Exponential fertilization and plant competition effects on the growth and N nutrition of trembling aspen and white spruce seedlings
Ya-Lin Hu, Yue Hu, De-Hui Zeng, Xiao Tan, and Scott X. Chang

Abstract: Exponential fertilization has been shown to be a useful technique for improving seedling quality during nursery production. In this study, we evaluated (i) the impact of exponential vs. conventional fertilization on trembling aspen (Populus tremuloides Michx.) and white spruce (Picea glauca (Moench) Voss) seedlings during nursery production and (ii) the growth performance and nitrogen (N) utilization of those seedlings in response to foxtail barley (Hordeum jubatum L.) competition after the transplantation of seedlings in a greenhouse experiment. Exponential fertilization with an application rate higher than the conventional fertilization increased the internal N reserve in trembling aspen and white spruce seedlings during nursery production and also increased new leaf, new stem and old stem biomass and N retranslocation rates in trembling aspen seedlings but not in white spruce seedlings after transplantation. Foxtail barley competition decreased N concentrations in seedlings and soil N uptake by the seedlings; however, increased N retranslocation rates with foxtail barley competition were observed in white spruce seedlings but not in trembling aspen seedlings. Our results suggest that the growth performance of seedlings was improved by N loading, whereas the impact of vegetation management was species specific.

Key words: exponential fertilization, internal N reserve, N-loaded seedling, net N retranslocation rate, vegetation competition.

Introduction
Vegetation management is one of the most critical silvicultural practices for maximizing postplanting tree seedling survival and growth during the early establishment phase of plantations (Lowery et al. 1993; Cole et al. 2003; Rose and Ketchum 2003). Non-crop vegetation competes with crop tree species for nutrients, water, and light and is one of the most important causes of markedly decreased tree seedling survival and forest productivity (Fisher and Neumann 1987; Woods et al. 1992). However, there is increasing public criticism on the use of chemical herbicides to alleviate vegetation competition because of the environmental risk associated with the use of herbicides (Ervin and Jussaume 2014). An alternative approach of planting “nutrient-loaded” seedlings has been recognized as part of integrated vegetation management practices (Imo and Timmer 2002). The so-called nutrient-loaded seedlings have higher internal nutrient storage when they are lifted from the nursery. The nutrients stored in the nutrient-loaded seedlings are immediately available to the newly planted seedlings after transplantation of seedlings in a greenhouse experiment. Exponential fertilization with an application rate higher than the conventional fertilization increased the internal N reserve in trembling aspen and white spruce seedlings during nursery production and also increased new leaf, new stem and old stem biomass and N retranslocation rates in trembling aspen seedlings but not in white spruce seedlings after transplantation. Foxtail barley competition decreased N concentrations in seedlings and soil N uptake by the seedlings; however, increased N retranslocation rates with foxtail barley competition were observed in white spruce seedlings but not in trembling aspen seedlings. Our results suggest that the growth performance of seedlings was improved by N loading, whereas the impact of vegetation management was species specific.
utilized by small seedlings at the early nursery stage; they can also cause nutrient deficiency in the later stages (Hawkins et al. 2005). The principle of steady-state nutrition, characterized by stable or increasing nutrient concentrations in seedlings, is applied by delivering fertilizers at an exponential rate corresponding to the exponential growth of seedlings during nursery production (Timmer 1996). Exponential fertilization regimes can induce luxury uptake and result in greater nutrient reserves that will be available for new tissues through retranslocation of nutrients from older tissues after being transplanted in the field (Salifu et al. 2009b). Improved seedling quality (e.g., increased internal nitrogen (N) reserve) and growth performance through exponential fertilization have been demonstrated in nursery production (e.g., Timmer 1996; Imo and Timmer 2002; Close et al. 2005; Salifu et al. 2009b). However, studies on the responses of nutrient-loaded seedlings combined with soil nutrient and water stresses such as those that can be caused by vegetation competition after transplantation in the field are needed (Timmer 1996; Malik and Timmer 1998; Salifu et al. 2009b), considering their species- and site-specific nature (Imo and Timmer 2002; Hawkins et al. 2005; Cuesta et al. 2010).

Trembling aspen (Populus tremuloides Michx.) and white spruce (Picea glauca [Moench] Voss) are important tree species for the reclamation of disturbed lands in the Athabasca Oil Sands District (AOSR) in northeastern Alberta, Canada, where approximately 715 km² of boreal forests have been disturbed and 10% of the disturbed lands are in the process of being reclaimed (Poweda and Lipsett 2014). To stabilize recently reclaimed oil-sands sites, grass species are usually seeded before the planting of tree seedlings. Planting of tree species for reclamation typically occurs after the seeding of a nurse crop or grass species. The current system requires the planting of quality trembling aspen and white spruce seedlings that can regenerate successfully while in competition with these seeded grass species. Traditional management practices in oil-sands reclamation typically involve fertilization at the time of or after planting, and the applied fertilizers feed both the planted seedlings and the weeds. Broadcast-compensate for incomplete root exploitation compensate for incomplete root exploitation applied fertilizers cause a loss of nutrients when the applied nutrients are not fully utilized and increase the competition between the grass and the seedlings. Nutrient loading can minimize both of these potential negative effects. However, little information exists on exponential fertilization of trembling aspen and white spruce during nursery production (Schott et al. 2013), and there is no information on their growth performance and N nutrition after transplantation on reclaimed lands with severe vegetation competition.

In this study, we conducted two related studies on the growth performance and N nutrition of trembling aspen and white spruce seedlings during nursery production and postplanting with foxtail barley (Hordeum jubatum L.) weed competition in greenhouse conditions. We hypothesized that (i) exponential fertilization during nursery production would increase the internal N reserve in seedlings, (ii) N-loaded seedlings would have improved growth after transplantation, (iii) competing vegetation would decrease seedling growth and soil N uptake because of interspecific competition for nutrients, and (iv) the negative impact of vegetation competition on seedling growth would be alleviated for the N-loaded seedlings.

Materials and methods
Seedling nursery production and fertilization regimes
Seeds of trembling aspen and white spruce were sown into 615A styroblocks (45 cavities per block, 340 ml per cavity) filled with peat moss and perlite (9:1 by volume) on 20 August 2010 in the Northern Forestry Centre of the Canadian Forest Service, Alberta, Canada (53°29′27″ N, 113°32′34″ W). For each species, 810 seedlings (18 styroblocks × 45 cavities) were germinated and raised under standard greenhouse growing conditions, where the temperature ranged from 18°C to 30°C, relative humidity ranged from 65% to 85%, and the photoperiod was 20 h, with light intensity at 250 μmol·m⁻²·s⁻¹ provided by sodium vapor lamps. Styroblocks were watered when the water content of the peat-perlite mixture dropped below 80% water holding capacity, either daily or on alternate days. The styroblocks were completely randomly arranged and rotated weekly to reduce possible edge effects in the greenhouse.

During nursery culture in the greenhouse, three fertilization regimes were set up, and each treatment contained 270 seedlings in six styroblocks for each of the two species. In this part of the experiment, each styroblock was a replication, and the styroblocks were randomly arranged and rotated weekly to reduce possible edge effects in the greenhouse. For trembling aspen seedlings, the conventional fertilization delivered a seasonal total of 120 mg N per seedling (AC120) at a constant rate delivered weekly, and exponential fertilization delivered seasonal totals of 240 and 500 mg N per seedling (AE240 and AE500, respectively), with an addition schedule based on a modified exponential model (Fig. 1a). For white spruce seedlings, the conventional fertilization delivered a seasonal total of 300 mg N per seedling (SC300) at a constant rate delivered weekly, and exponential fertilization delivered seasonal totals of 450 and 900 mg N per seedling (SE450 and SE900, respectively), with an addition schedule also based on a modified exponential model (Fig. 1b). The fertilizer addition rates for the conventional treatments were based on rates used in the Smoky Lake Forest Nursery in Alberta, Canada. The rates used for the exponential fertilization treatments were based on the optimum fertilization rates identified in an earlier study, which produced N-loaded seedlings (Hu 2012). In the exponential fertilization treatments, the fertilizer addition rates in the compensation period (Fig. 1) were increased at the start of the fertilization period to compensate for incomplete root exploitation and low nutrient availability in the growth media, and the extra fertilizer used in the compensation period was subtracted from the last application to avoid possible bud damage before dormancy onset due to excess fertilization (Timmer 1996). Fertilization started after germination and was delivered weekly using a commercial watersoluble compound fertilizer (20:20:20 N:P₂O₅:K₂O plus micronutrients; Plant Products Co. Ltd.). The total amount of fertilizer described above was added at 12 and 22 weeks for trembling aspen and white spruce seedlings, respectively, based on their different growth characteristics. After 12 or 22 weeks of the growth period, the seedlings were exposed to lower temperatures (12–18°C) and a shorter photoperiod (8 h) using blackout curtains to induce bud setting or hardening for 2 weeks. The seedlings were then transferred to cold storage at −2°C to overwinter for a 4-month period.

Seedling transplantation and plant competition
After overwintering, the growth performance of the fertilized seedlings with or without plant competition was assessed in a greenhouse experiment at the University of Alberta (53°31′34″ N, 113°31′40″ W). A completely randomized 2 × 2 factorial design for trembling aspen and white spruce seedlings was used as follows: two levels of plant competition (with or without foxtail barley) and three levels of fertilization treatment (conventional and two rates of exponential nutrient loading) imposed during the nursery phase as described earlier. In July 2011, 16 seedlings were selected from each nursery fertilization treatment. Individual seedlings were transplanted into separate 3.78 L pots (diameter 16 cm and height 20 cm) filled with a reclamation soil (peat—mineral soil mix, PMM) widely used for land reclamation in the AOSR. The soil used had 7.52% C, 0.3% N, 46% sand, 32% silt, and 22% clay and a pH of 7.24. Before transplantation, seedlings were sorted by size in each fertilization treatment, and seedlings with an average size were used to reduce possible confounding
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(NH₄)₂SO₄ fertilizer labelled with ¹⁵N at 60 atom percent excess weekly to reduce possible edge effects.

dropped below 80% water holding capacity. The pots were rotated period, the pots were watered daily when soil moisture content among tree species and foxtail barley during the postplanting period. The 16 pots were seeded with foxtail barley, a common weed species found across Canada. In each pot, the foxtail barley plants were thinned to 15 plants per pot after germination. The trembling aspen seedlings were grown for 10 weeks and white spruce seedlings were transplanted into pots immediately to avoid desiccation of exposed roots. To assess the competition effect, half of the 16 pots were seeded with foxtail barley, a common weed species found across Canada. In each pot, the foxtail barley plants were thinned to 15 plants per pot after germination. The trembling aspen seedlings were grown for 10 weeks and white spruce seedlings were grown for 13 weeks, with a mean temperature of 23 °C, relative humidity of 65%–85%, and a light level of 746 μmol·m⁻²·s⁻¹. To avoid water stress and competition for water among tree species and foxtail barley during the postplanting period, the pots were watered daily when soil moisture content dropped below 80% water holding capacity. The pots were rotated weekly to reduce possible edge effects.

To determine N uptake from the soil after transplantation, (NH₄)₂SO₄ fertilizer labelled with ¹⁵N at 60 atom percent excess was applied evenly over the soil surface in solution (10 mL) at the 1st and 6th week with an equal rate of 2.5 mg N per seedling during the transplanting experiment. No other fertilizer application was used for the transplanting experiment.

Plant sampling and chemical analysis
Root-collar diameter (RCD) and shoot height of seedlings were measured before and after transplantation. Five seedlings with an intermediate size in each fertilization treatment were randomly selected before transplantation and separated into leaves, stems, and roots, and five of the eight seedlings from each treatment combination were randomly selected and separated into new leaves, old leaves, new stems, old stems, and roots at the end of the greenhouse experiment. At each sampling, seedlings were washed free of soils from the root system and dust from the leaves before they were separated into components. In washing out the roots, the majority of the roots were recovered by carefully removing the potting soil from the seedling root system. The roots that broke off from the root system were manually collected as much as possible based on the thickness and color of the roots, with the tree-seedling roots being thicker and bigger and a lighter color than the grass roots, which were more fibrous and a darker color. Plant samples were oven-dried for 72 h at 60 °C and weighed to determine dry biomass. The samples were then ground with a ball mill for N concentration and ¹⁵N abundance analysis using a Carlo Erba NA 1500 elemental analyzer (Carlo Erba Instruments, Milano, Italy) linked to a stable isotope ratio mass spectrometer (OptimaEA; Micromass, Crewe, UK) at the Lethbridge Research Centre of Agriculture and Agri-Food Canada.

Net N retranslocation rates from old tissues were calculated based on N content differences in plant tissues before and after transplantation (Malik and Timmer 1998; Salifu and Timmer 2001). For the net N transfer methodology, N losses from the seedling due to volatilization or exudation of secondary metabolites from leaves, needles, or roots are assumed negligible for short-term trials such as ours (Salifu and Timmer 2001).

\[
N_{\text{net}} = \frac{N_{\text{ini}} \times B_{\text{ini}} - N_{\text{ini}} \times B_{\text{ini}}}{N_{\text{ini}} \times B_{\text{ini}}} \times 100\%
\]

where \(N_{\text{net}}\) is net N retranslocation rate, \(N_{\text{ini}}\) and \(B_{\text{ini}}\) are N concentration and biomass, respectively, of seedling components (i.e., old leaves, old stem, and roots) before transplantation, and \(N_{\text{ini}}\) and \(B_{\text{ini}}\) are N concentration and biomass of seedling components (i.e., old leaves, old stem, and roots), respectively, after transplantation.

Statistical analysis
All statistical analyses were done using the open-source statistical software R (version 2.14.1). Residuals from all response vari-
were lower in SE450 than in SC300. Stem N concentrations in AE240 and AE500 increased by 65% and 72% respectively; and SE450 and SE900, exponential fertilization regimes with 450 and 500 mg N per white spruce seedling, respectively, and SE450 and SE900, exponential fertilization regimes with 450 and 900 mg N per white spruce seedling. Values followed by different lowercase letters in the same row indicate significant difference at the level of p < 0.05 among fertilization regime treatments (all p < 0.01). Seedling size and biomass after transplantation

There were no significant interactions between fertilization regime and weed competition on the growth of both trembling aspen and white spruce seedlings (Table 5). Shoot height increases of trembling aspen seedlings in AE500 were lower than that in AC120 (p = 0.023) (Fig. 3a); however, RCD increments of white spruce seedlings were 37% greater in SE450 than in SC300 (p = 0.013) (Fig. 3b). Weed competition resulted in a lower shoot height increment of trembling aspen seedlings (p = 0.002) (Table 5). New leaf, new stem, and old stem biomass of trembling aspen seedlings 10 weeks after transplantation were greater in the exponential than in the conventional N fertilization treatments (all p < 0.05) (Fig. 4); however, root biomass was not affected by the fertilization regime. Weed competition did not change the biomass of new stems, old stems, and roots of trembling aspen seedlings, although a decrease in new leaf biomass of trembling aspen (p = 0.009) was observed (Table 5). For white spruce, the N fertilization regime and weed competition did not affect biomass in any of the components studied 13 weeks after transplantation (Table 5).

Seedling N concentration, soil N uptake, and N retranslocation after transplantation

There were no significant interactions between fertilization regime and weed competition on N concentrations, soil N uptake, and N retranslocation rates of both trembling aspen and white spruce seedlings after transplantation (Table 5). Stem N concentrations in SE900 increased by 18% compared with SC300 (p = 0.011) and root N concentrations in SE450 and SE900 increased by 34% and 48%, respectively, compared with SC300 (p < 0.001).

Table 1. Biomass and N concentration of different components in trembling aspen and white spruce seedlings before transplantation.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Trembling aspen</th>
<th>White spruce</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>AC120</td>
<td>AE240</td>
</tr>
<tr>
<td>Biomass (g·seedling−1)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf</td>
<td>nd</td>
<td>nd</td>
</tr>
<tr>
<td>Stem</td>
<td>1.80b (0.21)</td>
<td>1.75b (0.22)</td>
</tr>
<tr>
<td>Root</td>
<td>1.53b (0.30)</td>
<td>1.48b (0.22)</td>
</tr>
<tr>
<td>N concentration (mg·g−1)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf</td>
<td>nd</td>
<td>nd</td>
</tr>
<tr>
<td>Stem</td>
<td>13.76b (0.92)</td>
<td>22.75a (1.25)</td>
</tr>
<tr>
<td>Root</td>
<td>13.52b (0.76)</td>
<td>19.60a (1.81)</td>
</tr>
</tbody>
</table>

Note: AC120 and SC300, conventional fertilization regimes with 120 and 300 mg N per seedling for trembling aspen and white spruce seedlings, respectively; AE240 and AE500, exponential fertilization regimes with 240 and 500 mg N per trembling aspen seedling, respectively; and SE450 and SE900, exponential fertilization regimes with 450 and 900 mg N per white spruce seedling. Values followed by different lowercase letters in the same row indicate significant difference at the level of p < 0.05. Values in bold indicate significant level at p < 0.05.

Table 2. ANOVA table for root-collar diameter (RCD), shoot height, biomass of leaves (Leaf_bio), stems (Stem_bio), and roots (Root_bio), and N concentration in leaves (Leaf_Ncon), stems (Stem_Ncon), and roots (Root_Ncon) in trembling aspen and white spruce seedlings for exponential N fertilization vs. conventional fertilization before transplantation.

<table>
<thead>
<tr>
<th>RCD</th>
<th>Height</th>
<th>Leaf_bio</th>
<th>Stem_bio</th>
<th>Root_bio</th>
<th>Leaf_Ncon</th>
<th>Stem_Ncon</th>
<th>Root_Ncon</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trembling aspen</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>0.729</td>
<td>11.26</td>
<td>nd</td>
<td>17.93</td>
<td>5.980</td>
<td>nd</td>
<td>15.34</td>
</tr>
<tr>
<td>Pr&gt;F</td>
<td>0.4889</td>
<td>&lt;0.001</td>
<td>nd</td>
<td>&lt;0.001</td>
<td>0.016</td>
<td>nd</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>White spruce</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>2.642</td>
<td>0.094</td>
<td>0.503</td>
<td>1.057</td>
<td>1.363</td>
<td>0.144</td>
<td>4.868</td>
</tr>
<tr>
<td>Pr&gt;F</td>
<td>0.082</td>
<td>0.910</td>
<td>0.617</td>
<td>0.378</td>
<td>0.293</td>
<td>0.867</td>
<td>0.028</td>
</tr>
</tbody>
</table>

Note: nd, not determined. Values in bold indicate significant level at p < 0.05.
tion decreased N concentrations in new leaves and roots of trembling aspen seedlings by 6.8% ($p = 0.005$) and 14% ($p = 0.03$), respectively, 10 weeks after transplantation (Tables 3 and 5), and decreased N concentrations in new leaves, new stems, old leaves, old stems, and roots of white spruce seedlings by 26%, 20%, 12%, 18%, and 16%, respectively, 13 weeks after transplantation (all $p < 0.001$) (Tables 3 and 5).

The fertilization regime did not affect the recovery of $^{15}$N from fertilizer applied to the soil after transplantation, but weed competition decreased the recovery of $^{15}$N in all plant components of both trembling aspen and white spruce seedlings (all $p < 0.05$) (Tables 4 and 5).

For trembling aspen seedlings, N retranslocation rates from the old stems of trembling aspen seedlings significantly increased in the order of AC120 < AE240 < AE500 (Fig. 5b). However, weed competition did not change N retranslocation rates of trembling aspen seedlings 10 weeks after transplantation (Table 5). For white spruce seedlings, the fertilization regime did not change N retranslocation rates, whereas weed competition increased N retranslocation rates in the old leaves of white spruce seedlings 13 weeks after transplantation ($p = 0.02$) (Table 5).

**Discussion**

**Exponential fertilization effect was species specific**

Shoot height and stem and root biomass of trembling aspen seedlings in the AE500 treatment increased compared with conventional fertilization when assessed during nursery seedling production. Schott et al. (2013) suggested that shoot growth should be terminated prematurely to produce nutrient-loaded trembling aspen seedlings because of their indeterminate growth strategy. However, in this study, we observed no difference in the biomass of trembling aspen seedlings between the AE240 and AC120 treatments. The increased biomass of trembling aspen seedlings in AE500 during nursery culture may be related to a higher fertilizer application rate. The lack of impact of exponential fertilization on leaf, stem, and root biomass of white spruce seedlings was consistent with McAlister and Timmer (1998) who reported no exponential fertilization effect on the growth of white spruce seedlings. Trembling aspen has an indeterminate growth habit that allows trembling aspen seedlings to continuously grow as long as the growth conditions are favorable (Schott et al. 2013); however, white spruce is a determinate species. Our results suggested that the impact of exponential fertilization on seedlings growth was...
species specific and related to the growth strategy of the seedlings.

Exponential fertilization with a higher fertilization rate than the typical conventional fertilization increased N concentrations in the stems and roots for both trembling aspen and white spruce seedlings. The error bars are standard errors (n = 10). Different lowercase letters on bars indicate significant differences at p < 0.05. Please see the caption of Fig. 1 for an explanation of the treatment codes (AC120, AE240, and AE500).

Fig. 5. Effects of fertilization regime on (a) N concentration (mg·g⁻¹) of new leaves and (b) net N retranslocation rate (%) of old stems of trembling aspen seedlings 10 weeks after transplantation. The error bars are standard errors (n = 10). Different lowercase letters on bars indicate significant differences at p < 0.05. Please see the caption of Fig. 1 for an explanation of the treatment codes (AC120, AE240, and AE500).

...
Table 3. Effects of weed competition on N concentration in different components of trembling aspen and white spruce seedlings after transplantation.

<table>
<thead>
<tr>
<th>Component</th>
<th>N concentration (mg·g⁻¹)</th>
<th>F</th>
<th>Pr&gt;F</th>
<th>N concentration (mg·g⁻¹)</th>
<th>F</th>
<th>Pr&gt;F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aspen</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No weed</td>
<td>18.42a (0.26)</td>
<td>1.77b (0.35)</td>
<td>1.362</td>
<td>8.124 (0.35)</td>
<td>1.632 (0.208)</td>
<td>0.961</td>
</tr>
<tr>
<td>Weed</td>
<td>17.25a (0.54)</td>
<td>10.52a (0.29)</td>
<td>13.30a (0.45)</td>
<td>7.15a (0.16)</td>
<td>11.01a (0.26)</td>
<td>0.781</td>
</tr>
</tbody>
</table>

Table 4. Effects of weed competition on the recovery of ¹⁵N in different components of trembling aspen and white spruce seedlings after transplantation.

<table>
<thead>
<tr>
<th>Component</th>
<th>Recovery (%)</th>
<th>F</th>
<th>Pr&gt;F</th>
<th>Recovery (%)</th>
<th>F</th>
<th>Pr&gt;F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aspen</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No weed</td>
<td></td>
<td>1.67a (0.17)</td>
<td>1.45b (0.26)</td>
<td>3.17a (0.18)</td>
<td>4.11a (0.26)</td>
<td>7.46a (0.34)</td>
</tr>
<tr>
<td>Weed</td>
<td></td>
<td>1.66a (0.13)</td>
<td>1.26a (0.15)</td>
<td>1.82a (0.15)</td>
<td>5.06a (0.40)</td>
<td>0.427</td>
</tr>
</tbody>
</table>

Table 5. Two-way ANOVA testing of fertilization regime, weed competition, and their interaction on increment of root-collar diameter and seedling height, biomass, N concentration, recovery of ¹⁵N in new leaves, old leaves, new stems, old stems, and roots, and N retranslocation rate from old leaves, old stems, and roots in trembling aspen and white spruce seedlings after transplantation.

<table>
<thead>
<tr>
<th>Component</th>
<th>Increment</th>
<th>F</th>
<th>Pr&gt;F</th>
<th>Height</th>
<th>F</th>
<th>Pr&gt;F</th>
<th>N concentration</th>
<th>F</th>
<th>Pr&gt;F</th>
<th>Recovery</th>
<th>F</th>
<th>Pr&gt;F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aspen</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No weed</td>
<td>17.25a (0.54)</td>
<td>10.52a (0.29)</td>
<td>13.30a (0.45)</td>
<td>7.15a (0.16)</td>
<td>11.01a (0.26)</td>
<td>0.781</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weed</td>
<td>12.81b (0.21)</td>
<td>8.45b (0.37)</td>
<td>11.67b (0.30)</td>
<td>5.87b (0.14)</td>
<td>9.22b (0.26)</td>
<td>0.427</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: Values followed by different lowercase letters in the same column indicate a significant difference at p < 0.05 for trembling aspen or white spruce seedlings. Data in parentheses are standard errors (n = 15). nd, not determined.
1996b; Chang and Preston 2000). Weed competition for soil nutrients and (or) water is one of the most important causes of reduced seedling growth and N concentrations (Woods et al. 1992; Chang and Preston 2000; Kabba et al. 2011). For our study, watering was done daily to avoid water competition between tree seedlings and weeds. We found that the recoveries of \(^{15}\)N in all components of trembling aspen and white spruce seedlings were reduced by weed competition, suggesting that weed competition decreased soil N uptake by the seedlings (Chang et al. 1996b). However, weed competition increased N retranslocation rates in white spruce seedlings, which might account for the absence of decreases of white spruce seedling growth under weed competition and suggest that nutrient retranslocation was an adaptive strategy for nutrient conservation (Malik and Timmer 1998). Our results suggest that the impact of weed competition on seedling growth and N concentrations depends on the species-specific phenotypic plasticity and functional strategy (Cuesta et al. 2010).

The lack of interaction between the N fertilization regime and weed competition on growth and N concentrations indicated that the nutrient-loaded seedlings did not alleviate the competition of foxtail barley in our study. Therefore, vegetation management prescriptions should be considered to minimize competing vegetation for the establishment of tree seedlings (Wagner 1993). This is in contrast with Timmer (1996) and Malik and Timmer (1998) who reported that higher nutrient reserves and the improved nutrient balance in the N-loaded tree seedlings alleviated vegetation competition and improved seedling growth. Alleviation of negative effects from competing vegetation by planting N-loaded seedlings may be more likely to occur on sites with high weed competition rather than on sites with low weed competition (Imo and Timmer 2002). However, we only chose one weed species in this study, and thus other more competitive weed species should be assessed on N-loaded seedlings considering that species differ greatly in their competitiveness. Another reason for the lack of nutrient-loading effect may be the short-term nature of the greenhouse experiment. Long-term field experiments should be conducted to further test the utility of the nutrient-loading technique for trembling aspen and white spruce to overcome competing vegetation that establishes on a site over the longer term.

Conclusions

Exponential N fertilization with a higher application rate than conventional fertilization increased the internal N reserve in trembling aspen and white spruce seedlings during nursery culture. The growth performance of N-loaded trembling aspen seedlings was improved due to increased internal N reserve and N retranslocation rates after transplantation. However, improved growth performance was not observed for white spruce seedlings even though their internal N reserve increased during seedling nursery production. This implied that production of N-loaded seedlings may be a useful silvicultural technique to improve the out-planting performance but such benefits are likely species specific. Control of weed competition increased N concentrations in both trembling aspen and white spruce seedlings associated with a higher soil N uptake. However, the effectiveness of the N-loaded seedlings to overcome weed competition was not observed. Future research should evaluate the competitive relationship between N-loaded seedlings and weeds considering the various growth and competitive strategies of tree and weed species.

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