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Effects of compaction and water content on lodgepole pine seedling growth

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Abstract

Soil disturbance by heavy machinery usually causes a decrease in porosity and an increase in soil strength, which may limit access to nutrients and compromise seedling survival and growth. This study used a soil strength and a greenhouse experiment to assess the impact of compaction on lodgepole pine (*Pinus contorta* Dougl. Ex. Loud. var. *latifolia* Engelm.) seedling growth and the degree to which soil water influences the effects of compaction. A silt loam soil was collected from a forest landing in the central interior of British Columbia (BC) in the Sub-Boreal Spruce Biogeoclimatic zone. The silt loam soil was used in a soil strength experiment where soil with four water content levels (0.10, 0.18, 0.27, and 0.36 $cm^3\ cm^{-3}$) was packed into 0.21 cm^3 cores with three levels of compaction (74, 79, and 84% of maximum bulk density (MBD)). Soil strength was strongly affected by compaction and water content. In the greenhouse experiment, three water content levels (0.10–0.15, 0.20–0.30, and 0.30–0.35 $cm^3\ cm^{-3}$) and three levels of compaction (67, 72, and 76% of MBD) were applied to soil in pots and 1-year old lodgepole pine seedlings were grown in the pots. Soil strength was highest (1275 kPa) for the high compaction and dry water content treatment in the greenhouse experiment. Though the soil strength for this treatment did not exceed 2500 kPa, the effect of compaction on growth was noticeable, with a decrease in diameter growth, total shoot mass, and new root mass as compaction increased at the dry water content. At dry water content and high compaction, foliar nutrient concentrations were greatest. Generally, water content had a greater impact on seedling growth than did compaction, at the levels of compaction used in this study. This study indicates that if there is a critical value for mechanical impedance of the conifer roots, it likely occurs below 2500 kPa. Our results are consistent with the explanation that soil strength incrementally affects root growth below 2500 kPa for this soil type. Expensive rehabilitation techniques may not be needed on lightly disturbed soils similar to that used in this study if soil water content is high enough throughout the conifer growing season to alleviate the effects of compaction on soil strength.

Keywords: Soil compaction; Soil water content; Soil bulk density; Lodgepole pine seedlings

1. Introduction

Excessive soil disturbance by harvesting machinery may displace topsoil and compact underlying soil (McNabb, 1994) leading to a decrease in long-term site productivity. Soil of temporary access areas such as forest landings (areas of cutblocks where harvested trees are processed and loaded onto trucks) and skid trails may become so degraded that these areas are lost from the productive forest. Soil rehabilitation practices in British Columbia (BC) are carried out on excessively disturbed sites to improve soil conditions so that these sites may be replanted and that tree growth may increase. Since soil rehabilitation practices are expensive to apply, information is needed to better understand the factors that control seedling establishment and growth on degraded soils.

Compaction causes a decrease in porosity and an increase in soil bulk density and consequently in soil strength. Poor aeration, and reduced permeability to water (and therefore available soil water), may cause decreased tree growth (Rab, 1996; Grigal, 2000), but detrimental effects are not universal, and are affected by soil type (Gomez et al., 2002), climate (Miller et al., 1996), and the level of compaction (Jansson and Wästerlund, 1999; Kabzems and Haeussler, 2005; Sanchez et al., 2006). Research by da Silva et al. (1994) has attempted to

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combine soil aeration, water content, and strength into a single measurable parameter—the least limiting water range. The removal of the topsoil layer and reduced mobility of soil nutrients in compacted soils may result in nutrient deficiencies that seriously limit plant growth (Unger and Kaspar, 1994).

Several greenhouse studies have investigated the effects of soil compaction on the seedling growth of a variety of tree species. A study by Jordon et al. (2003) found the seedling growth and N uptake of two species of oak (*Quercus rubra* L., and *Quercus coccinea* Muencch) to be severely impeded by soil compaction. In particular, they found decreased seedling height, total dry matter (roots, stems, and leaves) production, and N uptake. Soil microbial activity was also reduced as a result of compaction.

Another greenhouse study by Siegel-Issem et al. (2005) utilized ponderosa pine (*Pinus ponderosa* var. *scopulorum* Dougl. Ex Laws), shortleaf pine (*Pinus echinata Mill.*), and loblolly pine *(Pinus taeda* L.) seedlings grown in PVC cylinders to examine the effect of compaction and water content on seedling root growth. Their research found root growth to decrease with compaction, with water content regulating the effect of compaction on all species. The results of their regression analysis indicated that seedling root growth response was both soil series and species specific. Siegel-Issem et al. (2005) also showed that one species, loblolly pine, did quite well at low aeration conditions (either high compaction or high water content). The reason for this may relate to root aerenchyma, which can occur in pines adapted to very wet soil conditions (Smirnoff and Crawford, 1983; Topa and McLeod, 1986).

Compaction studies by Conlin (1996) carried out on loam soils from the Interior Douglas-fir biogeoclimatic zone in BC, in PVC tubes, found root growth in both Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) and lodgepole pine (*Pinus contorta* Dougl. Ex. Loud. var. *latifolia* Engelm.) decreased in response to increasing levels of compaction. Those studies showed a decrease in the root:shoot ratio of lodgepole pine with increasing levels of compaction. Higher compaction levels increased shoot height of lodgepole pine, regardless of water table level. Higher water table treatments had lower mean concentration of soil O_2 as both compaction and soil depth increased. Most notable was the observation that the soil penetration resistance in all cases remained below 2500 kPa, a value which is often thought to be growth limiting (Greacen and Sands, 1980; Ball and O'Sullivan, 1982; Abercrombie, 1990).

The primary objective of our study was to assess the impacts of three levels of water content and three compaction levels of a silt loam soil on lodgepole pine seedling growth (stem height, average needle length, stem biomass, root biomass, foliar biomass, new root growth) and foliar nutrient levels in a greenhouse experiment. Another objective of the study was to examine the degree to which soil water influences the effects of compaction on lodgepole pine seedling growth by measuring soil strength at four levels of volumetric water content and three levels of compaction and comparing these results with the results from the greenhouse experiment.

2. Materials and methods

2.1. Soil

On October 5, 2002, mineral soil was collected to a depth of approximately 30 cm from a roadcut near a forest landing at a study site located approximately 20 km north of Williams Lake, BC (52°19′25″N, 122°5′28″W). The site was chosen for a related study because the silt-rich soils were uniform and nearly free of coarse fragments (Blouin et al., 2005). The soil on the site was classified as Orthic Dystric Brunisol (Lord and Walmsley, 1988). The collected soil was stored in plastic containers underneath a tarp at Simon Fraser University greenhouses until the initiation of the greenhouse experiment in April 2003. The soil was passed through a 2 mm sieve to remove coarse fragments and coarse woody debris and then the soil was thoroughly homogenized and air-dried to $0.15\ \mathrm{cm^3\ cm^{-3}}$ before it was compacted. The soil was a silt loam with 25% sand, 53% silt, and 22% clay. The standard Proctor test (American Society for Testing Materials, 2000) was used to determine the soil maximum bulk density (MBD), which was $1798\ \mathrm{kg\ m^{-3}}$, while optimal water content (i.e., the water content at which maximum compaction occurs) was $0.16\ \mathrm{cm^3\ cm^{-3}}$. The mean particle density and total C content for this soil were found to be $2597\ \mathrm{kg\ m^{-3}}$, and 1%, respectively. Soil water retention characteristics were determined at a range of bulk densities by compacting the soil into 8.2 cm diameter by 4.0 cm high cores, then using a metal ring to extract a $35\ \mathrm{cm^3}$ core of compacted soil. Samples were sent to the BC Ministry of Forests and Range Analytical Laboratory in Victoria, BC to determine soil water content at −5, −10, −33, −300, and $-1500\ \mathrm{J\ kg^{-1}}$ on a pressure plate apparatus (Klute, 1986). Total porosity was determined by weighing each sample following its removal from a saturation tank and subtracting the oven dry soil weight. The water retention characteristics for the soil are provided in Table 1.

2.2. Soil strength experiment

A laboratory experiment was carried out to determine the strength of the soil (that was used subsequently in the greenhouse experiment) at three levels of compaction and four levels of water content. Five replicates of each treatment were used in this experiment. Sub-samples of the air-dried soil were moistened to four levels corresponding to 0.10, 0.18, 0.27, and $0.36\ \mathrm{cm^3\ cm^{-3}}$ water content and were left overnight in tightly sealed plastic bags to equilibrate to uniform soil water content. The four water content levels were chosen to represent a range of values from near permanent wilting point to above field capacity (Table 1). The following day, soil was placed into 8.2 cm diameter by 4.0 cm high cores for each of the 12 compaction and water content combinations, for a total of 60 samples. Soil was compacted by hitting the soil in the core with a metal hammer (2.5 kg weight) in three layers. The three levels of compaction corresponded to 74, 79, and 84% (bulk densities of 1331, 1420, and $1510\ \mathrm{kg\ m^{-3}}$) of the MBD for this soil (i.e., $1798\ \mathrm{kg\ m^{-3}}$). These compaction levels reflect a wide range of

Table 1
Water retention characteristics for the soil used in the study at varying bulk density levels (measured for 4–8 samples per bulk density level)

Bulk density ($g\ cm^{-3}$)	Percent of maximum bulk density ($cm^3\ cm^{-3}$)	Total porosity ($cm^3\ cm^{-3}$)	Water content ($cm^3\ cm^{-3}$)	
			Field capacity at 10 $J\ kg^{-1}$	Permanent wilting point at 1500 $J\ kg^{-1}$
1510	84	0.43	0.31	0.22
1420	79	0.45	0.29	0.21
1366	76	0.48	0.27	0.19
1331	74	0.48	0.27	0.19
1295	72	0.50	0.25	0.17
1205	67	0.51	0.24	0.16

mechanical disturbance impacts (from minimal compaction to severely compacted soils) as this study was also part of a larger soil strength study involving soil collected from several sites throughout BC.

The compacted cores were probed with an IMADA digital force gauge (with a standard 4 mm basal diameter and 30° cone tip) that was lowered using a Chatillon motorized test stand (LTCM-6) that ran downwards at 50 mm min^{-1}. Strength readings (measured in kg cm^{-2} and converted to kPa) were recorded by a handheld Allegro computer (Juniper Systems) every 2.5 s. Each core was probed three times and an average strength reading was generated. The soil core was then weighed and oven-dried at 105 °C for 24 h. The soil was weighed again after oven drying and gravimetric water content was determined. These values were then converted to volumetric water content. The calculated volumetric water contents were found to be very close to the target water contents.

2.3. Greenhouse experiment

The greenhouse experiment was laid out as a 3 × 3 factorial experiment in a randomized complete block with nine treatments. Treatments consisted of three levels (dry, moist, and wet) of water content and three levels (low, medium, and high) of compaction. The nine treatments were applied to 15 replicates for a total of 135 pots. Pots that were 22 cm high, with a 22 cm inside diameter (7.5 L) were used. Landscaping mesh was placed at the bottom of the pots over the drainage holes to prevent soil from flowing out of the pots during watering. Fine crush granite rocks were placed over the mesh, followed by a layer of coarse sand and then fine sand to create a gradation of barriers against soil loss.

The soil had a water content of 0.15 g g^{-1} when it was compacted into the pots. Soil compaction levels were classified as low, medium, and high corresponding to 67, 72, and 76% of MBD (1205, 1295, and 1367 kg m^{-3}). These levels of bulk density were chosen to reflect light to moderate compaction, typical of the levels commonly reached in field experiments (Powers et al., 2005) and because information on the effects of light compaction is essential to determining the operational relevance of commonly used growth-limiting thresholds for soil strength. For the low compaction treatment the soil was hand-compacted and it served as an experimental control. The medium compaction treatment involved packing the soil in each pot in three layers, using five blows of a standard compaction hammer (base diameter of 5 cm, 2.5 kg weight) per layer. The hammer was dropped from a height of 40 cm. For the high compaction treatment the soil was packed in a similar fashion, using seven blows of the compaction hammer to each of three layers within a pot.

Volumetric water contents were maintained at 0.10–0.15, 0.20–0.30, and 0.30–0.35 $cm^3\ cm^{-3}$ for dry, moist, and wet water content levels, respectively. These water contents were chosen because they range from near the permanent wilting point to near the point where less than 10% of the pore space would be occupied by air for this soil. Soil water content was maintained by weighing each of the pots three times a week to determine the gravimetric water content and adding water to each pot to make up the appropriate weight. An additional 18 pots, with two replicates of each treatment, were used to check volumetric water contents twice a week, using a ThetaProbe soil moisture sensor model ML2 (Delta T Devices). Seedlings were also watered on weekends towards the end of July and beginning of August 2003, when the weather was warmer, to prevent seedling fatality in the low water content treatments.

Treatments were randomly assigned to pots and soil was added to the pots two weeks before planting the seedlings. This allowed the target soil water regime to be in place and the settling of soil prior to planting. One-year old seedlings of one stocktype (Pli stocktype PCT 410 and seedlot 61153) were planted in the pots on May 5–6, 2003. A soil core was removed from the centre of each pot using an Oakfield-type soil sampler (2.54 cm diameter) and seedling root plugs were placed in each hole and the core of soil was replaced around the top of the root plug.

The treatment pots were rotated every three weeks using a randomized procedure to level out the effects of different light intensities found in different areas of the greenhouse space. Seedlings were grown in the greenhouse for 16 weeks. At the end of the experiment, seedlings were harvested and all of the loose mineral soil was removed from the seedling roots. Entire root systems were then washed with cold running water over a 1.0 mm mesh screen.

2.3.1. Seedling growth measurements

Ten representative seedlings from the initial seedling batch were measured to determine seedling fresh weight, root and shoot dry weight, foliar biomass, basal diameter, root plug length, and shoot length. Initial seedling height, root plug length, and basal diameter were measured for each seedling planted in the pots. After seedlings were harvested, stem height was measured and rooting depth and root proliferation observations were recorded. Needle length was measured for three needles from new shoot growth on each seedling. Seedlings were then separated into roots, stems, and current year's, and past years' foliage. In addition, 100-needle weights were determined for each sample. Total root, stem and foliar biomass were measured by weighing each component. The difference in total foliage mass was calculated for each seedling by subtracting the average mass of foliage calculated from the representative seedlings at the beginning of the experiment from the total mass of foliage at the end of the growing season. New roots were cut from the old root plugs and new roots were weighed.

2.3.2. Seedling tissue analysis

Five replicate seedlings for each of the nine treatments were randomly selected for element analysis. Samples of current foliage were milled and analyzed for total P, K, Ca, Mg, S, Fe, Mn, B, Zn, Cu, and Al with an ICAP spectrometer following digestion in nitric acid with microwave heating (Kalra and Maynard, 1991). Total N concentration was determined with high temperature combustion on a Fisons NA-1500 NCS Analyzer (McGill and Figueiredo, 1993; Tiessen and Moir, 1993).

2.4. Statistical analyses

The soil strength data from the laboratory experiment were analyzed as a 4 × 3 factorial experiment in a randomized complete block design involving three compaction levels and four water content levels and five replications using JMP (SAS Institute Inc., 2001). Tukey's HSD multiple comparison test was used when necessary to assess differences between treatments. For the soil strength experiment, multiple regression analysis was carried out to predict soil strength based on bulk density and water content. Soil strength for the greenhouse experiment was estimated using the results from the multiple regression analysis. Seedling data from the greenhouse experiment were analyzed as a 3 × 3 factorial experiment in a randomized complete block design involving three compaction levels, three water content levels, and 15 replications using JMP (SAS Institute Inc., 2001). An α level of 0.05 was considered to be significant.

3. Results and discussion

3.1. Soil strength experiment

Soil strength was affected by both compaction and water content (Fig. 1). The effects of compaction were most pronounced when the soils were dry. At the highest water content (0.36 $cm^3\ cm^{-3}$), compaction treatments had no effect on soil strength. At 0.27 $cm^3\ cm^{-3}$ water content, the 84% of MBD compaction treatment had significantly greater soil strength than the 74% of MBD compaction treatment. At 0.18 $cm^3\ cm^{-3}$ water content, 84 and 79% of MBD compaction had greater soil strength than 74% of MBD. The greatest soil strength (2871 kPa) was obtained for the lowest water content (0.10 $cm^3\ cm^{-3}$) and highest compaction (84% of MBD) treatment. This was the only soil strength to exceed 2500 kPa, a value that has been reported to impede conifer root growth (Greacen and Sands, 1980; Busscher et al., 1986). Both the 79 and 84% of MBD compaction levels had bulk densities greater than the suggested growth-limiting value of 1350 $kg\ m^{-3}$ given by Corns (1988).

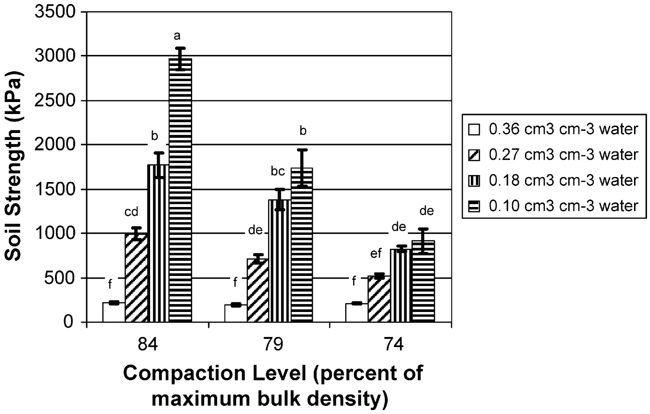

Fig. 1. Mean strength of soil collected from a forest landing at Lynes Creek, BC at four compaction and four water content treatments. Bars with the same letter are not significantly different at $p < 0.05$.

We used the data from the soil strength experiment to produce a regression equation for predicting soil strength based on measurements of volumetric water content and bulk density.

$$
\begin{aligned}
&\text{Soil strength (predicted)}\\
&\quad = -8298 - 7517\,(\text{volumetric water content})\\
&\qquad + 7.69\,(\text{bulk density}) \qquad (1)
\end{aligned}
$$

This equation has an r^2 value of 0.83, thus a considerable amount of the variation in soil strength can be explained by volumetric water content and bulk density. Fig. 2 shows how a certain soil strength can be found across a wide combination of bulk density and water content values.

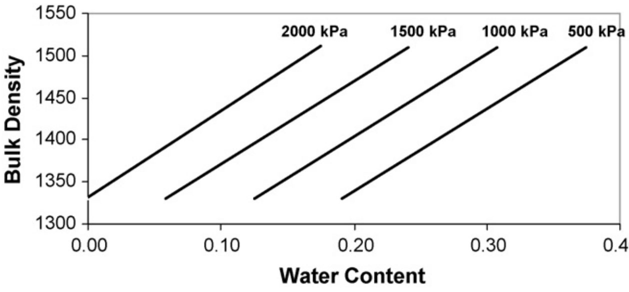

Fig. 2. Predicted soil strength values at various bulk density ($g\ cm^{-3}$) and water content ($cm^3\ cm^{-3}$) levels, based on the regression equation (1). This is a graphical representation which extends beyond the range of the data in our study and is for illustrative purposes only.

Table 2
Mean dry biomass and growth of lodgepole pine seedlings harvested after one growing season for high, medium, and low compaction (76, 72, and 67% of maximum bulk density) and wet, moist and dry water content (either 0.30–0.35, 0.20–0.30, and 0.10–0.15 $cm^3\ cm^{-3}$)

Treatment		Basal diameter growth (mm)	Stem mass (g)	100-needle mass (g new foliage)	Total root mass (g)	New root mass (g)	Root:shoot ratio
Compaction	Water						
High	Wet	2.56a (0.13)	2.99a (0.14)	0.70ab (0.04)	9.9a (0.3)	5.4a (0.3)	1.19cd (0.03)
Medium	Wet	2.31ab (0.13)	2.81ab (0.11)	0.56abc (0.02)	9.0a (0.3)	4.7ab (0.2)	1.21cd (0.04)
Low	Wet	2.66a (0.18)	2.93a (0.13)	0.74a (0.05)	8.7a (0.4)	5.0ab (0.3)	1.10d (0.03)
High	Moist	1.74bc (0.14)	2.41bc (0.13)	0.47bcd (0.04)	8.8a (0.3)	4.2b (0.3)	1.34c (0.06)
Medium	Moist	2.13ab (0.14)	2.34cd (0.09)	0.43cde (0.09)	9.3a (0.2)	4.4ab (0.2)	1.44bc (0.06)
Low	Moist	2.16ab (0.17)	2.29cd (0.10)	0.58abc (0.06)	8.5a (0.3)	4.1b (0.2)	1.36bc (0.04)
High	Dry	0.45e (0.11)	1.14f (0.06)	0.20e (0.02)	5.3c (0.4)	0.7d (0.1)	1.86a (0.08)
Medium	Dry	0.87de (0.11)	1.53ef (0.09)	0.31de (0.06)	6.1bc (0.3)	1.3d (0.1)	1.60b (0.06)
Low	Dry	1.42cd (0.17)	1.87de (0.07)	0.42cde (0.02)	7.0b (0.3)	3.1c (0.3)	1.32cd (0.05)
p value			<0.001	<0.001	<0.001	<0.001	<0.001

[Z] Values in the same column followed by a different letter are significantly different according to Tukey's test.

[Y] Standard error ($n = 15$) in the brackets.

3.2. Greenhouse experiment—seedling growth and biomass response

Compaction influenced seedling growth and biomass at dry water content, but not at moist or wet water contents (Table 2, Fig. 3). The moist and wet water contents appear to have decreased the strength of the soil and alleviated the effects of compaction. As compaction increased at dry water content, average needle length, and new root mass decreased. This was in agreement with findings from compaction experiments by Conlin and van den Driessche (1996) on lodgepole pine seedlings, and Buttery et al. (1998) on beans who found decreases in plant growth due to increased compaction levels at low water contents. At dry water content, stem mass and basal diameter were significantly greater for low compaction compared to high compaction treatment (Table 2). These results suggest that soil strength played a key role in inhibiting root growth and restricting access to nutrients and water. The increased bulk density at higher compaction levels resulted in higher soil strength (as seen earlier in this paper for the soil strength experiment) and decreased macroporosity. Generally, these factors create unfavourable conditions for plant germination, establishment, and growth.

We used the regression equation developed from the soil strength experiment (Eq. (1)) to estimate soil strength for some of the treatments used in the greenhouse experiment. Estimates of soil strength for the greenhouse experiment were only made for the high compaction treatments as the bulk densities for the medium and low compaction treatments in the greenhouse experiment were outside the range studied in the soil strength experiment. Soil strength for the high compaction/wet water content treatment was estimated as 0 kPa, for the high compaction/moist water content treatment as 335 kPa, and for the high compaction/dry water content treatment as 1275 kPa. Soil strength for the medium compaction and low water content treatment was estimated as being lower than 825 kPa, which is the soil strength measured at 74% of MBD and 0.18 $cm^3\ cm^{-3}$ water content. These estimates suggest that soil strength was well below growth-limiting levels for the moist and wet water content treatments, regardless of

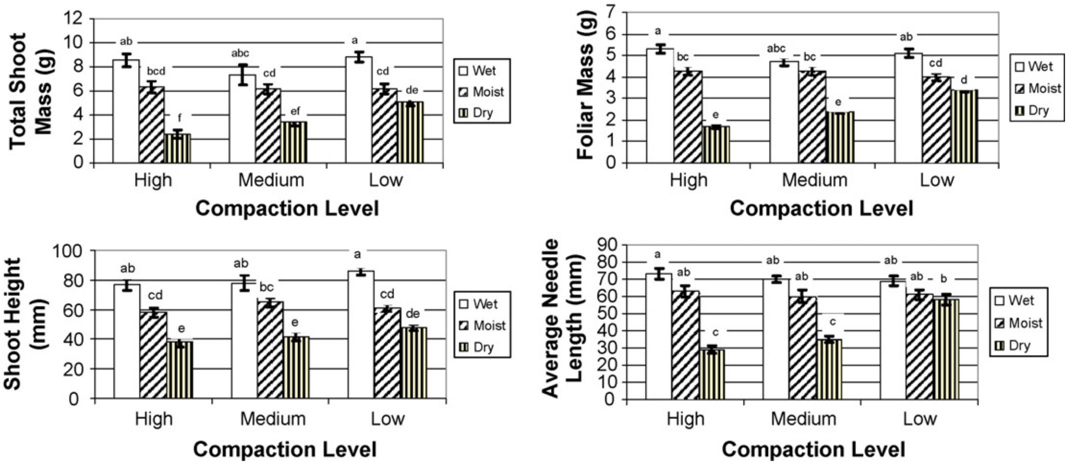

Fig. 3. Total shoot mass, foliar mass, shoot height, and average needle length of greenhouse seedlings of lodgepole pine seedlings harvested after one growing season for high, medium, and low compaction (76, 72, and 67% of maximum bulk density) and wet, moist and dry water content (0.30–0.35, 0.20–0.30, and 0.10–0.15 $cm^3\ cm^{-3}$). Bars with the same letter are not significantly different at $p < 0.05$.

compaction level. Thus, soil strength did not appear to have limited growth for these treatments as indicated by a lack of differences in seedling biomass or growth for moist and wet water content treatments. The greatest soil strength was obtained for the high compaction/dry water content treatment, but even this treatment did not have very high soil strength in relation to values commonly considered limiting to root growth.

It is expected that a combination of high soil strength and low water content inhibited seedling growth for the dry water content treatments since the compacted soils had fewer roots than the uncompacted treatments for all the dry water contents, and because the soil was below wilting point and water stress was likely. It is possible that (a) the critical soil strength value falls below 2500 kPa for this soil and/or (b) soil strength has incremental effects on seedling growth below 2500 kPa. Even though 2500 kPa has been used as a threshold for growth-limitation (Ball and O'Sullivan, 1982; Busscher et al., 1986; Abercrombie, 1990), several studies have shown that plant growth can be affected by compaction in soils where the soil strength is less than 2500 kPa. For example, Zou et al. (2000) indicated that increasing soil strength affected the root growth of radiata pine (*Pinus radiata* D. Don) at values lower than 2500 kPa, and the effect was independent of soil texture. Bulmer and Simpson (2005) showed that 2500 kPa soil strength was a better threshold for effects on survival of lodgepole pine, than for growth, but that the 2500 kPa threshold was still only able to explain 40% of the effect of soil strength on growth. Our study provides further evidence that soil strength can have effects on growth in lightly compacted soils, and that water content levels play a key role in determining the mechanical impedance experienced by growing plant roots.

A study by Sands and Bowen (1978) showed that the root and shoot growth of radiata pine seedlings on sandy soil decreased as soil bulk density increased from 1350 to 1600 kg m^{-3}. Root growth for lodgepole pine (Conlin and van den Driessche, 1996) and oak (Jordon et al., 2003) decreased, and the depth of rooting became shallower (Conlin and van den Driessche, 1996) with increased compaction. A study by Corns (1988) with lodgepole pine and white spruce (*Picea glauca* (Moench) Voss) seedlings on silty clay, clay loam, sandy loam/clay loam, and silt loam/loam soils in west-central Alberta found that the poorest growth occurred at high levels of bulk density (up to 1500 kg m^{-3}), but growth was not slowed down until the bulk density surpassed 1350 kg m^{-3}. In our study, soil bulk density levels of 1205, 1295, and 1367 kg m^{-3} corresponded to the low, medium, and high levels of compaction, respectively, and only the latter surpassed the bulk density level stated by Corns (1988).

Compaction can produce soil water conditions that are characteristic of a fine-textured soil (Greacen and Sands, 1980; Conlin and van den Driessche, 1996) by increasing the water retention of coarse textured soils and improving water availability on soils that would normally drain rapidly. Other studies have shown that adequate water supply tends to alleviate a large part of the adverse effects of soil compaction (Buttery et al., 1998). In our study, water content had a greater effect on seedling growth and biomass than did compaction (Table 2). Regardless of compaction level, measurements of stem height growth, basal diameter growth, stem mass, foliage mass, total root mass, and new root mass were greatest for the wet and/or moist water contents.

A number of studies have also looked at the allocation of biomass within seedlings of various species. McMillin and Wagner (1995) concluded that growth and establishment of ponderosa pine seedlings can be significantly affected by water stress that occurs during the early season shoot growth period. Prior et al. (1997) showed that longleaf pine (*Pinus palustrus* Mill.) seedlings that experienced water stress were shorter and had smaller stem diameters compared to the seedlings that were well-watered. A study by Nautiyal et al. (1994) showed similar results for a Eucalyptus hybrid (*Eucalyptus camaldulensis* × *Eucalyptus teriticornis*), *Casuarina equisetifolia*, and *Melia azedarach,* which experienced increasing water stress on a 2:1:1 ratio of garden soil, sand, and manure. A drastic decrease in tree heights was observed with increased water stress. This same study showed that the increase in stress led to an increase in the palisade parenchyma in *Eucalyptus* spp. and *Casuarina* spp., and to a decrease in the number, density, length, and width of stomata in all three tree species. Water stressed plants may experience stomatal closures, which may lead to decreases in photosynthetic rates per unit of leaf area (Nautiyal et al., 1994) and decreases in evapotranspiration.

Research by Topa and McLeod (1986) has found that two species of pine (*Pinus serotina* Michx. and *P. taeda* L) can adapt to low aeration conditions by increasing root lenticel and aeraenchyma formation, which provides a mechanism to increase root porosity and therefore increase root biomass. These types of physiological changes that affect the photosynthetic and respiration rates of the plants ultimately affect the plants' ability to allocate biomass. It is possible that the lodgepole pine seedlings in our study that were subject to high water contents were able to physiologically adapt to lower aeration conditions through the production of more lenticels and aerenchyma. The soils in our wet treatment were not saturated, thus root aerenchyma likely did not play a major role.

Visual observations of root growth within pots revealed that the seedling roots of the wet water content treatments had thick lateral roots that densely occupied the entire volume of the pot, regardless of compaction level, indicating that aeration was adequate in all treatments. The high compaction/dry water content treatment produced so few roots that they barely left the volume of space occupied by the nursery plug. The medium compaction and dry water content treatment produced a few vertical and lateral roots. The roots of the high compaction/medium water content treatment resembled that of the dry water content/medium compaction treatment. The roots of the low/medium compaction and moist water content treatments were slightly less dense than for the wet water contents (Fig. 4).

3.3. Nutrient response

The high compaction/dry water content treatment had significantly higher concentrations of all elements except Ca, Mg, and S in new foliage (Table 3) than all other treatments.

Fig. 4. Dry root morphology of the greenhouse seedlings grown in (A) high compaction, (B) medium compaction and (C) low compaction soil with dry, moist, and wet water contents (from left to right).

The high compaction/dry water content treatment also had the smallest shoot mass of all treatments (Fig. 3). The combination of small shoot mass and high nutrient concentration suggests that nutrient uptake may not have been impeded by high compaction and low water content at the levels of these factors imposed in our study. Factors other than nutrient uptake, such as mechanical impedance of roots and water availability, were likely responsible for the decreased growth associated with high compaction and low water content. The relationship between element concentration and physiological development is complex, particularly in seedlings. The high element concentrations and small shoot mass for the high compaction/dry water content treatment may reflect the ‘‘Steenbjerg Effect’’ from mismatched physiological stages of seedling development (Steenbjerg, 1954).

Compaction did not influence the concentration of any elements in new foliage (Table 3) at the wet and moist water contents, but compaction did have an effect at the dry water content. At dry water content, the high compaction treatment had significantly higher concentrations of all elements except Ca, Mg, and S than did the low compaction treatment. Soil water content also had a significant influence on element concentrations in new foliage with the dry water content treatment generally having higher concentrations of elements (except Ca and Mg) than the wet water content treatment. Lower element concentrations associated with low compaction as compared to high compaction at dry water content and with wet water content as compared to dry water content are most likely due to a dilution effect (Timmer and Morrow, 1984). The treatments that had the largest stem mass tended to have the smallest element concentrations, which suggests that the elements were taken up and were diluted for treatments with the best growth and were more concentrated for treatments with the poorest growth. The lower element concentrations and larger stem mass of seedlings at low compaction compared to high compaction could reflect the ‘‘Piper-Steenbjerg Effect’’ in which growth rates exceed uptake rates (Piper, 1942; Steenbjerg, 1954; Wikstrom, 1994).

Contrary to our results, Conlin and van den Driessche (1996) found generally decreased concentrations of nutrients in lodgepole pine shoots as soil compaction increased and as soil water content increased. The levels of compaction and of soil water content were more extreme in the study of Conlin and van den Driessche (1996) and the methods of compaction and of soil wetting differed from our study. These differences likely account for the dissimilar results of the two studies.

Comparison of nutrient concentrations from new foliage with levels presented by Ballard and Carter (1986) and Brockley (2001) show that deficiencies in N were likely and deficiencies in P, K, and S were possible for wet water contents at all compaction levels. It is not surprising that the silt loam soil was not able to supply adequate N to the seedlings in the wet water content since only mineral soil with relatively low organic matter content (2%) was used in the greenhouse

Table 3
Mean concentrations of foliar elements from the new foliage of lodgepole pine seedlings grown in the greenhouse after one growing season for high, medium, and low compaction (76, 72, and 67% of maximum bulk density) and wet, moist and dry water content (0.30–0.35, 0.20–0.30, and 0.10–0.15 $cm^3\ cm^{-3}$)

Treatment		N ($g\ kg^{-1}$)	P ($g\ kg^{-1}$)	K ($g\ kg^{-1}$)	Ca ($g\ kg^{-1}$)	Mg ($g\ kg^{-1}$)	S ($g\ kg^{-1}$)
Compaction	Water						
High	Wet	10.5c (0.7)[z]	0.73b (0.03)	4.6bc (0.1)	5.48abc (0.53)	2.38ab (0.15)	0.99bc (0.03)
Medium	Wet	10.8c (0.5)	0.76b (0.01)	4.1c (0.3)	4.68abc (0.25)	2.34ab (0.12)	0.87c (0.07)
Low	Wet	10.7c (0.5)	0.75b (0.04)	4.4bc (0.3)	6.06ab (0.49)	2.48ab (0.14)	1.05bc (0.03)
High	Moist	13.1bc (0.4)	0.71b (0.04)	3.5c (0.3)	5.59abc (0.33)	2.34ab (0.08)	0.97bc (0.05)
Medium	Moist	15.5b (0.9)	0.92b (0.08)	4.8bc (0.5)	6.21a (0.57)	2.57a (0.23)	1.21ab (0.05)
Low	Moist	14.6b (0.3)	0.73b (0.03)	4.4bc (0.4)	5.96ab (0.61)	2.23ab (0.11)	1.00bc (0.02)
High	Dry	21.0a (0.9)	1.82a (0.11)	8.4a (0.3)	3.62c (0.22)	1.87b (0.13)	1.40a (0.10)
Medium	Dry	19.5a (0.9)	1.52a (0.11)	6.0b (0.6)	4.17bc (0.24)	2.11ab (0.06)	1.44a (0.08)
Low	Dry	15.9b (0.8)	0.92b (0.04)	4.6bc (0.4)	5.53abc (0.34)	2.11ab (0.10)	1.78ab (0.05)
p value		<0.001	<0.001	<0.001	0.0008	0.02	<0.001

[Z] Values in the same column followed by a different letter are significantly different according to Tukey’s test.
[Y] Standard error ($n = 15$) in the brackets.

experiment. It is likely that seedlings grew well in the wet water content treatment due to good water availability and low soil strength, but that availability of some nutrients was limiting. Nutrient deficiencies were unlikely to occur at dry water contents and growth at dry water content was likely limited by low water availability rather than nutrient availability.

3.4. Soil strength and greenhouse experiments

In general, results of the greenhouse and soil strength experiments show that soil water content influenced the compaction effects on plant growth and nutrient uptake. This is similar to findings by Zainol et al. (1991) and Buttery et al. (1998) who found decreased plant growth with increased compaction. Our greenhouse results may be overstated compared to results found in the field due to the higher soil strength that the rigid pot sides would impose on the plant roots (Sands and Bowen, 1978), and because the roots of trees growing on field sites preferentially exploit any zones of weakness or cracks in the soil. This higher soil strength may be counterbalanced by the greater aeration near the pot walls (Wall and Heiskanen, 2003) due to the slight shrinkage during the drying process, which makes this area a preferential zone for root growth. In addition, drainage boundary conditions would differ for soil in greenhouse pots as compared to the field. Drainage would likely occur consistently throughout field soils and rapidly at the soil–sand/gravel interface in greenhouse pots.

Results from some field studies have shown either no detrimental effect on tree height or increases in tree growth with moderate levels of compaction (Brais, 2001; Ares et al., 2005; Eisenbies et al., 2005; Kranabetter et al., 2006). Reasons suggested in the literature for improved or unaffected tree growth in disturbed areas include: reduced competition, increased water retention, and increased N mineralization. These factors were not directly addressed in our greenhouse study, but must be considered when applying our results to the field.

4. Conclusions

The interaction between water content and compaction levels was clearly shown in the growth differences among the lodgepole pine seedlings. Growth parameters such as new root mass and stem basal diameter decreased as compaction increased, at dry water contents. Stress from poor water availability affects the plants' ability to photosynthesize and allocate biomass and seemed to have a greater impact on seedling growth and biomass than compaction. Foliar nutrient concentrations were not affected by compaction at the moist and wet water contents, but concentrations of most nutrients were lower for the low compaction treatment compared to the high compaction treatment at dry water contents. Lower nutrient concentrations were likely due to a dilution effect associated with the better growth on more optimal treatments. The lower nutrient concentrations could also reflect the ‘‘Steenbjerg Effect’’ from mismatched physiological stages of seedling development.

The results of this study suggest that if there is a critical value for mechanical impedance of lodgepole pine roots, it occurs below 2500 kPa. It is also possible that soil strength incrementally affects root growth below 2500 kPa for this silt loam soil. Findings of this study are useful for forest managers since they show that effects of compaction depend on the climate, and that under certain conditions (i.e., dry conditions for our soil) light compaction can have significant impacts on tree growth. Although the relevance of our greenhouse study to field conditions needs further elucidation, this is of interest because the harvesting machinery typically used in BC and elsewhere creates substantial amounts of such ‘‘light’’ disturbance. The productivity effects of ‘‘light’’ mechanical soil disturbance might be considered acceptable under current climatic conditions, but if site conditions became drier due to climate change, negative effects could potentially occur (for fine-textured soils).

Our results also illustrate how the effects of soil compaction can be alleviated for certain soil types if the soil water content is high enough throughout the conifer growing season. The soils in the wet treatment in our study were not saturated, however a common problem with many BC forest soils is that after compaction, soils are poorly drained and consequently saturated for lengths of time. We suggest that future work should include treatments with higher levels of water content.

By combining the results of this study with other similar studies based on a variety of soil types and site conditions, forest managers will be better equipped to assess the effects of mechanical disturbance on forest productivity. In turn, this will allow them to prescribe the most efficient forest practices, while upholding environmental standards.

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