligned}$$

$$\begin{aligned}
\text{MBt} &= \text{total microbial biomass (mg } C_{mic}\ g^{-1} \text{ soil)} \\
&= 0.0815CN + 0.37
\end{aligned}$$

$$\begin{aligned}
\text{EDI} &= \text{energy limitation index} \\
&= [(C - B) \div B] \times 100\%
\end{aligned}$$

$$\begin{aligned}
\text{NDI} &= \text{nutritional deficiency index} \\
&= [(CN - C) \div C] \times 100\%
\end{aligned}$$

The conversion factor used to transform respiration rates to microbial biomass was based on the equation of Anderson and Domsch (1978).

Statistical analyses

The effects of soils, seedlings and soil × seedling interactions on all measured variables were tested using two-way ANOVA. Unless otherwise stated, *F* values with corresponding probabilities $\leq$0.05 were accepted as significant. The simple effects of seedlings were tested within each soil using one-way ANOVA. Significant differences between treatment means were determined using Duncan's multiple range test ($p \leq 0.05$). All statistical analyses were performed using GLM procedures of SAS statistical software (SAS Institute Inc., 1984).

Table 2. Characterization of organic horizon from three experimental sites

Analyses	Soils		
		Spruce-*Kalmia* sites	
	Birch site	Rich	Poor
pH (1:10 = soil:water)	4.1 (0.06)	4.0 (0.07)	3.8 (0.09)
Nitrogen			
Total-N (mg g^{-1})	8.63 (0.49)	7.36 (0.66)	10.05 (0.75)
Extractable NH_4^+–N (μg g^{-1})	89.7 (6.6)	3.6 (0.97)	2.6 (0.71)
Extractable NO_3^-–N (μg g^{-1})	0.13 (0.03)	<0.01 (0.009)	0.17 (0.15)
Mehlich III extractable			
Ca (μg g^{-1})	78 (8.4)	62 (7.1)	52 (6.8)
Mg (μg g^{-1})	14 (3.1)	12 (2.4)	18 (3.9)
P (μg g^{-1})	0.55 (0.10)	0.39(0.08)	0.53 (0.08)
K (μg g^{-1})	8.5 (1.8)	8.0 (2.1)	8.0 (1.6)
Analytical pyrolysis			
Tannin (mg g^{-1})	7.7 (0.6)	29.3 (1.6)	40.9 (1.2)
Coumaric (mg g^{-1})	0.30 (0.09)	0.45 (0.06)	0.65 (0.14)
Phenol (area* μg^{-1})	267 (51)	427 (59)	482 (35)
Lignin (area* μg^{-1})	886 (99)	1605 (81)	1680 (118)

Means and standard errors are for n = 3, except for analytical pyrolysis for which n = 2.
* Relative measurement only.

Results

Initial soil tests

The initial pH of the organic humus from each site was acidic and the pH range (birch site > rich *Kalmia* site > poor *Kalmia* site) was small (Table 2). Total N and Mehlick III extractable nutrients were also in the same range and Ca concentrations showed the same trend as pH. There was a large extractable NH_4^+ pool present in humus from the birch site as compared to humus from either *Kalmia* site. Extractable NO_3^-–N concentrations were negligible in all three soils. Analytical pyrolysis revealed a decreasing trend in organic matter quality (i.e. increasing concentrations of tannin, coumaric acid, phenol and lignin) from the birch site to the rich *Kalmia* site to the poor *Kalmia* site. The differences in pyrolysate concentrations were generally larger between the birch site and the two *Kalmia* sites than between the two *Kalmia* sites. The 0 to 25 cm mineral soil horizon from each site had mineral-N and exchangeable cation concentrations an order of magnitude lower, but a slightly higher pH value, than their respective organic horizon (data not shown).

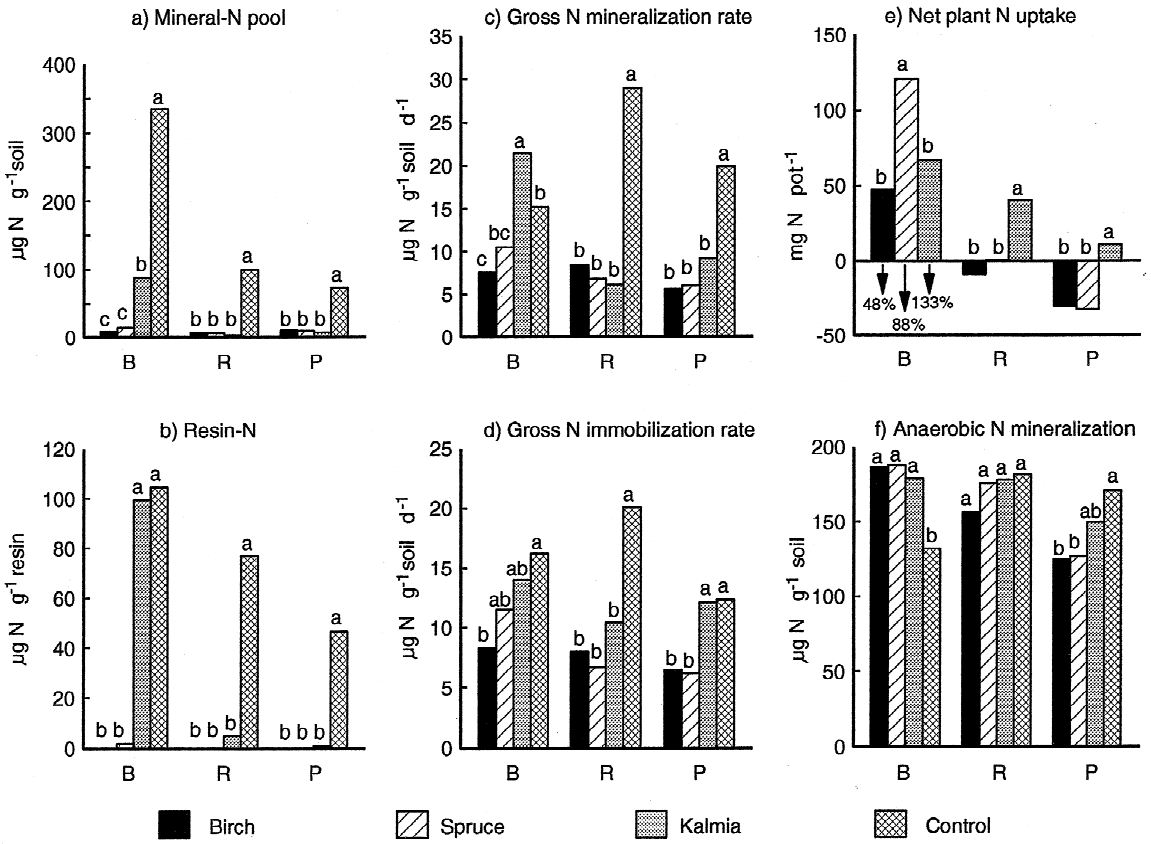

Figure 1. Effect of species on six post–bioassay soil-N measurements. Each cluster of four vertical bars represents a different soil (B = birch site, R = rich *Kalmia* site, P = poor *Kalmia* site). Bars within the same cluster with a different lower-case letter differ significantly (Duncan's Multiple Range Test, $p < 0.05$). Mean plant N uptake (Figure 1e) on soil from the birch site is also expressed as a % of initial plant N.

Post-bioassay N measurements

Soil × species interactions were statistically significant for all N measurements except for gross N immobilization rates where only the species effect was significant.

The mineral-N pool in each treatment consisted mainly of NH_4^+–N and negligible amounts of NO_3^-–N. Within each soil, a significantly larger mineral-N pool was found in the control treatment (Figure 1a). The soil mineral-N pool was 3.5 times larger in the control treatment from the birch site than in the control treatment from either *Kalmia* site, with the rich site having slightly higher concentrations than the poor site. In soil from the birch site, the mineral-N pool was significantly larger under *Kalmia* seedlings than under spruce or birch seedlings.

The effect of treatments on resin-NH_4^+ accretion over the course of the 20 wk bioassay (Figure 1b) was similar to the effect on soil mineral-N pools. The significant correlation between the two measurements is best described by a log-log linear regression ($n = 53$, $R^2 = 0.77$).

In soil from the birch site, the gross rate of N mineralization was significantly decreased by birch seedlings but significantly increased by *Kalmia* seedlings (Figure 1c). Gross N mineralization rates were significantly reduced by all seedlings grown in soils from both *Kalmia* sites. In soil from each of the three sites, gross N immobilization rates (Figure 1d) were highest in the control treatment followed by the *Kalmia* seedling treatment.

Plant N uptake (Figure 1e) was highest from the birch site soil and lowest from soil from the poor *Kalmia* site. When grown in the birch soil, spruce seedlings took up the largest amount of N followed by *Kalmia* and birch seedlings, although relative N uptake expressed as a % of the initial plant N content was highest in *Kalmia* seedlings. When grown in soils from the

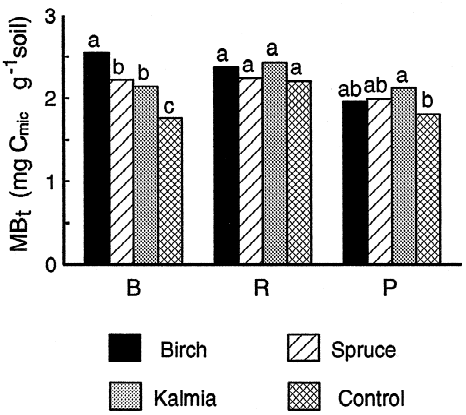

Figure 2. Effect of species on total microbial biomass (MBt) in each soil. Bar clusters are defined as in Figure 1. Bars within the same cluster with a different lower-case letter differ significantly (Duncan's Multiple Range Test, $p < 0.05$).

Table 3. Significant effects of soils and species on the energy and nutritional deficiency indices (EDI and NDI) of soil microbial communities and on gravimetric soil moisture content (M.C.); note that soil × species interactions are not significant for all three measurements (results from two-way ANOVA)

	EDI (%)	NDI (%)	M.C. (%)
Main soil effects			
Birch site	147 c	17.0 a	212 b
Rich *Kalmia* site	267 a	9.3 a	170 c
Poor *Kalmia* site	194 b	12.8 b	232 a
Main species effects			
Birch	219 a	12.3 ab	183 b
Spruce	226 a	14.8 a	172 b
Kalmia	249 a	9.0 b	232 a
Control	136 b	14.6 a	242 a

Mean values in the same grouping followed by a different lowercase letter differ significantly by Duncan's multiple range test ($p < 0.05$).

two *Kalmia* sites, *Kalmia* seedlings gained N whereas birch and spruce seedlings either lost or absorbed no N at all.

All seedlings significantly increased anaerobic N mineralization (Figure 1f) in soil from the birch site. In soil from the rich *Kalmia* site, none of the treatments differed significantly. In soil from the poor *Kalmia* site, all seedlings decreased the amount of N mineralized anaerobically, although the *Kalmia* seedling treatment did not differ significantly from the control.

Microbial biomass fractions

The effects of soil, species and soil × species interactions on the energy deficient (MBe) and total (MBt) soil microbial biomass were significant. Soil was the only factor affecting the nutritionally deficient microbial biomass (MBn). The mean MBn of the birch soil was significantly higher than that of either *Kalmia* soil. MBn was consistently an order of magnitude smaller than MBe across all treatments and therefore differences in MBt were primarily a reflection of differences in MBe. In soil from the birch site, birch seedlings increased MBt significantly over spruce and *Kalmia* seedlings which in turn increased MBt significantly over the control treatment (Figure 2). In soil from the rich *Kalmia* site, there were no significant differences in MBt between treatments. In soil from the poor *Kalmia* site, *Kalmia* seedlings increased MBt significantly over the control treatment.

Physiological indices of microbial communities

EDI and NDI were both affected by soils while NDI was also affected by species (Table 3). There were no significant interactions between soils and species in controlling the two ratios. EDI was lowest in the birch soil and highest in the rich *Kalmia* soil. All three seedling species increased EDI significantly over the control treatments and EDI was highest with *Kalmia* seedlings. The average NDI was higher in soil from the birch site than in soil from either *Kalmia* site. *Kalmia* seedling growth consistently resulted in the lowest NDI.

Soil moisture

Based on visual and tactual inspection, all three soils with *Kalmia* seedlings were wetter at each of the watering dates. There were significant soil and species effects ($p < 0.0001$) on the average measured soil moisture content at time of harvest (Table 3). All three soils with *Kalmia* seedlings had retained more water over the course of the final 10 days than those treated with spruce or birch seedlings. Soil × species interactions had a weaker effect ($p \approx 0.05$) on soil moisture.

Discussion

Although the scope and scale of the study precluded the use of replicated sites, the main findings are consistent with what is known about ericaceous shrubs and their interactions with site quality. The integrated nature of this study allows development of hypotheses regarding humus quality, soil mineral-N, the effect of *Kalmia* on gross N mineralization and immobilization rates, long-term N availability, rhizodeposition, soil microbial communities and plant nutrient acquisition. Ultimately, these mechanisms interact to determine successional pathways in this ericaceous system.

Initial humus quality

Humus chemical quality is inversely related to high concentrations of tannins, coumaric acid and other phenolics, which have been linked to allelopathic effects on spruce seedling growth (Gallet, 1994; Zhu and Mallik, 1994), as well as to high concentrations of lignin which retard litter decomposition and nutrient release (Melillo et al., 1982). Humus chemical quality at the birch site was much higher than that at the two *Kalmia* sites. Soils from each *Kalmia* site could be considered as belonging to the same class with a slightly higher humus quality being found at the rich site. The small NH_4^+–N pool in soil from each *Kalmia* site could have been related to the higher lignin concentrations limiting N mineralization rates, or to higher concentrations of phenolics and tannins forming stable complexes with labile forms of N (Handley, 1961; Howard and Howard, 1993).

Post-bioassay soil mineral-N

The inorganic soil-N pool is labile, and mineral-N consumption and production rates are expected to vary over short periods of time (Adams et al., 1989). Resin disk extracts reflected, however, the cumulative mineral-N in each treatment over the 20 wk bioassay. It is interesting to note that higher amounts of mineral-N and especially of resin-N were found in the birch site soil in which *Kalmia* seedlings were grown compared to the same soil in which either birch or spruce seedlings were grown. Four independent hypotheses may be used to explain this phenomenon:

(1) Kalmia *seedlings make low demands on the mineral-N pool because of slow growth.* This hypothesis is not tenable since N uptake by *Kalmia* seedlings grown in the birch-site soil was higher than in the other two soils.

(2) Kalmia *seedlings make low demands on the mineral-N pool because they utilize mainly organic-N.* Leake and Read (1989) reported that ericoid mycorrhizae successfully absorbed N from stable tannin-protein complexes. Organic-N thus assimilated by the fungal symbiont can be readily transferred to the host plant (Bajwa et al., 1985). However, the ability to assimilate organic forms of N does not necessarily preclude the ability to assimilate mineral forms as well.

(3) Kalmia *exudates hinder microbial acquisition of mineral-N in the birch site soil.* Ericaceous plants generally raise the concentration of free phenolics in the rhizosphere (De Montigny and Weetman, 1990) which may favor the establishment of microbes specialized in metabolizing N complexed with phenolic compounds (Shafer and Blum, 1991).

(4) Kalmia *growth in soil from the birch site promoted the mineralization of soil-N.* As corroborating evidence, gross N mineralization rates increased under *Kalmia* seedlings and decreased under spruce and birch seedlings.

It is, however, difficult to reconcile the increased cycling of mineral-N in the birch humus with *Kalmia*'s reputation for reducing soil-N availability (Damman, 1971). Even if the present data do not unequivocally show *Kalmia* acquiring organically bound nutrients, the occurrence of this mechanism would preclude the need for *Kalmia* to increase the mineralization of soil-N. Curiously, *Kalmia* seedlings reduced gross N mineralization rates on soils from the two *Kalmia* sites. Root-humus interactions such as these warrant a more rigorous interpretation of the data.

Effect of Kalmia *on gross N mineralization rates*

Kalmia roots created a *milieu* favorable to the mineralization of N in soil from the birch site, but the exact mechanism for this is unknown. The simplified model that has traditionally been used to explain gross mineralization rates (Kirkham and Bartholomew, 1954; Nishio et al., 1985; Tietema and Wessel, 1992) confounds all organic-N pools, including the microbial-N pool. Based on concepts of (1) trophic levels among soil microbial populations (Clarholm, 1985) and (2) chemical immobilization of soil proteins (Handley, 1961), the net transformation of soil-N from a nutrient bound within a complex organic molecule to free

NH_4^+–N probably involves many intermediate steps. There is no way of demonstrating unequivocally that *Kalmia* seedlings actually improved microbial access to recalcitrant organic-N in the birch soil.

Another explanation that is more consistent with the allelopathic nature of *Kalmia* and its dominance over soil nutrient cycles is that *Kalmia* root systems were repressing native microbial populations in the birch site soil at the time of harvest. In an analogous study, Schimel et al. (1992) treated organic forest floor material with a biocide and found that the biocide increased gross N mineralization rates relative to a control treatment. In the same study, forest floor material that was treated with starch had lower gross N mineralization rates because microbial uptake of starch competitively inhibited the use of N-containing organic matter for energy. In the present study, birch and spruce seedling growth in the birch site soil resulted in lower gross N mineralization rates, and this may have been the effect of high rhizodeposition emulating the effect of starch.

Effect of Kalmia *on gross N immobilization rates*

Gross N immobilization rate is a complicated measurement to interpret since it can be a function of (1) the biological process of microbial N acquisition, and (2) the chemical complexing of mineral-N with phenolic compounds. Furthermore, if gross N immobilization obeys first order kinetics (as many natural processes do) then its rate is implicitely related to the size of the mineral-N pool. The equations used to determine the parameters *i* and *m* (Kirkham and Bartholomew, 1954) are zero-order models. Therefore, the high gross N immobilization rates observed in control treatments of each soil were probably related to larger mineral-N pools in these treatments rather than a reduction of these rates due to seedlings. Gross N immobilization rates were consistently higher under *Kalmia* seedlings than under birch or spruce seedlings in spite of the small mineral-N pools in these treatments. It is therefore possible that biochemical immobilization of N was due to a higher occurrence of N-binding polyphenolics under *Kalmia* seedlings.

Anaerobic N mineralization

Anaerobically mineralized soil-N can be used as an index of long-term plant N availability (Keeney, 1980; Powers, 1980). Results from this study therefore suggest that the growth of all seedlings increased the long-term supply rate of soil-N on the humified organic matter from the birch site, had no such effect on the lignified organic matter of the rich *Kalmia* humus and depressed N fertility in the poor *Kalmia* humus. These results are consistent with the average seedling N uptake from each soil as well as with results from a study by Bradley and Fyles (1996a) which showed that the effect of seedlings on anaerobic N mineralization rates depends on the degree of humification of the soil organic matter.

Soil moisture

Low soil water content in all pots with birch and spruce seedlings suggests that transpiration, and by implication photosynthesis, was high in these two species. High rates of photosynthesis relative to N uptake may lead to a high allocation of photosynthates to the roots (Campagna and Margolis, 1989). However, roots of these two species were not observed to exploit the soil volume as thoroughly as *Kalmia* did, suggesting that allocation of C to the roots of spruce and birch resulted in higher rhizodeposition rates relative to *Kalmia* seedlings. Conversely, high soil moisture in pots with *Kalmia* seedlings implies that this species exchanged little gas with the atmosphere compared to birch or spruce seedlings. Therefore, *Kalmia* seedlings either had (1) a more water-efficient photosynthetic system than birch and spruce seedlings, or (2) a lower rate of photosynthesis relative to N uptake. If the latter is true, then rhizodeposition rates would likely have been lower in the *Kalmia* rhizosphere, which is consistent with the large root mats that developed in pots with *Kalmia* seedlings.

Properties of soil microbial communities

Bachmann and Kinzel (1992) proposed that plant × soil interactions be characterized by the relative control plants gain on soil nutrient cycling. Microbial biomass responded markedly to different seedlings in the birch site soil whereas seedlings had less or no effect on microbial biomass in the two *Kalmia* site soils. Plants thus exerted a stronger dominance over microbial populations, and therefore nutrient cycling, in the birch site soil than in the two *Kalmia* site soils.

The birch site humus had a lower EDI and a higher NDI than humus from the two *Kalmia* sites, which suggests that microbial communities in the birch humus had a lower C to N requirement, perhaps as a result of conditioning to the lower C to N ratio of well-

humified substrates. *Kalmia* seedlings increased EDI and decreased NDI ($p<0.10$) relative to other seedlings and to the control treatment which implies that microbial communities associated with *Kalmia* roots had a relatively higher energy to nutrient demand. Higher EDI in *Kalmia* site soils is consistent with findings by Read (1992) that respiration rates increase dramatically in heathland soils treated with glucose-C. It is also consistent with the hypothesis we inferred from soil moisture measurements, that belowground C allocation by *Kalmia* seedlings resulted in greater C retention within the roots and lower rhizodeposition compared to birch and spruce seedlings.

Plant nutrient acquisition

Nutrient acquisition mechanisms are central to a species' competitive ability. Nutrient acquisition by birch and spruce appears to involve high C fixation by the plant and high C allocation to the rhizosphere. This plant strategy, that we describe as *photosynthesis-driven nutrient acquisition*, involves mitigating energy deficits in nutrient-mineralizing rhizomicrobial communities using root-derived labile-C substrates. Past studies have correlated high rhizodeposition rates with increased nutrient cycling on humified soil organic matter (Berendse et al., 1989; Bradley and Fyles, 1995; Robinson, 1991), which is consistent with the observed high N-uptake by spruce and birch seedlings on the birch site soil in this study. It has also been shown, however, that the presence of tree roots can actually retard nutrient mineralization in moderately decomposed organic horizons (Bradley and Fyles, 1996a; Parmelee et al., 1993). This, in turn, is consistent with the observed low N uptake by both spruce and birch seedlings in humus from both *Kalmia* sites in this study. Since nutrient cycling in a photosynthesis-driven system appears to depend in part on the state of decomposition of above-ground litter, and in part on the stimulation of soil microbial activity by root exudates, a species' aboveground litter quality coupled with its ability to raise soil available C concentrations should determine its capacity to acquire nutrients. These are factors which determine specific growth patterns of birch and spruce.

In contrast to birch and spruce, the strategy of ericaceous plants such as *Kalmia* for acquiring soil nutrients may depend more on the ability of its associated ericoid mycorrhizae to readily assimilate organically-bound soil nutrients and transfer these to the plant host (De Montigny and Weetman, 1990; Leake and Read, 1989). We describe this strategy as *mycorrhizal-driven nutrient acquisition*. In spite of recent reports that other types of mycorrhizae associated with coniferous forest trees can utilize N from protein-tannin complexes (Northup et al., 1995), the mechanism by which heathland shrubs gain access to refractory soil-N appears to be exclusive to the order Ericales. Ericoid mycorrhizae have been shown to excrete phenol oxydase, ligninase and chitinase into the soil (Read, 1992) which can depolymerize structural components of organic matter and expose more labile forms of nitrogenous substrates. Evidence of the ecological importance of the ericoid symbionts was given by Read (1992) who estimated that 80% of CO_2 flux from heathland soils came from the respiration of the mycorrhizae alone. The same study suggested that ericaceous plants exert regulatory functions over the expression of the enzymes produced by the symbiotic fungus rather than provide the fungus with photosynthates as in other types of mycorrhizal associations. The uptake of soil organic N by the fungus implies a concomitant assimilation of reduced C. Consequently, it may not be necessary for *Kalmia* seedlings to provide photosynthates for the energy requirements of their symbionts. This conjecture is consistent with the hypothesis that *Kalmia* seedlings can cycle soil-N more efficiently with less photosynthate than birch and spruce seedlings.

Implications for nutrient cycling and succession

In nature, the performance of a given species can be discussed in terms of its competitive effect on, and response to, other species. Miller and Werner (1987) found competitive interactions to be asymetric, in that species able to exert strong competitive effects on other species displayed in turn a weak response to the others, and vice-versa, leading to a hierarchy of competitive ability in plant communities. In Newfoundland's boreal forest, a species' competitive ability is determined in part by the effect of the humus it produces on other plant species, and in part on its own nutrient acquisition mechanisms. In this study, *Kalmia* humus inhibited birch and spruce seedling growth more than it inhibited *Kalmia* seedling growth, presumably because of *Kalmia*'s symbiotic association with ericoid mycorrhizae. Birch and spruce seedlings did not appear to possess a mechanism by which they could gain access to nutrients in the *Kalmia* humus. However, humus from the birch site was appropriate for photosynthesis-driven species to thrive in, as well as for *Kalmia* seedlings. Although well-humified humus mainly con-

tain fulvic and humic acids which ericoid mycorrhizae are unable to utilize as C and N sources (Stribley and Read, 1980), *Kalmia* seedlings can still secure ample N for growth from the fertile birch site soil by scavenging the large mineral-N pool.

As gross immobilization rates of mineral-N were generally higher under *Kalmia* seedlings than under spruce or birch seedlings, we hypothesize that *Kalmia* roots also increased the biochemical immobilization of N. The production of N-binding compounds in the *Kalmia* rhizosphere may therefore play a determinant role in assuring its dominance over disturbed sites, with high tannin concentrations in *Kalmia* litter leading to the establishment of a positive feedback loop through which once-forested sites may be degraded to heaths of low nutrient availability. For example, fertilization trials have shown that the competitive ability (Prescott et al., 1995) and production of leaf tannins (Titus et al., 1993) by *Kalmia* increases with decreasing N fertility. Although sites were unreplicated, humus from the poor site was higher in tannins and other phenolic compounds and lower in extractable NH_4^+–N than humus from the rich site. It remains to be shown whether good softwood growth on richer *Kalmia* sites is the result of an initial threshold level of N fertility that neutralizes the N-binding potential of *Kalmia* humus and allows spruce seedlings to grow to maturity, to close canopy and to suppress *Kalmia* by shading. If the suppression of *Kalmia* on disturbed sites in central Newfoundland depends on the swiftness with which *photosynthesis-driven* N cycling can be established, then judicious fertilizer-N application during the early stages of softwood growth may be a viable silvicultural prescription.

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