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Complete List of Authors:	Kranabetter, John Marty; British Columbia Ministry of Forests and Range Dube, Stephane ; College of New Caledonia Lilles, Erica; British Columbia Ministry of Forests Lands and Natural Resource Operations
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An investigation into the contrasting growth response of lodgepole pine and
white spruce to harvest-related soil disturbance

J.M. Kranabetter¹, S. Dube² and E.B. Lilles³

¹British Columbia Ministry of Forests, Lands and Natural Resource Operations

P.O. Box 9536, Stn Prov Govt, Victoria, B.C., Canada V8W 9C4

Tel: 1 250 952-4172, Fax: 1 250 952-4119

Marty.Kranabetter@gov.bc.ca

²Applied Research and Innovation, College of New Caledonia

3330 22nd Ave., Prince George, B.C., Canada V2N 1P8

³British Columbia Ministry of Forests, Lands and Natural Resource Operations

BAG 6000, Smithers B.C., Canada V0J 2N0

Abstract

Losses in forest productivity through poor soil management are typically evaluated by changes in crop production, but conflicting growth responses among co-occurring species can challenge criteria for sustainability. In this study we evaluate species response to compaction and organic matter removal by contrasting the growth and foliar attributes at age 20 of lodgepole pine (*Pinus contorta* Dougl. ex Loud.) and hybrid white spruce (*Picea glauca* x *engelmannii* [Moench] Voss) in sub-boreal forests of central British Columbia. Bole volume increment was stable for lodgepole pine, averaging a 6% difference across treatments. White spruce, in contrast, often had large growth increases on forest floor retained – compacted plots (average of 63% gain), but reductions in productivity on the forest floor removed – compacted plots (40% decline). Foliar nitrogen concentrations converged across treatments for both species, despite the removal of over 50% of the site N capital. Some key differences in species traits were suggested by foliar $\delta^{15}\text{N}$, attributed to deeper rooting of pine, and foliar $\delta^{13}\text{C}$, indicating possibly higher CO_2 assimilation potential for spruce. The implication is that standard metrics of sustainable forestry are contingent upon tree autecology, and that comprehensive assessments of land management require a measure of collective species response.

Keywords: compaction, whole-tree harvest, ^{13}C , *Pinus contorta*, *Picea glauca*

Introduction

The post-harvest maintenance of soil productivity is a widely accepted and fundamental principle of sustainable forestry (Powers et al. 1999, Schoenholtz et al. 2000, Moffat 2003), and the impetus behind many studies of management issues such as biomass harvesting and heavy machine traffic (Thiffault et al. 2011, Ampoorter et al. 2011, Achat et al. 2015). Soil productivity has been primarily defined and quantified by the production of crops over a unit of time (i.e., net primary productivity, $\text{kg ha}^{-1} \text{ yr}^{-1}$), where any changes in tree growth can be attributed to differences in soil conditions, rather than silvicultural influences such as regeneration delay, stand tending, or removal of competing vegetation (Morris 1997). While a number of key soil properties that support crop production can be fairly readily measured, particularly nutrient and water availability (Paré et al. 2002, Duchesne and Houle 2008, Brandtberg and Olsson 2012), assessments of management impacts are often based ultimately on tree growth (e.g., Kabzems 2012, Fleming et al. 2014), with a suggested threshold of 15% productivity loss as defining detrimental soil disturbance (Powers et al. 1999). Other important functions of soils, such as the maintenance of site hydrology, provision of biotic habitat, and sequestration of carbon are acknowledged (Moffat 2003, Burger et al. 2008, Scott et al. 2014), but along with the expressed goal of nondeclining trends in forest productivity over multiple rotations (Nambiar 1996).

Inherent site productivity varies widely depending upon abiotic features, including climate, soil parent materials, and topography. The productive capacity of a soil may be altered both positively and negatively by management activities, particularly harvest-related soil disturbances. Two key changes to soils include reductions in soil porosity (compaction) and removal of site organic matter (OM), and recognition of these risks to soil productivity prompted a large, co-ordinated research effort to quantify these combined disturbance effects on forest plantations (the Long-term Soil Productivity study [LTSP]; Powers 2006). Synthesis of study results up to year 10 post-treatment have not found evidence of

consistent, negative effects of site organic matter removal or compaction on tree growth, but experimental outcomes have varied depending on site vulnerability (defined in part by soil texture and mineralogy) and tree species (Powers et al. 2005, Ponder et al. 2012). In some circumstances the autecology of a tree species might explain unique responses to compaction or organic matter removal, such as how the regeneration success of aspen (*Populus tremuloides* Michx.) depends upon the timing of soil disturbance (Stone and Kabzems 2002). With other tree species, however, the mechanisms for a diverging growth response are more obscure, and could involve a variety of species traits, including rooting patterns, nutritional demands, drought or frost tolerance, and mycorrhizal associations (Ponder et al. 2012). There are also some uncertainties as to whether these species effects might only be ephemeral, with some convergence in biomass production as saplings more fully accommodate to disturbed site conditions over time (Heninger et al. 2002, Egnell 2011). Sustainable production of diverse forests is a key management objective in many jurisdictions, making it important to better define the mechanisms behind tree species response to harvest-related soil disturbance, and to confirm if these effects persist past the establishment phase of a forest rotation.

Lodgepole pine (*Pinus contorta*) and hybrid white spruce (*Picea glauca* x *engelmannii*) are native conifer species widely utilized in reforestation throughout central and northern British Columbia (Canada). Both species have comparable growth potential (site indices at 50 years of approximately 19 m) on mesic sites (Wang 1998), with an expected rotation age of 80 years, although lodgepole pine has much greater initial growth rates than white spruce (Eis et al. 1982). Kranabetter et al. (2006), in a LTSP trial of 10 years in duration, described how white spruce growth declined under severe soil disturbances (forest floor removed and compacted mineral soil), in contrast to lodgepole pine, making it difficult to demonstrate unequivocal losses in site productivity. Large differences in foliar N concentrations between these two species indicated discrepancies in N acquisition as a possible mechanism leading to a diverging growth response. Another factor in species response to soil disturbance may be related to

water use and photosynthetic capacity (Gomez et al. 2002b, Choi et al. 2005), a potentially important difference among tree species given the sometimes beneficial increase in water-holding capacity found with soil compaction (Fleming et al. 1998, Brais 2001, Gomez et al. 2002a, Ares et al. 2005). Commercial forestry throughout the northern hemisphere use related species of pine and spruce (e.g., Thiffault et al. 2007, Helmisaari et al. 2011), each perhaps with similar autecology to *P. contorta* and *P. glauca*, so a better understanding of long-term response to harvest-related soil disturbances by these conifer species may prove relevant to vast areas of managed forests.

In this study we present the 20 year results from OM removal and compaction treatments in the Sub-Boreal Spruce zone of central British Columbia. We examine the most recent volume increment (years 15-20) of lodgepole pine and hybrid white spruce to test whether initial contrasting trends in productivity (Kranabetter et al. 2006) have converged over time. Foliar nutrient concentrations and natural isotope (^{13}C and ^{15}N) abundance, which integrate plant responses to resource gradients (Dawson et al. 2002), were examined for evidence of ecological traits separating the growth responses of these conifer species to soil disturbance (Gomez et al. 2002b, Choi et al. 2005, Tan et al. 2006). The objectives of our study were to 1) establish the extent of productivity changes due to organic matter removal and soil compaction after 20 years in the Sub-Boreal Spruce zone; 2) test whether co-occurring conifer species respond differently to harvest-related soil disturbance via growth rates and nutrition; and 3) elucidate possible mechanisms related to species autecology that would explain differences in treatment response. Our hypotheses at the onset of the LTSP study were that losses in site organic matter and reductions in soil porosity would be detrimental to forest soils (i.e., > 15% decline in productivity), with parallel losses in productivity between conifer species.

Materials and Methods

Site Descriptions

The LTSP installations in central British Columbia are located in the Sub-boreal Spruce biogeoclimatic zone (SBS), characterized by cold, snowy winters and relatively warm, moist and short summers (Meidinger and Pojar 1991). Three subzones were selected as sites (blocks) to replicate the LTSP experiment across a relative range of climatic conditions encompassed by SBS forests. Climate variables of mean annual temperature (MAT), precipitation (MAP) and heat:moisture index ($AH:M = [MAT+10]/[MAP/1000]$) were obtained for the 2001-2010 decade at each study site by querying ClimateWNA (Wang et al. 2006) with latitude, longitude and elevation. The three test sites include the moist, cold SBSmc subzone near Topley, BC (54°36'43"N, 126°18'25"W, elev. 1100 m, MAT 1.7°C, MAP 614 mm, AH:M 18.2); the wet, cool SBSwk near Prince George, BC (54°21'57"N, 122°36'48"W, elev. 785 m, MAT 3.3°C, MAP 897 mm, AH:M 14.8); and the warm, dry SBSdw near Williams Lake, BC (52°18'54"N, 121°54'51"W, elev. 1050 m, MAT 3.8°C, MAP 559 mm, AH:M 24.7). The sites are located within an approx. 200 km radius. Each site has deep, moderately well-drained to well-drained soils derived from ablation till, with textures ranging from sandy loam to loam (SBSmc 52% sand, 27% silt, 21% clay; SBSwk 44% sand, 40% silt, 16% clay; SBSdw 56% sand, 35% silt, 9% clay; Krzic et al. 2004), up to 40% coarse fragments, and mor humus forms approximately 7 cm thick. Sites were level (SBSdw), or had slopes ranging from 2-12%. Preharvest stands were 112-140 years old and comprised predominantly of subalpine fir (*Abies lasiocarpa* [Hook.] Nutt), hybrid white spruce and lodgepole pine. Site indices, based on preharvest stands, averaged 17.5 m at 50 yrs.

Experimental Design

Each LTSP site has nine plots (40 x 70 m each), arranged in a factorial combination of three organic matter removal treatments:

OM1 - Stem (boles) only removed, logging slash retained;

OM2 - Stems and crowns removed (whole-tree harvesting);

OM3 - Whole-tree and forest floor removed (scalped to mineral soil);

135 and three soil compaction treatments:

136 C0 - No compaction;

137 C1 - Light compaction (2 cm impression into mineral soil);

138 C2 - Heavy compaction (4 cm impression).

139 Each site was hand-felled in the winter to minimize soil disturbance. Logging slash was removed
140 by hand, and forest floors were extracted with an excavator and bucket attachment, with as little
141 mineral soil removal as possible. Soil compaction to the required depths was done with an excavator-
142 mounted hydraulic tamping plate. On the bole-only removal treatment, the logging slash was piled into
143 rows to allow compaction without impressing the slash into the soil and then respread. The treatment
144 plots were split (40 x 35 m) and planted with copper-treated 1+0 211 PSB (polystyrene blocks) lodgepole
145 pine or untreated 2+0 415 PSB hybrid white spruce. Local provenances were used for planting stock,
146 and seedlings were planted at 2.5 x 2.5 m spacing in the spring following treatment installation. In the
147 centre portion of each split-plot we tagged 100 seedlings (10 x 10 rows) for remeasurement, with the
148 outer two rows providing a buffer on all sides to minimize edge effects. Vegetation surrounding the
149 seedlings was clipped and removed up to a 50 cm radius for the first 5 years to reduce competition
150 effects. Any seedling mortality during the course of the study was not replaced. The experimental
151 installation was completed in 1993 for the SBSwk and SBSmc sites, and in 1994 for the SBSdw site.

152 Some key site variables related to the treatments were described previously (Sanborn et al.
153 2000, Kranabetter and Chapman 2004, Kranabetter et al. 2006) and summarized here: logging slash
154 averaged 34.6 tonnes ha⁻¹, equivalent to 58 kg N ha⁻¹; forest floor mass averaged 65 tonnes ha⁻¹,
155 equivalent to 815 kg N ha⁻¹; mineral soil N (to a 20 cm depth) averaged 1664 kg ha⁻¹; pre-treatment bulk
156 density (< 2 mm fraction) averaged 1.07 g cm⁻³, and increased to 1.42 g cm⁻³ with light compaction and
157 1.49 g cm⁻³ with heavy compaction (no statistical difference in bulk density between C1 and C2
158 treatments). Maximum bulk density, which is the theoretically highest compactability value based on

post-harvest mineral soil % C content (Krzic et al. 2004), averaged 1.61 g cm^{-3} for SBSdw, 1.55 g cm^{-3} for SBSwk, and 1.51 g cm^{-3} for SBSmc. Daily average mineral soil temperature (10 cm depth) over the growing season increased by 1°C to 3°C with whole-tree removal and scalping, respectively, and by approx. 0.5°C with compaction.

Tree and soil measures

Tree survival, height and diameter (at root collar initially, then at 1.3 m as trees reached pole size) were measured every 5 years (up to 20 years post-treatment) and bole volume was calculated with juvenile taper equations for each species (Kovats 1977). Differences in average bole volume by split-plot were determined between years 15 and 20 to derive the most recent growth increment. Volume increment was presented as a percent change to standardize treatment responses between species and sites (Thiffault et al. 2011). The percent change was calculated as the difference between each treatment plot from the least disturbed (OM1C0) treatment (e.g., $[\text{OM2C0}-\text{OM1C0}]/\text{OM1C0} \times 100$). Site index (metres at 50 yrs) was calculated from tree height and age using Forests Site Tools 3.3 (B.C. Ministry of Forests 2004).

All soil sampling took place within the central portion of each split-plot (the 10×10 rows of tagged trees). Chemical properties of forest floors and mineral soils (to 20 cm depth) were collected preharvest and at years 1, 5, 10, 15 and 20 post-treatment. Up to year 5, 25 subsamples were taken randomly throughout a plot and bulked into five samples, after which we collected three bulked subsamples of five sampling points (15 in total) per species split-plot. Soils were air-dried and sieved (2 mm) for analysis. Soil bulk density (BD) was determined by excavation to 20 cm at pre-harvest and years 1, 5, 10 and 20, starting with 10 random points per plot and then, by year 5, five random points per split-plot. Fine fraction BD ($< 2 \text{ mm}$) was calculated with an assumed specific gravity of the coarse fragments of 2.65 g cm^{-3} , and relative bulk density (RBD) was determined as $\text{BD}/\text{Maximum Bulk Density}$ (Zhao et al. 2010). Starting in year 5 post-treatment, foliar sampling was undertaken at 5 year intervals for each

species, with single bulked samples (10 trees combined) initially that was increased to three bulked subsamples (15 trees in total) per split-plot in years 15 and 20. Foliar samples were taken from the current year's growth in the top quarter of each tree in the fall (September – October) when growth had ceased. In 2015 (22 years post-treatment), soil moisture of the mineral soil (0-20 cm) was measured every three weeks (mid-May to mid-September) at the SBSmc site. A soil auger was used to extract five cores per split-plot, and these were bulked into one sample for gravimetric moisture determination (105°C for 24 hours) of the fine fraction (< 2 mm).

Foliar mass was determined on 100 needles, and foliar nutrient concentrations determined by dry combustion with a Leco CHN-600 analyzer (LECO Corp. St. Joseph, MI). Macronutrients were analyzed by inductively coupled plasma-atomic emission spectroscopy following microwave digestion. Mineralizable N concentrations of soils were measured via a 2-week anaerobic lab incubation (Kalra and Maynard 1991). The relative abundance of ^{13}C and ^{15}N , reported as $\delta^{13}\text{C}_{\text{vpdb}}$ and $\delta^{15}\text{N}_{\text{air}}$ respectively, was determined on approximately 5 mg of finely milled, oven dry (70°C) foliage and soils using a Flash 2000 elemental analyzer coupled to a ConFlo IV interface and DELTA Advantage isotope ratio mass spectrometer (all instruments Thermo Fisher Scientific, Waltham, MA). Instrument calibration was performed using certified reference materials EMA-P2 ($\delta^{13}\text{C}_{\text{vpdb}}$ -28.19‰, $\delta^{15}\text{N}_{\text{air}}$ -1.57‰), Sorghum Flour B2159 ($\delta^{13}\text{C}_{\text{vpdb}}$ -13.68‰, $\delta^{15}\text{N}_{\text{air}}$ -1.58‰) and USGS40 ($\delta^{13}\text{C}_{\text{vpdb}}$ -26.39‰, $\delta^{15}\text{N}_{\text{air}}$ -4.52‰). Reference materials EMA-P2 and Sorghum Flour purchased from Elemental Microanalysis Ltd, Okehampton, UK, traceable to isotope standards IAEA-CH-6 and IAEA-N-1. USGS40 purchased from National Institute of Standards and Technology (NIST), USDA. All reported values were calculated using Isodat3.0 gas isotope ratio MS software (Thermo Fisher Scientific) and subject to post-run two point linear normalization (Paul et al. 2007) to correct for instrument drift and changes in calibration gas. Foliar $\delta^{13}\text{C}$ was tested as absolute values and in relation to the least disturbed (OM1C0) treatment (e.g., $\Delta\delta^{13}\text{C} = \text{OM2C0} - \text{OM1C0}$).

Statistics

The experiment is a randomized block split-plot design. The main-plot factors (OM and Comp) are arranged as a full factorial design replicated in three blocks (sites), with species (pine and spruce) as the split-plot factor. For foliar and growth data, subsamples and individual trees were averaged beforehand, yielding a single value for each combination of site/OM/Comp/species. For soil data (chemistry and bulk density), where species split-plot was not used in early sampling, we focus on OM and Comp effects by averaging subsamples for each combination of site/OM/Comp.

Data from year 20 (the most recent sampling) were modelled as randomized block split-plot design using the Mixed Procedure (Method=REML) in SAS (SAS Institute 2011). Both site and the pooled main-plot error term (site x OM x Comp) were handled as random effects. All model assumptions were assessed graphically. For example, overall model fit and the additivity assumption (Montgomery 2008) were examined by plotting the observed volume increment versus their model predicted value to ensure a relationship close to 1:1 (i.e. the model fit well to the data). Survival (per 100 tree split-plot) was modelled using an overdispersed generalized linear mixed model (GLMM) via Proc Glimmix in SAS (SAS Institute 2011). The model included the same terms as those used for the Mixed Procedure (OM/Comp/Species), but here the distribution (conditional on the random effects) was assumed to be binomial.

Multi-year data of plot attributes were fitted to a repeated measures extension of the Mixed Procedure model. In the case of repeated foliar sampling, year was handled as a split split-plot factor, site x species x OM x Comp was incorporated as an additional random factor, and the covariance of each subject (site x species x OM x Comp) was modelled as a generalized ar(1) process with unequal time steps (e.g. sp[pow][year] in Proc Mixed; SAS Institute 2011). For soil chemistry and bulk density we removed the species factor from the repeated measures model as the split-plot was not designated in the early years of post-treatment sampling. Statistical significance was set at $p < 0.10$ in recognition of the inherent variability associated with field studies.

The relationships between tree productivity (volume) and foliar traits were tested by step-wise regression using a general linear model (GLM) with type III sums of squares (SAS Institute 2011). Site, species and either foliar N% or $\delta^{13}\text{C}$ were tested with a full set of interactions (e.g., site x species x N%), and then refitted without the three- or two-way interactions if these terms were insignificant.

Results

Soil properties

The focus of this element of our study is species growth response to harvest-related soil disturbances, and so we present select post-treatment soils data here to define key parameters of the study sites. The removal of forest floor was still evident 20 years post-treatment, with a high percentage (approx. 75%) of mineral soil exposure and little humus accumulation during this time. Post-treatment bulk density of the uncompacted soils averaged 1.19 g cm^{-3} (SE 0.016) up to year 20, significantly less dense than light ($1.37 [0.017] \text{ g cm}^{-3}$) and heavy ($1.32 [0.018] \text{ g cm}^{-3}$) compaction treatments, respectively ($p = 0.01$). This increase in soil bulk density was equivalent, on average, to a relative bulk density of 0.86 across the compaction treatments. We found a marginal reduction ($p = 0.08$) in mineralizable N of the mineral soils (0-20 cm) with organic matter removal (OM1 = $23.0 [SE 0.81] \text{ mg kg}^{-1}$, OM2 = $26.3 [1.28] \text{ mg kg}^{-1}$, and OM3 = $17.9 [0.60] \text{ mg kg}^{-1}$) over the post-treatment period, but no effect of compaction ($p = 0.49$). Forest floor mineralizable N (OM1 and OM2 only) was not affected by the treatments (p values for OM = 0.79, Comp = 0.83). Bulk soil $\delta^{15}\text{N}$ averaged 4.44‰ (SE 0.16) for mineral soil and 0.54‰ (0.24) for forest floor at 20 years post-treatment. Differences in soil moisture content over the 2015 growing season, measured at the SBSmc site, were most pronounced with forest floor removal, reaching a 50% decline at mid-July in comparison to the plots with forest floor retained (Fig. 1).

Tree response

Lodgepole pine was almost twice as tall as white spruce at year 20, on average, with heights of 6.6 (SE 0.3) m and 3.3 (0.3) m, respectively (Table 1). Wide differences in inherent productivity among the three sites were also evident, with the largest trees at the SBSwk site (average pine and spruce height of 8.4 [SE 0.2] m and 4.7 [0.2] m, respectively), followed by SBSmc (pine and spruce heights of 6.4 [0.07] and 3.7 [0.3] m, respectively), and the SBSdw site (pine and spruce heights of 4.9 [0.1] m and 1.6 [0.1] m, respectively). Site index (at 50 years) estimates on the least disturbed (OM1C0) plots predict fairly even growth trajectories between species, with an average of 19.4 m (pine) and 19.0 m (spruce) at SBSwk, 15.6 m (pine) and 16.2 m (spruce) at SBSmc, and 13.8 m (pine) and 9.0 m (spruce) at SBSdw.

Plots were well stocked through year 20 for both species, averaging 89% (SE 1.2) survival for pine and 90% (2.1) for spruce, with no effect of soil disturbance on mortality (Table 2). Bole volume increment between years 15 and 20 was relatively stable for lodgepole pine, averaging a 6% difference across the treatments in relation to OM1C0 (Fig. 2). White spruce, in contrast, had much greater amplitude in volume increment, resulting in both Species $\times$ OM and Species $\times$ OM $\times$ Comp interactions (Table 2). Spruce often had growth increases on forest floor retained – compacted plots (average of 63% [SE 17] gain) but reductions in productivity on the forest floor removed – compacted plots (average of 40% [8] decline) (Fig. 2).

Over the first two post-treatment decades foliar N concentrations of spruce had fluctuated more broadly than pine (Species $\times$ Year $p < 0.001$), with a large decline after year 5 that partially recovered over the subsequent 10 years (Fig. 3). Some early differences between OM treatments in foliar N% at year 5 were not sustained over time (repeated measures p values; OM = 0.64, Compaction = 0.45, and OM $\times$ Comp = 0.45), nor did we detect any significant species $\times$ treatment interactions (Species $\times$ OM $p = 0.56$, Species $\times$ Comp = 0.99, Species $\times$ OM $\times$ Comp = 0.58). At year 20, foliar N concentrations were significantly greater for lodgepole pine (mean = 1.11% [SE 0.03]) than white spruce (1.04% [0.01]), with no effects of soil disturbance treatments (Table 2). Foliar $\delta^{15}\text{N}$ values differed

among species as well, with pine significantly less depleted on average than spruce (mean = -2.24‰ [SE 0.18] and -3.71‰ [0.19], respectively) (Table 2, Fig. 4). Foliar $\delta^{15}\text{N}$ values also differed significantly among OM treatments, becoming less depleted with full organic matter removal (Table 2, Fig. 4). Other foliar macronutrient concentrations such as P, Ca and Mg, along with needle mass, differed between tree species but were also unaffected by the disturbance treatments (Table 3). Some positive effects of OM removal and compaction were found for foliar S and K concentrations, although the increase was < 10% (Supplemental Figure).

The natural abundance of $\delta^{13}\text{C}$ in year 20 foliage was marginally different among OM treatments ($p = 0.09$), with values of -26.36‰ (SE 0.22), -26.22‰ (0.23), and -26.65‰ (0.18) for bole-only, whole-tree harvest, and forest floor removal plots, respectively. A test of $\Delta\delta^{13}\text{C}$ (in relation to OM1C0) to standardize site differences revealed stronger effects of OM removal and tree species on C discrimination (Table 2, Fig. 5). $\delta^{13}\text{C}$ became more negative with forest floor removal, as noted previously, while pine had more consistent depletion in ^{13}C on average than spruce, particularly where forest floors were retained (mean $\Delta\delta^{13}\text{C} = -0.17\text{‰}$ [SE 0.09] and 0.30‰ [0.09], respectively, for OM1 and OM2 treatments combined) (Fig. 5).

The relationship between tree volume and foliar attributes related to photosynthetic capacity (foliar N%, $\delta^{13}\text{C}$) were not consistent between tree species. A species interaction with $\delta^{13}\text{C}$ ($p = 0.015$) was caused by a negative slope with lodgepole pine and tree volume, in contrast to a positive slope with white spruce, at least for two of the three sites (Fig. 6). Foliar N% did not have a similar species interaction ($p = 0.20$), nor did it relate overall with volume ($p = 0.76$). There was significant covariation between foliar N% and $\delta^{13}\text{C}$ at the SBSwk site ($p = 0.035$), but not at the SBSmc ($p = 0.59$) or SBSdw ($p = 0.40$) sites.

Discussion

Organic matter removal and soil compaction effects on productivity, both negative and positive, were apparent 20 years post-treatment for white spruce, but not for lodgepole pine. Harvest-related soil disturbance effects on crop production, based on a 15% threshold (Powers et al. 1999), could therefore be interpreted in this trial as simultaneously positive, negative, or of no consequence, depending upon tree species. While the lack of consistency in growth response may be a challenge in crafting non-specific guidelines on best management practices (Page-Dumroese et al. 2000, Curran et al. 2005), it also reflects important aspects of co-occurring species autecology in boreal ecosystems.

One of the stronger treatment effects was the full removal of site organic matter (whole-tree harvest and forest floor scalping; OM3), as indicated by the reductions in soil moisture and mineralizable N. Compaction of these scalped soils had a particularly detrimental effect on spruce productivity through 20 years, estimated at a 40% reduction in volume increment. Lodgepole pine, however, was more tolerant of these compacted soils, as evident by the neutral response to OM3C1 and OM3C2 treatments, which may reflect the more robust development of vertical roots with pine as suggested by Zhao et al. (2010). Compacted mineral soils with an intact forest floor (OM1 and OM2), on the other hand, were often beneficial to spruce growth (10 of the 12 compacted-forest floor plots had increased spruce productivity, with 6 plots > 90% gains), despite an RBD > 0.8, possibly because the mulch layer minimized evaporative loss of water and the onset of root-restricting soil strength (Bulmer and Simpson 2005). Similar gains in tree growth with compaction have been noted previously over the LTSP network, and generally attributed to improved soil temperature and moisture storage capacity (Ponder et al. 2012). Our results are in contrast, however, to a negative growth response of white spruce with compaction on boreal LTSP sites in northeast British Columbia (Tan et al. 2006, Kabzems 2012), perhaps due to finer soil texture and flat topography that can lead to prolonged soil saturation and the onset of anoxic conditions (Startsev and McNabb 2009). One question to be evaluated as stands mature will be

whether rooting in compacted soils is limited to surface organic horizons and shallow mineral layers such that available rooting volume eventually constrains tree growth (Ludovici 2008).

Nutrient status of the trees, as judged by foliar concentrations, was largely equivalent across the treatments at year 20, despite some of the initial (year 5) separation in foliar N% with OM removal. Nutritional studies of these conifer species have consistently found strong correlations, of an approximate two-fold range (e.g., 0.8 to 1.5%), in foliar N% with soil fertility (Kranabetter and Simard 2008, Lilles et al. 2014), so the most parsimonious interpretation of the LTSP foliar data is for little change in N supply and uptake across treatments, even with the removal of over 50% of the site N capital through slash and forest floors. The increase in soil temperature of the mineral soil with forest floor removal (Kranabetter and Chapman 2004) may have allowed earlier and deeper root egress, with perhaps greater availability of N at depth, which could have compensated for N loss of the forest floor itself (Prescott et al. 2000). Other key nutrients such as Ca, Mg and K were considered vulnerable to excessive losses by organic matter removal and compaction treatments (Arocena 2000), but as yet we have found no foliar evidence of diminished cation availability. These findings are generally consistent with much of the LTSP network in North America (e.g., Kabzems 2012, Holub et al. 2013, Curzon et al. 2014), although more significant OM removal effects have been found on sites with lower inherent soil fertility or greater proportion of site nutrient capital in aboveground biomass (Wiebe et al. 2012, Hazlett et al. 2014, Himes et al. 2014, Morris et al. 2014).

Strong discrimination against the ^{15}N isotope, as demonstrated by $\delta^{15}\text{N}$ of approx. -4‰ across OM1C0 plots, is typical of ectomycorrhizal conifers (Craine et al. 2009), but the species effect suggests interesting differences in some aspects of nitrogen nutrition. The reduced $\delta^{15}\text{N}$ values for pine may be largely explained by the deeper rooting of pine compared to spruce, which would provide access to more depleted ^{15}N organic matter from lower in the soil profile (Houle et al. 2014). We have also found young pine stands to be well colonized by *Suillus tomentosus*, a tuberculate ectomycorrhizal fungus with

associated N-fixation (Chapman and Paul 2012) that may have contributed some amount of fixed-N with $\delta^{15}\text{N}$ values near 0‰. Differences in foliar %N at year 20 suggests lodgepole pine may have a competitive advantage over spruce on mesic sub-boreal sites with relatively low soil N availability through these root-related adaptations. The significant effect of OM removal on foliar $\delta^{15}\text{N}$ for both species can be partly explained by the sharp difference in available rooting substrates (4.44‰ for mineral soil and 0.54‰ for forest floor), which should narrow over time as forest floors re-establish.

Mesic sub-boreal forests have a less severe summer drought than more southern LTSP locations, which could affect the sensitivity of foliar $\delta^{13}\text{C}$ to soil moisture deficits (Gomez et al. 2002b, Tan et al. 2006). While species differences in $\Delta\delta^{13}\text{C}$ were apparent, and matched the species interaction in growth increment to some degree, we conclude that the variation among study sites and typically subtle treatment effects (< 1‰ change in enrichment; Gomez et al. 2002b) probably limited our ability to find a consistent influence of soil compaction or OM removal on C discrimination. The species interaction in $\delta^{13}\text{C}$ regressions with tree biomass (at least for two of the test sites), however, along with the species differences in $\Delta\delta^{13}\text{C}$ (spruce had more consistent gains in ^{13}C than pine, particularly where forest floors were retained), suggests some fruitful areas for future study. A number of field studies involving juvenile trees have reported both positive and negative relationships in $\delta^{13}\text{C}$ with productivity, which Marguerit et al. (2014) attributed to specific physiological mechanisms; positive slopes in $\delta^{13}\text{C}$ result from different assimilation rates of CO_2 , whereas negative slopes imply stomatal conductance as the limit to CO_2 uptake. The improved photosynthetic capacity attributed to spruce by patterns in $\delta^{13}\text{C}$ may be partly explained by concomitant increases in foliar N%, although we found inconsistent relationships between these two traits across the study sites. An additional mechanism would possibly be an uplift in mesophyll conductance of CO_2 with spruce (Warren 2008), in contrast to pine, on plots with large productivity gains due to favourable increases in soil moisture and temperature after soil disturbance (e.g., Duan et al. 2009).

Co-occurring native conifer species (*Pinus*, *Picea* and *Abies*) of boreal forests typically inhabit partially overlapping niches along edaphic gradients (Coates et al. 2013), which we suggest would be well aligned with the interactions found in this LTSP trial. Lodgepole pine is a shade-intolerant species that dominates low fertility sites (dry, N-poor soils with thin forest floors) through adaptations such as high water-use efficiency, deep rooting and associated N-fixation. White spruce (along with *Abies*) is a shade-tolerant species with a high growth capacity, particularly on sites with rich, moist soils and well-developed forest floors. Consistent with these realized niches are the significantly larger gains in tree volume and foliar N% for spruce and *Abies* compared to lodgepole pine along natural edaphic productivity gradients (Kranabetter and Simard 2008, Lilles and Astrup 2012). The implication for forest management is that severe soil disturbances (forest floor scalping and compaction) has relegated site suitability to only lodgepole pine, foregoing the opportunity to productively manage the other conifer species native to these mesic soils. This restriction in productive capacity may even extend beyond the current rotation if soil recovery continues to be slow (e.g., Walmsley et al. 2009). In this way the collective tree species response, where any member of the forest community has been negatively impacted, can be considered a significant loss in site potential.

Conclusions

At twenty years post-treatment, both the losses and gains in productivity for hybrid white spruce associated with organic matter removal and soil compaction greatly exceeded a 15% threshold, whereas no disturbance effects were detected on lodgepole pine. Foliar N and cation concentrations were not reduced by OM removal for either species, despite the loss of over 50% of the site N capital in slash and forest floors. Some key differences in species traits were suggested by foliar $\delta^{15}\text{N}$, attributed to deeper rooting of pine, and a species interaction in foliar $\delta^{13}\text{C}$ regressions with tree biomass, indicating possibly higher CO_2 assimilation potential for spruce. The results of this trial have implications in assessing sustainable forestry through crop production, and as such we recommend a measure of

396 collective tree species response, whereby a loss in site potential should be defined by a negative impact
397 on any member of the native forest community.

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Table 1. Survival, height, and stem diameter for lodgepole pine and hybrid white spruce at year 20 post-treatment (average of 3 sites, SE in brackets).

	OM1C0*	OM1C1	OM1C2	OM2C0	OM2C1	OM2C2	OM3C0	OM3C1	OM3C2
Pine									
Survival (%)	90 (3.7)	86 (4.3)	89 (4.9)	86 (5.2)	87 (6.4)	90 (3.8)	93 (3.2)	90 (3.2)	88 (1.9)
Height (m)	6.35 (0.10)	6.82 (0.11)	6.64 (0.11)	6.95 (0.13)	6.63 (0.12)	6.61 (0.10)	7.04 (0.13)	6.59 (0.11)	6.75 (0.10)
DBH (cm)	9.6 (0.2)	10.3 (0.2)	10.5 (0.2)	10.6 (0.2)	10.7 (0.2)	10.3 (0.2)	10.9 (0.3)	10.0 (0.2)	10.4 (0.2)
Spruce									
Survival (%)	94 (3.2)	89 (1.2)	87 (4.0)	95 (4.2)	86 (6.2)	88 (9.7)	95 (0.6)	83 (15.5)	96 (1.2)
Height (m)	3.46 (0.9)	3.38 (0.9)	3.97 (0.9)	3.31 (0.9)	3.96 (1.3)	3.83 (1.1)	3.14 (1.1)	3.03 (0.9)	2.56 (0.8)
RCD* (cm)	7.1 (0.2)	7.1 (0.2)	8.2 (0.3)	7.0 (0.2)	8.5 (0.4)	8.1 (0.3)	7.4 (0.3)	6.9 (0.2)	5.9 (0.2)

*OM1 = bole-only removal; OM2 = whole-tree harvest; OM3 = scalped to mineral soil; C0 = no compaction; C1 = light compaction; C2 = heavy compaction. Spruce diameter measured at root collar, rather than 1.3 m, because of shorter stature

Table 2. Statistical significance (*p* values < 0.10 in bold) of organic matter removal, compaction and tree species on survival, percent change in bole volume increment (%Δ vol inc) and foliar attributes of lodgepole pine and white spruce at year 20 post-treatment.

Treatment variable	Num DF*	Den DF	Survival	%Δ vol inc	Foliar N%	Foliar δ ¹⁵ N	ΔFoliar δ ¹³ C
OM removal	2	14	0.878	0.048	0.445	< 0.001	0.021
Compaction	2	14	0.147	0.238	0.173	0.781	0.896
OM × Comp	3	14	0.940	0.205	0.601	0.251	0.847
Species	1	16	0.133	0.169	0.002	< 0.001	0.001
OM × Species	2	16	0.860	0.003	0.924	0.755	0.462
Comp × Species	2	16	0.134	0.361	0.947	0.756	0.512
OM × Comp × Species	3	16	0.471	0.099	0.431	0.361	0.232

*degrees of freedom for the numerator and denominator of the Proc Mixed model.

Table 3. Statistical significance (p values < 0.10 in bold) of organic matter removal, compaction and tree species on foliar macronutrient concentrations and needle mass at year 20 for lodgepole pine and white spruce (mean of 3 sites, SE in brackets). Degrees of freedom for the statistical model as shown in Table 2.

Tree species	P	S	Ca	K	Mg	Mass
	(%)	(%)	(%)	(%)	(%)	(g)
Lodgepole pine	0.12 (0.001)	0.080 (0.001)	0.22 (0.005)	0.42 (0.006)	0.12 (0.007)	1.88 (0.08)
White spruce	0.18 (0.005)	0.077 (0.002)	0.45 (0.017)	0.59 (0.009)	0.10 (0.004)	0.56 (0.01)
Treatment p value						
OM removal	0.549	< 0.001	0.442	0.275	0.466	0.994
Compaction	0.127	< 0.001	0.917	0.005	0.972	0.789
OM × Comp	0.663	0.109	0.776	0.882	0.813	0.995
Species	< 0.001	0.069	< 0.001	0.001	< 0.001	< 0.001

Figure 1. Gravimetric moisture content of the mineral soil for OM removal treatments, SBSmc site only, during the 2015 growing season (May 15 to Sept 17; mean of 3 compaction treatments per data point).

Figure 2. Bole volume increment between years 15 and 20 for lodgepole pine and white spruce in relation to the least disturbed plot (OM1C0) (mean of 3 sites, SE as bars). OM1 = bole-only removal; OM2 = whole-tree harvest; OM3 = scalped to mineral soil; C0 = no compaction; C1 = light compaction; C2 = heavy compaction.

Figure 3. Average foliar N concentrations by OM removal treatments between years 5 and 20 post-treatment for a) lodgepole pine and b) white spruce (each marker the mean of 3 sites and 3 compaction treatments, n = 9, SE as bars).

Figure 4. Average foliar $\delta^{15}\text{N}$ (‰) by tree species and OM removal treatments (each bar the mean of 3 sites and 3 compaction treatments, n = 9, SE as bars).

Figure 5. Average difference in foliar $\delta^{13}\text{C}$ by tree species and OM removal treatments in relation to the least disturbed plot (OM1C0) (mean of 3 sites and 3 compaction treatments [n = 9], with the exception of stem only [n = 6], SE as bars).

Figure 6. Plot mean of foliar $\delta^{13}\text{C}$ (‰) in correlation with tree bole volume (dm^3), by site, for a) lodgepole pine and b) white spruce. Species x $\delta^{13}\text{C}$ interaction p value = 0.057 for SBSwk, 0.027 for SBSmc, and 0.161 for SBSdw.

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

a)

b)

Fig. 6

An investigation into the contrasting growth response of lodgepole pine and white spruce to harvest-related soil disturbance

J.M. Kranabetter, S. Dube, and E.B. Lilles

Supplementary Fig. S1. Foliar sulphur (S) concentrations by pine and spruce across (a) organic matter removal and (b) compaction treatments; (c) foliar potassium (K) concentrations by pine and spruce across compaction treatments.

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