Nitrogen Accumulation by Conifer Seedlings and Competitor Species From ^{15}Nitrogen-labeled Controlled-Release Fertilizer

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ABSTRACT

A major impediment to the establishment of outplanted conifer seedlings is competition for available soil N by early successional species. The objective of this field study was to determine the fate of controlled-release fertilizer (CRF) N in soils with outplanted white spruce (*Picea glauca* [Moench] Voss.) and jack pine (*Pinus banksiana* Lamb.) seedlings, and the effect of weed control or vegetation management (VM) on fertilizer N accumulation. Nitrogen-15 labeled CRF was placed next to the seedling root plug during planting at four boreal mixed wood sites. After one growing season in the control plots, fertilizer N recovery as a percentage of ^{15}N added was 4% in seedlings, 3% in competing vegetation, <1% leached, and 85% residual CRF. After two growing seasons, fertilizer N recovery was 15% in seedlings, 20% in competing vegetation, <1% leached, and 58% residual CRF. Overall, VM increased seedling fertilizer N uptake by almost 300% compared with conifer seedlings in control plots. In VM plots, fertilizer bags contained more N than in control plots after two growing seasons. In both treatments, >50% of the fertilizer N remained in the fertilizer bag, presumably remaining available in subsequent seasons. Calamagrostis (*Calamagrostis canadensis*) was the primary competitor for fertilizer N in both growing seasons, with minor competition from fireweed (*Epilobium angustifolium* L.), and aspen (*Populus tremuloides* Michx.). The use of a point source CRF delivery method resulted in high fertilizer use efficiency (FUE), and minimized losses to competing vegetation and leaching.

In the boreal forest, outplanted white spruce and jack pine seedlings are vulnerable to lethargic growth or mortality during the early establishment phase because of poor seedling uptake of nutrients, particularly N (Brockley, 1988; Robinson et al., 1998). Fertilization often is used to improve seedling survival and growth during this early establishment phase, alleviating the competition between outplanted conifer seedlings and early successional species for available soil N. In the past, the most commonly used method of applying nitrogenous fertilizer at time of planting was a broadcast application across the soil surface. However, this is an inefficient method for supplying N to outplanted seedlings in the boreal forest. Even when interspecific competition for fertilizer N is reduced through weed control or VM, very little of the broadcast fertilizer is taken up by the target seedling (Staples et al., 1999). Studies using ^{15}N to examine the fate of broadcast nitrogenous fertilizers have reported low FUE, with uptake by the outplanted seedlings during the first year or two ranging from 0.4 to 10.1% of the applied fertilizer ^{15}N (Preston and Mead, 1994; Staples et al., 1999), compared with 22.0% taken up by native early successional species (Preston et al., 1990). The excess fertilizer N not taken up by crop or noncrop vegetation is rapidly immobilized by soil microbes (Preston and Mead, 1994) or lost from the ecosystem by leaching or gaseous losses (Hulm and Killham, 1990; Preston et al., 1990; Houle and Babeux, 1994). Furthermore, depending on soil type and the rate of fertilizer application, losses of excess fertilizer N to runoff or leaching could lead to environmental problems with respect to groundwater contamination or eutrophication of surface waters (Fisher and Binkley, 2000).

Unlike broadcast applications of fertilizer N that often lead to growth stimulation of noncrop plant species (Chang et al., 1996; Thevathasan et al., 2000), the use of individual seedling fertilization methods that involve a point source of CRF, such as ‘tea bags’, are less likely to promote the growth of noncrop vegetation (Anonymous, 1995). These fertilizer bags are effective in alleviating a variety of site-limiting factors such as interspecific competition and poor soil fertility (Munson et al., 1993). Many studies have discussed the associated benefits and risks of using individual seedling fertilization methods on white spruce and jack pine growth (Burdett et al., 1984; Houle and Babeux, 1994; Anonymous, 1995). However, no attempts have been made using tracers, such as ^{15}N, to determine the fate of added CRF-N during the early establishment phase after outplanting. The objective of this study was to determine the fate of CRF-N when applied with outplanted white spruce and jack pine seedlings in the boreal forest, and the effect of VM on uptake of fertilizer N by conifer seedlings.

MATERIALS AND METHODS

Study Sites

Two white spruce and two jack pine field sites were established in the boreal mixed wood forests of Saskatchewan. One white spruce, and one jack pine site were located near Alcott Creek, approximately 40 km southeast of Meadow Lake, Saskatchewan (108°34′ W long., 53°88′ N lat., and 108°32′ W long., 53°86′ N lat., respectively). The second pair of white spruce and jack pine sites was located near Wabeno Lake, approximately 80 km northwest of Prince Albert, Saskatchewan (106°44′ W long., 54°33′ N lat. and 106°43′ W long., 55°33′ N

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Abbreviations: CRF, controlled-release fertilizer; FUE, fertilizer-use efficiency; LSD, least significant difference; PVC, polyvinyl chloride; RCD, root collar diameter; VM, vegetation management.

lat., respectively). The Alcott sites were mechanically harvested and delimbed at the stump and the Wabeno sites were mechanically whole-tree harvested. All of the sites were harvested between the summer and fall of 1998. The soils at each site were classified as Typic Haplocryalfs (Orthic Gray Luvisols at the Alcott and Wabeno white spruce sites, and Brunisolic Gray Luvisols at the Alcott and Wabeno jack pine sites) that have 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). Mean annual temperatures ranged from −1.6 to −1.0°C, with average January and July temperatures of −21 and 17°C, respectively, and approximately 80 frost-free days. The mean annual precipitation was 450 mm with 70% occurring from May to September (Rostad and Ellis, 1972; Head et al., 1981).

Experimental Design

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 by 12 m) were established at each site, and in the spring of 1999, 49 (seven rows of seven seedlings) 1-yr old container-grown seedlings of white spruce or jack pine were planted by a single planter within each treatment plot (2 m spacing or 2400 stems ha^{-1}). Plots were separated by a 5-m buffer zone containing seedlings planted at the same density as the treatment plots. At time of planting, four seedlings within each treatment plot were planted with a Reforestation Technologies International (RTI, Salinas, CA) fertilizer bag containing 5 g of polyurethane-coated, controlled-release (12–14 mo), ^{15}N-labeled urea (7.5 atom% ^{15}N enrichment). The fertilizer blend was 20-6-12-6 (N-P-K-S) with micronutrients (Zn, Fe, Mg, Cu, B, Mn, Mo). Using a 2 by 2 m seedling spacing, the equivalent fertilizer rate would be approximately 6 kg N ha^{-1}. The remainder of the treatment plot seedlings was planted with a fertilizer bag containing nonlabeled urea fertilizer of equivalent blend. The fertilizer bag was placed 5 to 7 cm from the root plug in the same planting hole. Seedlings in the buffer zone were planted without fertilizer bags.

Treatment plots either had no weed control (Control), or weed control (VM) during the growing season. Three times during each growing season, weed control within the VM plots was maintained by aboveground scalping at ground level of noncrop vegetation using brush saws. Vegetation within a 30 cm radius of each seedling was removed by hand. All vegetation growing around seedlings planted with ^{15}N-labeled fertilizer was kept for ^{15}N analysis.

Seedling Survival and Growth

Initial shoot height and root collar diameter (RCD) of the 25 measurement seedlings in the center of each treatment plot were recorded immediately following outplanting and at the end of the first and second growing seasons (September 1999 and September 2000, respectively). Seedling growth responses for each treatment plot were based on the mean of the 25 measurement seedlings.

Plant Sampling

In the control treatments, a 1-m^2 plot (seedling-centered) was placed over each ^{15}N-labeled seedling prior to harvesting to determine percent cover and average height of the early successional species. The aboveground understory vegetation was harvested and separated into respective species prior to plant ^{15}N analyses. At the end of the first growing season, two of the four ^{15}N-labeled seedlings in each treatment plot were randomly harvested. The remaining two ^{15}N-labeled seedlings were harvested after the second season. The ^{15}N-labeled seedlings were excavated using small hand tools to recover the entire seedling root system and minimize fine root losses. Percentage of cover, average height, and ^{15}N enrichment data for the conifer seedlings and early successional species for each treatment plot were based on the mean of the two sampled plots. Four random root cores (10-cm diam.) were taken within the 1-m^2 plot to a 20 cm depth to determine ^{15}N content in the roots of early successional species.

Soil Sampling

Prior to excavating the ^{15}N-labeled seedling, the remnants of the fertilizer bag were excavated. After the first growing season (103 d after fertilizer ^{15}N addition), following the removal of the fertilizer bag, a soil core (30-cm depth) was removed from directly below the RTI bag and sectioned into 5-cm increments to quantify the leaching of the fertilizer N. After the second season (464 d after the fertilizer ^{15}N addition), the soil was sampled to a depth of 60 cm and sectioned into 10-cm increments. In addition, at each site at the start of the experiment four polyvinyl chloride (PVC) tubes (10-cm diam. by 1-m length) were installed and a fertilizer bag placed in the tube at approximately the 7-cm depth in the mineral soil. The PVC tubes were used to quantify the vertical movement of fertilizer N without the confounding effects of competing root systems. At the end of each growing season, two of the tubes were excavated and the soil sectioned into 10-cm increments.

Nitrogen-15 Analysis

Shoots and roots of the excavated seedlings were separated and the roots washed free of soil. Seedling shoots and roots, aboveground biomass and roots of early successional species were oven-dried (60°C for 72 h) and weighed. All plant tissue samples were ground separately in a Wiley mill (0.425 mm mesh) and reground in a rotating ball-bearing mill. Plant tissues were analyzed for total N and ^{15}N enrichment using a TracerMass mass spectrometer interfaced to a RoboPrep sample converter (Europa Scientific, Crewe, UK). Soil samples and excavated fertilizer bags were oven-dried (60°C for 72 h), ground in a rotating ball-bearing mill and analyzed for total N and ^{15}N enrichment in the same manner as the plant samples.

Vector Diagnosis

Growth and N status (i.e., concentration and content) of the conifer seedlings grown in control and VM plots were evaluated by the vector diagnosis technique (Timmer, 1991; Haase and Rose, 1995). This technique has been applied previously to studies on the effect of VM and fertilization on the early growth of white spruce seedlings (Munson et al., 1993).

Statistical Analyses

Seedling growth parameters, percentage of cover, height, and ^{15}N enrichment data for all sites were analyzed using the General Linear Models 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. Homogeneity of variances and normality of distributions of all data sets were checked before any statistical analysis was performed, and no data transformations were necessary.

Table 1. Mean ($n = 3$) aboveground characteristics and fertilizer N uptake of species growing in control plots (i.e., no vegetation management) at the end of the first growing season. See Appendix for Latin names.

Species	Biomass	Ground cover	Average height	Uptake of fertilizer N†
	g m^{-2}	%	cm	%
		Alcott White Spruce		
White Spruce seedling	9.53c‡	2c	34.2a	16.5a
Trees§	38.52b	11b	33.0a	0.0b
Shrubs¶	32.85b	20b	10.7b	0.0b
Herbs#	3.52c	2c	12.5b	0.0b
Forbs††	107.23a	41a	12.2b	0.0b
Grasses‡‡	31.66b	24b	27.5a	13.7a
Total	223.31			30.2
		Alcott Jack Pine		
Jack Pine seedling	5.16b	2b	24.1a	9.1a
Shrubs	15.51b	6b	9.4b	0.0b
Forbs	35.08a	16ab	9.6b	0.0b
Grasses	21.29ab	18a	21.0a	15.8a
Total	77.04			24.9
		Wabeno White Spruce		
White Spruce seedling	7.40b	2c	36.2a	25.2a
Trees	35.25a	25a	35.0a	0.0b
Shrubs	2.38b	3c	5.0b	0.0b
Forbs	19.48ab	20ab	15.6b	0.0b
Grasses	33.08a	15b	20.0ab	25.9a
Total	97.59			51.1
		Wabeno Jack Pine		
Jack Pine seedling	8.39b	2b	28.7a	30.3a
Trees	20.07ab	6b	22.5a	0.0c
Shrubs	36.45a	3b	8.5b	0.0c
Forbs	36.37a	4b	8.4b	0.0c
Grasses	5.72b	14a	20.0a	4.3b
Total	107.00			34.6

† Percentage of fertilizer N released from fertilizer bag.
‡ For each site, means within a column followed by the same letter are not significantly different ($P > 0.05$) by LSD.
§ Species included: aspen and birch.
¶ Species included: blueberry, dry-ground cranberry, gooseberry, green alder, honeysuckle, Labrador tea, low-bush cranberry, raspberry, rose, twinflower, and willow.
# Species included: Bicknell's geranium, Canada thistle, dandelion, narrow-leafed hawk's-beard.
†† Species included: bishop's-cap, bunchberry, dewberry, fireweed, horsetail, Lindley's aster, palmate-leafed colt's-foot, pea vine, sarsaparilla, Solomon's seal, starflower, strawberry, and vetch.
‡‡ Calamagrostis was the only grass species present.

RESULTS

Early Successional Species Distribution

The total biomass of noncrop vegetation present within control plots after the first growing season ranged from 71.88 g m^{-2} (Alcott jack pine) to 213.78 g m^{-2} (Alcott white spruce) (Table 1; see Appendix for Latin names). Calamagrostis, aspen, and fireweed were the major early successional species in the control plots during the first growing season on all sites. The Alcott white spruce site had the greatest total biomass production and diversity of early successional species. Considering all sites together, during the second growing season, the principal early successional species within the control plots were calamagrostis, aspen, fireweed, raspberry, and blueberry. The Alcott white spruce site continued to have the greater diversity and abundance of early successional species; however, the vegetation biomass on the other three sites increased considerably from the first growing season. At the end of the second growing season, the total biomass of noncrop vegetation present within the control plots ranged from 241.42 g m^{-2} (Alcott jack pine) to 375.85 g m^{-2} (Alcott white spruce) (Table 2).

Seedling Establishment and Growth

Prior to the second growing season there was extensive browsing of some seedlings at the Alcott jack pine site. These browsed seedlings were not included in the subsequent seedling growth analysis. Overall, seedling mortality was low for all study sites, with >98% survival after the second growing season and no differences between the treatments on any site. Vegetation management increased white spruce seedling height, RCD, and stem volume growth increments after the first and second growing season at both sites (Table 3). At the Wabeno jack pine site, VM increased jack pine volume growth increment after the first growing season and height, RCD, and stem volume growth increments after the second growing season (Table 3). There were no differences in seedling growth increments between treatments at the Alcott jack pine site. Except for the Alcott white spruce site, there were no differences in seedling root biomass between the treatments on any site after the first or second growing season (statistics not shown). At the end of the second growing season, seedling root biomass was greater than after the first growing season for white spruce and jack pine growing

Table 2. Mean (n = 3) aboveground characteristics and fertilizer N uptake of species growing in control plots (i.e., no vegetation management) at the end of the second growing season. See Appendix for Latin names.

Species	Biomass	Ground cover	Average height	Uptake of fertilizer N†
	g m^{-2}	%	cm	%
		Alcott White Spruce		
White Spruce seedling	12.46c‡	3b	34.9b	16.8b
Trees§	73.25b	8b	61.7a	10.1b
Shrubs¶	123.44a	6b	26.9b	0.0d
Herbs#	25.04c	7b	38.1b	0.0d
Forbs††	98.49a	8b	23.7b	4.9c
Grasses‡‡	55.63b	44a	61.3a	49.3a
Total	388.31			81.1
		Alcott Jack Pine		
Jack Pine seedling	11.18c	3c	32.2b	12.5b
Trees	3.37c	9c	18.6b	1.1c
Shrubs	64.52b	15bc	18.2b	0.0d
Herbs	2.56c	4c	23.5b	0.0d
Forbs	68.58b	26b	16.3b	7.9b
Grasses	102.39a	43a	60.7a	52.6a
Total	252.60			74.1
		Wabeno White Spruce		
White Spruce seedling	21.23c	3c	39.2bc	30.4a
Trees	23.42c	6c	44.4ab	6.8b
Shrubs	98.09a	28a	25.1bc	0.0c
Herbs	21.42c	16bc	17.8c	0.0c
Forbs	74.64ab	25ab	25.0bc	10.4b
Grasses	59.65b	22ab	61.7a	30.8a
Total	298.45			78.4
		Wabeno Jack Pine		
Jack Pine seedling	30.08b	3c	44.8ab	60.4a
Trees	39.26b	12bc	32.4bc	0.0c
Shrubs	195.29a	42a	30.7bc	0.0c
Forbs	38.70b	21b	21.2c	0.0c
Grasses	32.45b	22b	54.0a	20.9b
Total	335.78			81.3

† Percentage of fertilizer N released from fertilizer bag.
‡ For each site, means within a column followed by the same letter are not significantly different ($P > 0.05$) by LSD.
§ Species included: aspen and birch.
¶ Species included: blueberry, dry-ground cranberry, gooseberry, green alder, honeysuckle, Labrador tea, low-bush cranberry, raspberry, rose, twinflower, and willow.
# Species included: Bicknell's geranium, Canada thistle, dandelion, narrow-leafed hawk's-beard.
†† Species included: bishop's-cap, bunchberry, dewberry, fireweed, horsetail, Lindley's aster, palmate-leafed colt's-foot, pea vine, sarsaparilla, Solomon's seal, starflower, strawberry, and vetch.
‡‡ Calamagrostis was the only grass species present.

in control plots and for white spruce growing in VM plots (Table 4).

Fate of Applied Fertilizer Nitrogen

There were no significant differences in the accumulation of fertilizer N by the outplanted white spruce and jack pine seedlings between the two treatments after the first growing season (Table 5). At all sites, calamagrostis was the only early successional species to take up fertilizer N during the first growing season. Competing vegetation accounted for 0.7 to 3.2% of the applied fertilizer ^{15}N. Except for the Wabeno white spruce site, there were

Table 3. Mean (n = 3) height (HT), root collar diameter (RCD), and stem volume (VOL) growth increments for out-planted white spruce and jack pine seedlings for each growing season.

Species	Site	Treatment	Year 1 HT	Year 1 RCD	Year 1 VOL	Year 2 HT	Year 2 RCD	Year 2 VOL	Since start HT	Since start RCD	Since start VOL
			cm yr^{-1}	mm yr^{-1}	cm^3 yr^{-1}	cm yr^{-1}	mm yr^{-1}	cm^3 yr^{-1}	cm yr^{-1}	mm yr^{-1}	cm^3 yr^{-1}
White Spruce	Alcott	Control	9.65	2.53	1.39	5.25	0.96	1.71	15.46	3.84	4.05
		Vegetation management†	10.67‡	2.89‡	2.03‡	7.64‡	2.60‡	4.23‡	17.14‡	5.14‡	6.25‡
	Wabeno	Control	8.02	3.12	2.53	8.25	3.06	5.64	17.34	6.20	8.15
		Vegetation management	9.36‡	3.83‡	2.91‡	11.62‡	4.42‡	9.86‡	19.61‡	8.29‡	12.76‡
Jack Pine	Alcott	Control	12.93	1.92	1.02	10.77	2.25	3.64	23.72	4.20	4.64
		Vegetation management†	13.12	1.99	1.11	10.86	3.32‡	4.84	21.07	5.03	5.78
	Wabeno	Control	13.45	2.24	1.45	20.89	6.57	14.95	34.97	8.84	16.41
		Vegetation management	14.21	2.82	1.83‡	31.05‡	7.82‡	25.88‡	44.35‡	10.66‡	27.72‡

† Because of heavy browsing prior to second growing season each replicate is a mean of <25 seedlings.
‡ Values are different from the corresponding control ($P < 0.05$) by LSD.

Table 4. Root biomass of out-planted conifer seedlings growing in control and vegetation management plots after the first and second growing season.

Growing season	Alcott White Spruce	Alcott Jack Pine	Wabeno White Spruce	Wabeno Jack Pine
	g			
	Control Plots			
Year 1	14.01	6.48	11.64	9.36
Year 2	20.01†	11.64†	17.56†	14.27†
	Vegetation Management Plots			
Year 1	9.71	7.91	12.41	10.04
Year 2	15.05†	8.97	16.56†	13.27

† Values are different from the previous year ($P < 0.05$) by LSD.

no differences in the amounts of fertilizer N remaining in the fertilizer bags between the treatments after 1 yr. Leaching losses of the fertilizer N were negligible after the first growing season, ranging from 0.3 to 0.5% of the applied fertilizer N. Total recovery of the ^{15}N-labeled fertilizer in the plant tissue (i.e., crop and noncrop species), excavated fertilizer bag, and soil ranged from 85.6% (Alcott jack pine) to 92.9% (Wabeno white spruce) after the first growing season.

At the end of the second growing season, the conifer seedlings grown in the VM plots at the Alcott sites and the Wabeno white spruce site had accumulated larger amounts of fertilizer N compared with seedlings grown in the controls (Table 6). During the second growing season, calamagrostis, aspen, and fireweed were the only early successional species to take up fertilizer N, ranging from 9.8 to 28.1% of the applied ^{15}N-labeled fertilizer. Except for the Wabeno jack pine site, there were larger amounts of fertilizer N remaining in the fertilizer bags within the VM plots compared with the control plots after two growing seasons. Similar to the first year,

Table 5. Fertilizer N recovered (percentage of original) from out-planted conifer seedlings, competing vegetation, soil, and remnants of fertilizer bag after one growing season.

Treatment	Seedling	Competing vegetation†	Fertilizer bag	Leached‡	Total fertilizer N recovered
		Alcott White Spruce			
Control	2.6	2.2	84.2	0.3	89.6
Vegetation management	4.2	NA§	85.3	0.5	90.3
		Alcott Jack Pine			
Control	1.8	3.2	79.9	0.4	85.6
Vegetation management	1.5	NA	84.3	0.4	86.5
		Wabeno White Spruce			
Control	2.7	2.8	89.2	0.4	92.9
Vegetation management	3.7	NA	85.6¶	0.5	89.8
		Wabeno Jack Pine			
Control	4.8	0.7	84.1	0.5	89.9
Vegetation management	6.1	NA	85.4	0.5	91.8

† Calamagrostis was the only vegetation to accumulate fertilizer N during the first growing season.
‡ Recovered from soil cores (30 cm depth) taken below the excavated fertilizer bag.
§ Not Applicable.
¶ Values are different from the corresponding control ($P < 0.05$) by LSD.

Table 6. Fertilizer N recovered (percentage of original) from out-planted conifer seedlings, competing vegetation, soil, and remnants of fertilizer bag after two growing seasons.

Treatment	Seedling	Competing vegetation†	Fertilizer bag	Leached‡	Total fertilizer N recovered
		Alcott White Spruce			
Control	5.8	22.2	65.5	0.8	94.6
Vegetation management	11.4§	NA¶	80.9§	1.3	93.8
		Alcott Jack Pine			
Control	5.7	28.1	54.4	0.8	89.2
Vegetation management	12.6§	NA	78.2§	0.7	91.1
		Wabeno White Spruce			
Control	12.3	19.4	59.6	0.5	91.7
Vegetation management	16.8§	NA	73.5§	0.6	90.6
		Wabeno Jack Pine			
Control	28.4	9.8	53.0	0.6	91.8
Vegetation management	29.1	NA	62.0	0.4	91.6

† Calamagrostis, fireweed, and aspen were the only vegetation to accumulate fertilizer N after two growing seasons.
‡ Recovered from soil cores (60-cm depth) taken below the excavated fertilizer bag.
§ Values are different from the corresponding control ($P < 0.05$) by LSD.
¶ Not Applicable.

leaching losses of the fertilizer N were negligible after two growing seasons: ranging from 0.5 to 1.3% of the applied fertilizer N. Of the applied ^{15}N-labeled fertilizer, from 89.2% (Alcott jack pine) to 94.6% (Alcott white spruce) was accounted for in plant tissue, fertilizer bag, and soil collected after two growing seasons.

There were no differences in the amounts of fertilizer N leached between treatments at any site, with the majority of the fertilizer N located within 5 and 10 cm below the bag after the first and second growing seasons, respectively (data not shown). Also, there were no differences in the amount of fertilizer N leached below the fertilizer bags isolated in PVC tubes compared with bags placed in control and treatment plots (data not shown). The random root cores taken throughout each measurement plot after each growing season to assess ^{15}N content in roots of early successional species indicated no ^{15}N-enrichment of root tissue (data not shown).

Vector Diagnosis

The vector diagrams (Fig. 1) compare the relative responsiveness of white spruce and jack pine seedlings to VM in terms of seedling biomass (diagonal lines), N concentration (x-axis) and N content (y-axis) using the seedlings grown in the control plots as the reference which is normalized to 100. Only the response vectors for the Alcott white spruce site are drawn in Fig. 1, to reduce clutter. After both growing seasons, vector diagnosis revealed enhanced N uptake, N concentration, and biomass production (i.e., moving toward the right across diagonal lines) in conifer seedlings grown in VM plots compared with those grown in the control plots. This vector represents a typical deficiency response because of improved N availability (Shift C; Timmer, 1991). Vegetation management increased conifer seed-

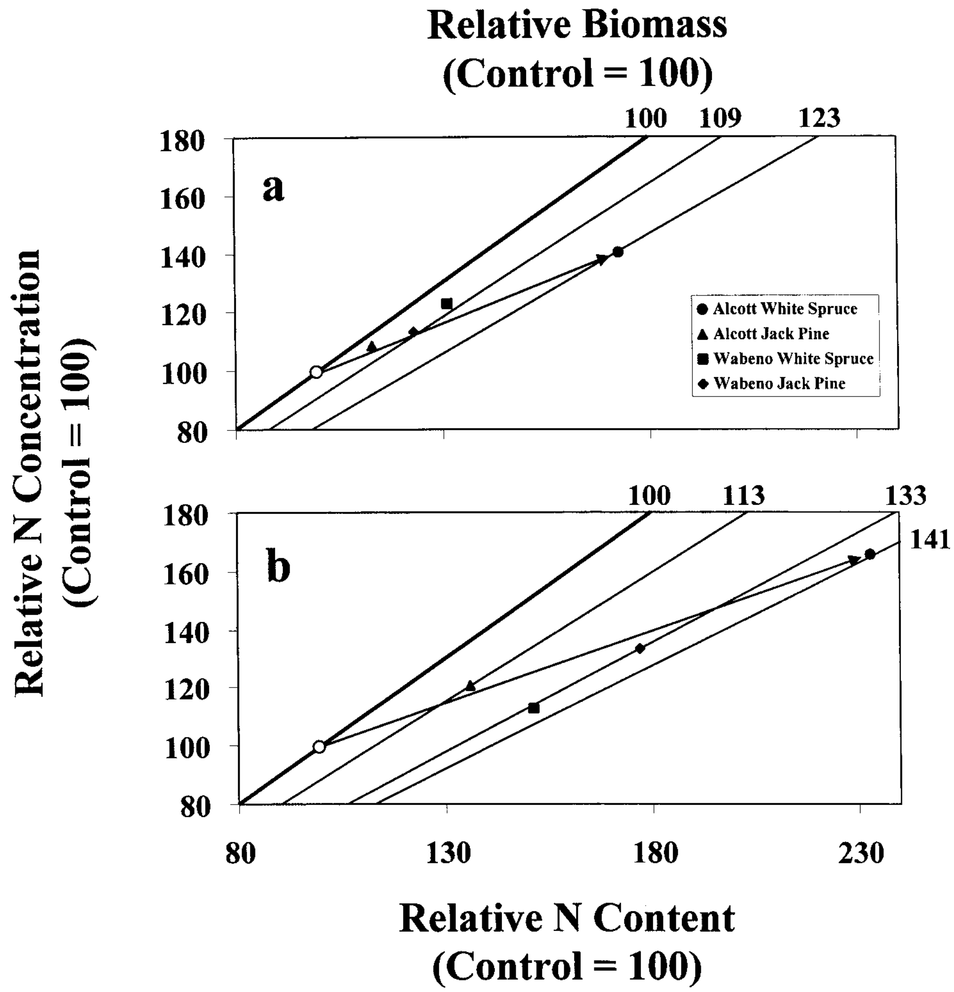

Fig. 1. Vector nomograms of relative differences in N concentration, N content, and conifer seedling biomass for vegetation management treatment plot seedlings after the (a) first and (b) second growing season. Biomass and N status of seedlings grown in control plots (i.e., no vegetation management) served as the reference and was normalized to 100. Only vectors associated with the site showing the strongest positive response (i.e., Alcott white spruce) to vegetation management are shown.

ling N uptake and biomass production up to 73 and 23%, respectively, after the first growing season (Fig. 1a). Nitrogen uptake and biomass increased by as much as 133 and 41%, respectively, after the second growing season, compared with the seedlings grown in control plots (Fig. 1b).

DISCUSSION

Fate of Applied Fertilizer Nitrogen

The point source CRF delivery method was effective at minimizing losses of applied N from the ecosystem. When averaged over all sites and treatments, over 90% of the applied fertilizer N was recovered in plant tissue and soil samples, and remnants of the fertilizer bag after two growing seasons. Considering that any microbial immobilization of the fertilizer N would probably be accounted for in the soil cores taken after each growing season, the missing fertilizer N probably is attributed to sampling error (i.e., located outside of the coring area). Although the high percentage recovery of applied fertilizer N is primarily attributed to the high residual fertilizer N remaining in the fertilizer bag after two growing seasons, this fertilizer N still is available for conifer seedling uptake in following growing seasons. When calculated in terms of fertilizer N released from the fertilizer bag (data not shown), the FUE by the outplanted conifer seedlings ranged from 9.1 to 41.8% and 12.5 to 76.6% during the first and second growing seasons, respectively. These values generally are well above the range of 0.4 to 15.4% for seedlings grown in control or VM plots using broadcast applications (Clinton and Mead, 1994; Staples et al., 1999).

Unlike broadcast fertilizer N that is taken up by early successional species (Staples et al., 1999) or rapidly immobilized by soil microorganisms (Chang et al., 1997; Chang and Preston, 2000), the majority of the added N in this study remained in the fertilizer bag after the second growing season. When averaged over all sites, >58% remained in the fertilizer bag in the control plots and 73% in the VM plots. Varying the thickness of the polyurethane coating on the fertilizer pellets contained within the fertilizer bag allows for a more controlled-release of the fertilizer N over time (Garry Hargrove, Pursell Technologies Inc., personal communication, May 2001). Furthermore, placing the fertilizer bag at depth should minimize microbial immobilization because the majority of microbial activity in boreal forest soils occurs in the humus layer of the forest floor, with comparatively low activity in the mineral soil (Walley et al., 1996). Soil microorganisms often immobilize the majority of broadcast fertilizer N within hours of application (Chang et al., 1997; Chang and Preston, 2000) and this N can remain unavailable for uptake by outplanted seedlings or early successional species even 8 yr after application (Preston and Mead, 1994). Therefore, under broadcast fertilization, early successional species are relatively small sinks for the applied N compared to the amount of fertilizer N immobilized in the soil. The use of a CRF contained in a fertilizer bag placed at depth probably minimizes the loss of fertilizer N to this effective sink and ensures that the conifer seedling takes up more of the applied fertilizer N (Table 2).

Within the boreal forest, outplanted white spruce and jack pine seedlings often cease shoot growth by late July or early August because of a limited number of growing degree-days (Brand and Janas, 1988; Hudson, 2000). This short growing season may help to explain the limited seedling fertilizer N uptake during the first year because of insufficient root growth by the outplanted seedlings (Hudson, 2000). By the second year, however, there was greater root biomass on the outplanted seedlings and a proliferation of roots near the fertilizer bag was observed when excavating the seedlings. Localized proliferation of root mass is considered a response mechanism to exploit fertile microsites (Jackson et al., 1990; Robinson, 1996) and has been reported elsewhere (Krasowski et al., 1999). This proliferation of roots probably caused enhanced N uptake from the fertilizer bag, as was indicated by the apparent greater fertilizer N uptake during the second growing season (Table 4).

At the end of each growing season, there was very little movement of the fertilizer N below the fertilizer bag (Tables 5 and 6), with or without (i.e., PVC tube) competing root systems, suggesting that the fertilizer bags minimized fertilizer N losses to leaching. Regardless of the site, after the second year, the majority of the leached fertilizer N (i.e., within 10 cm of the fertilizer bag) would still be accessible to the white spruce and jack pine root systems at this depth (Strong and La Roi, 1983; Krasowski et al., 1996). Although there were no differences in leaching depth of fertilizer N between the sites, greater leaching of the fertilizer N was expected at the Alcott jack pine site because of the coarser-textured soils. During both growing seasons, the Alcott jack pine site received from 35 to 40% lower than normal rainfall (data not shown). The limited leaching of fertilizer N at this site may in part be attributed to the relatively low amount of precipitation received.

Relative Competitiveness of Early Successional Species for Fertilizer Nitrogen

The lower fertilizer N uptake by conifer seedlings grown in control plots compared with VM plots is the result of two competitive mechanisms: direct competition for the uptake of applied fertilizer N with early successional species, and indirect competition by the early successional species for other site resources, thus inhibiting overall conifer seedling growth, resulting in reduced fertilizer N uptake. Optimizing silvicultural practices (i.e., VM and fertilization) in young conifer plantations requires an understanding of the relative competitiveness of early successional species, which affect the survival and growth of outplanted seedlings during the early establishment phase (Bell et al., 2000). Early successional species distribution within the ^{15}N-labeled seedling measurement plots indicated that the majority of the principal competitors in boreal forest plantations were present (Bell, 1991); however, only calamagrostis, fireweed, and aspen were able to take up measurable amounts of the fertilizer N. The lack of fertilizer N uptake by other very competitive species was surprising. This is especially true for red raspberry, which is a strong competitor for site resources (Bell, 1991) and was abundant at the Wabeno sites. In the present study, calamagrostis was the only species to accumulate fertilizer N during the first growing season and the primary species in the second growing season, although there were numerous woody species present in the ^{15}N-labeled seedling measurement plots. This supports the highly competitive nature of this perennial grass species reported by others (Eis, 1981; Lieffers et al., 1993).

The ability of early successional species to take up the applied fertilizer N is dependent on root morphological and physiological characteristics. The capacity of calamagrostis to absorb N released from the fertilizer bag is indicative of its capability to exploit soil resources through an extensive fibrous root system (Ländhausser and Lieffers, 1994; Hangs, 2001). Hangs (2001) reported calamagrostis to exhibit the greatest maximal uptake rates (i.e., I_{max}) and affinity (i.e., K_m) for NH_4^+ and NO_3^- uptake among selected early successional species in the boreal forest. Furthermore, the relative competitiveness of calamagrostis to inhibit shoot and root growth and fertilizer N uptake by planted white spruce and jack pine seedlings was greater than aspen and fireweed (Hangs, 2001). Calamagrostis was capable of taking up over 60% of the applied NH_4NO_3 after the 90-d growth period, compared with <10% uptake for fireweed and <3% uptake for aspen (Hangs, 2001).

Finally, the lower amount of fertilizer N remaining in the fertilizer bags within control plots compared with the treated plots at the end of the second growing season is because of uptake by early successional species. Furthermore, the lower fertilizer N uptake by early successional species at the Wabeno jack pine site compared with the other sites probably is a function of the lower abundance of calamagrostis at this site (data not shown).

Conifer Seedling Growth

Interspecific competition affected conifer shoot growth by the end of the first growing season and continued through the second growing season. Outplanted conifer seedlings grown within the control plots (i.e., no VM) had smaller shoot growth increments compared with seedlings growing in the VM plots at all sites except the Alcott jack pine site (Table 3). Although white spruce and jack pine seedling height generally does not show a consistent response to competition (Brand, 1990; Morris et al., 1990), the height growth increment of both of these conifers after two growing seasons was reduced by competitive pressure from early successional species within the control plots. The sensitivity of white spruce and jack pine stem diameter growth to competitive conditions is well documented (Sutton, 1995). In our study both white spruce and jack pine seedlings within the control plots had lower RCD growth compared with the VM plots. The influence of interspecific competition on height and RCD growth directly affects the stem volume and signifies a response to root competition (Ländhausser and Lieffers, 1998).

CONCLUSIONS

When fertilizer N uptake is expressed as a percentage of the fertilizer N released from the fertilizer bag, results from this study support the hypothesis that using a point source CRF delivery method promotes high FUE by outplanted white spruce and jack pine seedlings. Despite some accumulation of fertilizer N by calamagrostis, the use of a CRF contained in fertilizer bags resulted in minimal losses to competing vegetation within the ^{15}N-labeled seedling measurement plots. Except for minor accumulation of fertilizer N by fireweed and aspen during the second growing season, there was no fertilizer N uptake by any other early successional species after 2 yr. Unlike broadcast applications, where microbial N immobilization reduces fertilizer N availability, the use of CRF resulted in more than 50% of the original fertilizer N remaining available for conifer seedling uptake after two growing seasons. Some leaching of the fertilizer N occurred, although the fertilizer N still was accessible by the conifer seedling root system.

Although the CRF-N was applied in a fertilizer bag placed close to the conifer seedling root plug, calamagrostis was capable of accumulating significant amounts of the fertilizer N. Future research is needed to assess the fate of fertilizer ^{15}N using other individual seedling fertilization methods (i.e., nutrient-loaded root plugs containing CRF). Finally, the ability of calamagrostis to successfully compete with the outplanted conifers for the applied fertilizer N, despite the placement of the fertilizer close to the seedling root plug, clearly indicates the tenacity of this grass species in the field during the early establishment phase. Prioritizing the removal of calamagrostis from plantations should increase the FUE and benefit the early growth of outplanted white spruce and jack pine seedlings in boreal forest sites.

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APPENDIX

Early successional species common names and Latin nomenclature.

Common name	Latin nomenclature
Aspen	*Populus tremuloides* (Michx.)
Bicknell's geranium	*Geranium bicknelii* Britt.
Birch	*Betula papyrifera* Marsh.
Bishop's-cap	*Mitella nuda* L.
Blueberry	*Vaccinium angustifolium* Ait.
Bunchberry	*Cornus canadensis* L.
Calamagrostis	*Calamagrostis canadensis* (Michx.) Beauv.
Canada thistle	*Cirsium arvense* (L.) Scop.
Dandelion	*Krigia biflora* (Walt.) Blake
Dewberry	*Rubus pubescens* Raf.
Dry-ground cranberry	Vaccinium vitis-idaea *(Lodd)*
Fireweed	*Epilobium angustifolium* L.
Gooseberry	*Ribes oxyacanthoides* L.
Green alder	*Alnus crispa* (Ait.) Pursh.
Honeysuckle	*Lonicera involucrate*
Horsetail	*Equisetum sylvaticum* L.
Jack pine	*Pinus banksiana* Lamb.
Labrador tea	*Ledum groenlandicum*
Lindley's aster	*Aster ciliolatus* Lindl.
Low bush cranberry	*Viburnum edule* (Michx.) Raf.
Narrow-leafed hawk's-beard	*Crepis tectorum* L.
Palmate-leafed colt's-foot	*Petasites palmatus* (Ait.) A. Gray
Pea vine	*Lathyrus venosus* Muhl.
Raspberry	*Rubus idaeus* L.
Rose	*Rosa acicularis* Lindl.
Sarsaparilla	*Aralia nudicaulis* L.
Solomon's-seal	*Smilacina trifolia* (L.) Desf.
Starflower	*Trientalis borealis* Raf.
Strawberry	*Fragaria virginiana*
Twinflower	*Linnaea borealis* L.
Vetch	*Vicia Americana* Muhl.
White spruce	*Picea glauca* (Moench) Voss
Willow	*Salix humilis* Marsh.

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