Assessing N Competition Between Outplanted Conifer Seedlings and Early Successional Plants Using Ion-Exchange Membranes

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Abstract

During the early establishment phase, outplanted white spruce (*Picea glauca* (Moench) Voss.) and jack pine (*Pinus banksiana* Lamb.) seedlings are vulnerable to lethargic growth or mortality because of interspecific competition for soil nutrients, particularly nitrogen (N). Accurately quantifying the degree of N competition is essential for supporting effective vegetation management decisions. This study evaluated N competition at four boreal forest sites, three years following outplanting, using two-week *in situ* burials of ion-exchange membrane (IEM) in plots with and without vegetation management (VM). The effect of noncrop N uptake on soil N availability also was assessed using conventional 2*N* KCl extractions. Vegetation management continued to support increased conifer seedling growth, with no effect on survival compared to control plots. Although the N supply rate measured using IEM (Plant Root Simulator™-probes) were not correlated ($P > 0.05$) with 2*N* KCl-extracted N concentration, there was a correlation ($R^2 = 0.68$ to 0.76, $P < 0.01$) between N supply rate and seedling growth. Ammonium-N supply rate was better correlated than NO_3^--N with conifer seedling growth, which is in agreement with preferential NH_4^+-N uptake by conifer species. The results of this study support the use of *in situ* IEM burials for monitoring soil N bioavailability during the early establishment phase.

Introduction

White spruce (*Picea glauca* (Moench) Voss.) and jack pine (*Pinus banksiana* Lamb.) are important commercial tree species in the boreal forest and annually account for more than 40 % of the replanted area in Canada (B. Haddon, Canadian Forest Service, personal communication). With increasing public concern regarding sustainable forest management, forest land managers are obligated to ensure adequate restocking of seedlings on harvested sites. The ability of early successional plant species to inhibit the growth of white spruce and jack pine is well documented (Eis 1981; Bell et al. 2000; Hangs et al. 2002; 2003a). Under conditions of adequate soil moisture, interspecific competition for soil nitrogen (N) often is the principal cause of decreased white spruce and jack pine seedling growth during the early establishment phase (Staples et al. 1999; Robinson 2001). Measuring soil N availability, with and without the presence of competitor species, and accurately relating it to outplanted seedling growth, therefore, should provide a useful index of belowground competition for supporting effective VM strategies.

Conventional soil tests, based on chemical extractions, historically have failed in this regard because the data provided are poorly correlated with seedling nutrient uptake and growth (Fisher and Binkley 2000). The objective of this study was to assess the interspecific competition between outplanted white spruce and jack pine seedlings and noncrop vegetation by measuring N supply rates in different VM treatment plots using Plant Root Simulator (PRS)™-Probes. The hypothesis tested was that *in situ* burials of IEM would provide biologically more meaningful data compared with a conventional soil extraction, making IEM more effective for studying N competition during the early establishment phase.

Materials and Methods

Study sites

Two white spruce and two jack pine field sites were established in the boreal mixedwood forests of Saskatchewan. One white spruce and one jack pine site were located near Alcott Creek, approximately 40 km southeast of Meadow Lake, Saskatchewan. The second pair of white spruce and jack pine sites was located near Wabeno Lake, approximately 80 km northwest of Prince Albert, Saskatchewan. The soils at each site were classified as Orthic Gray Luvisols (Alcott and Wabeno white spruce sites) and Brunisolic Gray Luvisols (Alcott and Wabeno jack pine sites), developed on glacial till with clay loam surface textures (Alcott and Wabeno white spruce sites) or glacial till overlain by a layer of well-sorted sandy material and sandy loam (Alcott jack pine) and silty loam (Wabeno jack pine) surface textures (Rostad and Ellis 1972; Head et al. 1981). The ecological classification unit of each site prior to harvesting was: Alcott white spruce (E26-b3.3/SM4:8r-10CL); Alcott jack pine (E26-c1.2/SD2:3r-40SL); Wabeno white spruce (E18-b3.3/SM4:8r-10CL); and, Wabeno jack pine (E18-b1.1/SM3:8r-10SiL) (Beckingham et al. 1996). For the first three years following outplanting, the principal competitor species were calamagrostis (*Calamagrostis canadensis*), fireweed (*Epilobium angustifolium* L.), and aspen (*Populus tremuloides* Michx.). For a list of successional species diversity and abundance at each site, refer to Hangs et al. (2003a).

Experimental design

For a complete description of the field study, refer to Hangs et al. (2003a). Briefly, the experimental design was completely randomized, with two VM treatments (with and without weed control) replicated three times at each site. Six treatment plots (12 m x 12 m) were established at each site, and in the spring of 1999, 49 (seven rows of seven seedlings) one-year old white spruce or jack pine container-grown seedlings were planted by a single planter within each treatment plot (2 m spacing or 2400 stems/ha). Treatment plots either had no weed control (Control), or weed control (VM) during the growing season. Initial shoot height and root collar diameter (RCD) of the 25 measurement seedlings in the centre of each treatment plot were recorded immediately following outplanting and at the end of three growing seasons (September, 1999, 2000, and 2001, respectively). Seedling volume was calculated assuming a conical form. Seedling growth responses for each treatment plot were based on the mean of the 25 measurement seedlings. Only the third year seedling growth data are reported.

Soil N availability indices

PRS™-Probes

Plant Root Simulator™-probes were used to measure soil N availability (i.e., relative N competition) within control and VM plots, three years following outplanting, for correlation with seedling growth. Two nests of PRS™-probes were installed within each treatment plot and each nest consisted of two pairs of PRS™-probes (i.e., two cation- and two anion-exchange). The PRS™-probes were inserted vertically into the Ae horizon and left in the soil for two weeks, from July 24-Aug 7. Each nest of PRS™-probes were buried inside of polyvinyl chloride (PVC) cylinders (10 cm diameter x 20 cm long) to avoid the confounding effects of root competition. It was assumed that PVC cylinders did not significantly affect soil temperature and moisture and, therefore, soil N supply to the IEM compared to bulk soil (Adams et al. 1989; Hart and Firestone 1991; Huang and Schoenau 1997). The PRS™-probes within each nest were combined during the analysis. The soil N supply rate within each VM treatment measured using the PRS™-probe was expressed as μg of N (NH_4^+-N, NO_3^--N, or total) adsorbed per 10 cm^2 of IEM surface area over the two-week burial period (i.e., μg N/10 cm^{-2}/2 weeks).

2 M KCl Extractions

For comparison purposes, the effect of noncrop N uptake on soil N availability was assessed using conventional 2*N* KCl extractions and correlated with seedling growth. At time of PRS™-probe insertion, two subsamples from the Ae horizon were collected from each VM treatment plot for analysis. Each subsample was a composite from ten soil cores taken randomly within the plot to account for any microscale variability. Samples were bagged, placed in cold storage prior to transport, and stored at 4^{o}C until being further processed.

Statistical analyses

Seedling growth parameters and soil N availability data for all sites were analysed independently using the GLM procedure in SAS (Version 8.0, SAS Institute Inc. Cary, NC). Means comparisons were performed using least significant differences (LSD) at a significance level of 0.05. The LSD option was used to carry out pairwise *t* tests (equivalent to Fisher's protected LSD) of the different means between VM treatments. Homogeneity of variances and normality of distributions of all data sets were checked before any statistical analysis. No data transformations were necessary. Simple linear regressions were performed using the REG procedure in SAS (Version 8.0, SAS Institute Inc. Cary, NC) with pooled (n=24) data from all sites to quantify the relationship between the two soil N availability indices and seedling growth.

Results

Conifer seedling establishment and growth

Overall, seedling mortality was low for all study sites, with greater than 96 % survival after the third growing season and no significant difference (P >0.05) between the VM treatments at any site. Seedling growth differences between the two VM treatments followed a similar trend to the first two years (Hangs et al. 2003a; Table 1). There was no significant difference (P >0.05) in seedling growth between VM treatments at the Alcott jack pine site.

Vegetation management increased white spruce seedling height, RCD, and stem volume growth increments at the Wabeno site and conifer seedling stem volume growth increments on all sites except Alcott jack pine (Table 1). The larger percent difference in seedling growth response to VM each year was most prevalent with stem volume growth increment. Averaging all seedling growth parameters and sites, seedling growth was 16, 42, and 62 % greater in the VM plots than in the control plots after each growing season, respectively (Hangs et al. 2003a; Table 1). The outplanted seedlings at the Wabeno jack pine site clearly had the largest growth of all sites after three growing seasons.

Soil N availability

For all sites except Alcott jack pine, the total N supply rate was larger in the VM plots than in the control plots (Table 2). At both Wabeno sites, there were larger NH_4^+-N and NO_3^--N supply rates measured in the VM plots compared with the control plots. Except for the Alcott white spruce site, NH_4^+-N was the predominant inorganic N species at all sites (Table 2). Soil NO_3^--N availability was below the mdl for both the PRS™-probe and 2*N* KCl extraction at the Alcott jack pine site. There was no significant difference ($P > 0.05$) in N availability measured using conventional 2*N* KCl extractions between the VM treatments at any site (Table 2). There was no correlation ($R^2 = 0.03$-0.54, $P > 0.05$) between total N, NH_4^+-N, or NO_3^--N measured using PRS™-probes and 2*N* KCl extractions within VM treatments at any site. The Wabeno jack pine site had noticeably larger soil N supply rates compared with the other sites, although this difference was not statistically tested (Table 2).

Table 1. Mean (n = 3) Height (HT, cm/yr), Root Collar Diameter (RCD, mm/yr), and Stem Volume (VOL, cm^3/yr) Growth Increments for White Spruce and Jack Pine Seedlings in Vegetation Management Treatments Three Years After Outplanting.

Species	Site	Treatment	Year 3 HT	Year 3 RCD	Year 3 VOL	Since Start HT	Since Start RCD	Since Start VOL
White Spruce	Alcott	Control	12.03a*	1.27a	3.67b	27.73a	5.00b	8.40b
		Vegetation Management	11.37a	2.20a	8.23a	28.73a	7.33a	13.73a
	Wabeno	Control	12.57b	2.37b	12.50b	28.47b	8.70b	20.83b
		Vegetation Management	18.80a	4.33a	20.43a	39.30a	12.67a	33.27a
Jack Pine	Alcott†	Control	13.30a	2.73a	10.13a	38.07a	8.40a	15.13a
		Vegetation Management	18.07a	4.30a	12.63a	40.17a	8.70a	19.40a
	Wabeno	Control	50.33a	8.07a	90.90b	85.80a	17.03b	107.80b
		Vegetation Management	43.30a	12.43a	166.33a	88.30a	23.17a	194.67a

* For each site, means within a column followed by the same letter are not significantly different (*P* >0.05) by LSD.

† Each replicate is a mean of <25 seedlings due to heavy browsing prior to the second growing season.

Table 2. Mean (n = 3) Total N, NH_4^+-N, and NO_3^--N Measured Late-Season Using PRS™-probes (µg/10cm^{-2}/2 weeks) and 2*N* KCl Extractions (µg/g) in Vegetation Management Treatments Three Years After Outplanting.

			PRS™-probes			2*N*KCl		
Species	Site	Treatment	Total N*	NH_4^+-N	NO_3^--N	Total N	NH_4^+-N	NO_3^--N
White Spruce	Alcott	Control	10.8b†	9.3a	1.4b	4.63a	4.63a	< mdl
		Vegetation Management	22.3a	9.0a	13.3a	2.82a	2.75a	0.07
	Wabeno	Control	16.9b	13.2b	3.6b	3.14a	2.97a	0.17a
		Vegetation Management	50.2a	30.7a	19.5a	8.43a	3.86a	4.57a
Jack Pine	Alcott	Control	12.4a	12.3a	< mdl	2.06a	2.06a	< mdl
		Vegetation Management	9.1a	9.0a	< mdl	2.03a	2.00a	< mdl
	Wabeno	Control	86.9b	60.5b	26.4b	3.54a	3.54a	< mdl
		Vegetation Management	107.5a	74.7a	32.9a	4.47a	4.10a	0.37

* Based on the addition of NH_4^+-N and NO_3^--N prior to adjusting for method detection limits (mdl).
† For each site, means within a column followed by the same letter are not significantly different (P >0.05) by LSD.

Relationship between soil N availability and seedling growth

Linear regressions comparing total N (i.e., NH_4^+-N + NO_3^--N) availability, measured using PRS™-probes and 2*N* KCl extraction, with third year white spruce and jack pine seedling growth are shown in Figure 1. Using pooled (n=24) data from both VM treatments for all sites, PRS™-probe N supply rate was correlated with seedling height, RCD, and stem volume increments; however, there was no correlation (P > 0.05) between 2*N* KCl-extractable N and seedling growth (Fig. 1). There was no correlation (R^2 = 0.08-0.50, P > 0.05) between 2*N* KCl-extractable total N, NH_4^+-N, or NO_3^--N and seedling growth increment within VM treatments at any site. The PRS™-probe total N, NH_4^+-N, and NO_3^--N supply rate data were better correlated with jack pine than white spruce seedling growth regardless of VM treatment (data not shown). However, due to the limited data from which these regressions were derived, small differences in R^2 values should be interpreted cautiously. Although both NH_4^+-N and NO_3^--N supply rates were correlated with outplanted conifer seedling growth, there was a stronger correlation with NH_4^+-N supply rate (Fig. 2).

Discussion

Conifer seedling growth

The ability of early successional plant species to inhibit the growth of outplanted white spruce and jack pine seedlings, which was apparent in the first two years (Hangs et al. 2003a), continued into the third growing season. The increased conifer seedling growth response to VM over the first three years illustrates the compounding effects of interspecific competition over

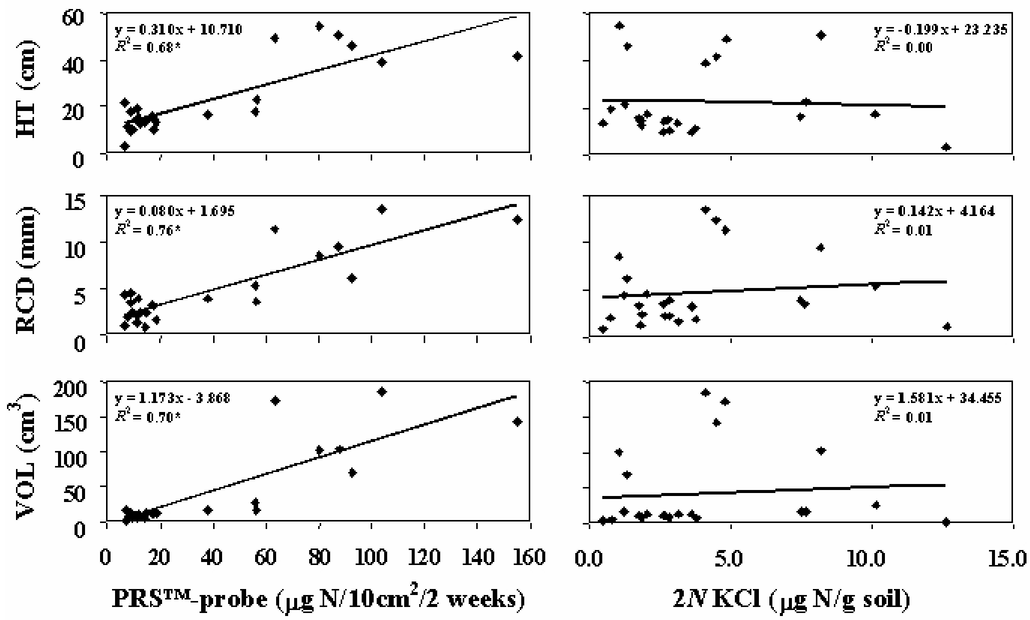

Figure 1. Correlations (n=24) of PRS™-probe total nitrogen (NH_4^+-N and NO_3^--N) supply rates and 2*N* KCl-extracted concentration measured late-season with outplanted conifer seedling height (HT), root collar diameter (RCD), and stem volume (VOL) growth increments at four sites in the boreal mixedwood forest of Saskatchewan. Coefficient of determination (R^2) significance of P <0.01 indicated by *.

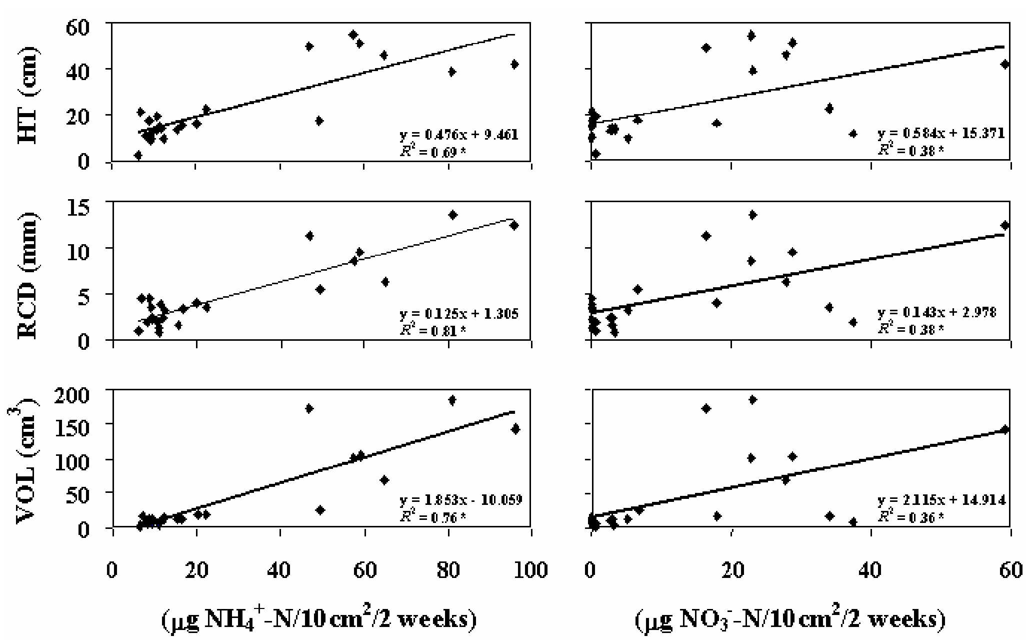

Figure 2. Correlations (n=24) of PRS™-probe NH_4^+-N and NO_3^--N supply rates measured late-season with outplanted conifer seedling height (HT), root collar diameter (RCD), and stem volume (VOL) growth increments at four sites in the boreal mixedwood forest of Saskatchewan. Coefficient of determination (R^2) significance of P <0.01 indicated by *.

time and has been reported elsewhere (White and Newton 1990; Munson et al. 1993; Rose and Ketchum 2002). The continued lack of differences in seedling growth increments between VM treatments at the Alcott jack pine site can be attributed to the relative lack of competing vegetation at this site even after three years. The outplanted seedlings at the Wabeno jack pine site had the greatest growth of all sites in this study, probably due to the larger soil N supply rates (Table 2).

Soil N availability

The increased soil N supply rates within VM plots compared with the control plots primarily is due to the lack of N uptake by noncrop vegetation, thereby supporting increased conifer seedling growth in the VM plots. The NH_4^+-N and NO_3^--N availability measured using PRS™-probes and conventional 2*N* KCl extractions in this study were consistent with values reported elsewhere for Ae horizon soil (Huang and Schoenau 1997; Maynard 1997; Johnson et al. 2001). The relative lack of noncrop vegetation at the Alcott jack pine site probably accounted for there being no significant difference (P >0.05) in soil N availability between the VM treatments (Table 2). The undetectable NO_3^--N levels at the Alcott jack pine site probably is attributable to the coarse-textured soils at this site allowing NO_3^--N leaching below the depth of sampling. In view of the lack of significant differences (P >0.05) observed for soil N availability between the VM treatments measured using 2*N* KCl extractions compared with the PRS™-probes (Table 2), it appears that the PRS™-probes provided a more sensitive measure of N availability in forest soils in this study.

Relationship between soil N availability and seedling growth

When validating new soil testing methodologies, the convention is to correlate its nutrient availability index with traditional testing practices. Although the N supply rate measured using PRS™-probes was not correlated (P >0.05) with 2*N* KCl-extractable N, the PRS™-probe N supply rate was the only N availability index correlated with seedling growth (Fig. 2). This is not surprising considering cumulative N supply rate, determined by removing buried PRS™-probes after some weeks and re-inserting fresh PRS™-probes in the same soil slot, is well correlated (R^2 >0.74, P <0.05) with outplanted conifer seedling tissue N concentration (D. Maynard, unpublished data). The apparent indifference of 2*N* KCl extractions toward the VM treatments (Table 2) and conifer seedling growth (Fig. 2) illustrates the shortcoming of conventional soil extractions in measuring nutrient availability that correlate with plantation productivity, thus precluding their use in routine forest management practices (Kraske et al. 1989). The better correlation of PRS™-probe NH_4^+-N supply rate than NO_3^--N with white spruce and jack pine seedling growth increment is not surprising, considering that these conifer seedlings preferentially take up NH_4^+-N (Hangs et al. 2003b). The indiscriminate adsorption of inorganic N by IEM compared with conifer species suggests a need for caution when modelling seedling N uptake and growth based on total N supply rates.

Conclusion

The capacity of early successional plant species to outcompete outplanted white spruce and jack pine seedlings for available N in soil is well known; however, biologically meaningful indices for quantifying this interspecific competition are lacking. Compared with a conventional 2*N* KCl extraction, *in situ* burials of IEM provided the necessary sensitivity and precision to measure differences in N supply rates between VM treatments and helped explain the variability present in the early growth of conifer seedlings between the VM treatments. Results of this study support the hypothesis that *in situ* burials of IEM provide biologically more meaningful data compared with a conventional 2*N* KCl extraction, making IEM more effective for studying N competition between boreal forest species during the early establishment phase.

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