EFFECTS OF SOIL COMPACTION ON THE GERMINATION AND GROWTH OF *PICEA MARIANA* AND *PINUS BANKSIANA*

by

Kristy Vannieuwenhuizen

FACULTY OF NATURAL RESOURCES MANAGEMENT

LAKEHEAD UNIVERSITY

THUNDER BAY, ONTARIO

April 2020

EFFECTS OF SOIL COMPACTION ON THE GERMINATION AND GROWTH OF *PICEA MARIANA* AND *PINUS BANKSIANA*

by

Kristy Vannieuwenhuizen

A Master's Thesis Submitted in Partial Fulfillment of the Requirements for the Masters of Science in Forestry Degree

Faculty of Natural Resources Management

Lakehead University

April 2020

Dr. Qing-Lai Dang

Thesis Supervisor

LIBRARY RIGHTS STATEMENT

Signature:______________________

Date: April 28, 2020

A CAUTION TO THE READER

This MScF thesis has been through defense review by at least two faculty members. It is made available for loan by the Faculty of Natural Resources Management for the purpose of advancing the practice of professional and scientific forestry.

The reader should be aware that conclusions in this document are those of the student and do not necessarily reflect the opinions of the thesis supervisor, the faculty, or Lakehead University.

ABSTRACT

Vannieuwenhuizen, K.R. 2020. The effects of soil compaction on the germination and growth of *Picea mariana* and *Pinus banksiana*. MScF thesis, Faculty of Natural Resources Management, Lakehead University, Thunder Bay, Ontario. pp. 66.

Keywords: bulk density, forest productivity, greenhouse experiment, *Picea mariana*, *Pinus banksiana*, regeneration, seedlings, silviculture, soil compaction.

Soil compaction has long been an issue for the forestry industry. Soil compaction can reduce soil aeration, porosity and drainage, and restrict the growth and success of trees and other plants. The objective of this study is to determine how the degree of soil compaction affects the seed germination and seedling growth of jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*). The study was carried out in a greenhouse at the Lakehead University Thunder Bay campus. Silty clay loam soil was used for the study and the treatment consisted of four levels of compaction with the bulk densities of 0.9 g/cm^3 (C), 1.1 g/cm^3 (C1), 1.2 g/cm^3 (C2), and 1.3 g/cm^3 (C3). The soil compaction was implemented in buckets of 36 cm in height and 30.2 cm in diameter. Each treatment level was replicated five times. Seed germination was tallied daily. Seedling height and root collar diameter were measured after 18 weeks of seedling growth. Then the seedlings were harvested. The foliage and root systems were scanned and analyzed using the Regen WinSeedle and WinRhizo systems, respectively, and the following parameters were subject to statistical analysis: root length and diameter, total root length, and projected and surface areas of roots, average needle length, average needle width, total leaf area and the number of needles per seedling. The biomass of roots, total biomass, as well as root to shoot ratios, were determined after the samples were dried in a drying oven at 80 C for 48h. It was found that root biomass, total biomass, root to shoot ratios, main root lengths, seedling height, total root length, average root diameter, root surface area, and the number of root tips were significantly affected by soil compaction and were generally significantly different between the two species, except for the root to shoot ratios. While root diameters increased under increased compaction, every other growth parameter faced general downward trends in growth. Under the most severely compacted soil (C3), total root lengths and number of root tips decreased by 64.6% and 76.2%, respectively in *Picea mariana*. Large reductions in the main root lengths and the number of root tips were found for *P. banksiana* under the most severely compacted soil as well, with reductions of 46.4% and 46.7%, respectively. The reductions by soil compaction of all the measured growth parameters were greater in *P. mariana* than in *P. banksiana*. Overall, this study illustrates that while the growth of both species was negatively affected by all levels of soil compaction, *P. banksiana* was less sensitive than *P. mariana*, suggesting that jack pine may have a competitive advantage over black spruce on sites with soil compaction. Therefore, all efforts should be made to avoid or minimize soil compaction in forestry operations to maintain the forest productivity of the site.

ACKNOWLEDGEMENTS

This work was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) - Alexander Graham Bell Canada Graduate Scholarship, and funding from Dr. Q.L Dang to K. Vannieuwenhuizen.

I would like to acknowledge and thank my supervisor Dr. Qing-Lai Dang, as well as Dr. Lense Meyer and Dr. Rongzhou Man (co-supervisors) for helping me complete this Master's thesis. I would also like to thank Mr. Eric Searle, Mr. Robert Timoon, and Keri Pidgen for their aid in data analysis, geotechnical support, and greenhouse support, respectively.

A special thank you also goes to the friends and family members who have also aided me in completing my thesis.

CONTENTS

TABLES

FIGURES

APPENDICES

INTRODUCTION

Soil compaction refers to the compression of soil particles into smaller volumes, leading to reduced aeration porosity of the soil (McKenzie 2010). Soil compaction can have a substantial impact on the regeneration and growth of trees and other plants on logged sites and reduce the productivity of the site (Cambi et al. 2015, Lockaby and Vidrine 1984, Zhang et al. 2017). However, the relationship between the degree of soil compaction and the regeneration and growth of different tree species is currently not well understood.

In forestry, soil compaction is mainly caused by heavy machinery with low floatation (Kozlowski 1999). The severity of soil compaction varies with soil type and the type and floatation of the machinery. For example, heavier soils such as loams and clays are more prone to compaction than sandy soils (Voyle and Hudson 2014). The weight of operational machines can range from 5-40 metric tons (Jansson and Wasterlund 1999). Over time, many of these pieces of machinery have become more powerful and efficient, but in a lot of cases, also heavier, leading to more severe soil compaction (Horn et al. 2007).

In general, soil compaction increases soil bulk density but decreases the connectivity and macro to micro-pore ratios in the soil, impacting soil hydraulic conductivity (Horn et al. 1995, Kozlowki 1999). Reductions in water infiltration in compacted soils lead to increased occurrences of water ponding, surface runoff, waterlogging, reduced soil oxygen contents and soil erosion, all of which would further degrade the soil (Soane and van Ouwerkerk 1994). These changes will lead to the deterioration of soil properties for tree growth and reduce site quality (Kozlowski 1999).

Soil compaction has various negative impacts on the physiology and morphology of trees. It retards the elongation of the main and 1st and 2nd order lateral roots and reduces total root length (Kozlowski 1999). However, the number and diameter of 1st order lateral roots generally increase in response to increasing soil compaction, while the taproot becomes shorter and thicker (Cambi et al. 2015, Gilman et al. 1987, Sands and Bowen 1978). Shorter taproots limit the tree's access to nutrients in deeper soil layers and reduce nutrient uptake (Cambi et al. 2015). Soil compaction reduces the ability of roots to penetrate a larger soil volume and into deeper soil layers and can lead to oblique (non-vertical) growth, which in turn can result in desiccation and mortality (Skinner et al. 2009). Compaction also affects established and regenerating forests by having a negative influence on fine root development, overall tree growth, seed germination, and seedling growth (Malo and Messier 2011). Furthermore, soil compaction can lead to the loss of nutrients from the site because of increased surface runoff and reduced nutrient absorption by roots (Kang and Lal 1981, Cole 1982, Silverbush et al. 1983). Reduced aeration due to soil compaction can lead the shift of root respiration from aerobic to an anaerobic pathway which is much less efficient in the utilization of carbohydrates and energy production, resulting in declines in root growth, shoot growth, and overall tree health (Kozlowski & Pallardy 1997). Although the effects of soil compaction on trees are primarily negative, there can be beneficial ones as well. For example, if the competing vegetation is more sensitive to soil compaction than the crop tree species, a certain level of soil compaction can suppress the competition and promotes the establishment and growth of crop trees. However, the specific effects depend on the soil type and the composition of plant species (Zhang et al. 2017).

There are various challenges for conducting soil compaction research in the field, such as variations in site conditions and difficulties in controlling the levels of soil compaction (Kozlowski 1999). Therefore, it is extremely difficult to use field experiments to investigate the response patterns of trees to a range of soil compaction severity and with reasonable replications. In this greenhouse research, jack pine (*Pinus banksiana* (Lamb.)) and black spruce (*Picea mariana* (Mill.) b.s.p.) were exposed to a wide range of soil compaction with the soil bulk densities of 0.9 g/cm^3 (C), 1.1 g/cm^3 (C1), 1.2 g/cm^3 (C2), and 1.3 g/cm^3 (C3). This range covers a typical array of compaction that occurs in forestry operations (Kozlowski 1999). Jack pine and black spruce are two important commercial tree species in the boreal forest. However, there is a lack of information in the literature on the effects of soil compaction on those species. Since soil compaction is a common phenomenon in the boreal forest, particularly during forest operations in the summer, such knowledge is critically important for the scientific management of the boreal forest (Cambi et al. 2015). This study investigated the responses of seed germination and seedling growth of the two species to the above range of soil compaction. It is hypothesized that more severe soil compaction would exert progressively greater limitation to seed germination and seedling growth, as the deterioration of soil properties generally increases with increases in the severity of soil compaction (Soane and van Ouwerkerk 1994, Kozlowski 1999). The two species have contrasting growth rates and different rooting patterns: black spruce is a slow-growing species with a fibrous root system; jack pine, in contrast, is a fast-growing tree species with a taproot system (Strong and La Roi 1983). A taproot system is believed to better able to penetrate compacted soils than a fibrous root system (Clark et al. 2003). Therefore, it is hypothesized that jack pine would be more resistant to soil compaction than black spruce.

LITERATURE REVIEW

CAUSES OF SOIL COMPACTION

Soil compaction can be a result of both natural and human activities. In a natural setting, loose soils can become compacted as a result of natural settling and/or slumping, which is often the case for soils that are very wet (Koolen & Kuipers 1983). As trees grow, they can also contribute to compaction by transmitting their weight onto the surrounding soil. Likewise, severe forest fires can contribute to compaction and produce water-repellent surface layers (Wright & Bailey 1982).

Tillage tools may also contribute to soil compaction, as well as other forms of machinery and heavy equipment. In forestry, these types of machinery often include skidders, trucks, and other heavy equipment with low floatation. The masses of these vehicles typically range from anywhere between 5 and 40 metric tons (Jansson & Wasterlund 1999). In recent years, many of these types of machinery have become more powerful and efficient, but also heavier, leading to an increase in their compaction on forest soils (Horn et. al 2007). The highest degree of compaction tends to occur in the top 30 cm of the soil profile, which also normally contains most of the root masses (Wingate-Hill & Jakobson 1982). Vehicles contribute to compaction by exerting force in three ways: 1) through the normal vertical force due to the load on the tires; 2) through the shear stress caused by the wheel slippage; and, 3) due to the vibration of the engine through the tires. Compaction generally occurs after the first few passes of a vehicle; subsequent passes do not usually cause further compaction to the soil. The impact, however, does vary with the load of the vehicle, and the strength of the soil. Also, deeper soil levels could still become affected after more than a few passes of a vehicle, even if the overlying layers no longer were (Lockaby & Vidrine 1984, Shetron et al. 1988). Logging machinery can have a substantial compacting effect on soils. In the uppermost soil layers, skidders have been shown to increase bulk density by 41-52% (Miller et al. 1996) and logging machinery generally has resulted in increases of 5-25% (McNeel & Ballard 1992, Johnson et al. 1991).

EFFECTS ON SOIL CHARACTERISTICS

The main consequences of compaction on soil characteristics include increased bulk density (BD), increased aggregate breakdown, decreased soil porosity, decreased pore sizes and continuity, increases in shear strength, a decreased infiltration capacity, and the increase in water runoff and erosion (Kozlowski & Pallardy 1997a). Soil bulk density is a measure of soil mass per unit volume. The total soil porosity is the volume of pores as a proportion of the total soil volume. The total porosity can be divided into aeration porosity and water holding capacity. Also affected by compaction because it causes a decrease in the pore volume within the soil; a component that is essential for gas diffusion (Currie 1984). The oxygen consumed by plant roots is normally replaced by diffusion, but compaction has the effect of impeding this exchange. Further, these oxygen limitations vary based on the type of soil present, and more coarsely grained soils are less likely to have issues with a lack of aeration (Kozlowski & Pallardy 1997b).

Even minor soil compaction can drastically decrease the infiltration of water into deeper layers, leading to surface runoff, soil erosion and water deficits in the deep soil layers (Cole 1982). Water retention is also generally much lower in areas with timber harvesting than those without (Cullen et al. 1991, Lutz 1945). Surface runoff can increase the leaching of soil nutrients from the soil (Kang & Lal 1981).

The recovery of severely compacted soils is generally a very slow process. For example, there is no observable reversal of soil seven years after the occurrence of soil compaction at some forest sites in Australia (Cheatle 1991) and the reversal of soil compaction can take several decades in the boreal region of Canada (Corns 1998). For example, forest soils may suffer from the compacting effect of tractor skidding for more than 40 years in California. However, the rate of recovery depends on the severity and depth of the compaction. More severe and deeper compaction will take longer to recover (Thorud & Frissell 1976).

THE EFFECTS OF COMPACTION ON PLANT AND TREE GROWTH

Soil compaction generally decreases tree growth but can also increase tree growth under certain circumstances, depending on the degree of compaction, soil type and plant species. Cambi et al. (2015) have investigated the effects of compaction on soil properties and the growth of English oak seedlings (*Quercus robur*) under field conditions in Florence, Italy. They have found that soil compaction decreases the number of leaves by 22%, shoot biomass by 26%, the shoot-root ratio by 10%, and the main root length by 24%. The study concludes that the limited access to nutrients and water, as a result of the shortened root lengths, is a key contributing factor for the decreased growth (Cambi et al. 2015). In contrast, a twenty-year study in California shows that a 10-25% increase in the bulk density of sandy loam and clay loam soils has increased seedling growth by 15% and the increase in seedling growth is attributable to the suppression of competing vegetation by the soil compaction (Zhang et al. 2017). These results will help to shed light on the idea that even though compaction has many negative effects on seedling growth, there may also be the opportunity to increase seedling success as well, depending on the degree of compaction (Zhang et al. 2017).

Skinner et al. (2009) found that compaction harms root penetration, and results in much smaller root systems when compared to sites with lower compaction levels. As a consequence of this, young seedlings are more likely to dry out due to the inability to access water deeper in the soil. Skinner et al. (2009) contributes to the theory that soil compaction decreases root growth and has the potential of decreasing seedling survival rates as the trees grow. In other studies, it was also found that the absorption of water by plants decreased with increasing levels of soil compaction and that needle water potential was similarly reduced (Arvidsson & Jokela 1995, Sheriff & Nambiar 1995).

Hormone growth regulators were also studied for seedlings on compacted sites, and it was found that severe soil compaction tends to induce substantial increases in xylem abscisic acid (ABA) and ethylene (Tardieu et al. 1992, Tardieu 1994, Liang et al. 1996). ABA is an inhibitory hormone in plants that helps them adapt to stressful conditions. It plays a role in stomatal closure and delayed seed germination (Anon 2017a), while ethylene is a hormone that aids in the ageing process of plants (Anon 2017b). A study done on field beans (*Vicia faba*) determined that due to compaction, the rate of ethylene evolution increased up to 6 times that of a free-growing plant. When bulk densities are heightened, the increase of these two hormones works to alleviate the pressures of poor site conditions by reducing stomatal conductance, delaying seed germination to a preferable time, and attempting to increase growth (Mulholland et al. 1996).

Other studies aimed to determine the effects of compaction on the mineral nutrition of plants and their ability to absorb nutrients. Several studies contribute to the theory that severe compaction decreases the absorption by roots of major mineral nutrients, especially nitrogen (N), phosphorus (P), and potassium (K) (Kang and Lal 1981, Cole 1982, Silverbush et al. 1983). They found that mineral uptake by the plants is reduced as compaction increases, due to nutrient losses from the soil, the decreased root access, and the lowered ability of roots to take up the nutrients. A study done on lodgepole pine (*Pinus contorta*) shoots determined that the concentrations of mineral nutrients were much smaller as the compaction levels became greater (Conlin & van den Driessche 1996), while another found that shoot nutrient concentrations of various other tree species were also reduced with increased compaction (Comerford et al. 1984). These reductions in nutrient levels harm the growth of woody species and can impede their productivity.

Another consequence of compaction is decreased photosynthesis and respiration rates. The rates of photosynthesis are decreased when stomatal closure is associated with leaf water deficits (Kozlowski 1972a); it is also due to smaller leaf areas and more frequent leaf abscission (Kozlowski & Pallardy 1997a). Photosynthesis of plants on compacted sites is also related to the availability of mineral nutrients. These limited resources reflect decreased chlorophyll synthesis, as well as stomatal closure and a lower capacity for photosynthetic electron transport (Kozlowski Pallardy 1997a). As soil compaction shifts conditions to a more anaerobic state, with lower soil oxygen contents, the prevalence of anaerobic respiration is more apparent than aerobic respiration. However, aerobic root respiration is essential for mineral uptake, the synthesis of protoplasm, and cell maintenance. Thus, without aerobic respiration, not enough energy is released to properly carry out many of these essential functions and most likely lead to the decline in root growth, shoot growth, and overall health (Kozlowski & Pallardy 1997a).

Numerous studies focus on the effects of soil compaction on tree growth specifically and the regeneration of forest stands. One study showed that compaction negatively affects stand regeneration by inhibiting seed germination and seedling growth, and by increasing the prevalence of seedling mortality (Kozlowski 1999). It has been found that in some cases the number of trees per hectare at a particular site can be reduced 88-91% by compaction. On skid trials specifically, compaction can result in 74% less volume and 41% fewer trees than adjacent forest areas (Lockaby & Vidrine 1984). Compaction decreases the elongation of main roots, first and second-order lateral roots and total root length. However, it has also been found that the number of first-order lateral roots and their diameters increase in response to higher levels of compaction (Sands & Bowen 1978). Similarly, it has been found that root systems become shortened and thickened but also show increased branching as a response to compaction (Gilman et al. 1978). Compaction also results in a decrease in fine root growth and has the potential to limit the productivity of residual trees left on a harvested block, through their decreased water and nutrient uptake. The implications of such a loss could be significant, and ultimately determine the success and survival of the remaining trees in an area after logging has occurred (Malo & Messier 2011).

Another way that trees may be lost is due to the potential for the decreased structural integrity of trees; the inability to penetrate deeper in the ground will result in shallow root systems that are more likely to become uprooted during a storm. This could create a hazardous situation as the trees grow and produce trees with weak foundations (Hutchison 2017). One study concludes that it is possible to carry out forestry operations if the weight of the machinery is kept below a particular threshold and if only a small number of passes are made with the machinery (Jansson & Wasterlund 1999).

MATERIALS & METHODS

PLANT MATERIALS

This experiment took place in the greenhouse at Lakehead University, Thunder Bay, ON. The *P. banksian*a and *P. mariana* seeds were sourced in 2011 from Nelson River, MB and Tracadie, NB, respectively, and were provided by the National Tree Seed Centre (NTSC). They were stratified before planting. Stratification involved putting the seeds in sealed containers with enough moisture so that the contents were moist, but not oversaturated with pooling water. About ¼ cup vermiculite and ¼ cup gravelly material were in the container. 1 tsp of powdered copper fungicide was sprinkled in as well to prevent fungal growth. The containers were stored in a refrigerator for two weeks before planting.

PREPARATION OF SOIL

Silty clay loam soil was obtained from Murillo, ON. The soil was pasteurized to kill weed seeds, soil-borne insects, and pathogens. The soil in aluminum pans covered with aluminum foil was heated to 180 degrees Fahrenheit in a ventilated drying-over and kept at that temperature for 30 minutes. The aluminum foil was then removed, and the soil was oven-dried for 24 hours at 105 degrees Fahrenheit (Pennsylvania State University 2007). Finally, the soil was sieved through a #4 sieve to remove large clumps.

COMPACTING THE SOIL

5-gallon buckets (30.2 cm x 36 cm) were used as the container for the experiment and drainage holes were drilled in the bottom which was then lined with filter paper at the bottom to prevent soil from escaping. There were four levels of soil compaction with the following bulk densities: 0.9 g/cm^3 (C), 1.1 g/cm^3 (C1), 1.2 g/cm^3 (C2), and 1.3 g/cm^3 (C3). These compaction levels were chosen based on USDA bulk density values which display specific levels of compaction that are considered limiting for tree growth (USDA 1999, Appendix III, Table 5). These bulk densities were also chosen based on typical bulk density levels one would find in the field (Kozlowski 1999) and based on how dense we could physically pack the soil in the pots without damaging them. The soil compacting was conducted in the Lakehead University Civil Engineering laboratory. The dry soil without any artificial compacting had a bulk density of 0.9 g/cm^3 and served as the control (C) for the experiment. 14.4 kg of dry soil was added into each control bucket. To obtain the bulk density of 1.1g/cm^3 (C1), 660g of lukewarm water was added into 4.4 kg of dry soil. The soil and water were thoroughly mixed, and any clumps were broken apart. The soil was then poured into the bucket and compacted down to a specified depth with a 2x4 wood block. The first layer of soil was compacted down to a mark on the bucket, equivalent to a volume of 4 L; the second layer was pressed down to an 8 L mark, the third to a 12 L mark, and the fourth and final layer to a 16 L mark. Each layer consisted of a mixture of 4.4kg of dry soil and 660g water. The compacting process was the same for the next two bulk densities, except the amount of water and dry soil differed: 720g of lukewarm water was added to 4.8kg dry soil for the 1.2 g/cm^3 bulk density (C2) and 780g water was added to 5.2kg soil for the 1.3 g/cm^3 (C3) bulk density. Also, for this last compaction level, a cylindrical manual rammer was used in combination with the 2x4 to compact the soil down.

There were 5 buckets per species for each compaction level. The locations of the buckets on the bench were completely randomized. The soil was moistened before seed planting. Nine *P. banksiana* seeds were planted in each bucket in groups of three at equal distance from each other. Because tests showed a lower germination rate for *P. mariana*, 18 seeds were planted in each bucket in groups of 6 (Appendix IV, Figure 11). The seeds were covered with soil after sowing. The soil was misted each day until germination began. The subsequent seedlings were fertilized twice a week with a starter fertilizer solution (11-41-8: 100.1mg/L N, 373.1 mg/L P and 72.8 mg/L K) for the first two weeks. The fertilizer solution was then changed to the forestry seedling standard fertilizer 20-8-20 (N-P-K) at 50mg/L N, 20mg/L P and 50mg/L K to 200mg/L N, 80mg/L P and 200mg/L K for two months as recommended by Richard (2015). Regular watering also occurred based on a predetermined and consistent watering schedule. The greenhouse environmental conditions were controlled as follows: day/night temperature 22°C/17°C, RH 45 %, and a photoperiod 15 h.

<u>OBSERVATION AND MEASUREMENTS</u>

Seed germination was tallied throughout the experiment. Seedling height and root collar diameter were measured 18 months after the completion of germination. The seedlings were then harvested. To avoid damages to the root system, particularly fine roots, the buckets were cut open down the side with a circular saw and the seedlings were extricated by washing soil particles away from the roots with a garden hose. The seedlings were then stored in cold storage in plastic bags until analysis. The length of the main/taproot was measured with a ruler. The whole root system was then scanned and analyzed using the Regen WinRHIZO system 3.9 (Regent Instrument Inc., Quebec City, Quebec). The following parameters were subjected to the scanning software: total root length (cm) the total projected root area, total surface area, average root diameter, and the number of root tips. The foliage was scanned and analyzed using the Regen WinSEEDLE system V 4.3B (Regent Instrument Inc., Quebec City, Quebec). The foliage parameters used for further analyses were total projected leaf area of the seedling, average projected area per needle, average needle length, average needle width, the total number of needles, and the total accumulative length of all the needles. Following those measurements, all the seedlings were oven-dried at 80 ^{o}C for 48 h. The dry mass of roots, and total biomass were measured on a Sartorius® CP Series Analytical Balance, and then the root to shoot ratios were calculated (CP 124S, Sartorius AG, Goettingen, Germany).

DATA ANALYSIS

Seedling Growth

The data were analyzed using the R software package 3.6.2 (R Development Core Team 2019). The seedling data were examined for the assumptions of normality and homogeneity before being subjected 2-way Analysis of Variance (ANOVA) using the following linear model:

$$Y_{ijk} = \mu + a_i + b_j + ab_{ij} + \varepsilon_{ijk}$$

Where μ is the overall mean, a_i is the fixed effect of the compaction level (4 levels), b_j is the fixed effect of species (2 species), ab_{ij} is the effect of the fixed interaction (8 combinations) between compaction level and species, and $\varepsilon_{(ij)k}$ is the residual or random error. If the interaction and/or soil compaction effect was significant ($p \leq 0.05$), Tukey's post-hoc tests were conducted.

Seed Germination

Seed germination was tested using an offset Poisson regression for count data. Refer to the following model:

$$\log \mu_x = \log t_x + \beta'_0 + \beta'_1 x$$

Where μ_x is the expected count for those with covariate x, β'_0 and β'_1 are the counts for seed germination per species, $\log t_x$ is the offset to account for the difference in seeds planted per species.

RESULTS

Jack pine and black spruce both showed significant declines in root biomass in response to increases in soil compaction (Table 1, Figure 1). Because the probability for the species-compaction was very close to the threshold value (0.06 vs. 0.05) and our sample size was small, the results of the two species were presented separately. As compared to the control, the root mass of *P. banksiana* decreased by 27.85% at soil compaction treatment C1, 22.2% at C2, and 31.5% at C3 (Figure 1). However, the difference between C2 and the control was not statistically significant (Figure 1). The root biomass of *P. mariana* decreased by 10.1%, 31.9%, and 46.4% at the three levels of soil compaction. Statistically, the decline was significant only in the most serious soil compaction treatment (C3). Black spruce suffered a greater decline in root biomass than jack pine at the highest compaction level (46.4% vs. 32%, Figure 1).

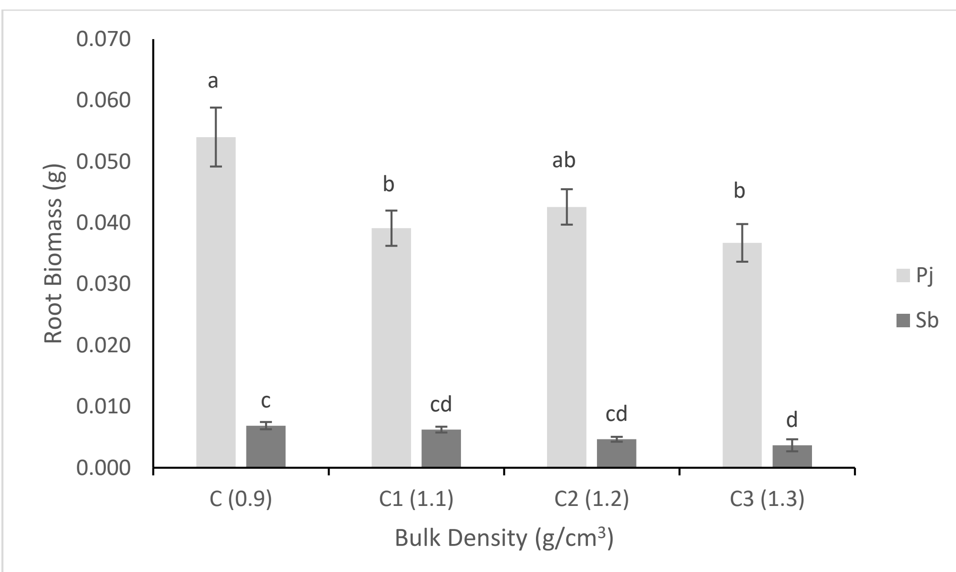

Figure 1. Responses of root biomass (g) to soil compaction in *Pinus banksiana* (Pj) and *Picea mariana* (Sb). Means with no common letter were significantly different from each other ($p \leq 0.05$); determined through Tukey's post-hoc test.

Table 1. Results of two-way ANOVA for all parameters; excluding seed germination.

Variable	Df	Sum Sq.	F value	Pr.
Root Biomass				
Compaction	3	3.19	10.43	<0.001
Species	1	105.21	1030.78	<0.001
Compaction*Species	3	0.79	2.39	0.06
Total Biomass				
Compaction	3	0.04	10.43	<0.001
Species	1	105.21	1030.78	<0.001
Compaction*Species	3	2.43	2.39	0.171
Root to Shoot Ratio				
Compaction	3	2.99	15.4	<0.001
Species	1	0.32	0.7	0.4
Compaction*Species	3	0.94	4.22	0.007
Main Root Length				
Compaction	3	680	11.35	<0.001
Species	1	7906	395.91	<0.001
Compaction*Species	3	162	2.71	0.05
Seedling Height				
Compaction	3	9.6	32.37	<0.001
Species	1	237.2	2398.44	<0.001
Compaction*Species	3	0.29	0.97	0.41
Total Root Length				
Compaction	3	4.71	18.6	<0.001
Species	1	51.39	608.98	<0.001
Compaction*Species	3	1.71	6.74	<0.001
Root Surface Area				
Compaction	3	3.03	14.06	<0.001
Species	1	80.87	1124.43	<0.001
Compaction*Species	3	1.48	6.85	<0.001
Average Root Diameter				
Compaction	3	0.04	31.43	<0.001
Species	1	0.21	457.45	<0.001
Compaction*Species	3	0.002	1.67	0.18
# of Root Tips				
Compaction	3	5.82	17.59	<0.001
Species	1	66.68	604.74	<0.001
Compaction*Species	3	2.25	6.81	<0.001

Soil compaction significantly affected total biomass and there was no significant interaction between species and soil compaction (Table 1, Figure 2). The total biomass had a general downward trend, and when compared to the control, the reductions were 20.8%, 16.8%, and 19%, for C1, C2, and C3, respectively. C1 and C3 were statistically different from the control, while C2 was not (Figure 2).

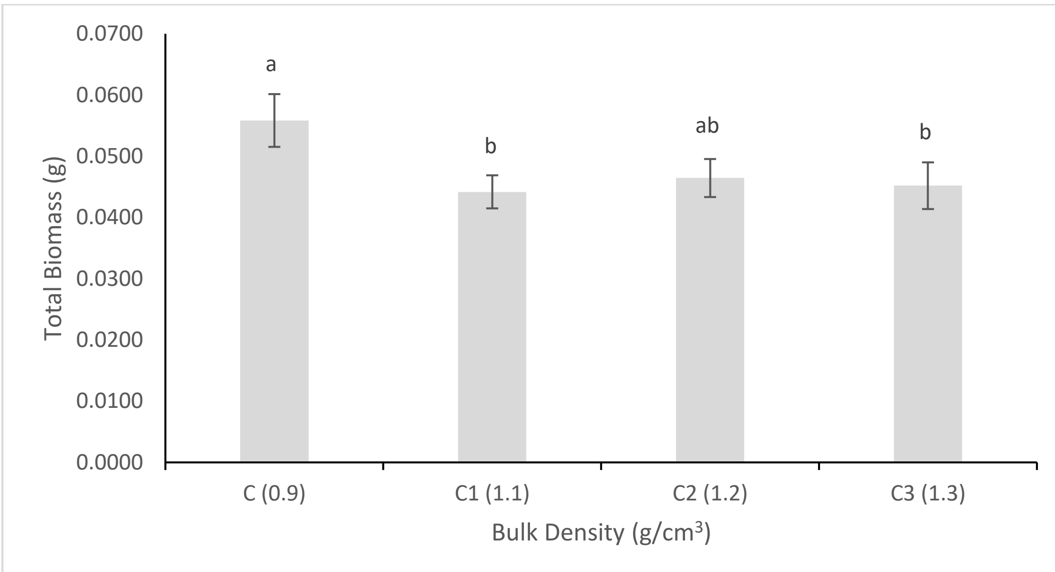

Figure 2. Total biomass (g) of *Pinus banksiana* and *Picea mariana*. Means with no common letter were significantly different from each other ($p \leq 0.05$); determined through Tukey's post-hoc test.

The root to shoot ratios for both jack pine and black spruce were significantly affected by soil compaction (Table 1, Figure 3). In this case, there is a significant species-compaction interaction, but the general trend of the responses was similar in the two species, i.e., the root to shoot ratios declined with increasing severity of soil compaction. The average decline for *P. banksiana* was 11.8%, 8.2%, and 32.4% for treatment C1, C2, and C3, respectively. The corresponding declines in *P. mariana* were greater than jack pine, with a decline of 13.2%, 38.5%, and 36.7%, for treatment C1, C2, and C3, respectively. However, when comparing the interactions of the two species, one can see that under each treatment, the responses of the two species were not statistically different from one another (Figure 3).

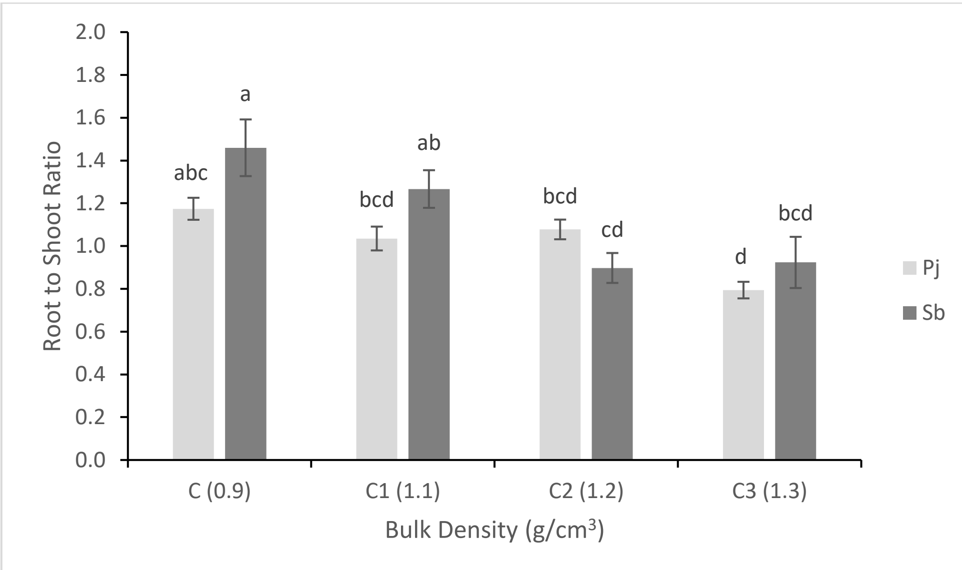

Figure 3. Responses of the root to shoot ratios to soil compaction in *Pinus banksiana* (Pj) and *Picea mariana* (Sb). Means with no common letter were significantly different from each other ($p \leq 0.05$); determined through Tukey's post-hoc test.

Soil compaction significantly reduced tap/main root length and the response was significantly different between the two species (Table 1). For *P. banksiana* the main root length decreased by 4.1%, 9.6%, and 46.4% in the soil compaction treatment of C1, C2, and C3, respectively, but the decline in C1 and C2 were not statistically significant (Figure 4). For *P. mariana* the decline in main root length became progressively greater with increasing compact severity: the decline was 9.4%, 33%, and 50.9% for treatment C1, C2 and C3, respectively (Figure 4).

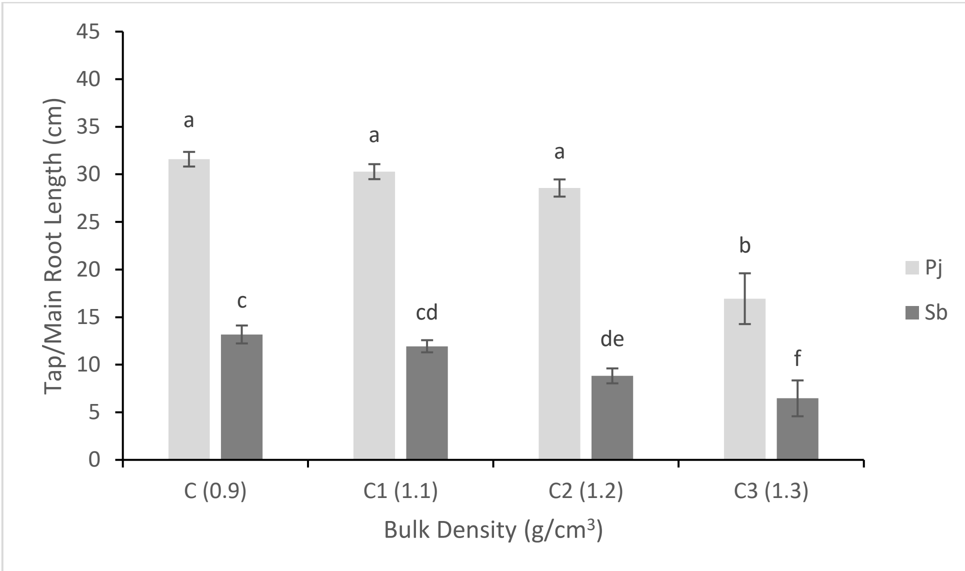

Figure 4. Responses of tap/main root length (cm) to soil compaction in *Pinus banksiana* (Pj) and *Picea mariana* (Sb). Means with no common letter were significantly different from each other ($p \leq 0.05$); determined through Tukey's post-hoc test.

Soil compaction significantly affected seedling height and there was no significant interaction between species and soil compaction (Table 1, Figure 5). The reductions in seedling height were by 6.1%, 3.5%, and 8.5%, for treatments C1, C2, and C3, respectively. However, only C1 and C3 were statistically different from the control (C), while C2 was not (Figure 5).

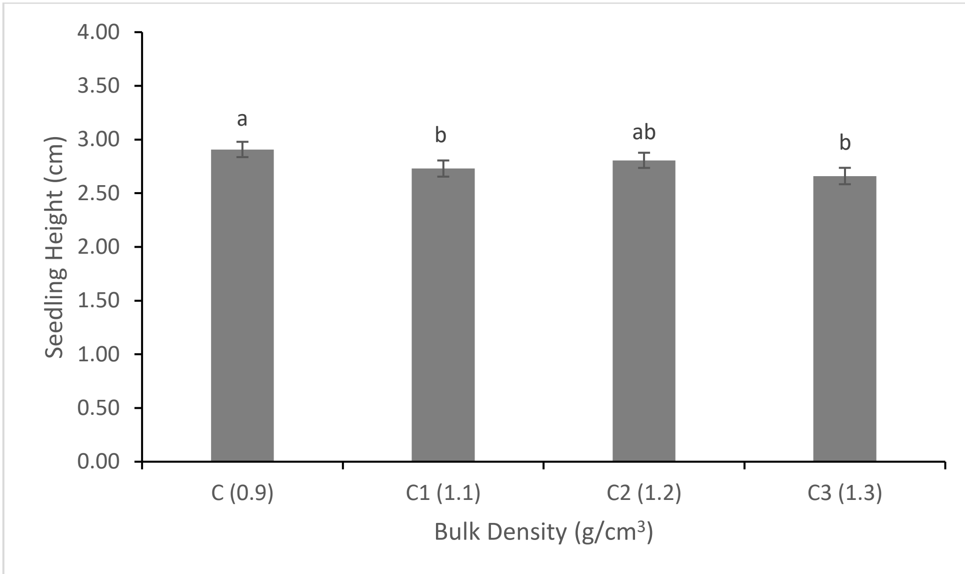

Figure 5. Seedling height (cm) of *Pinus banksiana* and *Picea mariana* per compaction level. Means with no common letter were significantly different from each other ($p \leq 0.05$); determined through Tukey's post-hoc test.

While there was a significant interactive effect of soil compaction and species on the total root length per seedling, the general trend of the response was similar in the two species, *i.e*., the total root length declined with increasing severity of soil compaction (Table 1, Figure 6). The average decline for *P. banksiana* was 28.8%, 32.1% and 43.2% for treatment C1, C2, and C3, respectively. The corresponding declines in *P. mariana* were 14.2%, 53.3% and 64.6%, respectively. However, not all pairwise differences were statistically significant (Figure 6).

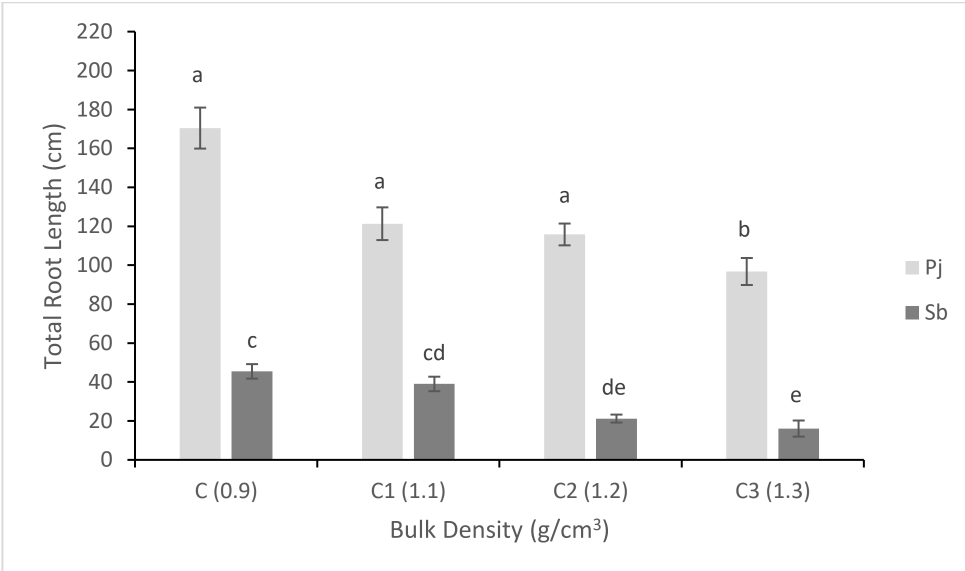

Figure 6. Total root length (cm) of *Pinus banksiana* (Pj) and *Picea mariana* (Sb). Means with no common letter were significantly different from each other ($p \leq 0.05$); determined through Tukey's post-hoc test.

The response patterns of the root surface area were similar to those of total root length: it declined with increasing soil compaction in both species (Table 1, Figure 7). However, the rates of the decline were different between the two species: the net reduction for jack pine was 27.8%, 25.1%, and 39.1%, for treatment C1, C2, and C3 respectively; the decline for black spruce was 7.4%, 44.5%, and 57.4%, respectively. Again, not all the pairwise differences were statistically different from each other (Figure 7).

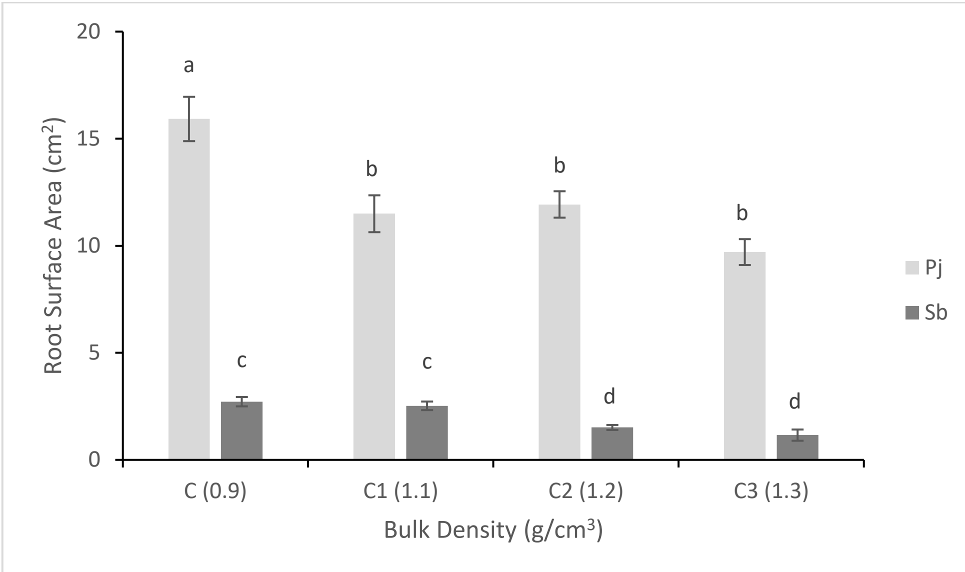

Figure 7. Root surface area (cm^2) of *Pinus banksiana* (Pj) and *Picea mariana* (Sb). Means with no common letter were significantly different from each other ($p \leq 0.05$); determined through Tukey's post-hoc test.

The response of average root diameter contrasted with those of root length and root surface area. Root diameter generally increases with increasing severity of soil compaction (Table 1, Figure 8) and the two species responded similarly, *i.e.*, no significant interaction between species and soil compaction (Table 1). The net increase in root diameter was 6.6%, 15%, and 13.6% for treatment C1, C2 and C3, respectively, although not all the increases were significant statistically (Figure 8).

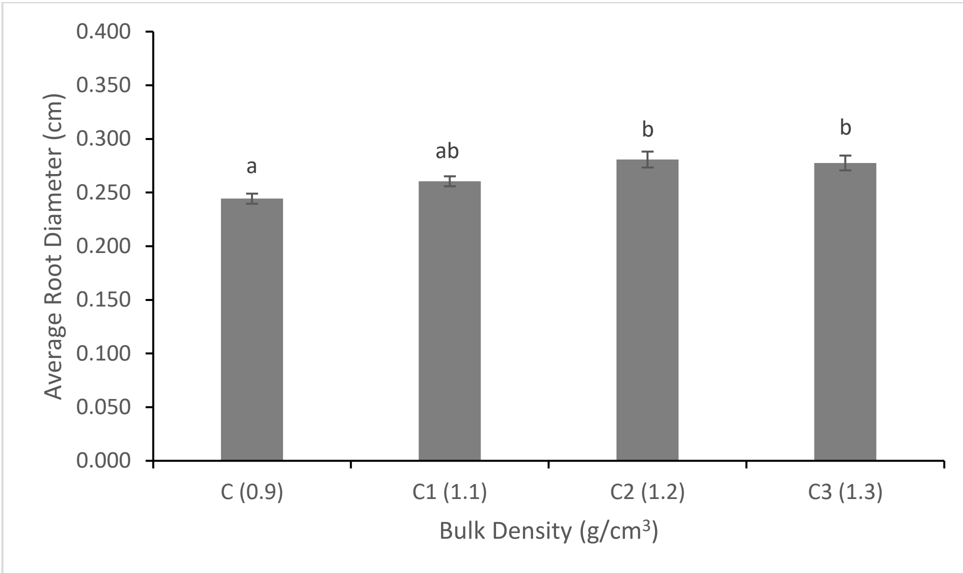

Figure 8. Average root diameter (cm) of *Pinus banksiana* and *Picea mariana*. Means with no common letter were significantly different from each other ($p \leq 0.05$); determined through Tukey's post-hoc test.

Lastly, the number of root tips generally declined with increasing level of soil compaction in the two species (Table 1, Figure 9). However, the rate of decline was smaller for jack pine than black spruce: For *P. banksiana*, the decline was 22.6%, 30.6%, and 46.7% for soil compaction treatment C1, C2 and C3, respectively while the corresponding decline for *P. mariana* was 29.3%, 57.1%, and 76.2%, respectively (Figure 9).

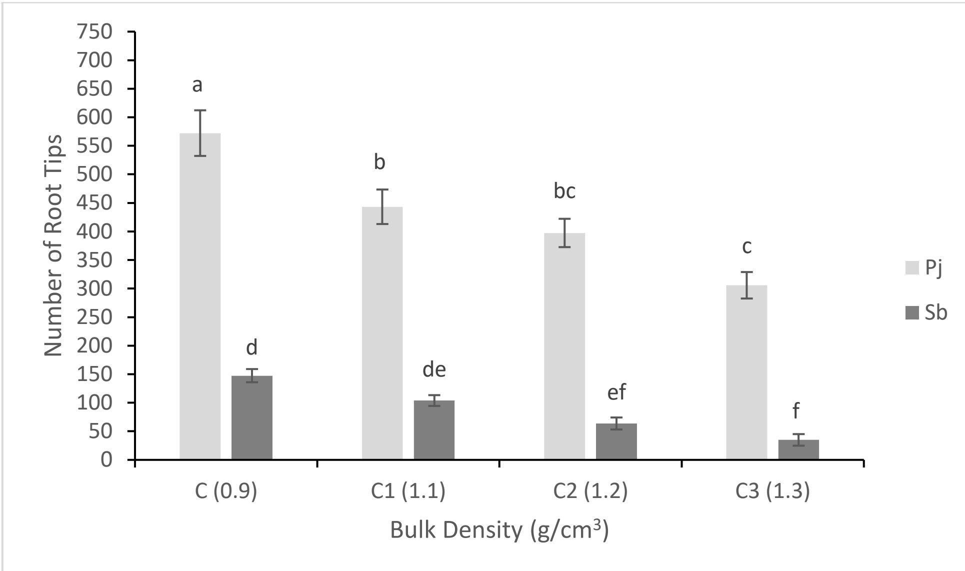

Figure 9. Number of root tips of *Pinus banksiana* (Pj) and *Picea mariana* (Sb). Means with no common letter were significantly different from each other ($p \leq 0.05$); determined through Tukey's post-hoc test.

The seed germination of black spruce and jack pine were not significantly different within or between species (Table 2, Figure 10).

Table 2. Results of Poisson regression for seed germination.

Variable	Chi-Squared	Df	Pr.
Seed Germination			
Compaction	1.36	3	0.71
Species	2.3	1	0.13
Compaction*Species	0.52	3	0.91

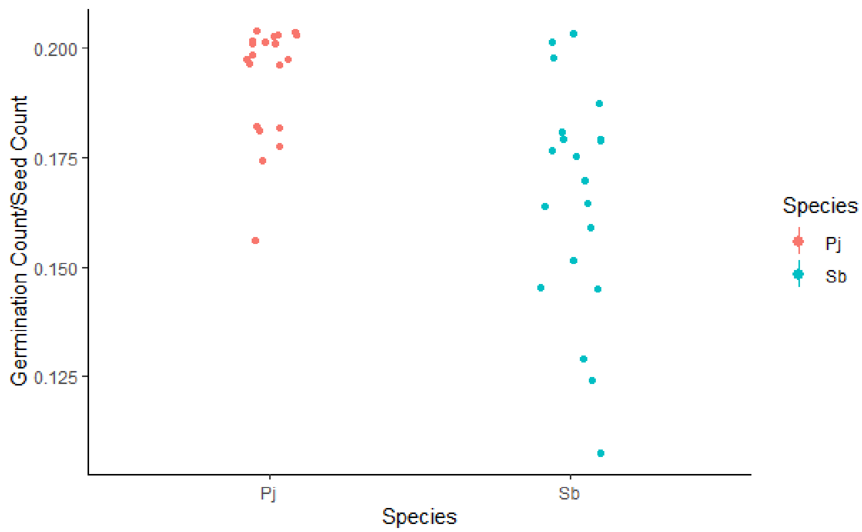

Figure 10. Germination count/seed count for *Pinus banksiana* (left) and *Picea mariana* (right).

DISCUSSION

The results of the study suggest that *Pinus banksiana* and *Picea mariana* are both very sensitive to soil compaction. Both species showed significant declines in the root biomass, and total biomass, root to shoot ratios, main/ taproot lengths, total root lengths, root surface area, and the number of root tips in response to soil compaction. The degree of the declines generally increased with increasing severity of soil compaction. These findings are consistent with the results of Cambi et al. (2015) and Gilman et al. (1987). Both species also displayed significant increases in their average root diameters in response to soil compaction. Sands and Bowen (1978) have reported similar findings. However, one result was generally contrary to the literature, *i.e*., Seed germination displayed results that did not align with most studies currently published. There was no significant effect of soil compaction on the germination within or between the two species. The general success of seed germination is likely a result of the environmental conditions that this experiment was subject to. In contrast to a field experiment, conditions would have been more ideal for their germination, except for the increase in bulk density itself. Due to the unexpected responses of seed germination, the hypothesis stating that more severe levels of compaction will exert progressively greater limitations to seed germination and seedling growth, can only be accepted for the seedling growth parameters, and not seed germination.

The results indicate that root growth was the most sensitive to soil compaction among all the seedling traits measured in this study, and black spruce was more sensitive than jack pine. In black spruce, the traits with the largest declines in response to soil compaction were total root lengths and the number of root tips. Overall, the total root length declined by 64.6% and the reduction in root tip numbers was 76.2% on the most severely compacted soil. In jack pine, however, the taproot length and the number of root tips were the most sensitive to soil compaction and declined 46.4%, and 46.7%, respectively, on the most severely compacted soil. The overall declines in both traits were much greater in black spruce than jack pine. These results support our hypothesis that black spruce would be more sensitive to soil compaction than jack pine because of the difference in their rooting patterns. These results can have great implications for the regeneration of forests and could result in changes to forest composition over time; one such change may be the reduction in *P. mariana* on heavily compacted sites. This is one of the many reasons why soil compaction needs to be taken into consideration by current and future forest managers. Furthermore, the large declines suggest that measures to minimize soil compaction in forest operations can have substantial effects on the site productivity, particularly during the establishment phase of the forest stand. Using equipment with high floatation and avoiding repeated use of the same path could be effective options.

In addition to this, there was also a substantial difference in the growth of the two species overall. In this current study, *P. mariana* was much more sensitive than *P. banksiana*. For instance, black spruce has almost a 30% lower number of root tips than jack pine under the highest level of compaction. Black spruce also had a 15%, 4.5%, and 18.3%, greater decline in root biomass, main root length, root surface area, respectively, when compared to jack pine under the highest level of compaction. The reason that *P. mariana* had more drastic declines in growth may have also been due to the sheer size of the seedlings as well as the lack of a taproot to penetrate the soil with the same force as

P. banksiana would have had. This aligns with research done by Skinner et al. (2009) which speaks of the importance of a taproot in penetrating deeper into the ground. An important aspect of resisting soil compaction is the ability of the root system to push through the compacted soil (Skinner et al. 2009, Kozlowski 1999). Another reason why black spruce may have responded more negatively than jack pine could be due to their shorter root systems. With a reduction in water penetration on more compacted soils comes a greater period where water is left standing on the soil. Thus, with a shorter root system, black spruce may have had more roots underwater, when compared to jack pine. In this experiment, the more compacted the soil was, the longer the water would sit on the surface of the soil after watering. Over time under these conditions, those treatments developed a very thin layer of green mosses/algae. It is believed that this contributed to the poor growth of *P. mariana* especially, given its greater growth reductions. This is surprising because black spruce is supposed to be more resistant to flooding than jack pine (Fryer 2014). Due to these wetter conditions, the oxygen content in the soil may have been lower as well and could have shifted the seedlings to a more anaerobic state. Aerobic root respiration is essential for mineral uptake, the synthesis of protoplasm, and cell maintenance. Thus, without aerobic respiration, not enough energy is released to properly carry out many of these essential functions and most likely lead to the decline in growth and overall health (Kozlowski & Pallardy 1997a).

The root to shoot ratios of the two species responded by following a similar downward trend. The ratios both gradually declined as the level of compaction increased, which aligns with past research (Kozlowski 1999). When comparing the two species to each other, jack pine tended to have a lower ratio than black spruce did, except for the moderate compaction level (C2), where it was slightly higher. The root biomass measurements revealed significant reductions in growth, which has led to the resulting root to shoot ratios. However, for every treatment, black spruce displayed greater declines than jack pine, which suggests that it is a more sensitive species, but also that soil compaction has a greater influence on the root growth of the seedlings, as opposed to the aboveground growth. This is a key feature to keep in mind when managing our forests and should be further explored in future experiments.

One of the benefits of this study, as previously mentioned, is that multiple bulk densities are experimented upon. This helps us to see the response pattern between the dependent variables and the varying levels of compaction. Soil compaction resulted in substantial declines in every single growth parameter, except for the average root diameters of the two species. There are some severe implications for these reductions, in the sense that it does not matter how light the compaction is because the growth of the seedlings is very sensitive to even minor levels of soil compaction and could still suffer considerable consequences. The significant reductions in this study demonstrate the importance of considering soil compaction when carrying out forest operations because it has an impact on soils, forest health, as well as productivity. It has been forecasted that severe compaction will be more prevalent in future years and will continue to have an impact on our forests. By further studying the effects that compaction has on *P. banksiana, P. mariana*, and other species, researchers may be better able to mitigate the effects, even if it is not possible to completely avoid them. This is a short-term study in a controlled environment. The literature suggests that the responses of trees to soil compaction can change with tree age (Kozlowski 1999). If the compaction is limited to the top layer of the soil, some of its impact on trees may decline after the root system penetrates below the compacted layer. The dynamics of freeze-thaw cycles may also modify the impact. Furthermore, different soil types and ground cover can influence the effect of soil compaction on trees. Longer-term field studies should be carried out in the future to assess the long-term effects of soil compaction on tree physiology, growth and forest productivity under different site conditions. Such studies should provide forest managers with more insights for developing more efficient measures to reduce soil compaction and to mitigate the negative effect of soil compaction.

LITERATURE CITED

Anonymous, 2017a. Abscisic acid (ABA) definition. Maximum Yield webpage. Retrieved November 1, 2017. https://www.maximumyield.com/definition/836/abscisic-acid-aba

Anonymous, 2017b. Ethylene definition. Maximum Yield webpage. Retrieved November 1, 2017. https://www.maximumyield.com/definition/1578/ethylene

Anonymous, 2018. What is R? The R Foundation. Retrieved April 10, 2018. https://www.r-project.org/about.html

Arvidsson, J. & Jokela, W. E. 1995. A lysimeter study of soil compaction effects on evapotranspiration in a barley crop. Swedish Journal of Agricultural Research. 39, pp. 109-118. Retrieved November 30, 2017. http://eds.b.ebscohost.com.ezproxy.lakeheadu.ca/eds/detail/detail?vid=4&sid=5d01e4d9-a1b2-45cd-93f8-a697350aaecd%40sessionmgr4010&bdata=JnNpdGU9ZWRzLWxpdmUmc2NvcGU9c2l0ZQ%3d%3d#AN=edsagr.SE9610706&db=edsagr

Cambi, M., Hoshika, Y., Mariotti, B., Paoletti, E., Picchio, R., Venanzi, R., and Marchi, E. 2015. Compaction by a forest machine affects soil quality and *Quercus robur* L. seedling performance in an experimental field. Forest Ecology and Management 384, pp. 406-414. Retrieved October 20, 2017. https://ezproxy.lakeheadu.ca/login?url=http://search.ebscohost.com/login.aspx?direct=true&db=edselp&AN=S0378112716308374&site=eds-live&scope=site

Cheatle, R. J. 1991. Tree growth on compacted Oxisol. Soil Tillage Res. 19, pp. 331–344. Retrieved November 30, 2017.

Clark L.J, Whalley W.R., Barraclough P.B. 2003. How do roots penetrate strong soil? Plant Soil 255:93-104.

Cole, D. N. 1982. Wilderness campsite impacts: effect of amount of use. USDA Forest Service Res. Pap. INT-284. Ogden, Utah. Retrieved November 30, 2017.

Comerford, N. B., Kidder, G. K. & Mollitor, A. V. 1984. Importance of subsoil fertility to forest and non-forest plant nutrition. *In* Stone, E. L. (ed.). Proceedings, Sixth North American Forest Soils Conference, pp. 381–404. University of Tennessee, Knoxville, TN. Retrieved November 25, 2017.

Conlin, T. S. S. & van den Driessche, R. 1996. Short-term effects of soil compaction on growth of *Pinus contorta* seedlings. Can. J. For. Res. 26: 727–739. Retrieved November 20, 2017.

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, pp. 75–84. Retrieved November 20, 2017.

Cullen, S.J., Montagne, C., Ferguson, H. 1991. Timber harvest trafficking and soil compaction in western Montana. Soil Sci. Soc. Am. J. 55, pp.1416-1421. Retrieved December 2, 2017.

Currie, J. A. 1984. Gas diffusion through soil crumbs: the effects of compaction and wetting. European Journal of Soil Science, 34 (1), pp. 1-10. Retrieved October 20, 2017. http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2389.1984.tb00253.x/abstract;jsessionid=D38F0CC86444A381D8836B97F2252EC9.f03t01

Franklin, J. & Mercker, D. 2009. Tree growth characteristics. The University of Tennessee Institute of Agriculture, USA. Retrieved April 13, 2018. https://extension.tennessee.edu/publications/Documents/W227.pdf

Fryer, J. L. 2014. Picea mariana. In: Fire Effects Information System. U.S. Department of Agriculture, Forest Service, Rocky Mountains Research Station, Fire Sciences Laboratory. Retrieved March 26, 2020. https://www.fs.fed.us/database/feis/plants/tree/picmar/all.html

Horn, R., Domzal, H., Slowinska-Jurkiewicz, A., and van Ouwerkerk, C. 1995. Soil compaction process and their effects on the structure of arable soils and the environment. Soil and Tillage Research, 35(1-2), pp. 23-36. Retrieved October 18, 2017. https://www.sciencedirect.com/science/article/pii/016719879500479C

Hutchinson, L.J. 2017. Urban forestry laboratory manual (14th Edition). Lakehead University, Faculty of Natural Resources Management. pp. 57-92.

Gilman, E. F., Leone, I. A. & Flower, F. B. 1987. Effect of soil compaction and oxygen content on vertical and horizontal root distribution. J. Environ. Hort. 5, pp. 33–36. Retrieved November 15, 2017.

Goss, M. 2017. Soil plant relations. University of Guelph, Ontario. Retrieved October 19, 2017. http://www.uoguelph.ca/~mgoss/three/410-N03f.html

Jansson, K.J. & Wasterland, I. 1999. Effect of traffic by lightweight forest machinery on the growth of young *Picea abies* trees. Scandinavian Journal of Forest Research. 14, pp. 581-588. Retrieved November 16, 2017. https://ezproxy.lakeheadu.ca/login?url=http://search.ebscohost.com/login.aspx?direct=true&db=aph&AN=6403076&site=eds-live&scope=site

Johnson, C. E., Johnson, A. H., Huntington, T. G. & Siccama, T. G. 1991. Whole-tree clear-cutting effects on soil horizons and organic matter pools. Soil Sci. Soc. Am. J. 55, pp. 497–502. Retrieved November 10, 2017.

Kang, B. T. & Lal, R. 1981. Nutrient losses in water runoff from agricultural catchments. *In* Lal, R. & Russel, E. W. (eds.). Tropical Agricultural Hydrology, pp. 153–161. Wiley, New York. Retrieved November 15, 2017.

Koolen, A. J. & Kuipers, H. 1983. Agricultural soil mechanics. Springer, Berlin. Retrieved November 2, 2017.

Kozlowski, T. T. 1972*a*. Shrinking and swelling of plant tissues. *In* Kozlowski, T.T. (editor). Water Deficits and Plant Growth, Vol. III, pp.1–64. Academic Press, New York. Retrieved November 1, 2017.

Kozlowski, T. T. & Pallardy, S. G. 1997a. Physiology of Woody Plants, 2nd ed. Academic Press, San Diego, CA. Retrieved November 1, 2017.

Kozlowski, T. T. & Pallardy, S. G. 1997b. Growth Control in Woody Plants. Academic Press, San Diego, CA. Retrieved November 3, 2017. https://ezproxy.lakeheadu.ca/login?url=http://search.ebscohost.com/login.aspx?direct=true&db=edsagr&AN=edsagr.US9705725&site=eds-live&scope=site

Kozlowski, T.T. 1999. Soil compaction and growth of woody plants. Scandinavian Journal of Forest Research, 14, pp. 596-619. Retrieved October 25, 2017. https://ezproxy.lakeheadu.ca/login?url=http://search.ebscohost.com/login.aspx?direct=true&db=aph&AN=6403084&site=eds-live&scope=site

Liang, J. Zhang, J. & Wong, M.H. 1996. Stomatal conductance in relation to abscisic acid concentrations in two tropical trees, *Acacia confusa* and *Litsea glutinosa*. Plant Cell Environ. 19, pp. 93-100. Retrieved December 12, 2017.

Lockaby, B. G. & Vidrine, C. G. 1984. Effect of logging equipment traffic on soil density and growth and survival of loblolly pine. South. J. Appl. For. 8, pp. 109–112. Retrieved November 10, 2017.

Lund, A., & Lund, M. 2013. One-way ANOVA. Laerd Statistics. Lund Research Ltd. Retrieved January 15, 2017. https://statistics.laerd.com/statistical-guides/one-way-anova-statistical-guide.php

Lutz, H. 1945. Soil conditions on picnic grounds in public forest parks. J. For. 43, pp. 121-127. Retrieved December 12, 2017.

Malo, C. & Messier, C. 2011. Impact of primary and secondary machinery tracks on fine root growth of sugar maple after selection cutting. Canadian Journal of Forest Research. 41(4), pp. 892-897. Retrieved November 10, 2017. https://ezproxy.lakeheadu.ca/login?url=http://search.ebscohost.com/login.aspx?direct=true&db=aph&AN=65536352&site=eds-live&scope=site

McKenzie, R.H. 2010. Agricultural soil compaction: Causes and management. Government of Alberta, Agriculture and Forestry. Retrieved October 18, 2017. http://www1.agric.gov.ab.ca/$department/deptdocs.nsf/all/agdex13331

McNeel, J. F. & Ballard, T. M. 1992. Analysis of site stand impacts from thinning with a harvester-forwarder system. J. For. Engin. 4, pp. 23–29. Retrieved November 1, 2017.

Mikulecky, P.J., Gilman, M.R., & Peterson, B. 2017. Plant biology: roots, shoots, stems, and leaves. Dummies education. Retrieved December 1, 2017. http://www.dummies.com/education/science/plant-biology-roots-shoots-stems-and-leaves/

Mitchell, M.L., Hassan, A.E., Davey, C.B., Gregory, J.D. 1982. Loblolly pine growth in compacted greenhouse soils. Trans. Am. Soc. Agric. Eng. 25, pp. 304-307, 312. Retrieved December 1, 2017.

Mulholland, B. J & Fullen, M. A. 1991. Cattle trampling and soil compaction on loamy sands. Soil Use Manage. 7, pp. 189-193. Retrieved November 1, 2017.

Pomeroy, K. B. 1949. The germination and initial establishment of loblolly pine under various surface soil conditions. J. For. 47, pp. 541–543. Retrieved November 5, 2017.

Regent Instruments Inc. 2017. WinRhizo: Analysis of washed roots and Arabidopsis seedlings. Regent Instruments Inc. Retrieved April 10, 2018. http://regent.qc.ca/assets/winrhizo_about.html

Sands, R. & Bowen, G. D. 1978. Compaction of sandy soils in radiata pine forests. II. Effects of compaction on root configuration and growth of radiata pine seedlings. Aust. For. Res. 8, pp. 163–170. Retrieved November 16, 2017.

Sheriff, D.W., Nambiar, E.K.S. 1995. Effect of subsoil compaction and three densities of simulated root channels in the subsoil on growth, carbon gain and water uptake of *Pinus radiata*. Aust. J. Plant Physiol. 22, pp. 1001-1013. Retrieved December 20, 2017.

Shetron, S.G., Sturos, J.A., Padley, E., Trettini, C. 1988. Forest soil compaction: effect of multiple passes and loadings on wheel track surface soil bulk density. North. J. Appl. For. 5, pp. 120-123. Retrieved December 15, 2017.

Silverbush, M., Hallmark, W. B. & Barber, S. A. 1983. Simulation of effects of soil bulk density and P addition on K uptake by soybeans. Commun. Soil Sci. Plant Anal. 14, pp. 287–296. Retrieved November 13, 2017.

Skinner, A. K., Lunt, I. D., Spooner, P., McIntyre, S. 2009. The effect of soil compaction on germination and early growth of *Eucalyptus albens* and an exotic annual grass. Austral Ecology, 34, pp. 698-704. Retrieved October 22, 2017. http://resolver.scholarsportal.info.ezproxy.lakeheadu.ca/resolve/14429985/v34i0006/698_teoscoaaaeag.xml

Soane, B.D. and van Ouwerkerk, C. 1994. Compaction in crop production. Elsevier Science B.V. Amsterdam, NL. pp. 684.

Strong, W.L., & La Roi, G.H. 1983. Root-system morphology of common boreal forest trees in Alberta, Canada. Canadian Journal of Forest Research, 13(6), pp. 1164-1173. https://doi.org/10.1139/x83-155

Tardieu, F., Zhang, J., Katerji, N., Bethenod, O., Palmer, S. & Davies, W. J. 1992. Xylem ABA controls the stomatal conductance of field-grown maize subjected to soil compaction or soil drying. Plant Cell Environ. 15, pp. 193–197. Retrieved November 4, 2017.

Thorud, D. B. & Frissell, S. S. 1976. Time changes in soil density following compaction under an oak forest. Minnesota Forestry Research Note 257. Retrieved November 21, 2017.

[USDA] United States Department of Agriculture, 2017. Physical properties of soil and soil water: bulk density. Plant and Soil Sciences eLibrary. Retrieved January 9, 2018. http://passel.unl.edu/pages/informationmodule.php?idinformationmodule=1130447039&topicorder=6

Voyle, G. and Hudson, H. 2014. What to do about compact soils. Michigan State University Extension, USA. Retrieved October 19, 2017. http://msue.anr.msu.edu/news/what_to_do_about_compacted_soil

Wingate-Hill, R. & Jakobson, B. F. 1982. Increased mechanization and soil damage in forests: a review. N Z J. For. Sci. 12, pp. 380–393. Retrieved November 1, 2017.

Wright, H. A. & Bailey, A. W. 1982. Fire Ecology. Wiley, New York. Retrieved November 1, 2017.

Zhang, J., Busse, M. D., Young, D. H., Fiddler, G. O., Sherlock, J. W., and Tenpas, J. D. 2017. Aboveground biomass responses to organic matter removal, soil compaction, and competing vegetation control on 20-year mixed conifer plantations in California. Forest Ecology and Management, 401, pp. 341-353. Retrieved October 20, 2017. https://ezproxy.lakeheadu.ca/login?url=http://search.ebscohost.com/login.aspx?direct=true&db=edselp&AN=S0378112717307971&site=eds-live&scope=site

APPENDICES

APPENDIX I: JACK PINE RAW DATA

Table 3. Jack pine raw data.

Bucket #	Species	Compaction Level	Tree ID	Shoot Biomass (g)	Root Biomass (g)	Total Biomass (g)	Root/Shoot Ratio	Main Root Length (cm)	Stem Diameter (mm)	Tree Height (cm)
1	Pj	C3	A	0.036	0.031	0.066	0.854	28.50	0.63	4.00
1	Pj	C3	B	0.044	0.029	0.073	0.653	21.00	0.61	4.40
1	Pj	C3	C	0.037	0.034	0.070	0.923	29.50	0.61	4.30
4	Pj	C1	A	0.035	0.035	0.071	1.003	25.80	0.60	4.10
4	Pj	C1	B	0.045	0.039	0.084	0.860	32.00	0.66	4.80
4	Pj	C1	C	0.025	0.030	0.055	1.198	28.00	0.48	3.70
5	Pj	C	A	0.063	0.088	0.151	1.396	31.00	0.68	4.50
5	Pj	C	B	0.070	0.064	0.134	0.916	30.00	0.74	4.30
5	Pj	C	C	0.054	0.092	0.146	1.709	33.80	0.70	4.40
8	Pj	C2	A	0.025	0.031	0.056	1.224	24.00	0.57	4.50
8	Pj	C2	B	0.037	0.054	0.091	1.441	22.50	0.61	4.80
8	Pj	C2	C	0.031	0.029	0.060	0.927	25.00	0.59	4.70
9	Pj	C1	A	0.034	0.037	0.071	1.082	35.00	0.61	4.70
9	Pj	C1	B	0.026	0.025	0.050	0.953	31.50	0.54	3.90
9	Pj	C1	C	0.042	0.051	0.093	1.208	32.00	0.65	4.20
11	Pj	C3	A	0.051	0.039	0.090	0.759	7.00	0.71	4.80
11	Pj	C3	B	0.040	0.035	0.075	0.873	4.00	0.60	3.90
11	Pj	C3	C	0.044	0.028	0.072	0.647	6.50	0.68	3.90
14	Pj	C2	A	0.024	0.031	0.055	1.321	30.50	0.65	4.00
14	Pj	C2	B	0.041	0.034	0.076	0.824	31.50	0.65	4.50
14	Pj	C2	C	0.026	0.032	0.057	1.225	28.50	0.64	3.80
16	Pj	C	A	0.030	0.036	0.066	1.203	26.00	0.71	3.70
16	Pj	C	B	0.043	0.042	0.084	0.981	30.50	0.74	4.50
16	Pj	C	C	0.037	0.041	0.077	1.115	34.70	0.96	4.00
18	Pj	C3	A	0.038	0.032	0.070	0.826	14.50	0.79	4.20
18	Pj	C3	B	0.034	0.019	0.053	0.543	12.70	0.71	3.60
18	Pj	C3	C	0.058	0.038	0.095	0.648	9.50	0.79	4.50
21	Pj	C1	A	0.031	0.026	0.057	0.863	28.00	0.62	4.70
21	Pj	C1	B	0.042	0.059	0.100	1.396	27.50	0.69	4.80
21	Pj	C1	C	0.036	0.050	0.086	1.413	28.90	0.65	4.30

Table 3. Jack pine raw data, continued.

Bucket #	Species	Compaction Level	Tree ID	Shoot Biomass (g)	Root Biomass (g)	Total Biomass (g)	Root/Shoot Ratio	Main Root Length (cm)	Stem Diameter (mm)	Tree Height (cm)
23	Pj	C	A	0.029	0.029	0.058	1.000	29.00	0.58	4.60
23	Pj	C	B	0.046	0.056	0.102	1.228	33.00	0.71	4.20
23	Pj	C	C	0.060	0.066	0.126	1.096	29.00	0.76	3.80
24	Pj	C2	A	0.054	0.053	0.107	0.996	33.70	0.62	4.50
24	Pj	C2	B	0.047	0.044	0.092	0.930	31.00	0.63	4.00
24	Pj	C2	C	0.042	0.037	0.080	0.877	26.50	0.65	4.20
27	Pj	C3	B	0.075	0.063	0.137	0.842	27.60	0.59	4.00
27	Pj	C3	C	0.049	0.052	0.101	1.051	25.00	0.68	3.90
28	Pj	C2	A	0.051	0.046	0.096	0.901	30.40	0.65	4.30
28	Pj	C2	B	0.061	0.063	0.124	1.033	31.80	0.63	4.60
28	Pj	C2	C	0.052	0.062	0.113	1.185	31.30	0.68	4.00
30	Pj	C1	A	0.058	0.048	0.106	0.833	31.90	0.59	4.70
30	Pj	C1	B	0.048	0.045	0.093	0.946	28.00	0.51	3.90
30	Pj	C1	C	0.041	0.052	0.093	1.283	32.40	0.59	3.80
31	Pj	C	A	0.054	0.064	0.118	1.187	29.20	0.67	4.60
31	Pj	C	B	0.053	0.058	0.111	1.098	36.20	0.72	4.80
31	Pj	C	C	0.037	0.042	0.079	1.116	32.00	0.68	4.20
34	Pj	C2	A	0.044	0.046	0.090	1.053	23.80	0.63	4.80
34	Pj	C2	B	0.032	0.038	0.070	1.171	31.00	0.64	4.80
34	Pj	C2	C	0.038	0.040	0.078	1.058	27.00	0.66	4.80
35	Pj	C	A	0.043	0.050	0.093	1.153	33.50	0.70	4.80
35	Pj	C	B	0.034	0.035	0.069	1.035	29.50	0.68	4.70
35	Pj	C	C	0.034	0.047	0.081	1.381	36.50	0.59	4.70
37	Pj	C3	A	0.041	0.037	0.079	0.896	26.40	0.68	4.70
37	Pj	C3	B	0.052	0.042	0.095	0.811	8.00	0.78	5.10
39	Pj	C1	A	0.031	0.024	0.055	0.784	27.30	0.53	4.10
39	Pj	C1	B	0.037	0.029	0.066	0.778	29.50	0.56	4.90
39	Pj	C1	C	0.039	0.036	0.075	0.928	36.50	0.52	3.90

Table 3. Jack pine raw data, continued.

Bucket #	Species	Compaction Level	Tree ID	Total Projected Needle Area (mm^2)	Average Projected Needle Area (mm^2)	Average Straight Needle Length (mm)	Average Straight Needle Width (mm)	# of Needles
1	Pj	C3	A	297.347	7.080	15.610	0.586	42
1	Pj	C3	B	358.085	7.460	14.855	0.626	48
1	Pj	C3	C	335.032	6.443	13.724	0.583	52
4	Pj	C1	A	308.322	6.703	14.669	0.588	46
4	Pj	C1	B	472.859	7.058	15.699	0.555	67
4	Pj	C1	C	205.018	6.407	13.685	0.570	32
5	Pj	C	A	464.716	8.012	17.025	0.668	58
5	Pj	C	B	558.981	8.734	16.604	0.659	64
5	Pj	C	C	433.648	8.503	16.282	0.664	51
8	Pj	C2	A	276.114	5.113	13.522	0.502	54
8	Pj	C2	B	368.938	6.361	15.003	0.562	58
8	Pj	C2	C	339.956	7.082	15.349	0.597	48
9	Pj	C1	A	310.265	6.332	14.060	0.577	49
9	Pj	C1	B	260.788	7.048	16.091	0.585	37
9	Pj	C1	C	411.390	7.762	16.051	0.628	53
11	Pj	C3	A	401.770	8.734	17.191	0.660	46
11	Pj	C3	B	342.250	7.606	15.812	0.608	45
11	Pj	C3	C	326.250	7.250	14.489	0.646	45
14	Pj	C2	A	226.774	5.154	12.640	0.526	44
14	Pj	C2	B	376.214	7.235	15.008	0.590	52
14	Pj	C2	C	290.903	5.818	14.071	0.546	50
16	Pj	C	A	266.057	6.187	14.136	0.552	43
16	Pj	C	B	370.200	8.227	16.564	0.644	45
16	Pj	C	C	376.372	5.974	13.435	0.588	63
18	Pj	C3	A	301.132	6.274	12.652	0.616	48
18	Pj	C3	B	294.860	6.018	13.990	0.581	49
18	Pj	C3	C	457.254	7.884	16.313	0.670	58
21	Pj	C1	A	306.637	7.131	16.575	0.569	43
21	Pj	C1	B	339.878	6.936	13.962	0.630	49
21	Pj	C1	C	308.759	7.351	16.472	0.569	42

Table 3. Jack pine raw data, continued.

Bucket #	Species	Compaction Level	Tree ID	Total Projected Needle Area (mm²)	Average Projected Needle Area (mm²)	Average Straight Needle Length (mm)	Average Straight Needle Width (mm)	# of Needles
23	Pj	C	A	244.910	6.619	14.197	0.585	37
23	Pj	C	B	408.931	7.302	14.608	0.607	56
23	Pj	C	C	361.727	6.237	13.994	0.605	58
24	Pj	C2	A	366.953	6.327	14.140	0.584	58
24	Pj	C2	B	288.738	6.277	14.753	0.535	46
24	Pj	C2	C	319.677	6.268	13.319	0.592	51
27	Pj	C3	B	338.487	6.908	16.423	0.538	49
27	Pj	C3	C	311.390	6.625	13.333	0.639	47
28	Pj	C2	A					53
28	Pj	C2	B					59
28	Pj	C2	C					52
30	Pj	C1	A					49
30	Pj	C1	B					43
30	Pj	C1	C					46
31	Pj	C	A					49
31	Pj	C	B					57
31	Pj	C	C					48
34	Pj	C2	A					60
34	Pj	C2	B					51
34	Pj	C2	C					51
35	Pj	C	A					59
35	Pj	C	B					42
35	Pj	C	C					46
37	Pj	C3	A					49
37	Pj	C3	B					54
39	Pj	C1	A					58
39	Pj	C1	B					50
39	Pj	C1	C					57

Table 3. Jack pine raw data, continued.

Bucket #	Species	Compaction Level	Tree ID	Total Straight Needle Length (mm)	Total Root Length (cm)	Root Projected Area (cm^2)	Root Surface Area (cm^2)	Average Root Diameter (cm)	# of Root Tips
1	Pj	C3	A	655.597	79.572	2.386	7.496	0.300	330
1	Pj	C3	B	713.039	62.522	2.178	6.841	0.348	213
1	Pj	C3	C	713.661	124.340	3.836	12.050	0.309	331
4	Pj	C1	A	674.773	127.931	3.458	10.863	0.270	470
4	Pj	C1	B	1051.831	149.466	4.603	14.459	0.308	603
4	Pj	C1	C	437.914	99.831	2.761	8.675	0.277	397
5	Pj	C	A	987.458	254.482	7.543	23.695	0.296	848
5	Pj	C	B	1062.672	179.043	5.522	17.347	0.308	516
5	Pj	C	C	830.357	227.282	7.007	22.013	0.308	688
8	Pj	C2	A	730.205	83.356	2.725	8.560	0.327	279
8	Pj	C2	B	870.166	144.567	4.825	15.157	0.334	484
8	Pj	C2	C	736.772	78.154	2.830	8.889	0.362	266
9	Pj	C1	A	688.943	130.014	4.169	13.096	0.321	310
9	Pj	C1	B	595.368	81.744	2.212	6.950	0.271	346
9	Pj	C1	C	850.694	172.106	5.078	15.952	0.295	557
11	Pj	C3	A	790.798	121.131	3.767	11.834	0.311	387
11	Pj	C3	B	711.520	88.622	3.019	9.484	0.341	212
11	Pj	C3	C	651.987	85.650	2.723	8.554	0.318	243
14	Pj	C2	A	556.148	93.775	2.770	8.704	0.295	274
14	Pj	C2	B	780.422	107.817	3.670	11.530	0.340	359
14	Pj	C2	C	703.564	124.293	3.798	11.931	0.306	466
16	Pj	C	A	607.841	157.090	4.404	13.835	0.280	575
16	Pj	C	B	745.373	147.453	4.640	14.577	0.315	554
16	Pj	C	C	846.379	165.488	5.608	17.617	0.339	542
18	Pj	C3	A	607.290	78.454	2.804	8.808	0.357	262
18	Pj	C3	B	685.510	64.218	2.124	6.674	0.331	227
18	Pj	C3	C	946.122	111.531	3.552	11.160	0.319	398
21	Pj	C1	A	712.708	85.223	2.734	8.590	0.321	334
21	Pj	C1	B	684.154	186.393	5.975	18.772	0.321	635
21	Pj	C1	C	691.820	134.456	4.368	13.723	0.325	594

Table 3. Jack pine raw data, continued.

Bucket #	Species	Compaction Level	Tree ID	Total Straight Needle Length (mm)	Total Root Length (cm)	Root Projected Area (cm^2)	Root Surface Area (cm^2)	Average Root Diameter (cm)	# of Root Tips
23	Pj	C	A	525.289	96.955	2.853	8.962	0.294	386
23	Pj	C	B	818.038	181.651	5.286	16.605	0.291	723
23	Pj	C	C	811.644	173.088	4.752	14.930	0.275	632
24	Pj	C2	A	820.107	131.037	4.024	12.643	0.307	437
24	Pj	C2	B	678.654	105.062	3.334	10.474	0.317	365
24	Pj	C2	C	679.260	98.643	3.291	10.339	0.334	352
27	Pj	C3	B	804.739	72.159	2.397	7.529	0.332	190
27	Pj	C3	C	626.671	115.488	3.625	11.390	0.314	367
28	Pj	C2	A		116.902	3.580	11.247	0.306	327
28	Pj	C2	B		138.718	4.255	13.366	0.307	510
28	Pj	C2	C		131.568	4.812	15.118	0.366	430
30	Pj	C1	A		112.332	3.149	9.894	0.280	447
30	Pj	C1	B		98.814	3.007	9.447	0.304	398
30	Pj	C1	C		145.904	4.332	13.608	0.297	531
31	Pj	C	A		157.051	4.909	15.423	0.313	469
31	Pj	C	B		221.707	6.604	20.748	0.298	854
31	Pj	C	C		141.433	3.929	12.345	0.278	435
34	Pj	C2	A		146.896	4.789	15.044	0.326	588
34	Pj	C2	B		106.757	3.454	10.851	0.324	345
34	Pj	C2	C		129.692	4.797	15.070	0.370	479
35	Pj	C	A		169.442	4.926	15.477	0.291	526
35	Pj	C	B		115.512	3.387	10.641	0.293	314
35	Pj	C	C		169.077	4.648	14.602	0.275	522
37	Pj	C3	A		121.459	3.696	11.612	0.304	406
37	Pj	C3	B		132.912	4.054	12.736	0.305	409
39	Pj	C1	A		78.598	2.550	8.011	0.325	278
39	Pj	C1	B		97.569	2.894	9.093	0.297	324
39	Pj	C1	C		119.445	3.599	11.307	0.301	425

APPENDIX II: BLACK SPRUCE RAW DATA

Table 4. Black spruce raw data.

Bucket #	Species	Compaction Level	Tree ID	Shoot Biomass (g)	Root Biomass (g)	Total Biomass (g)	Root/Shoot Ratio	Main Root Length (cm)	Tree Height (cm)
2	Sb	C	A	0.004	0.003	0.008	0.77	10.40	1.40
2	Sb	C	B	0.007	0.006	0.013	0.89	13.70	1.30
2	Sb	C	C	0.006	0.004	0.009	0.71	5.50	1.20
3	Sb	C1	A	0.006	0.006	0.011	1.05	15.40	1.20
3	Sb	C1	B	0.003	0.006	0.009	1.85	14.10	1.00
3	Sb	C1	C	0.003	0.004	0.007	1.44	9.70	1.00
6	Sb	C3	A	0.004	0.005	0.009	1.12	8.50	1.00
7	Sb	C2	A	0.005	0.005	0.010	1.06	7.30	1.00
7	Sb	C2	B	0.005	0.005	0.010	1.06	9.10	1.00
10	Sb	C	A	0.002	0.005	0.007	2.33	14.20	1.30
10	Sb	C	B	0.006	0.007	0.014	1.14	14.80	1.50
10	Sb	C	C	0.002	0.005	0.007	1.96	17.00	1.40
12	Sb	C2	A	0.005	0.004	0.008	0.87	7.40	1.40
12	Sb	C2	B	0.005	0.003	0.008	0.58	7.70	1.50
12	Sb	C2	C	0.003	0.004	0.007	1.41	8.30	1.30
13	Sb	C1	A	0.005	0.005	0.010	0.94	13.40	1.10
13	Sb	C1	B	0.003	0.004	0.007	1.09	7.00	1.20
13	Sb	C1	C	0.006	0.009	0.015	1.48	14.40	1.40
17	Sb	C2	A	0.006	0.006	0.012	0.94	10.50	1.40
17	Sb	C2	B	0.005	0.003	0.008	0.51	4.00	0.90
17	Sb	C2	C	0.005	0.005	0.010	1.06	14.90	1.10
19	Sb	C1	A	0.006	0.003	0.010	0.54	10.50	1.30
19	Sb	C1	B	0.005	0.006	0.011	1.22	11.00	1.20
19	Sb	C1	C	0.004	0.005	0.008	1.25	10.30	0.90

Table 4. Black spruce raw data, continued.

Bucket #	Species	Compaction Level	Tree ID	Shoot Biomass (g)	Root Biomass (g)	Total Biomass (g)	Root/Shoot Ratio	Main Root Length (cm)	Tree Height (cm)
20	Sb	C	B	0.006	0.007	0.014	1.18	15.70	1.40
20	Sb	C	C	0.006	0.009	0.016	1.54	14.80	1.80
22	Sb	C3	B	0.005	0.005	0.010	0.94	8.20	1.10
25	Sb	C1	A	0.005	0.007	0.012	1.33	12.90	1.00
25	Sb	C1	B	0.005	0.008	0.012	1.73	11.80	1.30
25	Sb	C1	C	0.006	0.008	0.014	1.37	15.40	1.30
26	Sb	C2	A	0.007	0.004	0.011	0.60	7.00	1.30
26	Sb	C2	B	0.005	0.005	0.010	1.02	12.50	1.00
26	Sb	C2	C	0.005	0.004	0.008	0.84	7.50	1.20
29	Sb	C3	B	0.002	0.002	0.004	0.71	2.70	1.10
32	Sb	C	A	0.007	0.009	0.016	1.28	7.20	1.40
32	Sb	C	B	0.005	0.011	0.016	2.14	13.20	1.20
32	Sb	C	C	0.005	0.008	0.013	1.55	13.00	1.40
33	Sb	C2	A	0.007	0.007	0.014	0.95	12.10	1.40
33	Sb	C2	B	0.005	0.003	0.008	0.54	5.30	1.20
33	Sb	C2	C	0.007	0.008	0.014	1.13	10.00	1.00
36	Sb	C	A	0.004	0.006	0.010	1.72	12.00	1.40
36	Sb	C	B	0.004	0.007	0.012	1.70	14.50	1.40
36	Sb	C	C	0.006	0.009	0.015	1.53	18.50	1.90
40	Sb	C1	A	0.007	0.008	0.015	1.15	9.00	1.40
40	Sb	C1	B	0.005	0.008	0.013	1.63	13.50	1.00
40	Sb	C1	C	0.008	0.008	0.016	0.91	10.70	1.10

Table 4. Black spruce raw data, continued.

Bucket #	Species	Compaction Level	Tree ID	Total Projected Needle Area (mm²)	Average Projected Needle Area (mm²)	Average Straight Needle Length (mm)	Average Straight Needle Width (mm)	# of Needles	Total Straight Needle Length (mm)
2	Sb	C	A	397.97	19.90	16.74	1.57	20	334.86
2	Sb	C	B	615.06	18.64	17.68	1.40	33	583.44
2	Sb	C	C	435.99	24.22	19.86	1.60	18	357.55
3	Sb	C1	A	471.90	18.88	16.32	1.54	25	407.92
3	Sb	C1	B	296.26	19.75	17.27	1.61	15	259.12
3	Sb	C1	C	235.98	21.45	16.60	1.81	11	182.62
6	Sb	C3	A	389.01	17.68	17.29	1.45	22	380.31
7	Sb	C2	A	398.46	23.44	19.65	1.62	17	334.13
7	Sb	C2	B	451.04	21.48	17.05	1.64	21	358.14
10	Sb	C	A	201.26	9.58	10.64	1.31	21	223.51
10	Sb	C	B	535.46	16.23	15.28	1.40	33	504.22
10	Sb	C	C	242.64	16.18	13.48	1.69	15	202.23
12	Sb	C2	A	350.58	18.45	16.27	1.54	19	309.05
12	Sb	C2	B	437.53	16.83	14.38	1.62	26	373.77
12	Sb	C2	C	298.15	15.69	14.85	1.42	19	282.12
13	Sb	C1	A	400.28	22.24	19.31	1.53	18	347.62
13	Sb	C1	B	324.19	19.07	17.26	1.47	17	293.37
13	Sb	C1	C	400.21	21.06	17.95	1.54	19	341.10
17	Sb	C2	A	547.43	19.55	16.61	1.60	28	465.07
17	Sb	C2	B	440.12	18.34	15.74	1.51	24	377.74
17	Sb	C2	C	333.15	15.14	14.13	1.43	22	310.77
19	Sb	C1	A	531.61	18.99	16.34	1.62	28	457.60
19	Sb	C1	B	351.56	18.50	16.76	1.48	19	318.52
19	Sb	C1	C	325.31	16.27	14.29	1.55	20	285.84

Table 4. Black spruce raw data, continued.

Bucket #	Species	Compaction Level	Tree ID	Total Projected Needle Area (mm^2)	Average Projected Needle Area (mm^2)	Average Straight Needle Length (mm)	Average Straight Needle Width (mm)	# of Needles	Total Straight Needle Length (mm)
20	Sb	C	B	363.67	17.32	15.74	1.46	21	330.46
20	Sb	C	C	369.34	17.59	16.93	1.42	21	355.58
22	Sb	C3	B	378.02	22.24	17.53	1.68	17	298.06
25	Sb	C1	A	364.93	16.59	14.42	1.58	22	317.13
25	Sb	C1	B	362.41	20.13	17.70	1.57	18	318.53
25	Sb	C1	C	512.71	23.31	17.78	1.79	22	391.26
26	Sb	C2	A	560.80	20.77	17.00	1.63	27	459.04
26	Sb	C2	B	446.07	21.24	16.72	1.73	21	351.18
26	Sb	C2	C	315.51	26.29	19.05	1.83	12	228.61
29	Sb	C3	B	178.79	13.75	12.29	1.60	13	159.73
32	Sb	C	A	481.42	19.26	17.26	1.46	25	431.44
32	Sb	C	B	374.94	20.83	17.51	1.58	18	315.20
32	Sb	C	C	413.17	22.95	18.26	1.60	18	328.66
33	Sb	C2	A	684.99	22.10	19.42	1.55	31	601.90
33	Sb	C2	B	419.12	20.96	18.01	1.57	20	360.14
33	Sb	C2	C	434.94	20.71	17.16	1.61	21	360.30
36	Sb	C	A	210.08	11.67	12.86	1.33	18	231.47
36	Sb	C	B	275.33	14.49	13.46	1.52	19	255.67
36	Sb	C	C	386.14	14.85	13.84	1.52	26	359.90
40	Sb	C1	A	400.84	21.10	19.78	1.43	19	375.76
40	Sb	C1	B	295.07	18.44	16.15	1.48	16	258.36
40	Sb	C1	C	502.70	17.33	16.56	1.39	29	480.36

Table 4. Black spruce raw data, continued.

Bucket #	Species	Compaction Level	Tree ID	Total Root Length (cm)	Root Projected Area (cm²)	Root Surface Area (cm²)	Average Root Diameter (cm)	# of Root Tips
2	Sb	C	A	36.29	0.72	2.27	0.20	109
2	Sb	C	B	50.36	1.08	3.39	0.21	166
2	Sb	C	C	29.65	0.62	1.94	0.21	106
3	Sb	C1	A	46.91	1.03	3.23	0.22	139
3	Sb	C1	B	28.27	0.62	1.94	0.22	98
3	Sb	C1	C	31.12	0.62	1.94	0.20	130
6	Sb	C3	A	22.70	0.50	1.57	0.22	42
7	Sb	C2	A	26.23	0.60	1.89	0.23	75
7	Sb	C2	B	18.14	0.43	1.36	0.24	68
10	Sb	C	A	29.19	0.55	1.74	0.19	75
10	Sb	C	B	46.22	0.92	2.89	0.20	171
10	Sb	C	C	43.41	0.70	2.21	0.16	161
12	Sb	C2	A	18.61	0.42	1.31	0.22	57
12	Sb	C2	B	16.98	0.38	1.21	0.23	42
12	Sb	C2	C	21.85	0.44	1.38	0.20	49
13	Sb	C1	A	23.91	0.58	1.81	0.24	54
13	Sb	C1	B	35.65	0.77	2.43	0.22	83
13	Sb	C1	C	68.58	1.30	4.09	0.19	202
17	Sb	C2	A	36.37	0.75	2.37	0.21	172
17	Sb	C2	B	15.31	0.31	0.97	0.20	48
17	Sb	C2	C	35.18	0.62	1.96	0.18	127
19	Sb	C1	A	23.80	0.54	1.70	0.23	52
19	Sb	C1	B	46.18	1.08	3.40	0.23	105
19	Sb	C1	C	70.39				72

Table 4. Black spruce raw data, continued.

Bucket #	Species	Compaction Level	Tree ID	Total Root Length (cm)	Root Projected Area (cm^2)	Root Surface Area (cm^2)	Average Root Diameter (cm)	# of Root Tips
20	Sb	C	B	44.87	0.84	2.64	0.19	144
20	Sb	C	C	48.81	1.05	3.29	0.21	150
22	Sb	C3	B	17.08	0.39	1.23	0.23	48
25	Sb	C1	A	46.61	1.14	3.58	0.24	110
25	Sb	C1	B	34.45	0.72	2.27	0.21	104
25	Sb	C1	C	35.91	0.76	2.40	0.21	108
26	Sb	C2	A	13.94	0.36	1.13	0.26	32
26	Sb	C2	B	21.22	0.51	1.59	0.24	46
26	Sb	C2	C	14.87	0.37	1.15	0.25	36
29	Sb	C3	B	8.48	0.21	0.66	0.25	15
32	Sb	C	A	73.82	1.28	4.02	0.17	232
32	Sb	C	B	71.19	1.42	4.45	0.20	198
32	Sb	C	C	45.01	0.81	2.56	0.18	120
33	Sb	C2	A	20.72	0.61	1.92	0.29	46
33	Sb	C2	B	10.53	0.31	0.97	0.29	35
33	Sb	C2	C	27.12	0.63	1.99	0.23	60
36	Sb	C	A	25.31	0.55	1.71	0.22	96
36	Sb	C	B	45.66	0.76	2.38	0.17	150
36	Sb	C	C	46.71	0.82	2.58	0.18	187
40	Sb	C1	A	29.11	0.70	2.20	0.24	92
40	Sb	C1	B	34.55	0.76	2.38	0.22	118
40	Sb	C1	C	29.71	0.63	1.99	0.21	92

APPENDIX III: USDA IDEAL AND RESTRICTING BULK DENSITY LIMITS

Table 5. United States Department of Agriculture limits for ideal and restricting bulk densities, based on soil type.

Soil Texture	Ideal bulk density	Bulk density restricts root growth
	----- g/cm^3 -----	
Sand, loamy sand	< 1.60	> 1.80
Sandy loam, loam	< 1.40	> 1.80
Sandy clay loam, clay loam	< 1.40	> 1.75
Silt, silt loam	< 1.30	> 1.75
Silty clay loam	< 1.40	> 1.65
Sandy clay, silty clay	< 1.10	> 1.58
Clay	< 1.10	> 1.47
USDA. 1999. Soil quality test kit guide. USDA Soil Quality Institute. Washington, D.C.		

APPENDIX IV: TOP-VIEW OF THE PLANTING BUCKETS

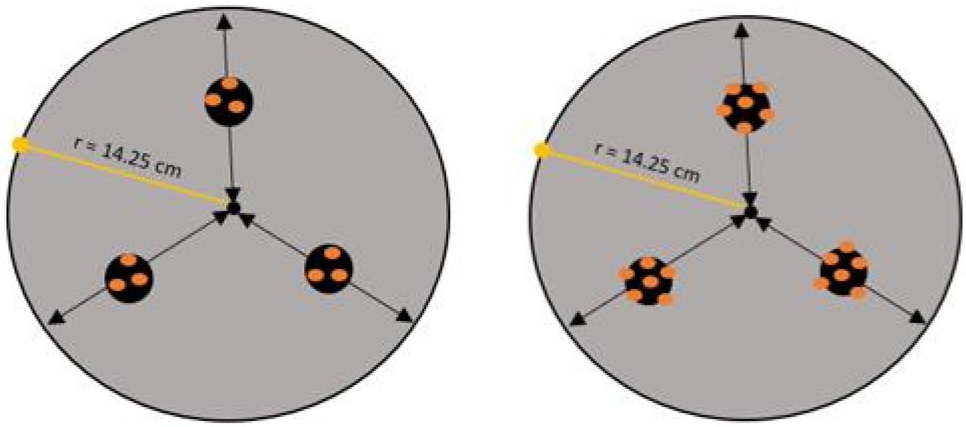

Figure 11. Top-view of the planting buckets, for *Pinus banksiana* (left) and *Picea mariana* (right). The black circles represent the planting sites, and the lighter ovals within represent the number of seeds planted.