The Contrasting Response to Soil Disturbance between Lodgepole Pine and Hybrid White Spruce in Subboreal Forests

J. M. Kranabetter,* P. Sanborn, B. K. Chapman, and S. Dube

ABSTRACT

Reductions in soil porosity through compaction and losses in nutrients through site organic matter removal are considered potentially detrimental effects of forest operations to site productivity. Defining sustainable forest practices is complicated, however, by the possible contrasting responses of commercial tree species to these disturbances. We compared the productivity and foliar nitrogen (N) nutrition of lodgepole pine (Pinus contorta Dougl. ex Loud.) and hybrid white spruce (Picea glauca × engelmannii [Moench] Voss) at Year 12 across organic matter removal and soil compaction treatments in the subboreal forests of central British Columbia. Nitrogen availability peaked in the years following tree harvest, and by Year 12 in situ rates of net N mineralization were uniformly low across treatments.

Low rates of N supply were partially offset by intermediate disturbances (forest floor removal alone or compaction through forest floors), which increased N uptake and height growth for hybrid white spruce. Lodgepole pine, in contrast, had near adequate foliar N concentrations and higher tree productivity across the complete gradient of soil disturbances. Some advantage in N nutrition for lodgepole pine might be provided by ectomycorrhiza through host-specific Suillus species. Fruiting bodies of Suillus species had, on average, 40% higher N concentrations than other common ectomycorrhiza (ECM) fungi found across the plots. The large and often contrasting differences in growth and N nutrition between lodgepole pine and hybrid white spruce demonstrate the possible challenges in defining universal criteria for detrimental soil disturbance.

The extent of soil disturbance caused by harvesting systems has been identified as a promising indicator for evaluating the sustainability of forest management (Curran et al., 2005). Soil disturbance can play a role in maintaining forest productivity in northern climates (Van Cleve and Dyrness, 1983; Kimmins, 1996; Prescott et al., 2000), but reductions in soil porosity through compaction and losses in nutrients through site organic matter removal are considered potentially detrimental consequences of forest operations (Jurgensen et al., 1997; Kozlowski, 1999). Quantifying the effects of these disturbances on soil properties and tree growth is an ongoing objective of the Long-Term Soil Productivity (LTSP) studies in North America (Powers, 2006). The results from these studies will provide scientific rationale for soil conservation and provide insight into soil–tree interactions affecting site productivity across major climatic regions and soil types.

One of the challenges in defining and regulating acceptable forest operations is the mixed response to soil disturbance sometimes found between tree species (Fleming et al., 2006). Pine species, for example, can be less sensitive to soil compaction or soil nutrient deficiencies than spruce species (Wästerlund, 1985; Egnell and Leijon, 1999; Péridé and Munson, 2000; Bothwell et al., 2001). Because of this, definitions of soil degradation that rely on measures such as soil strength, organic matter content, or N availability (Karlen et al., 1997; Powers et al., 1998; Schoenholtz et al., 2000) may not be necessarily universal, and productivity losses could depend on the species used in reforestation. A better understanding of how commercial tree species respond to soil disturbances, and the mechanisms involved, would be an important contribution to the discussion of best forest management practices.

At the LTSP installation in the subboreal forests of central British Columbia, we have found consistent and near adequate foliar N (~1.3% N) for lodgepole pine (Pinus contorta var. latifolia Doug. ex Loud.), but declining and sometimes very severely deficient foliar N (as low as 0.8% N) for hybrid white spruce (Picea glauca × engelmannii [Moench] Voss) over the 10 yr since establishment (N deficiencies defined by Carter, 1992; Brockley, 2001). It is unclear whether this diverging response in nutrition reflects species effects on soil N availability, or physiological differences in N uptake between species (Hobbie, 1992; Knops et al., 2002). Enhanced soil N accumulation and availability in young pine stands has been demonstrated in some ecosystems (Williams et al., 1979; Williams, 1992; Krause, 1998), although long-term effects may be less significant (Fyles and Côté, 1994; Pajuste and Frey, 2003). Alternatively, pine species may be well adapted to low fertility soils in part through access to intractable soil N sources (Miller et al., 1979). There is evidence for differences in the ability of ECM fungal species to mobilize recalcitrant forms of organic N, or directly utilize simple organic forms of N, rather than relying solely on inorganic N uptake (Lipson and Nasholm, 2001; Read and Perez-Moreno, 2003). If such ECM fungal species were limited in distribution to pine, and allowed enhanced N uptake, then the ECM community would provide an additional advantage over spruce on infertile soils (Bothwell et al., 2001).

Understanding the processes governing soil N supply and plant uptake is important because of the close relationship between foliar N and plant photosynthetic

Abbreviations: ECM, ectomycorrhizal; LTSP, Long-Term Soil Productivity; mc, moist and cold; SBS, subboreal spruce biogeoclimatic zone; wk, wet and cool.
capacity (Reich et al., 1997), and because N is generally considered the most common nutritional constraint on tree growth in boreal forests (Chapin, 1980). The objectives of this study were (i) to contrast the response in productivity and foliar N nutrition between lodgepole pine and hybrid white spruce; (ii) to examine whether the patterns in tree response reflect soil N supply differences between species or across soil compaction and organic matter removal treatments; and (iii) to explore the potential influence of ECM species and possible advantage to lodgepole pine by comparing N concentrations of host-specific and host-generalist ECM mycorrhizal trees.

In addition to the possible differences in tree species response, the results of this study will be used to discuss some of the broader implications of soil disturbance in enhancing or reducing site productivity in these subboreal forests.

**MATERIALS AND METHODS**

**Site Descriptions**

Full site characteristics and selected soil properties of these LTSP experimental plots were described in Kranabetter and Chapman (2004) and Krzic et al. (2004). Briefly, the LTSP installations in central British Columbia are located in the Subboreal Spruce bioclimatic zone (SBS), characterized by severe, snowy winters and relatively warm, moist, and short summers (Meidinger and Pojar, 1991). The results presented in this study were from two replicates: the moist, cold (mc) subzone near Houston, BC (54°37′ N lat., 126°18′ W long.); and the wet, cool (wk) near Prince George, BC (54°21′ N lat., 122°37′ W long.). Each site has deep, medium-textured, skeletal soils (>35% coarse fragments by volume), derived from morainal blankets, with typical soil moisture and nutrient status for the subzone (Banner et al., 1993; Delong et al., 1993). Soils were classified as Gleyed and Eluviated Dystric Brunisols (Cryochrepts) at the SBSwk site and Orthic and Gleyed Gray Luvisols (Borals) at the SBSmc site (Soil Classification Working Group, 1998). Soil textures ranged from silt loam to clay loam, with Hemimor humus forms approximately 7 cm thick (Green et al., 1993). Preharvest stands were approximately 140 yr old and comprised of subalpine fir (Abies lasiocarpa [Hook.] Nutt.), hybrid white spruce, lodgepole pine, and, for the SBSwk site only, Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco).

**Experimental Design**

For this study, we chose a subset of the LTSP plots (40 × 70 m each) for a detailed examination of N availability and tree response. The experiment is a factorial design, with each combination of treatments replicated once per site. The treatments include two levels of site organic matter removal: OM1—stem (boles) only removed, OM3—whole tree and forest floor removed (leaving only mineral soil); and three soil compaction treatments: C0—no compaction, C1—light compaction (2-cm depression into mineral soil), C2—heavy compaction (4-cm depression). Each site was hand-felled in the winter with at least a 50-cm snowpack and ground skidded through trails between plots to minimize soil disturbance. Forest floors from OM3 plots were carefully removed with an excavator and bucket attachment, with as little mineral soil displacement as possible. The compaction was done with an excavator and tamping plate, rather than logging equipment, to better control the uniformity and intensity of compaction. On the bole-only removal treatment (OM1), the logging slash was piled into rows to allow the compaction treatment and then respread. The experimental installation was completed in 1993. The plots were split and planted with two tree species: copper-treated 1 + 0 211 PSB (polystyro blocks) lodgepole pine, and untreated 2 + 0 415 PSB hybrid white spruce. Seedlings were planted at 2.5 × 2.5 m spacing in the spring following treatment installation. Vegetation surrounding the seedlings was clipped and removed up to a 50-cm radius for the first 5 yr to reduce competition effects.

Some selected core measures, which have been part of the ongoing LTSP monitoring, have been included to further characterize the treatments. These include forest floor mass, soil N mass, and mineralizable N concentrations collected preharvest, posttreatment (Year 1), Year 5 and Year 10. Total C and N were measured using combustion elemental analysis. Mineralizable N (Min-N) was determined through a 2-wk anaerobic incubation at 30°C, followed by a 4 M KCl extraction and colorimetric analysis for ammonium N (Kalra and Maynard, 1991; Carter, 1993). Mineral soil bulk density was determined to a 20-cm depth using excavations of approximately 1.5 L. The volume of the holes was determined with glass beads. The soils were oven-dried (105°C for 24 h) and the mass of the fine fraction (<2 mm) determined by grinding and sieving out the coarse fragments. A coarse fragment specific density of 2.65 g cm⁻³ was used for the calculation of coarse fragment volume. Nutrient concentrations were converted to mass (kg ha⁻¹) using mineral soil bulk density adjusted for coarse fragment content (<2 mm wt/total volume), while compaction treatments were characterized by fine fraction bulk density (<2 mm wt/2 mm volume). Forest floor mass was determined from a 20 × 20 cm area, with live roots removed from the sample. Five bulk density and forest floor samples were randomly located in each split-plot. Forest floors were not sampled from the OM3 plots posttreatment because almost no organic matter accumulation had occurred by Year 10. Slash loads were estimated in a post-harvest fuel load survey using the line-intercept method (Trowbridge et al., 1986; Sanborn et al., 2000).

**In Situ Nitrogen Mineralization**

During the early growing season (June 7 and 13, 2005, for the SBSwk and SBSmc sites, respectively), five sample points were randomly selected from each split plot for the measurement of mineral soil and forest floor N availability using in situ buried bags. For the OM1 treatments, we collected two forest floor (15-cm diam. circle) and mineral soil (0- to 20-cm depth) samples within 1 m of the selected point; on OM3 treatments, we collected only mineral soil samples since no continuous surface humus had accumulated since the establishment of the experiment. One forest floor or mineral soil sample was buried for 5 wk and the other used to obtain an initial measure of inorganic N. The in situ samples were placed into thin polyethylene bags, and then replaced into the hole, with the litter layer or a thin layer of mineral soil (for the OM1 and OM3 treatments, respectively) covering the buried bags. All soil samples from time 0 and Week 5 were run through coarse sieves (6.3 mm for forest floor, 4.8 mm for mineral soil) and a subsample taken for moisture content (105°C for 24 h). A second subsample was frozen for KCl extraction of inorganic N.

Inorganic NH₄–N and NO₃–N were determined using KCl extraction of a 5- and 2-g dry-soil equivalent of mineral soil and forest floor, respectively (Hart et al., 1994). The extracts were immediately frozen (−80°C), allowing all pre-incubation and post-incubation samples to be analyzed together. The NH₄–N and NO₃–N in the extracts were measured colorimet-
ically using an Alpkem Flow System IV analyser (OI Analytical, College Station, TX). Nitrogen results are presented as initial inorganic N, gross inorganic N over 5 wk, and net mineralized N (subtracting the initial concentration of soil inorganic-N from the post-incubation concentration of soil inorganic-N). Concentrations were converted to mass (kg ha\(^{-1}\)) using mineral soil bulk density adjusted for coarse fragment content (<2 mm w/total volume) and forest floor mass values collected in Year 10 posttreatment.

**Tree Growth and Foliar Nitrogen Attributes**

Nine trees were randomly selected from each split plot in mid-September 2005. Tree height and height increment were measured on each tree. Foliar samples were taken from the current year’s growth in the top quarter of each tree (all sides of the tree) and bulked into three subsamples (each subsample has three trees randomly assigned from the nine measured trees). Foliar samples were oven-dried (70°C for 24 h) and ground with a Wiley mill. Foliar specific mass was determined from 50 needles. Foliar N was analyzed by dry combustion with the Leco CHN-600 analyzer (LECO Corp., St. Joseph, MI). Macro and micronutrients were analyzed by inductively coupled plasma–atomic emission spectroscopy following microwave digestion (Kalra and Maynard, 1991; Carter, 1993).

**Mushroom Collections**

Ectomycorrhizal mushrooms were collected in mid-September from the OM1C0, OM1C2, OM3C0, and OM3C2 treatments in 2004 and 2005. We picked mushrooms that were relatively fresh and larval-free. Not all ECM species were consistently fruiting in each split-plot, but where present the mushrooms were abundant enough to allow for a bulk sample of >5 mushrooms per split-plot. Species identification followed Arora (1986). The mushrooms were dried at 70°C and ground with a Wiley mill. Mushroom N concentrations were determined by dry combustion with the Leco CHN-600 analyzer (LECO Corp., St. Joseph, MI).

**Statistics**

The LTSP experiment is a randomized block design, with sites as blocks. The treatments were tested by ANOVA using Proc Mixed in SAS (SAS Institute, 1988), with site and site interactions set as random factors. Mineral soils were tested for compaction and forest floor removal effects, while forest floors were only tested for compaction across OM1 treatments (OM3 treatment had no forest floor values to test). Tree response and N concentrations were tested with subsamples, while N mass was tested with the mean value (average concentration \(\times\) average bulk density) per split-plot. Mineralizable N was tested across sample year using repeated measures under Proc Mixed in SAS with site interactions set as random factors. Forest floor min-N from one plot at the SBSwk site in Year 10 was not included in this analysis because of inadequate drying during sample preparation.

**RESULTS**

**Selected Soil Properties**

Total soil N averaged 2697 kg ha\(^{-1}\) preharvest, which was reduced by 977 kg N (36%) after forest floor removal on the OM3 plots (Table 1). Mineralizable N, an index of plant-available N, averaged 55 kg ha\(^{-1}\) preharvest, and was reduced by 26 kg (51%) after forest floor removal on the OM3 plots (Table 1). Mineralizable N concentrations were tested with subsamples, while N mass was only tested for compaction across OM1 treatments (OM3 plots was likely limited to surface horizons, however, and deeper soils (>10 cm) were noticeably denser and greater in soil strength than uncompacted plots at Year 10.

**Soil Nitrogen In Situ Mineralization**

In situ N mineralization rates at Year 12 were quite consistent across treatments, and we did not detect any effects of compaction or forest floor removal on net N mineralized or gross inorganic N concentrations (Table 2; ANOVA results for gross inorganic N not shown). We also did not find any differences in these N mineralization measures between tree species. Overall, net mineralization rates were low, averaging 15.0 mg kg\(^{-1}\) NH\(_4\)\(^+\) and 1.0 mg kg\(^{-1}\) NH\(_3\)\(^+\) in forest floors and mineral soils, respectively, over 5 wk (Table 3). Nitrate was not detected in any soils at the end of the incubation.

The rates of NH\(_4\)\(^+\) mineralization for forest floors or mineral soils, when expressed as mass (kg ha\(^{-1}\)), were not significantly different across disturbance treatments or tree species either (Table 2). The mass of NH\(_4\)\(^+\) mineralized in forest floors at Year 12 was less than found for mineral soils, and was equal to 38% of the soil profile on average (Table 3). Forest floors and mineral soils combined (OM1) for 3.3 kg NH\(_4\)\(^+\) ha\(^{-1}\) mineralized over 5 wk, compared with 1.5 kg NH\(_4\)\(^+\) ha\(^{-1}\) for OM3 plots (Fig. 2).

<table>
<thead>
<tr>
<th>Year</th>
<th>Mass</th>
<th>Total N</th>
<th>C/N ratio</th>
<th>Min-N</th>
</tr>
</thead>
<tbody>
<tr>
<td>SBSmc</td>
<td>7.53 (0.4)</td>
<td>1097 (68)</td>
<td>34 (0.4)</td>
<td>31 (1.5)</td>
</tr>
<tr>
<td>SBSwk</td>
<td>7.82 (0.6)</td>
<td>856 (53)</td>
<td>33 (0.6)</td>
<td>21 (1.6)</td>
</tr>
</tbody>
</table>

† SBSmc, Subboreal Spruce Biogeoclimatic zone moist and cool; SBSwk, Subboreal Spruce Biogeoclimatic Zone wet and cool.

**Table 1. Selected preharvest properties of the Long-term soil productivity (LTSP) sites (mean and SD).**
Tree Growth and Foliar Response

There was evidence of an interaction between organic matter removal and compaction for tree height and height increment at Year 12 (Table 4 and Fig. 3). Tree productivity was generally higher with the intermediate disturbances (OM1C2 or OM3C0) and lower with either no soil disturbance (OM1C0) or severe disturbances (OM3C2). The relative differences in tree productivity were much larger for hybrid white spruce (up to 40 and 60% difference in height and height increment, respectively) than lodgepole pine (for current height increment, the OM × Comp interaction p = 0.051 for spruce and p = 0.189 for pine). Lodgepole pine trees on average were also twice as tall as hybrid white spruce trees, with a height increment almost threefold greater across the treatments in Year 12.

At Year 5 postharvest, lodgepole pine, and hybrid white spruce foliar N concentrations from these plots averaged 13.3 and 12.0 g kg⁻¹, respectively, with no significant difference detected between species (p = 0.389). By Year 12, foliar N concentrations of lodgepole pine, averaging 12.6 g kg⁻¹, were significantly higher than hybrid white spruce, at 9.2 g kg⁻¹ (Table 4). There was some evidence of a treatment interaction with species (p = 0.098): lodgepole pine had relatively consistent foliar N concentrations across treatments, while hybrid white spruce tended to peak with the intermediate treatments (OM × Comp interaction p = 0.106 for spruce, and p = 0.394 for pine; see Fig. 4a). Foliar specific mass (g per 50 needles) was not affected by the treatments for either pine or spruce, and patterns in foliar N content were no more diagnostic than N concentrations (data not shown). Overall, hybrid white spruce foliar N ranged from 7.0 to 12.8 g kg⁻¹ (very severely deficient to moderate deficiency; Carter 1992), and was positively correlated with height increment (p < 0.001, adj. r² = 0.48), while lodgepole pine foliar N ranged from 11.2 to 14.8 g kg⁻¹ (moderate deficiency to adequate; Brockley, 2001), with no correlation to height increment (Fig. 4b).

### Ectomycorrhizal Mushroom Nitrogen Concentrations

Nine species of ECM mushrooms were sampled, of which five were host-generalist fungi (occurring with both lodgepole pine and hybrid spruce) and four were host-specific fungi (Table 5). Fruiting by these ECM species was sporadic across the plots, which precluded a

### Table 2. ANOVA results for net NH₄⁺ mineralization in forest floors and mineral soils across soil disturbance treatments (organic matter removal and compaction) at Year 12 postharvest.

<table>
<thead>
<tr>
<th></th>
<th>Forest floor NH₄⁺</th>
<th>Mineral soil NH₄⁺</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(mg kg⁻¹)</td>
<td>(mg kg⁻¹)</td>
</tr>
<tr>
<td></td>
<td>(kg ha⁻¹)</td>
<td>(kg ha⁻¹)</td>
</tr>
<tr>
<td>Forest floor</td>
<td></td>
<td></td>
</tr>
<tr>
<td>OM removal</td>
<td>df (p &gt; F)</td>
<td>df (p &gt; F)</td>
</tr>
<tr>
<td>OM1</td>
<td>1</td>
<td>0.370</td>
</tr>
<tr>
<td>OM3</td>
<td>1</td>
<td>0.562</td>
</tr>
<tr>
<td>Compaction</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C0</td>
<td>2</td>
<td>0.263</td>
</tr>
<tr>
<td>C1</td>
<td>2</td>
<td>0.428</td>
</tr>
<tr>
<td>OM × Comp</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spruce</td>
<td>1</td>
<td>0.546</td>
</tr>
<tr>
<td>Pine</td>
<td>2</td>
<td>0.744</td>
</tr>
<tr>
<td>OM × Comp × Species</td>
<td>2</td>
<td>0.634</td>
</tr>
</tbody>
</table>

### Table 3. Forest floor and mineral soil (0–20 cm depth) NH₄⁺ mineralization measures (5 wk in situ incubation) at Year 12 postharvest, averaged across soil disturbance treatments and tree species.

<table>
<thead>
<tr>
<th></th>
<th>Initial NH₄⁺ (time 0)</th>
<th>Gross NH₄⁺ (5 wk)</th>
<th>Net NH₄⁺ (5 wk)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Conc., mg kg⁻¹</td>
<td>Conc., mg kg⁻¹</td>
<td>Conc., mg kg⁻¹</td>
</tr>
<tr>
<td>Forest floor</td>
<td>13.1 (1.3)</td>
<td>28.1 (2.2)</td>
<td>15.0 (2.1)</td>
</tr>
<tr>
<td>Mineral soil</td>
<td>1.3 (0.1)</td>
<td>2.4 (0.1)</td>
<td>1.0 (0.1)</td>
</tr>
<tr>
<td>Mass, kg ha⁻¹</td>
<td>1.0 (0.2)</td>
<td>2.1 (0.3)</td>
<td>1.1 (0.2)</td>
</tr>
<tr>
<td>Mineral soil</td>
<td>2.2 (0.2)</td>
<td>4.1 (0.4)</td>
<td>1.9 (0.3)</td>
</tr>
</tbody>
</table>

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more detailed analysis of possible differences in N concentrations across treatments. There were, in general, no clear differences in the N status of host-generalist fungi between tree species, averaging 28 g N kg$^{-1}$ dry mass between the five ECM species for both lodgepole pine and hybrid white spruce. The *Suillus* species, found only with lodgepole pine, had the highest N concentrations of the species sampled, averaging 38 g N kg$^{-1}$, which was 40% higher than the average N concentrations of all the other ECM species combined.

**DISCUSSION**

We found large differences in growth and N nutrition between lodgepole pine and hybrid white spruce that suggest there may be challenges in defining universal criteria for detrimental soil disturbance. The ability of lodgepole pine to maintain relatively adequate N status and good tree productivity was in sharp contrast to hybrid white spruce. The differences in tree species response were apparent both over time (from Year 5 to 12) and across soil disturbance treatments. The results emphasize the dynamic nature of these ecosystems after harvesting and the need to examine each species response to fully understand the implications of land management practices.

Soil N availability typically increases after tree harvest (the assart effect), and peaks after approximately 3 to 5 yr (Keenan and Kimmins, 1993), which would be generally consistent with the patterns of mineralizable N from our sites. The relative status of soil N in the midterm (>10-yr postharvest) is less clear, but some studies have reported N availability at levels below that of unharvested stands (Piatek and Allen, 1999; Finzi and Canham, 2000; Brais et al., 2002). A short-term pulse in available N would be consistent for the hybrid white spruce in this study, with foliar N concentrations as high as 16.5 g kg$^{-1}$ at Year 5, and declining by 22%, on average, by Year 12. Foliar N concentrations for many spruce trees are now severely deficient, and, unlike pine, generally reflect the low rates of N mineralization in mineral soils and forest floors (both only 1/3 the N mineralization rates found in 12-yr-old gaps in a temperate forest; J.M. Kranabetter, unpublished data, 2004). Such low rates of N mineralization might develop after significant losses of N from the ecosystem via leaching during the assart flush (Smethurst and Nambiar, 1990), and a decline in microbial activity with lower postharvest inputs of C (Finzi and Canham, 2000; Hassett and Zak, 2005). As a general pattern for subboreal forests, we suggest soil N availability increases rapidly in the first years following tree harvest, peaking and then declining.

![Fig. 2. Net NH$_4^+$ mineralized (kg ha$^{-1}$) in 5-wk in situ incubation for mineral soils + forest floors across soil disturbance treatments at Year 12 (sites and species split-plots combined; SE as error bars).](image)

![Fig. 3. Tree height and height increment of lodgepole pine and hybrid white spruce at Year 12 across soil disturbance treatments (both sites combined; SE as error bars).](image)

### Table 4. ANOVA results for soil disturbance (organic matter removal and compaction) effects on tree height, height increment, and foliar N concentrations at Year 12 postharvest.

<table>
<thead>
<tr>
<th></th>
<th>Tree ht</th>
<th>Ht inc.</th>
<th>Foliar N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>($p &gt; F$)</td>
<td>($p &gt; F$)</td>
</tr>
<tr>
<td>OM removal</td>
<td>1</td>
<td>0.318</td>
<td>0.873</td>
</tr>
<tr>
<td>Compaction</td>
<td>2</td>
<td>0.859</td>
<td>0.550</td>
</tr>
<tr>
<td>OM × Comp</td>
<td>2</td>
<td>0.083</td>
<td>0.056</td>
</tr>
<tr>
<td>Species</td>
<td>1</td>
<td>0.122</td>
<td>0.035</td>
</tr>
<tr>
<td>OM × Species</td>
<td>1</td>
<td>0.278</td>
<td>0.381</td>
</tr>
<tr>
<td>Comp × Species</td>
<td>2</td>
<td>0.816</td>
<td>0.774</td>
</tr>
<tr>
<td>OM × Comp × Species</td>
<td>2</td>
<td>0.564</td>
<td>0.217</td>
</tr>
</tbody>
</table>
by Year 10 to create a high potential for N limitations to growth.

Both negative and positive short-term effects of compaction and forest floor removal on N mineralization have been reported in the LTSP network (Gomez et al., 2002a; Li et al., 2003; Tan et al., 2005). We also observed early interactions in mineralizable N in this study, but little evidence for soil disturbance effects on N supply in the subsequent period (other than simply the reduction in N caused by forest floor removal). Soil microbial processes such as decomposition rates have proven fairly resilient to a range of soil disturbances (Kranabetter and Chapman, 2004; Shestak and Busse, 2005), which might result in little long-term difference in soil biological function and organic matter turnover after the initial assart flush. The consistent, albeit low, rates of N mineralization suggest that the differences in tree productivity or foliar N status cannot be explained solely by N supply. In fact, some of the most productive trees and highest foliar N concentrations for both species were found on plots with the lowest amounts of net mineralized and total N (OM3C0). The diverging response between tree species or across soil disturbance treatments is therefore more likely explained by processes governing N uptake.

Nitrogen uptake and tree growth, especially for hybrid white spruce, was higher with the intermediate combinations of soil disturbance. This response curve across soil disturbances might be explained by the influence of soil temperature and bulk density on N diffusion and root activity. Low soil temperatures limit productivity in boreal forests, and warming soils through organic matter removal or compaction (up to 3°C increase in average daily soil temperature; Kranabetter and Chapman, 2004) could affect N uptake by reducing water viscosity, increasing rooting depth, and lengthening the season for root growth (Bowen, 1991; Bonan, 1992). Higher bulk densities via compaction can increase the diffusion rate of N through greater unsaturated hydraulic conductivity and improved root–soil contact, both leading to a higher N status of the plant (Arvidsson, 1999; Gomez et al., 2002a). Compaction without the forest floor, however, exposed soils to more drying, which likely increased soil strength and mechanical resistance to the point where root development and growth was detrimentally affected (Bulmer and Simpson, 2005; Paged-Dumroese et al., 2006). An effort was made to manually control vegetation interactions, but differences in plant communities across treatments (Haeussler et al., 2002) and therefore varying levels of competition for N cannot be ruled out. Differences in competition for N between the crop tree and its surrounding vegetation would likely not explain the species effects we observed, however, because neither pine nor spruce were tall enough to affect the surrounding vegetation.

Better growing conditions created by a moderate amount of soil disturbance have also been found with some, but not all, tree species (Brais, 2001; Gomez et al., 2002b; Eisenbies et al., 2005; Ares et al., 2005; Kabzems and Haeussler, 2005), usually on mesic sites with medium- or coarse-textured soils. The beneficial effects of these soil disturbances would parallel some experi-
ences with mechanical site preparation and prescribed burning (e.g., Orlander et al., 1996; Bulmer et al., 1998; Kranabetter and Yole, 2000; MacKenzie et al., 2005). Our point is not to encourage widespread compaction or organic matter removal, but to recognize that a certain amount of soil disturbance in northern climates is perhaps necessary to maintain site potential, at least for some species such as hybrid white spruce. As Haussler and Knesew (2003) concluded, the most important limiting factor in nutritionally poor ecosystems, where rates of C and N cycling diminish over time, may well be insufficient rather than excessive disturbance during logging. It should be acknowledged that our treatments do not include the potentially detrimental disturbance associated with mineral soil displacement (Rygiewicz et al., 2004) (bladed trails, landings etc.), nor do we dismiss the potential for further shifts in treatment effects in the long-term.

Physiological mechanisms, such as greater retranslocation efficiency, might favor pine nutrition on poor soils as stands mature, but the early period of growth should depend largely on soil sources of N (Miller, 1995). Differences in N uptake between species, and the clear advantage to lodgepole pine, was perhaps affected by the benefits of host-specific Suillus ECM fungi. Suillus species generally persist or disperse well after forest disturbances, and are often prominent in young stands (Dahlberg and Finlay, 1999), so these fungi should be key contributors to the N status of these lodgepole pine trees (Bothwell et al., 2001). The higher N concentrations of Suillus mushrooms presumably reflect more N uptake by the mycelium (Vogt et al., 1981; Ohtonen, 1986; Gebauer and Taylor, 1999), perhaps through less accessible organic N sources, which could be shared with the host trees. Another intriguing possibility is the contribution of N fixation from bacteria within the peridium of the host trees. Another intriguing possibility is the contribution of N fixation from bacteria within the peridium of the host trees. Another intriguing possibility is the contribution of N fixation from bacteria within the peridium of the host trees.

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