Ammonium and Nitrate Uptake Characteristics of Hydroponically-Grown Boreal Forest Tree Species and Selected Understory Vegetation

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Abstract

With increasing public concern regarding sustainable forest management, forest land managers are obligated to ensure successful seedlings establishment and growth, particularly within the first few years. In order to achieve this goal there needs to be adequate seedling uptake of moisture and nutrients from the soil. Under conditions of adequate soil moisture, a reduction in early growth of planted white spruce and jack pine seedlings (two important commercial tree species in Saskatchewan) through *interspecific competition* with non-crop vegetation is primarily attributed to reductions in seedling uptake of soil nutrients, particularly N. Despite numerous reports on the competitive inhibition of young conifer seedlings by native understory vegetation, no attempts have been made to compare the relative N uptake ability of conifer planting stock with native boreal forest competitors. A depletion experiment was conducted to study the relationship between N concentration and subsequent ion absorption by roots of five competing boreal forest species. By monitoring the decrease in solution N concentration over time, the relative NH_4^+-N and NO_3^--N uptake capacity of each species was quantitatively determined. Results from this study indicate that white spruce and jack pine seedlings have a lower measured NH_4^+-N and NO_3^--N uptake capacity compared to native forest competitors, making these conifers relatively poor competitors for available N in soil. Calamagrostis exhibited a superior capacity for NH_4^+-N and NO_3^--N uptake, suggesting that silvicultural practices that reduce the establishment of this grass species in the field will benefit the growth of planted conifer seedlings. A greater understanding of the relative N uptake capacity between conifer seedlings and native understory competitors may, therefore, lead to improved silviculture practices and subsequent plantation productivity.

Introduction

Nitrogen (N) is considered to be the most limiting nutrient in the boreal forest (Wollum and Davey, 1975), therefore plants possessing a greater ability for sequestering soil N will have a competitive advantage in terms of resource capture, and hence, increased biomass accumulation and growth. In the past, poor conifer seedling performance in the first year or two following outplanting has placed the planted stock at a major disadvantage in the competition with native vegetation for available soil nutrients. However, through considerable advancements in seed selection and nursery growing protocol, current planting stock used in reforestation practices exhibit greater root growth capacity, vigor, and quicker growth. As a result, reduced growth following outplanting, know as *planting check*, is almost non-existent today (Derek Sitters, personal communication). However, it is still during this early establishment phase that outplanted conifer seedlings are the most vulnerable to lethargic growth or mortality because of reductions in seedling uptake of soil nutrients, particularly N (Woods et al., 1992). Apart from edaphic controls on nutrient availability, the ability of these competing species to sequester available N in soil depends primarily on plant physiological characteristics. Therefore, a greater understanding of the relative N uptake capacity between conifer seedlings and native competitor species may lead to improved silviculture practices and subsequent plantation productivity.

Since the development of a depletion technique by Claassen and Barber (1974), the dynamics of N (NH_4^+-N and NO_3^--N) uptake have been reported for a few boreal forest species (McFee and Stone, 1968; Kronzucker et al., 1995; Kronzucker et al., 1996). Although these studies are important for characterizing N uptake by various tree species, no attempt has been made to compare the relative NH_4^+-N and NO_3^--N uptake of conifer planting stock with native boreal forest competitors which typically inhabit plantations following harvesting and inhibit growth of outplanted seedlings.

The objective of this study is to determine the NH_4^+-N and NO_3^--N uptake characteristics for roots of jack pine (*Pinus banksiana*) and white spruce seedlings (*Picea glauca* (Moench) Voss.), along with three competitive common native boreal forest species: calamagrostis (*Calamagrostis canadensis* (Michx.) Beauv.), fireweed (*Epilobium angustifolium* L.), and aspen (*Populus tremuloides* Michx.). Determining the relative NH_4^+-N and NO_3^--N uptake capacities will be useful in quantitatively assessing competitive differences between these species.

Materials and Methods

Plant Material

Seeds of calamagrostis and fireweed were collected from the northern boreal forest. The seeds were germinated on filter paper in a petri dish, periodically moistened with deionized water. Seeds were maintained until root extension was sufficient to allow satisfactory transplantation (approximately 14 d; primary radicle was 2-3 cm long). Seedlings were transferred into 4 L pots containing Terra-Lite® RediEarth® potting soil (W.R. Grace and Co. Ajax, Ontario). Forty days after transplanting, the roots of 28 plants for each species were washed free of soil, and transferred into 40 L styrofoam tanks (50 cm x 33 cm x 32 cm) containing an aerated nutrient solution (Table 1). Plants were grown for an additional 30 days, to allow adequate time for acclimation to the hydroponic culture prior to the actual depletion experiment.

Table 1: Composition of Standard Nutrient Solution

Element	Concentration	Source	Element	Concentration	Source
N	700 µM	NH_4NO_3	Fe	80 µM	FeNaEDTA
P	15 µM	$CaH_4(PO_4)_2H_2O$	B	0.02 µM	H_3BO_3
K	500 µM	KCl	Cu	5 pM	$CuCl_2 \bullet 2H_2O$
Mg	200 µM	$MgSO_4 \bullet 7H_2O$	Mo	5 pM	$Na_2MoO_4 \bullet 2H_2O$
Ca	400 µM	$CaSO_4 \bullet 2H_2O$	Mn	0.01 µM	$MnCl_2 \bullet 4H_2O$
S	560 µM	$MgSO_4 \bullet 7H_2O + CaSO_4 \bullet 2H_2O$	Zn	0.03 µM	$ZnCl_2$

These nutrient concentrations were based on soil solution concentrations present in forest soils (Van Rees, unpublished data). Solution pH was monitored periodically and maintained between 4.5 and 4.7 using 0.05 M H_2SO_4 and NaOH. Nutrient solutions were continuously aerated using aquarium pumps. Water loss by evapotranspiration was compensated for with daily additions of deionized water to maintain solution volume. The solutions were completely changed every 4 d. The temperature of the nutrient solution was 18 ± 1 ^oC.

Seedlings of jack pine, white spruce, and aspen were nursery-grown and supplied as 1+0 container planting stock. The jack pine and white spruce seedlings were lifted in November, 1998 and subsequently cold-stored. The aspen were hot-lifted June 1, 1999. Twenty-eight seedlings of each species were randomly selected and their root systems washed free of soil and transferred to similar 40 L hydroponic culture tanks. These seedlings were grown for a 60 d period before the depletion experiment.

All species were grown in a controlled environment growth chamber. Air temperature was 22 ^oC in the day and 18 ^oC at night. Lighting (irradiance) was provided by racks of Cool White VHO fluorescent and incandescent lights (Sylvania, Drummondville, Ont.). Photon flux density was approximately 400 µmol m^{-2} s^{-1} at canopy level and was measured using a LI-COR quantum light meter (model LI-189; LI-COR, Lincoln, NE).

Depletion Experiment

A depletion experiment was conducted to study the relationship between N concentration and subsequent ion absorption at the root surface for roots of the five competing boreal forest species. By monitoring the decrease in solution N concentration over time, the relative NH_4^+-N and NO_3^--N uptake capacity of each species was quantitatively determined (Claassen and Barber, 1974). Four replicates of each species were grown in individual 2 L depletion vessels (11 cm dia. x 24 cm h) and randomly placed in the growth chamber. Depletion vessels were initially painted black to eliminate incidental light on the root systems, then painted white to minimize heating of root zones under the high intensity lights. The experiment was repeated two weeks later.

Forty-eight hours before the start of the depletion experiment, the root systems of all the species were rinsed with deionized water and placed in fresh standard nutrient solution without N. The purpose of this N deprivation was to induce starvation thereby eliciting a greater uptake response during the subsequent experiment. After this starvation period, eight plants from each species were randomly selected and transferred (in pairs) to four 2 L depletion vessels containing 1.5 L of the nutrient solution containing a known concentration of NH_4^+-N and NO_3^--N. In trial # 2 twelve individual tree seedlings were transferred (in triplets) to four vessels, while only one calamagrostis or fireweed plant was placed in each depletion vessel. In an attempt to ensure complete depletion of N from solution three tree seedlings (instead of two) were placed in a single depletion vessel, and the length of depletion experiment extended from 18 h to 24 h. However, for calamagrostis and fireweed, only a single plant (instead of two) was placed in each vessel. This was done in order to prolong the depletion period.

Sampling

For each depletion vessel, the solution N concentration (NH_4^+-N and NO_3^--N) was sampled immediately before root immersion, after 1/2 hour, and then every hour until the end of the depletion period. Samples were extracted in 5 mL aliquots taken midway up the depletion vessel. Samples were frozen until analysed for NH_4^+-N and NO_3^--N concentrations using an auto analyser (Technicon II autoanalyser). The N removed in sampling was < 5% of the total N at the start of the experiment, hence, N losses from sampling are assumed to be negligible. Decreases in solution volume resulting from sampling and transpiration were restored with deionized water. Upon completion of the depletion experiment, solution volume and pH for each vessel were measured.

At the conclusion of each depletion trial the tree seedlings and plant species were destructively harvested and separated into shoots and roots. The root systems from each vessel were rinsed, blotted dry using paper towel, and weighed to determine total fresh root weight. All samples have been cold-stored (4 ^oC) until further processing can be done. Total root length (L) will be estimated using a scanner and root length determination software (Bernston, 1992). Average root radius and root surface areas were calculated according to Barber (1984). Average root radius (r_o) is calculated from $r_o = (fresh\ weight/\pi L)^{0.5}$. This equation assumes a root density of 1.00 g/cm^3. In order to standardize values of uptake rate between species (with varying root morphology and biomass), total root surface area (A) is calculated using $A=2r_o\pi L$. This equation assumes a cylindrical root shape. Values of NH_4^+-N and NO_3^--N uptake can then be expressed in terms of root surface area (Table 2).

Table 2: Selected Plant Parameters from Depletion Vessels for all Species (means ± SD, n=8)

Species	Shoot Dry Weight (g)	Root Dry Weight (g)	Root Surface Area (m^2)
Calamagrostis	15.06 (1.55)	14.53 (1.97)	0.47 (0.04)
Fireweed	17.59 (4.13)	13.53 (1.92)	0.35 (0.02)
Aspen	24.33 (3.19)	14.85 (2.27)	0.20 (0.07)
White Spruce	37.24 (3.73)	15.28 (1.37)	0.23 (0.03)
Jack Pine	26.38 (2.94)	14.77 (1.77)	0.26 (0.09)

The uptake rates were determined by calculating the rate of NH_4^+-N and NO_3^--N disappearance from solution and based on the initial hour of the depletion period. Only the first hour of each depletion curve was used, since this represented a period of non-limiting uptake for all species (zero-order kinetics). After this period, the uptake of NH_4^+-N and NO_3^--N by calamagrostis was likely inhibited by low solution N concentrations, thereby making uptake comparisons between the species inappropriate. These uptake rates were then expressed on an uptake per day basis for the sake of providing numbers of reasonable magnitude for comparison.

Statistical Analysis

Uptake rates for each species are reported as a mean of a maximum of eight replications. Uptake means (n = 8) for NH_4^+-N and NO_3^--N for roots of each species were analysed using one-way ANOVA and LSD (0.05) are reported where appropriate.

Results and Discussion

Preferential NH_4^+-N Uptake

For all of the competitor species the uptake of NH_4^+-N was considerably higher than NO_3^--N until the NH_4^+-N was sufficiently depleted from solution. NO_3^--N uptake by conifer seedlings was almost non-existent. This preferential uptake of NH_4^+ by roots of the tree seedlings is in agreement with previous studies using various tree species (McFee and Stone, 1968; France and Reid, 1978; Keltjens, 1989; Marschner et al., 1991; Peuke and Tischner, 1991; Abbes et al., 1995; Kronzucker et al., 1996; Eltrop and Marschner, 1996). These higher observed uptake rates of NH_4^+-N compared to NO_3^--N are typical of forest tree species that have physiologically adapted to conditions where NH_4^+-N is the predominant N species in soil. The depletion curves of calamagrostis, fireweed, and aspen indicate a strong uptake capacity NO_3^--N as well as NH_4^+-N.

The capacity for simultaneous NO_3^--N uptake was most prevalent with calamagrostis. Increases in mineralization and nitrification following harvesting have been shown to significantly increase the levels of NO_3^--N in many forest soils (Vitousek and Melillo, 1979; Matson and Vitousek, 1981; Vitousek and Andariese, 1986; Robertson et al., 1987; Davidson et al., 1992; Walley et al., 1996). Smith et al. (1968) reported an 18-fold and 34-fold increase in the numbers of *Nitrosomonas* and *Nitrobacter*, respectively, after harvesting a forest in Connecticut. The greater flexibility for N absorption of the competitor species, in terms of a high capacity for NH_4^+-N uptake, coupled with an ability to simultaneously utilize NO_3^--N, helps to explain the highly competitive nature of these native plant species during subsequent replantation attempts following harvesting.

NH_4^+-N and NO_3^--N Absorption

When looking at NH_4^+-N and NO_3^--N absorption over time, calamagrostis was able to completely deplete NH_4^+-N and NO_3^--N from solution in less than four hours (Figures 1and 2).

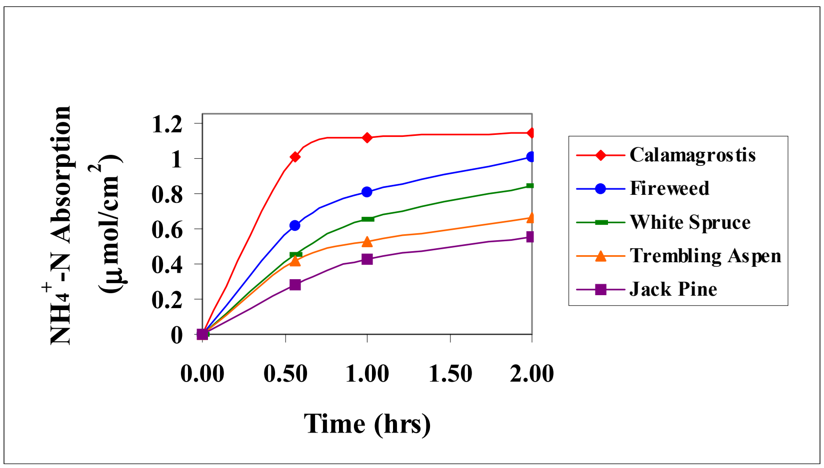

Figure 1: NH_4^+-N absorption curves for five boreal forest species.

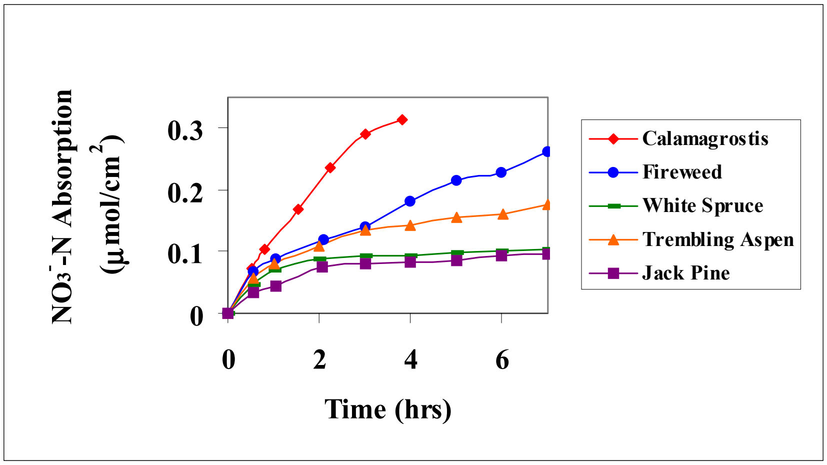

Figure 2: NO_3^--N absorption curves for five boreal forest species.

Because the uptake of NH_4^+-N and NO_3^--N by calamagrostis was so rapid, another depletion experiment was conducted using a larger depletion vessel (14 L) in order to extend the depletion period (data not shown). Unlike the native competitor species which seem proficient at utilizing NO_3^--N as the sole N source, white spruce, and jack pine seedlings were extremely limited in their capacity for NO_3^--N uptake. Hence, white spruce and jack pine had more than 90 % of the NO_3^--N remaining in solution after the 24 h depletion period.

NH_4^+-N and NO_3^--N Uptake Rates

Comparing the relative N uptake characteristics of the different species is useful for the preliminary characterization of the differing abilities of each species to absorb NH_4^+-N and NO_3^--N from solution. This is directly related to their relative competitive ability for acquiring N from the soil (Figure 3).

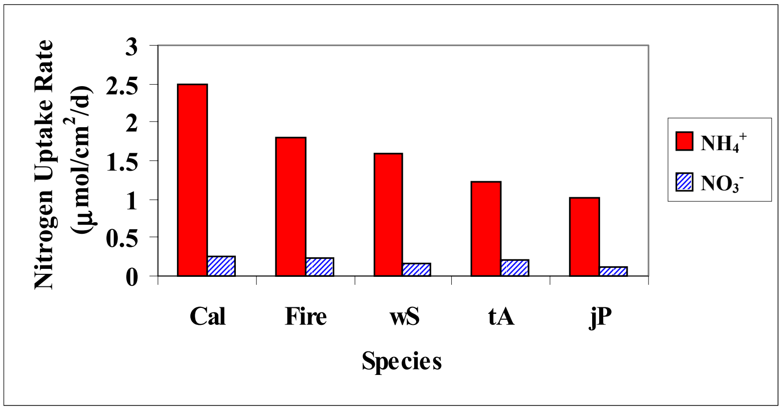

Figure 3: NH_4^+-N and NO_3^--N uptake rates between species (means, n=8). Similar coloured columns followed by the same letter are not significantly different (P < 0.05)

For all species tested, the rate of NH_4^+-N uptake is considerably greater than that of NO_3^--N. This is not surprising considering forest plant species have physiologically adapted to conditions where NH_4^+-N is the predominant inorganic N species present in these soils. Calamagrostis also has a significantly ($P < 0.05$) greater rate of NH_4^+-N uptake compared to all other species, and significantly ($P < 0.05$) greater rate of NO_3^--N uptake compared to the conifer seedlings. The measured NH_4^+-N and NO_3^--N uptake capacity of aspen is surprising considering it is typically a vigorous competitor on mixedwood blocks following harvesting. This might reflect the dependence a young aspen seedling has on the peripheral network of roots from which it suckers, for providing nutrients during its initial rapid growth following a disturbance rather than its inherent root uptake capacity. Unlike white spruce which has adapted to finer texture soils with greater fertility, the lowest measured NH_4^+-N and NO_3^--N uptake rates for jack pine compared to all other species tested, is indicative of the adaptation of this species for slow growth on coarse-textured forest soils with inherently poor fertility.

Conclusions

An understanding of the N uptake characteristics of conifer tree seedlings is important for developing silvicultural practices that improve N fertilizer use efficiency. Staples and Van Rees (1999) reported a low fertilizer use efficiency of ^{15}N fertilizer after a surface broadcast application, simply due to the more efficient uptake systems of surrounding competing vegetation. Studying the differential NH_4^+-N and NO_3^--N uptake of these competing species is important for understanding outplanted conifer seedling performance in Saskatchewan boreal forest ecosystems. This is of particular importance in young forests following logging, where increased mineralization and nitrification rates lead to relative increases in NO_3^--N availability.

Results from this study support the hypothesis that white spruce and jack pine seedlings have lower NH_4^+-N and NO_3^--N uptake rates compared to the native competitor species, hence making these conifers relatively poor competitors for available N in soil. The relative uptake characteristics between these five boreal forest species have important implications for silviculture management, because this study has shown calamagrostis to exhibit a superior capacity for NH_4^+-N uptake along with a physiological flexibility allowing it to absorb any available NO_3^--N. This will most certainly facilitate the rapid growth of this grass species and make it an efficient competitor for soil moisture, light, and space. Thus, suggesting that silvicultural practices (e.g. selective vegetation management) that reduces the establishment of this principal competitor species in the field, will greatly benefit the growth of planted conifer seedlings.

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