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; Périé 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* Dougl. 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

---

J.M. Kranabetter, British Columbia Ministry of Forests, BAG 6000, Smithers, BC, V0J 2N0 Canada; P. Sanborn, Univ. of Northern British Columbia, 3333 University Way, Prince George, BC, V2N 4Z9 Canada; B.K. Chapman, British Columbia Ministry of Forests, 200-640 Borland St., Williams Lake, BC, V2G 4T1 Canada; S. Dube, British Columbia Ministry of Forests, 1011 4th Ave., Prince George, BC, V2L 3H9 Canada. Received 21 Feb. 2006. *Corresponding author (marty.kranabetter@gov.bc.ca).

Published in Soil Sci. Soc. Am. J. 70:1591–1599 (2006).
Forest, Range & Wildland Soils
doi:10.2136/sssaj2006.0081

677 S. Segoe Rd., Madison, WI 53711 USA

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 mushrooms. 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 biogeoclimatic 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 (Boralfs) 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 ovendried (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 NH_4–N and NO_3–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 NH_4–N and NO_3–N in the extracts were measured colorimetrically 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 wt/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 × 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 (Table 1). Mineralizable N concentrations of the forest floors and mineral soils generally increased after harvest, peaking between Year 1 and 5 before declining by Year 10 to equal to or below preharvest levels (Fig. 1). These trends are approximate, however, as both mineral soils and forest floors had significant treatment interactions by year (OM × Year $p = 0.022$ and OM × Comp × Year $p = 0.014$, respectively).

Table 1. Selected preharvest properties of the Long-term soil productivity (LTSP) sites (mean and SE).

	Mass	Total N	C/N ratio	Min-N
	Mg ha^{-1}	kg ha^{-1}		kg ha^{-1}
		Forest floor		
SBSmc†	7.53 (0.4)	1097 (68)	34 (0.4)	31 (1.5)
SBSwk	7.82 (0.6)	856 (53)	33 (0.6)	21 (1.6)
		Mineral soil (0–20 cm)		
SBSmc	na	2269 (156)	21.0 (0.3)	46 (5)
SBSwk	na	1170 (108)	18.4 (0.5)	13 (1)

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

Slash loads averaged 36.2 Mg ha^{-1} for the OM1 plots at the SBSmc and SBSwk sites, equal to 75 kg N per ha. Forest floor mass at Year 10 averaged 7.5 (SE 0.5) kg m^{-2} across the OM1 treatments, which was a 15% reduction from preharvest mass, with no effects of compaction ($p = 0.191$) or species ($p = 0.291$). Mineral soil bulk density (<2 mm) at Year 10 averaged 1.14 (SE 0.23) Mg m^{-3} to a 20-cm depth, with evidence for a significant interaction between organic matter and compaction ($p = 0.037$). Bulk density increased with compaction under forest floors (from 1.00 to 1.30 Mg m^{-3}), but was more uniform where forest floors were removed (from 1.10 to 1.15 Mg m^{-3}). Any recovery in bulk density on 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 organic matter 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_4^+ 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).

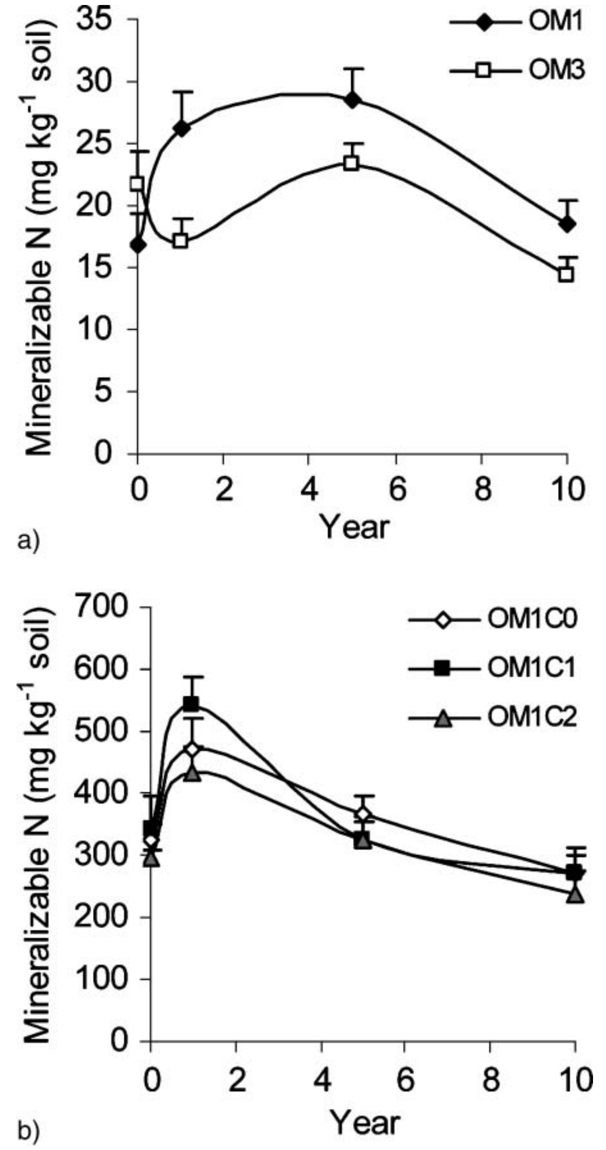

Fig. 1. Trends in mineralizable N concentrations between preharvest (Year 0), posttreatment (Year 1) and Years 5 and 10 for (a) mineral soil and (b) forest floors. (Selected plots only for SBSmc and SBSwk; SE as error bars). OM1–bole only removal; OM3-Whole-tree and forest floor removed; C0–no compaction; C1–light compaction; C2–heavy compaction.

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.

Table 2. ANOVA results for net NH_4^+ mineralization in forest floors and mineral soils across soil disturbance treatments (organic matter removal and compaction) at Year 12 postharvest.

		Forest floor NH_4^+		Mineral soil NH_4^+	
		mg kg^{-1}	kg ha^{-1}	mg kg^{-1}	kg ha^{-1}
	df	($p > F$)	($p > F$)	($p > F$)	($p > F$)
OM removal	1	na		0.370	0.244
Compaction	2	0.901	0.680	0.562	0.533
OM × Comp	2	na		0.263	0.603
Species	1	0.990	0.605	0.428	0.450
OM × Species	1	na		0.546	0.770
Comp × Species	2	0.495	0.543	0.744	0.724
OM × Comp × Species	2	na		0.634	0.668

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. $r^2 = 0.48$), 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 3. Forest floor and mineral soil (0–20 cm depth) NH_4^+ mineralization measures (5 wk in situ incubation) at Year 12 postharvest, averaged across soil disturbance treatments and tree species.

	Initial NH_4^+	Gross NH_4^+	Net NH_4^+
	(time 0)	(5 wk)	
		Conc., mg kg^{-1}	
Forest floor	13.1 (1.3)	28.1 (2.2)	15.0 (2.1)
Mineral soil	1.3 (0.1)	2.4 (0.1)	1.0 (0.1)
		Mass, kg ha^{-1}	
Forest floor	1.0 (0.2)	2.1 (0.3)	1.1 (0.2)
Mineral soil	2.2 (0.2)	4.1 (0.4)	1.8 (0.3)

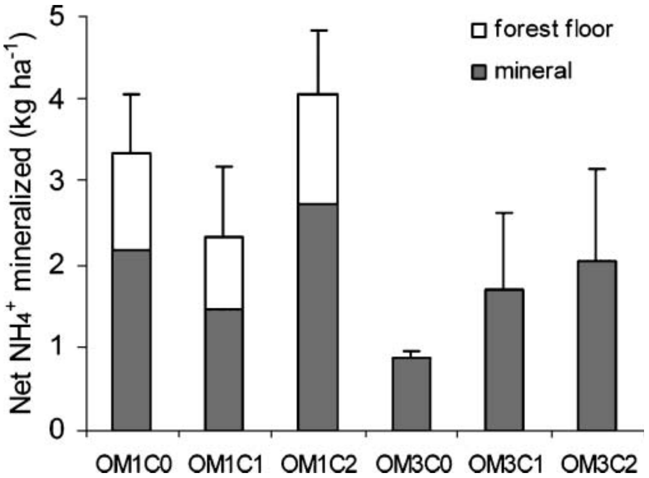

Fig. 2. Net NH_4^+ mineralized (kg ha^{-1}) in 5-wk in situ incubation for mineral soils + forest floors across soil disturbance treatments at Year 12 (sites and species split-plots combined; SE as error bars).

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

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.

		Tree ht	Ht inc.	Foliar N
	df	(p > F)	(p > F)	(p > F)
OM removal	1	0.318	0.873	0.793
Compaction	2	0.859	0.550	0.958
OM × Comp	2	0.083	0.056	0.294
Species	1	0.122	0.035	0.059
OM × Species	1	0.278	0.381	0.487
Comp × Species	2	0.816	0.774	0.422
OM × Comp × Species	2	0.564	0.217	0.098

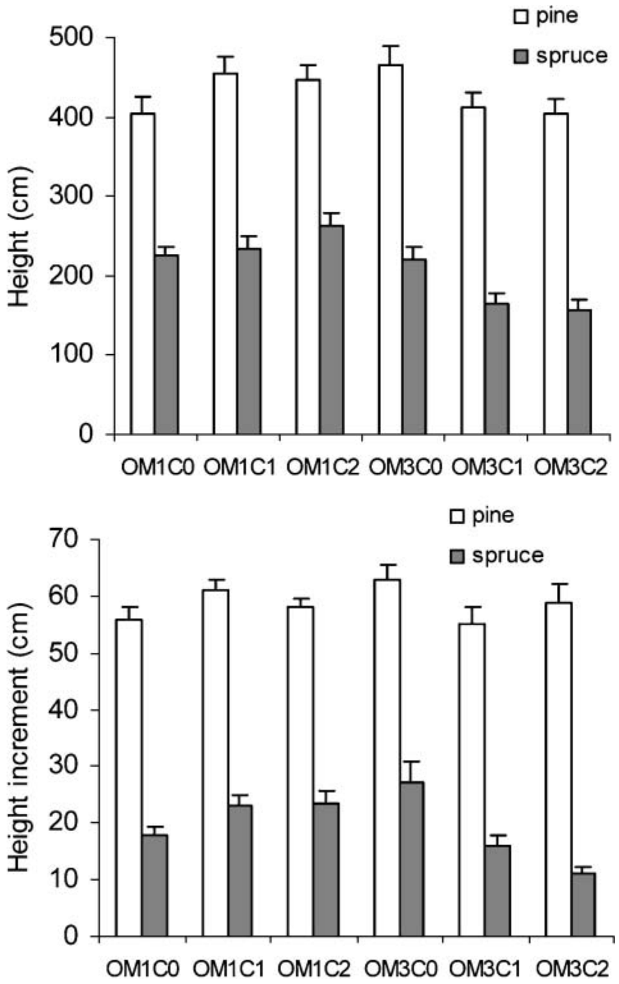

Fig. 3. Tree height and height increment of lodgepole pine and hybrid white spruce at Year 12 across soil disturbance treatments (both sites combined; SE as error bars).

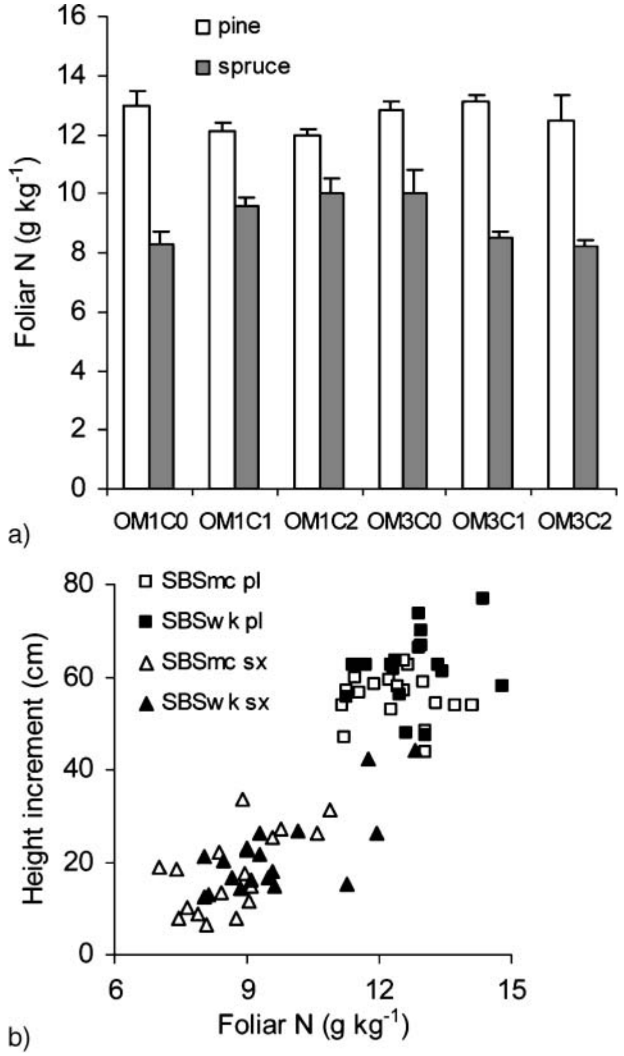

Fig. 4. (a) Foliar N concentrations of lodgepole pine and hybrid white spruce at Year 12 across soil disturbance treatments (both sites combined; SE as error bars), and (b) relationship between height increment and foliar N concentrations at Year 12 for lodgepole pine (pl) and hybrid white spruce (sx) for both sites (SBSmc, Subboreal Spruce Biogeoclimatic zone moist and cold; SBSwk, Subboreal Spruce Biogeoclimatic Zone wet and cool).

Table 5. Sporocarp N concentrations (mean and SE where plots sampled > 1) for host-generalist and host-specific ECM species with lodgepole pine and hybrid white spruce (*n* = number of plots sampled, max. 8).

Lodgepole pine	(*n*)	N, g kg^{-1}	Hybrid white spruce	(*n*)	N, g kg^{-1}
Host-generalist ECM species					
Thelephora terrestris	**5**	**27 (1.3)**	***Thelephora terrestris***	**3**	**26 (1.0)**
Laccaria laccata	**3**	**28 (2.2)**	***Laccaria laccata***	**3**	**29 (3.9)**
Hebeloma crustuliniforme	**1**	**29**	***Hebeloma crustuliniforme***	**2**	**28 (1.1)**
Cortinarius croceus	**2**	**30 (0.6)**	***Cortinarius croceus***	**4**	**31 (2.1)**
***Inocybe lanuginosa*-like**	**1**	**32**	***Inocybe lanuginosa*-like**	**1**	**24**
Host-specific ECM species					
Suillus brevipes	**7**	**37 (2.7)**	***Hygrophorus agathosmus***	**4**	**32 (0.8)**
Suillus tomentosus	**4**	**41 (3.1)**			
Chroogomphus rutilus	**8**	**20 (0.7)**			

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; Page-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 experiences with mechanical site preparation and prescribed burning (e.g., Örlander 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 Haeussler and Kneeshaw (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 *Suillus* tuberculate structure (Paul, 2002; Peterson et al., 2004). Early-seral ECM communities with spruce (including some host-generalist ECM species on pine), in comparison, would likely be at a relative disadvantage as soil inorganic N supplies decline over time (Kranabetter, 2004). Superior root development might also favor lodgepole pine nutrition, although field evidence has not consistently demonstrated large differences in rooting depth between these species (e.g., Nadeau and Pluth, 1997; Bothwell et al., 2001), nor indicated that lodgepole pine roots are insensitive to soil compaction (Corns, 1988; Wass and Smith, 1994; Conlin and van den Driessche, 1996; Bulmer and Simpson, 2005). Given the remarkable differences in foliar N nutrition, especially on bare, compacted mineral soils (over 50% higher than spruce), the nutritional benefits of *S. brevipes* and *S. tomentosus* to lodgepole pine, and the N fixation associated with tuberculate ectomycorrhiza, should be further explored.

In conclusion, the contrasting species response to soil compaction and organic matter removal in the first decade of this experiment indicate possible challenges in defining universal criteria for detrimental soil disturbance. Moderate levels of soil disturbance led to better tree growth and nutrition, especially for hybrid spruce, and these results lend support to the utility of treatments such as mechanical site preparation and prescribed burning in the management of boreal soils (Hawkins et al., 2006).

ACKNOWLEDGMENTS

We thank a number of individuals associated with the SBS LTSP, including Rick Trowbridge, Anne Macadam, and Marty Osberg for initiating the project, and a large number of summer students assisting in all aspects of the study. Marcel Lavigne, in particular, assisted in this buried bag installation and foliar/mushroom preparation for analysis. Clive Dawson and Dave Dunn of the Ministry of Forests Analytical Laboratory undertook the soil and foliar chemical analysis. Peter Ott and Wendy Bergerud of the Ministry of Forests Research Branch were consulted on the statistical analysis. Shannon Berch (Ministry of Forests Research Branch) has administered and participated in the LTSP study since the start. Funding for this project was supplied by the Forest Science Program administered through PriceWaterhouse Cooper.

REFERENCES

Ares, A., T.A. Terry, R.E. Miller, H.W. Anderson, and B.L. Flaming. 2005. Ground-based forest harvesting effects on soil physical properties and Douglas-fir growth. Soil Sci. Soc. Am. J. 69:1822–1832.

Arora, D. 1986. Mushrooms demystified. 2nd ed. Ten Speed Press, Berkeley.

Arvidsson, J. 1999. Nutrient uptake and growth of barley as affected by soil compaction. Plant Soil 208:9–19.

Banner, A., W. MacKenzie, S. Haeussler, S. Thomson, J. Pojar, and R. Trowbridge. 1993. A field guide to site identification and interpretation for the Prince Rupert Forest Region. Ministry of Forestry Field Handb. 26. Crown Publications, Victoria, B.C.

Bonan, G.B. 1992. Soil temperature as an ecological factor in boreal forests. p. 126–143. *In* H.H. Shugart et al. (ed.) System analysis of the global boreal forest. Cambridge Press, Cambridge.

Bothwell, K.S., C.E. Prescott, and M.D. Jones. 2001. Factors contributing to the superior growth and N nutrition of 11-year-old lodgepole pine compared with Sitka spruce on a N-poor cedar-hemlock cutover. Can. J. For. Res. 31:1272–1279.

Bowen, G.D. 1991. Soil temperature, root growth, and plant function. p. 309–330. *In* Y. Waisel et al. (ed.) Plant roots: The hidden half. Marcel Dekker, Inc. New York.

Brais, S. 2001. Persistence of soil compaction and effects on seedling growth in northwestern Quebec. Soil Sci. Soc. Am. J. 65:1263–1271.

Brais, S., D. Pare, C. Camire, P. Rochon, and C. Vasseur. 2002. Nitrogen net mineralization and dynamics following whole-tree harvesting and winter windrowing on clayey sites of northwestern Quebec. For. Ecol. Manage. 157:119–130.

Brockley, R.P. 2001. Foliar sampling guidelines and nutrient interpretative criteria for lodgepole pine. Ext. Note No. 52. B.C. Ministry of Forests, Victoria, B.C.

Bulmer, C., M.G. Schmidt, B. Kishchuk, and C. Preston. 1998. Impacts of blading and burning site preparation on soil properties and site productivity in the sub-boreal spruce zone of central British Columbia. Can. For. Serv. Inf. Rep. BC-X-377. Can. For. Serv. Victoria, BC.

Bulmer, C.E., and D.G. Simpson. 2005. Soil compaction and water content as factors affecting the growth of lodgepole pine seedlings on sandy clay loam soil. Can. J. Soil Sci. 85:667–679.

Carter, M.R. (ed.). 1993. Soil sampling and methods of analysis. Lewis Publishers, Boca Raton, FL.

Carter, R. 1992. Diagnosis and interpretation of forest stand nutrient status. p. 90–97. *In* H.N. Chappel et al. (ed.) Forest fertilization: Sustaining and improving nutrition and growth of western forests. Institute of Forest Resources. No. 73. University of Washington, Seattle.

Chapin, F.S., III. 1980. The mineral nutrition of wild plants. Ann. Rev. Ecol. Sys. 11:233–260.

Conlin, T.S.S., and R. van den Driessche. 1996. Short-term effects of soil compaction on growth of *Pinus contorta* seedlings. Can. J. For. Res. 26:727–739.

Corns, G.W. 1988. Compaction by forestry equipment and effects on coniferous seedling growth on four soils in the Alberta foothills. Can. J. For. Res. 18:75–84.

Curran, M.P., R.E. Miller, S.W. Howes, D.G. Maynard, T.A. Terry, R.L. Heninger, T. Niemann, K. van Rees, R.F. Powers, and S.H. Schoenholtz. 2005. Progress towards more uniform assessment and reporting of soil disturbance for operations, research, and sustainability protocols. For. Ecol. Manage. 220:17–30.

Dahlberg, A., and R.D. Finlay. 1999. Suillus. p. 33–64. *In* J.W.G. Cairney and S.M. Chambers (ed.) Ectomycorrhizal fungi. Key genera in profile. Springer-Verlag, NY.

Delong, C., D. Tanner, and M.J. Jull. 1993. A field guide for site identification and interpretation for the southwest portion of the Prince George Forest Region. B.C. Minist. For. Land Manage. Handb. No. 24. Victoria, B.C.

Egnell, G., and B. Leijon. 1999. Survival and growth of planted seedlings of *Pinus sylvestris* and *Picea abies* after different levels of biomass removal in clear-felling. Scand. J. For. Res. 14:303–311.

Eisenbies, M.H., J.A. Burger, W.M. Aust, and S.C. Patterson. 2005. Soil physical disturbance and logging residue effects on changes in soil productivity in five-year-old pine plantations. Soil Sci. Soc. Am. J. 69:1833–1843.

Finzi, A.C., and C.D. Canham. 2000. Sapling growth in response to light and nitrogen availability in a southern New England forest. For. Ecol. Manage. 131:153–165.

Fleming, R.L., R.F. Power, N.W. Foster, J.M. Kranabetter, D.A. Scott, F. Ponder, Jr., S. Berch, W.K. Chapman, R.D. Kabzems, K.H. Ludovici, D.M. Morris, D.S. Page-Dumroese, P. Sanborn, F.G. Sanchez, D.M. Stone, and A.E. Tiarks. 2006. Effects of soil compaction, organic matter removal, and vegetation control on 5-year seedling performance: A regional comparison of LTSP sites. Can. J. For. Res. 36:529–550.

Fyles, J.W., and B. Côté. 1994. Forest floor and soil nutrient status under Norway spruce and red pine in a plantation in southern Quebec. Can. J. Soil Sci. 74:387–392.

Gebauer, G., and A.F.S. Taylor. 1999. ^{15}N natural abundance in fruit bodies of different functional groups of fungi in relation to substrate utilization. New Phytol. 142:93–101.

Gomez, A., R.F. Powers, M.J. Singer, and W.R. Horwath. 2002a. N uptake and N status in ponderosa pine as affected by soil compaction and forest floor removal. Plant Soil 242:263–275.

Gomez, A., R.F. Powers, M.J. Singer, and W.R. Horwath. 2002b. Soil compaction effects on growth of young ponderosa pine following litter removal in California's Sierra Nevada. Soil Sci. Soc. Am. J. 66:1334–1343.

Green, R.N., R.L. Trowbridge, and K. Klinka. 1993. Towards a taxonomic classification of humus forms. For. Sci. Mono. 29:1–48.

Haeussler, S., L. Bedford, A. Leduc, Y. Bergeron, and J.M. Kranabetter. 2002. Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest. Silva Fennica 36:307–327.

Haeussler, S., and D. Kneeshaw. 2003. Comparing forest management to natural processes. p. 307–368. *In* P.J. Burton et al. (ed.) Towards sustainable management of the boreal forest. NRC Research Press, Ottawa, ON.

Hart, S.C., J.M. Stark, E.A. Davidson, and M.K. Firestone. 1994. Nitrogen mineralization, immobilization, and nitrification. p. 985–1018. *In* R.V. Weaver et al (ed.) Methods of Soil Analysis. Part 2. SSSA Book Series 5. SSSA, Madison, WI.

Hassett, J.E., and D.R. Zak. 2005. Aspen harvest intensity decreases microbial biomass, extracellular enzyme activity, and soil nitrogen cycling. Soil Sci. Soc. Am. J. 69:227–235.

Hawkins, C.B.D., T.W. Steele, and T. Letchford. 2006. The economics of site preparation and the impacts of current forest policy: Evidence from central British Columbia. Can. J. For. Res. 36:482–494.

Hobbie, S.E. 1992. Effects of plant species on nutrient cycling. Trends Evol. Ecol. 7:336–339.

Jurgensen, M.F., A.E. Harvey, R.T. Graham, D.S. Page-Dumroese, J.R. Tonn, M.J. Larsen, and T.B. Jain. 1997. Impacts of timber harvesting on soil organic matter, nitrogen, productivity, and health of inland northwest forests. For. Sci. 43:234–251.

Kabzems, R., and S. Haeussler. 2005. Soil properties, aspen and white spruce responses five years after organic matter removal and compaction treatments. Can. J. For. Res. 35:2045–2055.

Kalra, Y.P., and D.G. Maynard. 1991. Methods manual for forest soil and plant analysis. Forestry Canada, Northwest Region, Northern Forestry Centre, Edmonton, AB. Information Report NOR-X-319.

Karlen, D.L., M.J. Mausbach, J.W. Doran, R.G. Cline, R.F. Harris, and G.E. Schuman. 1997. Soil quality: A concept, definition, and framework for evaluation. Soil Sci. Soc. Am. J. 61:4–10.

Keenan, R.J., and J.P. Kimmins. 1993. The ecological effects of clearcutting. Environ. Rev. 1:121–144.

Kimmins, J.P. 1996. Importance of soil and role of ecosystem disturbance for sustained productivity of cool temperate and boreal forests. Soil Sci. Soc. Am. J. 60:1643–1654.

Knops, J.M.H., K.L. Bradley, and D.A. Wedin. 2002. Mechanisms of plant species impacts on ecosystem nitrogen cycling. Ecol. Lett. 5:454–466.

Kozlowski, T.T. 1999. Soil compaction and growth of woody plants. Scand. J. For. Res. 14:596–619.

Kranabetter, J.M. 2004. Ectomycorrhizal community effects on hybrid spruce seedling growth and nutrition in clearcuts. Can. J. Bot. 82:983–991.

Kranabetter, J.M., and B.K. Chapman. 2004. An analysis of litter nitrogen dynamics using artificial soils across a gradient of forest soil disturbances. Can. J. Soil Sci. 84:159–167.

Kranabetter, J.M., and D. Yole. 2000. Alternatives to broadcast burning in the northern interior of British Columbia: Short-term tree results. For. Chron. 76:349–353.

Krause, H.H. 1998. Forest floor mass and nutrients in two chronosequences of plantations: Jack pine vs. black spruce. Can. J. Soil Sci. 78:77–83.

Krzic, M., C.E. Bulmer, F. Teste, L. Dampier, and S. Rahman. 2004. Soil properties influencing compactability of forest soils in British Columbia. Can. J. Soil Sci. 84:219–226.

Li, Q., H.L. Allen, and C.A. Wilson. 2003. Nitrogen mineralization dynamics following the establishment of a loblolly pine plantation. Can. J. For. Res. 33:364–374.

Lipson, D., and T. Nasholm. 2001. The unexpected versatility of plants: Organic nitrogen use and availability in terrestrial ecosystems. Oecologia 128:305–316.

MacKenzie, M.D., M.G. Schmidt, and L. Bedford. 2005. Soil microclimate and nitrogen availability 10 years after mechanical site preparation in northern British Columbia. Can. J. For. Res. 35:1854–1866.

Meidinger, D., and J. Pojar. 1991. Ecosystems of British Columbia. Special Report Series No. 6. Crown Publications, Victoria BC.

Miller, H.G. 1995. The influence of stand development on nutrient demand, growth and allocation. Plant Soil 168–169:225–232.

Miller, H.G., J.M. Cooper, J.D. Miller, and O.J.L. Pauline. 1979. Nutrient cycles in pine and their adaptations to poor soils. Can. J. For. Res. 9:19–26.

Nadeau, L.B., and D.J. Pluth. 1997. Spatial distribution of lodgepole pine and white spruce seedling roots 10 years after deep tillage of a Gray Luvisol. Can. J. For. Res. 27:1606–1613.

Ohtonen, R. 1986. The effect of forest fertilization on the nitrogen content of the fruit-bodies of two mycorrhizal fungi, *Lactarius rufus* and *Suillus variegatus.* Ann. Bot. Fenn. 23:189–203.

Örlander, G., G. Egnell, and A. Albrektson. 1996. Long-term effects of site preparation on growth in Scots pine. For. Ecol. Manage. 86:27–37.

Page-Dumroese, D.S., M.F. Jurgensen, A.E. Tiarks, F. Ponder, Jr., F.G. Sanchez, R.L. Fleming, J.M. Kranabetter, R.F. Powers, D.M. Stone, J.D. Elioff, and D.A. Scott. 2006. Soil physical property changes at the North American Long-Term Soil Productivity study sites: 1 and 5 years after compaction. Can. J. For. Res. 36:551–564.

Pajuste, K., and J. Frey. 2003. Nitrogen mineralization in podzol soils under boreal Scots pine and Norway spruce stands. Plant Soil 257:237–247.

Paul, L.R. 2002. Tuberculate ectomycorrhizae on lodgepole pine (*Pinus contorta*) and associated nitrogen fixation. Ph.D. thesis, University of British Columbia, Vancouver, BC.

Périé, C., and A.D. Munson. 2000. Ten-year responses of soil quality and conifer growth to silvicultural treatments. Soil Sci. Soc. Am. J. 64:1815–1826.

Peterson, R.L., H.B. Massicotte, and L.H. Melville. 2004. Mycorrhizas: Anatomy and cell biology. NRC Research Press, Ottawa, ON.

Piatek, K.B., and H.L. Allen. 1999. Nitrogen mineralization in a pine plantation fourteen years after harvesting and site preparation. Soil Sci. Soc. Am. J. 63:990–998.

Powers, R.F. 2006. Long-term Soil Productivity: Genesis of the concept and principles behind the program. Can. J. For. Res. 36:519–528.

Powers, R.F., A.E. Tiarks, and J.R. Boyle. 1998. Assessing soil quality: Practicable standards for sustainable forest productivity in the United States. p. 53–80. *In* The Contribution of Soil Science to the development of and Implementation of Criteria and Indicators of Sustainable Forest Management. SSSA Special Pub. No. 53. SSSA, Madison, WI.

Prescott, C.E., D.G. Maynard, and R. Laiho. 2000. Humus in northern forests: Friend or foe? For. Ecol. Manage. 133:23–36.

Read, D.J., and J. Perez-Moreno. 2003. Mycorrhizas and nutrient cycling in ecosystems—A journey towards relevance? New Phytol. 157:475–492.

Reich, P.B., M.B. Walters, and D.S. Ellsworth. 1997. From tropics to tundra: Global convergence in plant functioning. Proc. Natl. Acad. Sci. USA 94:13730–13734.

Rygiewicz, P.T., D. Zabowski, and M.F. Skinner. 2004. Site disturbance effects on a clay soil under *Pinus radiata*– root biomass, mycorrhizal colonisation, ^{15}Ammonium uptake, and foliar nutrient levels. N.Z. J. For. Sci. 34:238–254.

Sanborn, P., J.M. Kranabetter, and B. Chapman. 2000. Nutrient removals in woody biomass: Preliminary estimates from the Sub-boreal Long-Term Soil Productivity study. LTSP Research Note 04, B.C. Forest Service, Victoria, B.C.

SAS Institute. 1988. SAS/STAT user's guide. Release 6.03 ed. SAS Institute Inc., Cary, NC.

Schoenholtz, S.H., H. Van Miegroet, and J.A. Burger. 2000. A review of chemical and physical properties as indicators of forest soil quality: Challenges and opportunities. For. Ecol. Manage. 138:335–356.

Shestak, C.J., and M.D. Busse. 2005. Compaction alters physical but not biological indices of soil health. Soil Sci. Soc. Am. J. 69:236–246.

Smethurst, P.J., and E.K.S. Nambiar. 1990. Distribution of carbon and nutrients and fluxes of mineral nitrogen after clear-felling a *Pinus radiata* plantation. Can. J. For. Res. 20:1490–1497.

Soil Classification Working Group. 1998. The Canadian System of soil classification. 3rd ed. Agriculture and Agri-Food Canada Pub. 1646. Canadian Government Publishing Center. Ottawa, Canada.

Tan, X., S.X. Chang, and R. Kabzems. 2005. Effects of soil compaction and forest floor removal on soil microbial properties and N transformations in a boreal forest long-term soil productivity study. For. Ecol. Manage. 217:158–170.

Trowbridge, R.L., B. Hawkes, A.M. Macadam, and J. Parminter. 1986. Field handbook for prescribed fire assessments in British Columbia: Logging slash fuels. B.C. Min. For., Land Manage. Handb. 11. Queen's Printer Publications, Victoria, B.C.

Van Cleve, K., and C.T. Dyrness. 1983. Introduction and overview of a multidisciplinary research project: The structure and function of a black spruce (*Picea mariana*) forest in relation to other fire-affected taiga ecosystems. Can. J. For. Res. 13:695–702.

Vogt, K.A., R.L. Edmonds, and C.C. Grier. 1981. Biomass and nutrient concentrations of sporocarps produced by mycorrhizal and decomposer fungi in *Abies amabilis* stands. Oecologia 50:170–175.

Wass, E.F., and R.B. Smith. 1994. Impacts of soil disturbance on root systems of Douglas-fir and lodgepole pine seedlings. Information Rep. BC-X-348. For. Can., Pacfic Forestry Centre, Victoria, BC.

Wästerlund, I. 1985. Compaction of till soils and growth tests with Norway spruce and Scots pine. For. Ecol. Manage. 11:171–179.

Williams, B.L. 1992. Nitrogen dynamics in humus and soil beneath Sitka spruce (*Picea sitchensis* (Bong.) Carr.) planted in pure stands and in mixture with Scots pine (*Pinus sylvestris* L.). Plant Soil 144:77–84.

Williams, B.L., J.M. Cooper, and D.G. Pyatt. 1979. Some effects of afforestation with lodgepole pine on rates of nitrogen mineralization in peat. Forestry 52:151–160.