Effects of soil compaction and vegetation weeding on the above-, and belowground growth of boreal evergreen conifer seedlings

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Research Article

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Abstract

If the soil compaction by the running of forestry machines does not suppress the growth of planted seedlings, this operation may be an alternative method to conventional weeding to control vegetation competition. To evaluate the effects of soil compaction and the weeding of vegetation on seedlings of three boreal evergreen coniferous species, the field experiment was conducted for two years. Under weeding conditions, the main target species, *Abies sachalinensis* seedlings with thick fine roots showed relatively robust belowground growth under soil compaction rather than the other *Picea* species with thin fine roots. The soil compaction suppressed the density and height of vegetation, mitigating the light conditions. In *A. sachalinensis* seedings, leaf mass per area, nitrogen content per leaf area, and specific root length of fine roots significantly respond to the weeding treatment without soil compaction. No weeding suppressed the relative growth rate in root collar diameter and aboveground volume, while these changes were not observed under soil compaction. Both the results of light conditions and the responses of seedlings indicated that the competitive conditions were weakened by soil compaction. These results suggested that when planting the functional type with thicker fine roots, such as *A. sachalinensis*, the machine running may contribute to the forest vegetation management.

Introduction

It is necessary for sustainable forest management to elucidate the environmental impacts of forestry operations (Rönnqvist et al. 2015, Marchi et al. 2018, Rossit et al. 2021). The use of forestry machines would improve the efficiency and safety of forestry operations (McEwan et al. 2020). In contrast, inappropriate or excessive use can negatively impact forest productivity and the ecosystem (Rossit et al. 2021). While previous studies have evaluated various negative impacts of soil compaction by running forestry machines on tree individuals and forest environments (e.g., Ares et al. 2007, Cambi et al. 2015, Collet et al. 2021), the improvement to suitable site preparation with heavy forestry machines for tree seedling growth has also been in progress (e.g., Yoshida et al. 2022, Reicis et al. 2023). Understanding the processes of tree responses to soil compaction would provide cues to find the availability of forestry machines suitable for local forest management (Marchi et al. 2018, Pandey et al. 2021).

Changes in soil physical environments due to forestry machine running can suppress the growth of planted seedlings (Sinnet et al. 2008, Cambi et al. 2015, Mariotti et al. 2020). Soil compaction occurs immediately after the forestry machine running, reducing soil porosity and increasing soil hardness (Cambi et al. 2015, Binkley and Fisher 2019). Physical changes by soil compaction induce the suppression of growth and function of roots (de Kroon and Visser 2003, Pandey et al. 2021) and inhibit nutrient acquisition (Kamaluddin et al. 2005, Correa et al. 2019). It has been reported the interspecific differences in these responses to soil compaction (Sinnet et al. 2008, Mariotti et al. 2020), where the species with tolerance to compaction can often develop relatively thicker roots and maintain root elongation rate against soil compaction (Bengough et al. 2011, Correa et al. 2019). Although root characteristics of tree species have been widely investigated under soil compaction (e.g., Sinnet et al. 2008, Sugai et al. 2020a), relatively few studies provided the ecological insights into the relationship between the growth tolerance to soil compaction and functional root characteristics (de Kroon and Visser 2003, Mariotti et al. 2020).

The impact of soil compaction is not limited to planted tree seedlings but also vegetation plants on forest floors (Godefroid and Koedam 2004, Cambi et al. 2015, Bockstette et al. 2017). Although the mechanisms of responses to soil compactions would have much in common between vegetation plants and woody plants (Bengough et al. 2011, Correa et al. 2019), the duration and degree of soil compaction would vary between vegetation plants and tree seedlings in fields (Ohsato et al. 1996, Sinnet et al. 2008, Reicis et al. 2023) because most vegetation relies on the natural regeneration while the seedlings are artificially planted after machine running. On the other hand, in the afforestation fields, the initial growth of seedlings is significantly suppressed by the shade effects of vegetation (Wagner et al. 2006, Harayama et al. 2022). Weeding vegetation to eliminate the shade effect often accounts for approximately half of the total reforestation costs in the first decade in temperate forests (Masaki et al. 2017), where vegetation growth is particularly vigorous. These studies suggest the effects of soil compaction on the growth of seedlings may vary with competitive conditions with sympatric vegetation. However, few studies evaluated the effects of soil compaction and weeding on seedlings (Ares et al. 2007, Reicis et al. 2023), and there is a lack of understanding of the processes by which soil compaction affects seedlings under competitive conditions.

This study investigated the growth responses of seedlings to soil compaction and weeding treatments. The main target species was *Abies sachalinensis*, the dominant species for afforestation in the northern island of Japan, Hokkaido (Hokkaido government 2021). It has been reported that the thicker fine roots and superior shade tolerance in *Abies* sp compared with *Picea* sp. (Doi et al. 2008). We have preliminarily observed the fine root thickness and the relatively flattened leaves of *A. sachalinensis* compared with other two spruce species , i.e., *P. glehni* and *P. jezoensis*, which are also native species in Hokkaido (Fig. 1). In Japan, the largest number of forestry machinery is in Hokkaido (Ministry of Agriculture, Forestry and Fisheries 2021), so it is a responsible region for considering the applicability of forestry machines. We first verified the tolerance to soil compaction of *A. sachalinensis*, by comparing with *P. glehni* and *P. jezoensis*. Then, we evaluated the interaction effects of soil compaction and weeding treatments on the growth of *A. sachalinensis* seedlings. We hypothesized that (i) the superior tolerance to soil compaction in *A. sachalinensis* due to the relatively thick root diameter, (ii) the soil compaction may mitigate the shade effects of vegetation on seedlings, and the growth of *A. sachalinensis* seedlings may not be suppressed even under no weeding conditions. If these hypotheses are correct, the operation of machine running may be an alternative method to previous weeding operations and may improve the cost of vegetation management. We evaluated the changes of above-, and belowground environments, the growth responses of seedlings, and the functional traits of fine roots and needle leaves as the indicators of response to light as well as soil compaction (de Kroon and Visser 2003, McCormack et al. 2015, Mariotti et al. 2020).

Material and Methods

Experimental design

This experiment was conducted from April 2021 to November 2022 at the nursery of the Hokkaido Research Institute, Forestry and Forest Products Research Institute (FFPRI), located at Sapporo City, Hokkaido (42°59'N, 141°23'E; 149 m a.s.l.). The region of study site shows cool temperate climate in boreal region, where the mean annual air temperature was approximately 7.5 °C and the total annual precipitation was 952 mm (Mizoguchi and Yamanoi 2015). The soil type of this nursery was well clay soil with dark brown color. In April 2021 before beginning the experiment, the nursery was completely plowed at a depth of approximately 30 cm. Due to the technical limitations of machine running in the field, a split-plot design was adopted based on previous studies (Mizuguchi 2011, Sugai et al. 2020a). Overview of experimental design was summarized in Fig. S1. In brief, three sets of both the track lines for soil compaction and the no track lines without any soil compaction were established. Each line was set for 12 m × 3 m. Next, each line was divided into four blocks. Each block was set for 2 m × 3 m and the distance between blocks was set for 1 m. Total 24 blocks were used for six blocks each for the following treatments; no-compaction of soil and no-weeding (NC+NW), no-compaction of soil and weeding (NC+W), compaction of soil and no-weeding (C+NW), and compaction of soil and weeding (C+W), respectively.

The compaction treatment was conducted on May 25, 2021, when there had been no precipitation for at least a week. To compact the soil only in the corresponding areas, the caterpillar-type excavator with approximately 1.08 ton g (PC10, Komatsu Ltd, Tokyo, Japan) was used. This machine ran multiple times fully across the corresponding areas in each track line. In parallel with machine running, surface soil hardness was evaluated by a tester (Yamanaka's Soil Hardness tester, Fujiwara Scientific Co., Ltd., Tokyo, Japan). The hardness of surface soil was set for approximately 12 kg cm^{-2} as the level of soil physical conditions (Fig. S1) that can inhibit a seedling growth of hybrid larch, a boreal forest species (Sugai et al. 2020a) as well as the realistic values that can occur in forests due to large mechanical running in Hokkaido (Sugai et al. 2020b). On May 26, 2021, soil bulk density was evaluated using a metal cylinder core (5 cm × 20 cm^2, Daiki Rika Kogyo Co., Ltd., Saitama, Japan). After carefully removing organic matters on surface, soil was collected from 5 cm depth by a metal core. The obtained cores were transported to the laboratory, and the dry weight was measured by using a 0.01 g scale (EB-3300SW, Shimadzu Co., Ltd., Kyoto, Japan) after drying at 105°C for three days. Finally, soil bulk density was calculated as the ratio of soil dry weight to core volume.

As experimental materials, *Abies sachalinensis*, *Picea glehni*, and *P. jezoensis* were adopted. They are the major dominant boreal conifer species in Hokkaido and are widely used not only for afforestation (Hokkaido government 2021) but also greening (Kayama et al. 2007). Seeds collected in the field of the Hokkaido Research Institute in FFPRI were sown at the nursery beside the experimental plots in 2016. The healthy five-year-old seedlings were selected on May 19, 2021 and were carefully dug out with avoiding damages on roots as much as possible. To prevent drying stresses, the roots of seedling were soaked in tap water and soils on above- and belowground were carefully removed. All seedlings were kept in approximately 10 °C for eight days before transplanting. Two seedlings of each species were randomly transplanted into each block of experimental plots on May 27, where the distance between seedlings in each block was set for 1 m. In transplanting, we used a commercial equipment of drill-type shovel (AD-574, Aida godo factory Co., Ltd, Niigata, Japan) and formed a cylindrical space with 25 cm deep and 9.5 cm wide. The depth was set based on the initial maximum root length of seedlings (details are described below). Seedlings were planted in holes with their root collar approximately at ground level and the soil produced by each space formation was used to softly fill the space. Finally, seedlings were irrigated with tap water.

Soil physical conditions and vegetation

To verify the manipulated soil physical conditions during experimental periods, the hardness of surface soil, the three phase fraction of soil, i.e., solid, liquid, and air fraction, bulk density, porosity, and maximum water capacity were evaluated on November 29, 2021, and November 24, 2022. In each measurement day, the surface soil hardness was firstly evaluated within each block at three randomly selected points approximately 20 cm away from each seedling, and the average value was obtained. For the bulk density and three phase fraction of soil, soil samples were then collected at three points in each block from a distance of at least 50 cm from seedlings after carefully removing organic matters on surface. After sampling, the metal core was immediately sealed with plastic tape to prevent drying, and transported to laboratory, and the fresh weight was measured by using a 0.01 g scale (PB503-S/PH, Mettler-Toledo International Inc., Greifensee, Switzerland). Then, the total volume fraction of solid and liquid was evaluated in each core by a digital volume analyzer (DIK-1150, Daiki Rika Kogyo Co., Ltd., Saitama, Japan). This measurement was repeated five times on the same sample and the average value was obtained. The difference between the volume of the core and their volume was calculated as the air volume fraction. The liquid volume fraction was evaluated by the difference of sample weight before and after drying at 105 °C for three days. In each core, soil bulk density, porosity, and maximum water capacity were calculated as the ratio of soil dry weight to core volume, the sum of liquid and air volume, and the ratio of porosity to 100 times bulk density.

The treatment of weeding vegetation was performed once a month from July through September in 2021 and 2022. The corresponding area was set as the size of a block, i.e., 2 m × 3 m. All vegetation on the ground surface was manually removed using scissors and the removed vegetation was brought outside the experimental plots to avoid covering seedlings and soil. In early July, August, and September 2021, the vegetation removed from 0.5 m × 0.5 m around a seedling was collected. This sampling was conducted repeatedly for each seeding throughout the period. The dry weight of collected vegetation was measured after drying at 75 °C for 7 days to evaluate the productivity of vegetation under soil compaction and no compaction. The total density of vegetation was calculated in each species of planted seedlings as the sum of the ratio of dry weight of vegetation to sampling area by month. For evaluating the effects of soil compaction on vegetation size, the representative height of vegetation was evaluated in middle July and late September 2021. The height was evaluated three times in the randomly selected three blocks in non-weeding plots, respectively. For evaluating the shade effects of vegetation, the illuminance sensors (UA-002-64, Pacico trade Co., Ltd., Tokyo, Japan) were set 20 cm above ground in 2021. In addition, all the sky photos 40 cm above ground were obtained by a 360 degree camera (THETA

SC2, Ricoh Co., Ltd., Tokyo, Japan) on September 10, 2021. In these photos, the artificial obstructions were eliminated the in the image analysis. Image analysis was conducted using an image analysis software (ImageJ, National Institutes of Health, Maryland, USA).

Growth traits of seedlings

Just before transplanting, the maximum root length of each seedling was measured using a ruler by 1 mm resolution. This root length was measured as the length of the longest root growing from the root trunk after soil on the roots was carefully removed. After transplanting, on July 9, 2021, the height size was measured using a ruler by 1 mm resolution, and the root collar diameter was measured using an electronic caliper (CDN-P20, Mitutoyo Corporation, Kanagawa, Japan) by 0.01 mm resolution. The diameter was measured in two perpendicular directions and the average value was obtained. The measurement of these aboveground sizes was conducted on November 20, 2022. From November 25 to 28 in 2022, when root growth was expected to be generally complete (Satoh 1995), a seedling in each species that appeared to be healthy and growing relatively well was selected within each block. Aboveground parts of seedings were firstly collected, and then belowground parts were dug up with shovels from a range of 0.5 m × 0.5 m and a depth of 40 cm. The collected belowground parts, i.e., roots with soil were soaked in tap water immediately after digging and covered against direct sunlight to prevent the drought impacts. The soil attached on roots was carefully removed using tap water and tweezers, and then the maximum root length of each seedling was measured again by the same method just before transplanting as above. The relative growth rate (RGR) of maximum root length, height, root collar diameter, and aboveground volume as the products of height and diameter squared were calculated using the following equation;

$$RGR = \frac{Log\ (S_2) - Log\ (S_1)}{t_2 - t_1}$$

where S_1 and S_2 denote the initial and final values of a seedling, and t_1 and t_2 denote the initial and final date when the size measurement was conducted. The values of annual RGR were calculated by multiplying the daily RGR values by 365. Roots in the soil that had settled in the bucket or were removed in the shower were collected as much as possible. The biomass of total aboveground parts of a seedling and total belowground parts of each seedling were evaluated after drying at 75 °C for 14 days. The ratio of aboveground biomass to belowground biomass was calculated as T/R ratio.

Morphological traits of fine roots

Four to seven intact, alive fine roots, i.e., roots less than 2 mm in diameter (McCormack et al. 2015), were collected from each seeding just before the removement of soil attached on roots using tweezers. In this study, the alive fine root was selected based on root color, texture, and shape (de Kroon and Visser 2003, McCormack et al. 2015). The collected fine roots were placed in plastic bags with zippers to prevent them from drying and stored in a refrigerator at approximately 4 °C until the subsequent measurements. For measuring fine root morphology, soil adhering to the surface of the collected fine roots was carefully removed at first. Next, the fine roots were immersed in an acrylic case filled with tap water, neatly rearranged to avoid overlapping roots each other, and a scanner (GTX-900, Seiko Epson Corporation, Nagano, Japan) was used to acquire a projected image of the roots. The acquired images were analyzed by a root morphometry application (WINRHIZO Pro 2021, Regent Instruments Inc., Quebec, Canada) to obtain the average diameter and total root length of the projected fine roots. From fine root collection to scanning, the process was completed in four days after digging out. After scanning, the dry weight of these fine roots was determined by 0.1 mg resolution (AG245, Mettler-Toledo International Inc., Greifensee, Switzerland) after drying at 55°C for seven days. Finally, specific root length (SRL, m g^{-1}) was calculated as the ratio of dry weight to total projected root length.

Leaf mass per area and nitrogen contents of needle leaves

The aboveground parts of seedlings were separated from the underground portion from the base and stored in plastic bags until the following analysis. A lateral current shoot developed from the stem in 2022, that showed healthy green and well development appearances, was selected in each individual. Intact 20 needle leaves were collected from the shoot and its projected image was obtained by a handy scanner (MSC10, King jim co. ltd., Tokyo, Japan). Total projected area of needle leaves was evaluated by an image analysis software (ImageJ, National Institutes of Health, Maryland, USA). Then, the dry weight was evaluated after drying at 75 °C for three days. Finally, the leaf mass per area (LMA) was calculated as the ratio of the dry weight to projected area of needle leaves. Using the needles, the total nitrogen content was determined by the dry combustion method using a nitrogen-carbon analyzer (SUMIGRAPH, NC-22F, Sumika Chemical Analysis Service, Ltd., Osaka, Japan). Based on the obtained values as the nitrogen content per leaf mass and LMA, the nitrogen contents per area (N_{area}) was calculated.

Statistical analysis

All statistical analyses were conducted by a commercial spreadsheet software (Microsoft Excel for Mac, Microsoft, Washington, USA) and a statistical analysis free software (R version 4.2.1, R core team 2020). A significant level of 5% was adopted for all statistical tests in this study. Based on the purposes of this study, two analysis frameworks were established for verifying (i) the interspecific difference in the responses of seedlings of the three species, *A. sachalinensis*, *P. glehni*, and *P. jezoensis*, to soil compaction without shade effects of competitive vegetation, and (ii) the interaction effects of soil compaction and vegetation weeding on growth of *A. sachalinensis* seedlings. The former analysis used the data regarding the treatments of vegetation weeding (i.e., NC+W and C+W) in all species, while the latter analyzed data of all treatments in *A. sachalinensis*. The following models were constructed based on the split-plot design (Mizuguchi 2011);

$$Y_{ijk} = \mu + C_i + \varepsilon_{ij} + S_k + C_i \times S_k + \varepsilon_{ijk} \qquad (1)$$

$$Y_{ijk} = \mu + C_i + \varepsilon_{ij} + W_k + C_i \times W_k + \varepsilon_{ijk} \qquad (2)$$

where Y_{ijk} denotes the evaluated traits, i.e., RGR of height, RGR of base diameter, RGR of maximum root length, RGR of aboveground volume, aboveground biomass, belowground biomass, total belowground biomass, height of seedlings in 2022, T/R ratio, average diameter of fine roots, SRL, LMA, N_{area}, and N_{mass} and the environmental conditions, i.e., the vegetation density, the hardness of surface soil, the three phase fraction of soil, i.e., solid, liquid, and air fraction, bulk density, porosity, and maximum water capacity, μ denote the fixed effects of blocks, C_i denote the fixed effects of soil compaction, ε_{ij} denote the error of whole-plot, S_k denote the fixed effects of species difference, W_k denote the fixed effects of weeding, and ε_{ijk} denote the error of spilt-plot. With these general linear models, the effects of soil compaction and species difference and the effects of soil compaction and weeding were evaluated by Two-way ANOVA, respectively. For this analysis, the values of data were used after logarithm transformation. Regarding the fixed effects of soil compaction on traits of seedlings, the continuous function factor of the soil environmental conditions evaluated in 2022 was provided instead of a categorical factor since the soil conditions could have been heterogeneously changed within two years. With the standardized value of obtained 6 soil physical factors, i.e., the three phase fraction of soil, bulk density, porosity, and maximum water capacity, principal component analysis (PCA) was performed. Among the obtained principal components, the one that best reflected the effect of soil compaction was set for the continuous function factors for each individual. In addition, the Tukey's multiple comparison test were performed to evaluate the variation of soil compaction and species difference and the variation of soil compaction and weeding, respectively. In the multiple comparison test, the fixed effect of soil compaction was set as a categorical factor.

Results

Manipulated environments of belowground and aboveground

The soil compaction treatment significantly changed all the evaluated soil properties in both years (Table 1, Table S1a), where the increases of surface soil hardness, liquid and solid ratios, and bulk density and the reductions of air ratio, porosity, and maximum water capacity were observed. The weeding treatment increased the surface soil hardness only in 2021 (Table 1, Table S1a) but no significant changes were observed in 2022. On the other hand, the significant effects of weeding treatment on other soil properties than surface soil hardness were observed in 2022 (Table S1a). For example, the significant increase of bulk density and the reduction of maximum water capacity occurred only under no soil compaction (Table 1, $p < 0.05$). Results of PCA showed that PC1 clearly reflected the differences by soil compaction with approximately 87.3%. The variation of PC1 showed that multiple soil conditions varied even in the soil compaction treatment and the no soil compaction treatment in this study (Fig. S2). Since the value of PC1 in an individual was able to be considered as the more responsible explanatory factor, these values were used for the following ANOVA analyses.

Table 1: Soil physical properties in 2021 and 2022.

		Treatment			
Year	Factor	NC+NW	NC+W	C+NW	C+W
2021	Soil hardness (kg cm^{-2})	1.63 ± 0.15 c	2.77 ± 0.14 b	6.02 ± 0.70 a	9.55 ± 1.16 a
	Liquid (%)	39.98 ± 1.03 b	39.65 ± 1.02 b	43.02 ± 0.37 a	42.24 ± 0.56 ab
	Soild (%)	34.05 ± 0.52 b	34.82 ± 0.59 b	43.04 ± 0.65 a	43.88 ± 0.69 a
	Air (%)	25.97 ± 1.13 b	25.53 ± 1.00 b	13.95 ± 0.60 a	13.88 ± 0.72 a
	Bulk density (g cm^{-3})	0.97 ± 0.01 b	0.97 ± 0.01 b	1.17 ± 0.01 a	1.20 ± 0.01 a
	Porosity (%)	65.95 ± 0.52 b	65.18 ± 0.59 b	56.96 ± 0.65 a	56.12 ± 0.69 a
	Maximum water capacity (%)	68.52 ± 1.45 b	67.19 ± 1.44 b	48.76 ± 1.14 a	47.20 ± 1.19 a
2022	Soil hardness (kg cm^{-2})	1.86 ± 0.36 b	1.38 ± 0.10 b	3.86 ± 0.14 a	4.31 ± 0.31 a
	Liquid (%)	36.10 ± 0.8 b	36.95 ± 0.65 b	42.59 ± 0.73 a	43.12 ± 0.44 a
	Soild (%)	30.89 ± 0.74 b	33.57 ± 0.46 b	37.93 ± 1.15 a	39.90 ± 0.64 a
	Air (%)	33.01 ± 0.86 b	29.49 ± 0.63 b	19.48 ± 1.40 a	16.97 ± 0.84 a
	Bulk density (g cm^{-3})	0.99 ± 0.02 c	1.07 ± 0.01 b	1.19 ± 0.02 a	1.24 ± 0.01 a
	Porosity (%)	69.11 ± 0.69 b	66.43 ± 0.46 b	62.07 ± 1.15 a	60.10 ± 0.64 a
	Maximum water capacity (%)	70.28 ± 1.61 c	62.38 ± 0.79 b	52.40 ± 1.74 a	48.72 ± 0.93 a

The abbreviations of treatments denote as follows; NC+NW: no-compaction of soil and no-weeding, NC+W: no-compaction of soil and weeding, C+NW: compaction of soil and no-weeding, and C+W: compaction of soil and weeding. Different letters denote significantly difference in each parameter and each year (Tukey, $p < 0.05$).

The soil compaction treatment significantly reduced total vegetation density in all species without any interspecific difference (Fig. 2, Table S1b). In 2021, the suppression of vegetation height in July and September was observed (Fig. 3a). Although the micro difference by only one measurement point per treatment should be considered, the relatively bright conditions under soil compaction in September and the little difference between weeding and no weeding condition under soil compaction were also observed (Fig. 3b, c). In addition, compared with the no soil compaction, the vegetation density were completely suppressed by soil compaction at least until July (Fig. S3). Although the vegetation density under soil compaction was gradually increased from July to September, the rate of increase were also suppressed by soil compaction (Fig. S3).

Responses to soil compaction under weeding conditions in the three tree species

The significant effect of soil compaction was observed only in RGR of maximum root length but not in other traits (Table 2, Fig. 4). In regard to RGR of maximum root length, the interaction effect of soil compaction and species difference was also significant (Table 2, $p < 0.05$) and the multiple comparison test showed that the significant reduction was observed only in *P. jezoensis* (Fig. 4d). Compared with the average values between soil compaction treatments, the highest reduction rate of RGR of maximum root length was approximately 53.7% in *P. jezonensis* and the second highest reduction rate was approximately 31.2% in *P. glenii*, while the lowest was approximately 14.3% in *A. sachalinensis* (Fig. 4d). In fine root morphological traits, such as the average diameter of fine roots and SRL, there was neither any significant responses to soil compaction nor the species-specific responses (Table 2), rather the significant species differences were observed (Table 2, $p < 0.001$). Results of multiple comparison test showed that the average diameter of fine roots of *A. sachalinensis* was higher than *P. jezonensis* (Fig. 4e) and the SRL of *A. sachalinensis* was lower than *P. jezonensis* (Fig. 4f).

Effects of soil compaction and weeding on *A. sachalinensis*

Significant effects of soil compaction were observed in RGR of root collar diameter, RGR of aboveground volume (Table 3, $p < 0.01$), aboveground biomass, belowground biomass, and total biomass (Table 3, $p < 0.05$). On the other hand, significant effects of weeding were observed in almost traits except for RGR of height (Table 3). In regard to RGR of aboveground volume, aboveground biomass, total biomass and height in 2022, both the effect of weeding and interaction with soil compaction were significant (Table 3). The multiple comparison test showed that the significant increases of RGR of root collar diameter, RGR of aboveground volume, and height in 2022 by weeding was observed only under no soil compaction (Fig. 5b, Fig. 5c, Fig. 5h). Furthermore, in regard to aboveground, belowground, and total biomass, both the significant increases by weeding and the increases by compaction under no weeding condition were observed (Fig. 5e, Fig. 5f, Fig. 5g).

Table 2: Results for ANOVA in both traits and total vegetation density between soil compaction and species difference under weeding conditions.

Trait	Compaction (C)	Species (S)	C × S
RGR of height (year^{-1})	0.22 | 0.66	2.64 | 0.10	1.52 | 0.24
RGR of diameter (year^{-1})	1.66 | 0.25	0.66 | 0.53	0.08 | 0.92
RGR of volume (year^{-1})	0.32 | 0.59	0.34 | 0.72	1.20 | 0.32
RGR of root length (year^{-1})	14.32 | <0.05	0.48 | 0.62	4.16 | <0.05
Fine root diameter (mm)	0.75 | 0.43	16.45 | <0.001	0.51 | 0.61
SRL (m g^{-1})	0.34 | 0.58	18.00 | <0.001	0.39 | 0.68

In each cell, left and right number denote *F* value and *p* value.

Table 3: Results for ANOVA in traits of *Abies sachalinensis* seedlings between soil compaction and weeding treatments.

Trait	Compaction (C)	Weeding (W)	C × W
RGR of height (year^{-1})	0.15 | 0.71	0.02 | 0.98	2.99 | 0.07
RGR of diameter (year^{-1})	32.33 | <0.01	14.19 | <0.001	1.43 | 0.26
RGR of volume (year^{-1})	30.16 | <0.01	9.31 | <0.01	4.77 | <0.05
RGR of root length (year^{-1})	0.12 | 0.75	6.14 | <0.01	0.02 | 0.98
Aboveground biomass (g)	11.21 | <0.05	29.53 | <0.001	4.59 | <0.05
Belowground biomass (g)	10.81 | <0.05	24.83 | <0.001	0.03 | 0.97
Total biomass (g)	8.52 | <0.05	70.03 | <0.001	10.15 | <0.001
Height in 2022 (cm)	5.12 | 0.07	3.9 | <0.05	15.09 | <0.001
Fine root diameter (mm)	2.18 | 0.20	8.60 | <0.01	1.75 | 0.20
SRL (m g^{-1})	5.00 | 0.08	7.66 | <0.01	0.97 | 0.40
T/R ratio	4.26 | 0.09	5.42 | <0.05	11.07 | <0.001
LMA (g m^{-2})	3.14 | 0.14	7.85 | <0.01	0.35 | 0.71
N_{area} (mgN cm^{-2})	0.09 | 0.78	8.75 | <0.01	12.12 | <0.05
N_{mass} (mgN g^{-1})	1.54 | 0.27	0.06 | 0.94	9.50 | <0.01

In each cell, left and right number denote *F* value and *p* value.

Regarding to fine roots, T/R ratio, and needle leaves, there was no significant effect of soil compaction whereas the significant effects of weeding were observed on almost traits except for N_{mass} (Table 3). However, the significant interaction effect of soil compaction and weeding was observed on T/R ratio, N_{area}, and N_{mass} (Table 3). The multiple comparison test showed that the effect of weeding significantly increased average diameter of fine root (Fig. 6a), LMA (Fig. 6d), and N_{area} (Fig. 6e) only under no soil compaction. In addition, the effect of weeding decreased T/R ratio under soil compaction (Fig. 6c). On the other hand, the effect of soil compaction significantly decreased N_{mass} only under weeding conditions (Fig. 6f).

Discussion

Interspecific variation of tolerance to soil compaction under weeding conditions

Previous studies have reported the interspecific difference in responses of seedlings to soil compaction (Sinnet et al. 2008, Ponder Jr et al. 2012, Mariotti et al. 2020). The meta-analysis showed the relatively lower sensitivity of conifer species to soil compaction (Mariotti et al. 2020). In addition, the relatively light disturbance by machine running may not be a critical issue for the growth of conifer seedlings (Blouin et al. 2008), although the degree of soil physical changes by machine running varied with soil types and water conditions (Cambi et al. 2015).

Results under weeding conditions showed no significant changes of aboveground growth to soil compaction in three boreal evergreen conifer species (Fig. 4, Table 2). The variation of soil bulk density (Table 1) indicated that the current impact degree of soil compaction might be relatively weak compared to previous studies (Kamaluddin et al. 2005, Mariotti et al. 2020). Nevertheless, the belowground growth was suppressed in *P. jezonensis*, while no significant change in *A. sachalinensis* seedlings (Fig. 4d). The interspecific difference in morphological traits of fine roots indicated that *A. sachalinensis* seedlings with the relatively thicker fine roots showed the relatively stable performance of belowground growth under soil compaction compared with *P. jezonensis* with relatively thinner fine roots (Table 2, Fig. 4e). Although any significant change was not observed in *P. glehnii* seedlings (Fig. 4), the tolerance of belowground growth to soil compaction under the weeding condition would be relatively higher in *A. sachalinensis* rather than *P. jezonensis* at least.

Functional variation of fine root morphology under weeding conditions

Root thickness indicates aeration and mass transport capacity, with thicker roots being able to elongate in anaerobic soil environments (Correa et al. 2019). Generally, roots subjected to soil physical resistance would be thicker, and its elongation can be reduced compared to those grown in softer soils (de Kroon and Visser 2003). In this study, no significant changes in the average diameter of fine roots under soil compaction were observed in all species under weeding conditions (Fig. 4e). Rather, the interspecific difference in the average diameter of fine roots was maintained regardless of soil compaction. These results would reflect the greater differences in fine root diameter between species than the responses capacity to soil compaction within species (Correa et al. 2019).

The pattern of species difference in fine root diameter was relevant to the variation of SRL (Fig. 4f). As functional traits of the resource absorption capacity as well as the construction cost of fine roots, high SRL and thin diameter would reflect the strategies that rely on root exudates and/or mycorrhizal symbiosis rather than morphology (McCormack et al. 2015). Roots would often relieve the physical limitations of soil by its elongation (de Kroon and Visser 2003). Probably since root exudates and mycelia may have a weak impact on soil physical properties than physical root cultivation by root elongation (Hallett et al. 2022), the growth of the functional type of seedlings with relatively higher SRL and thinner fine roots might be relatively vulnerable against soil physical stresses.

The interspecific variation in root morphological traits may be associated with the difference in life-history, especially the regeneration stage. Doi et al. (2008) reported that *P. jezonensis*, which often regenerates on fallen logs but is rare in soil, probably to avoid the pathogenic effects, localized roots on surface layers, while the roots of *A. mariessi* and *A. veitchii,* which can regenerate on forest soil, developed horizontal roots into the relatively deep soil layer. If these root developmental patterns might indicate the niche differentiation (Doi et al. 2008), the higher construction cost of thicker fine roots in *A. sachalinensis* reflects the strategy to extend fine roots into relatively deep and physically complex soils. In contrast, the lower construction cost of thinner fine roots in *P. jezonensis* reflects the strategy to compete for accessible substrates on the surface of fallen logs. Although there was no statistically significant interspecific variation in the relatively belowground growth rate (Fig. 4d), we also assumed that the root elongation rate might be associated with the observed root morphological variation, probably resulting in the temporal niche differentiation (de Kroon and Visser 2003, Doi et al. 2008).

On the other hand, it has been reported that *P. glehnii* was the most slow-growth type among the three species (Kayama et al. 2007). This species has relatively superior tolerance to stressful soil environments, such as acidic and serpentine soil, probably due to the defense strategies with mycorrhizal symbiosis (Kayama et al. 2007). The interspecific difference in root growth responses to soil compaction between *P. jezonensis* and *P. glehnii* might be associated with the functional variation between root exudation capacity or mycorrhizal symbiosis (McCormack et al. 2015, Hallett et al. 2022). In future studies, the functional significances should be provided from the spatiotemporal variation in root elongation rate, root exudation capacity, and mycorrhizal symbiosis under soil compaction.

Responses of *A. sachalinensis* seedlings to competition can vary by compaction

The growth of planted seedlings in fields could vary depending on not only the physical properties of soil but also the changes in above- and belowground competitive conditions induced by the soil modifications (Ares et al. 2007, Reicis et al. 2023). Although we did not directly evaluate belowground competitive conditions, the morphological changes of fine roots by weeding without soil compaction (Fig. 6a, b) might reflect the relatively weak belowground competitive conditions since the thinning root thickness could often be considered as the acclimation against competitive conditions (Sun et al. 2020). On the other hand, the soil compaction suppressed vegetation growth (Fig 2), which improved the light conditions for *A. sachalinensis* seedlings (Fig. 3). Therefore, the effects of aboveground competitive conditions on planted seedlings would not be the same degree between soil compaction treatments, i.e., the impacts of vegetation was relatively weak under soil compaction. In this context, LMA and N_{mass} can provide relevant information on light and soil conditions, respectively; LMA increases with increasing light intensities, whereas N_{mass} in leaves within a tree canopy is almost stable irrespective of growth light environments (Meir et al. 2002, Kitao et al. 2012). Hereafter, we focused on LMA as the response indicator to the aboveground light condition and N_{mass} as one to the belowground soil nutrient status.

Soil compaction differentially affected changes in LMA in response to weeding. Without weeding, LMA was significantly reduced under no soil compaction, but not under soil compaction (Figure 6d). That is, leaf morphological acclimation to shade conditions (Kitao et al. 2019, Ishizuka and Sugai 2021) did not occur due to the suppression of weed growth by soil compaction. Regarding N_{mass}, the decrease in N_{mass} was observed by soil compaction under weeding (Fig. 6f), which is consistent with the previous studies showing that soil compaction suppresses N acquisition (e.g., Kamaluddin et al. 2005). This might be relevant to the responses of T/R ratio. The reduction of T/R ratio due to soil compaction under weeding conditions (Fig. 6c) was not accompanied by a reduction in aboveground biomass (Fig. 5e), but by a slight increase in belowground biomass (Fig. 5f), suggesting that increased allocation to the belowground in acclimation against limited soil resource availability would prevent a decline in aboveground growth (Correa et al. 2019). Meanwhile, no weed effects on N_{mass} were observed (Table 3), indicating that the competition with vegetation for N would not be intense for *A. sachalinensis* seedlings. In fact, N_{mass} under compaction without weeding was comparable to that under no compaction with weeding, suggesting that vegetation may improve soil N status under compaction by alleviating soil physical properties (Table 1).

On the other hand, the reduction of N_{area} by no weeding under no soil compaction (Fig. 6e) would be the acclimation to shade effects caused by vegetation (Stenberg et al. 1998). Besides, the reduction of N_{area} by soil compaction under weeding conditions without shade effects would result from the inhibition of N acquisition (Kamaluddin et al. 2005). Interestingly, the shade acclimation of N_{area} would be driven by morphological changes rather than N_{mass} changes (Meir et al. 2002, Kitao et al. 2012). Thus, the relatively low N_{area} under soil compaction and no weeding conditions might result from the interaction of the weak shade condition, a slight morphological acclimation (Fig. 6d), and a slight increase of N_{mass} (Fig. 6e).

As a product of $N_{mass} \times LMA$, N_{area} is known to be positively related to the area-based light-saturated photosynthetic rate (Evans 1989; Niinemets et al. 2004), which could be a measure of photosynthetic capacity. Despite the reduction of N_{area} (Fig. 6e), the growth and biomass of seedlings were not decreased by soil compaction under weeding conditions (Fig. 5). This may be partly related to the response to soil water conditions, including drought, associated with changes in the carbon allocation (Correa et al. 2019, Mariotti et al. 2020). Soil compaction induced the higher carbon allocation to belowground (i.e., lower T/R ratio, Fig. 6c), probably due to the limited soil resource availability. This would consequently promote water acquisition capacity (Kitao et al. 2005, Correa et al. 2019). The soil moisture content was higher under soil compaction even though the amount of water the soil could potentially hold was reduced in both measurement periods (Table 1). Although the absolute difference in the liquid ratio was approximately 6% between soil compaction treatments, the relative difference in the liquid ratio to the maximum water capacity, i.e., the potential soil water content, was approximately 30%. In addition, because the period of little precipitation (< 5 mm a day: 4.5 mm for 1 day, and 0.5 mm for 3 days) was prolonged for $\approx$ 1.5 months with high temperatures in the summer of 2021 (Japan Meteorological Agency 2021), soil drought stress would have been severe during this period. The low T/R ratio under soil compaction without weeding can alleviate soil drought stress (Yamashita 2016, Harayama et al. 2021). Overall, the current results indicated the potentially dry condition under no soil compaction and weeding conditions, probably leading to similar growth performances between soil compaction and no soil compaction conditions. Further study is needed to elucidate the effects of soil compaction concerning drought tolerance and avoidance.

Conclusion

This study evaluated the potential of soil compaction, which could mitigate the competitive conditions and may not significantly suppress the growth of *A. sachalinensis* seedlings. Although our results were based on the relatively mild degree of manipulated soil physical properties (Kamaluddin et al. 2005, Mariotti et al. 2020) and the relatively short-term suppression of vegetation growth by soil compaction (Ohsato et al. 1996, Sinnet et al. 2008), these suggested that the mere machine running may partly contribute to the forest vegetation management when planting the functional type with thicker fine roots, such as *A. sachalinensis* (Wagner et al. 2006, Ares et al. 2007). It should note that the effects of soil compaction can vary depending on topography (Cambi et al. 2015). Particularly, most afforestation area in Japan are on steep slopes (Masaki et al. 2017, Ministry of Agriculture, Forestry and Fisheries 2021). Therefore, future studies should identify the suitable sites where machine operations should be avoided as well as predict the change degree of soil physical properties in plantation fields by evaluating the path of machine travel during harvesting and collection of timber. Given the possibility of reducing the forest management cost by machine running, it would be important to develop and optimize the novel methods of forestry machines considering the balance between its negative and positive impacts.

Declarations

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Author contributions: TS and MK contributed to set the experimental site. The study design, material preparation, data collection, and analysis were mainly performed by TS with supports by all other authors. The manuscript was written by TS with contributions from all other authors. All authors read and approved the final version of the manuscript.

Data availability: The data sets generated and analyzed in this study are available from the corresponding authors upon reasonable request.

Conflict of interest: The authors declare that they have no conflict of interest.

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Figures

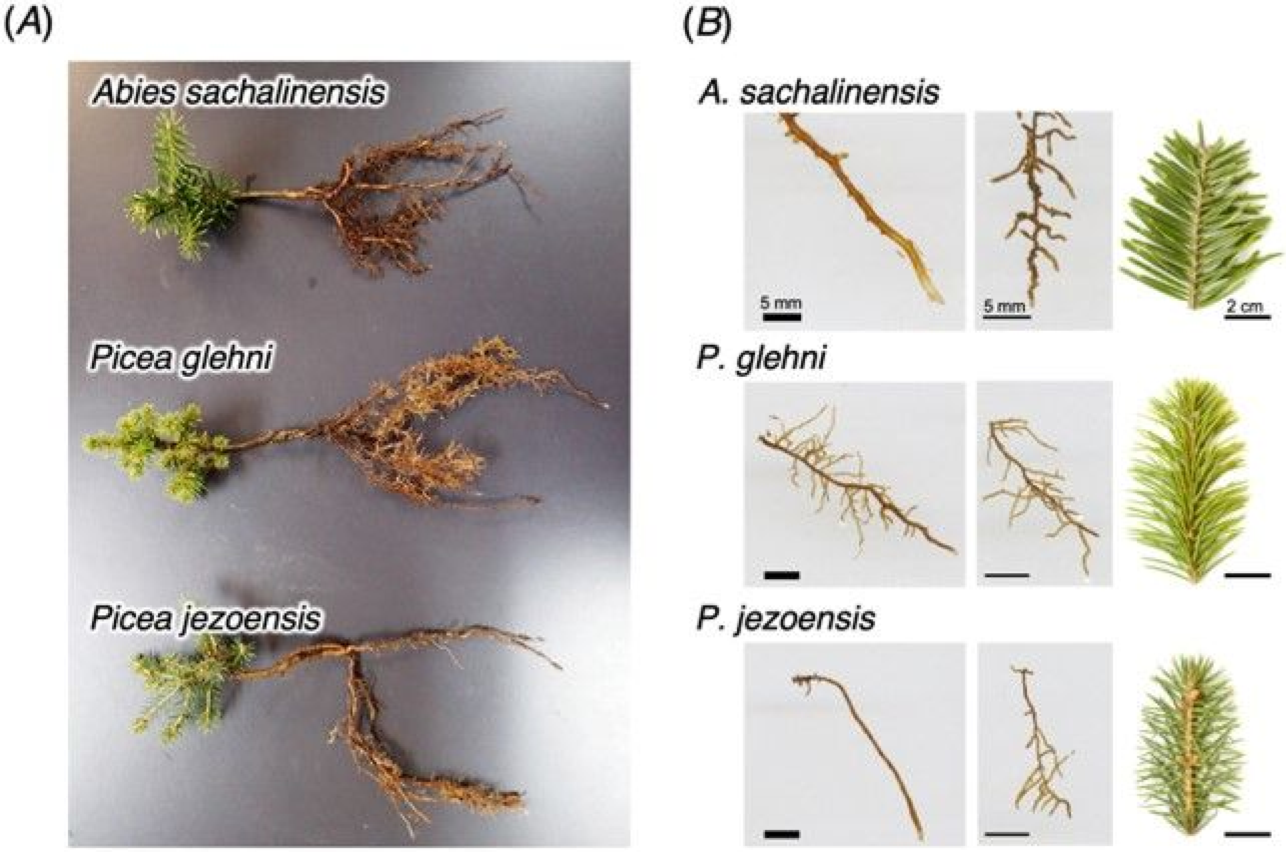

Figure 1

Shema for experimental materials. (a) Images at a whole plant level. (b) Images at individual root and shoot levels. Scale bars with common width indicate the same scale.

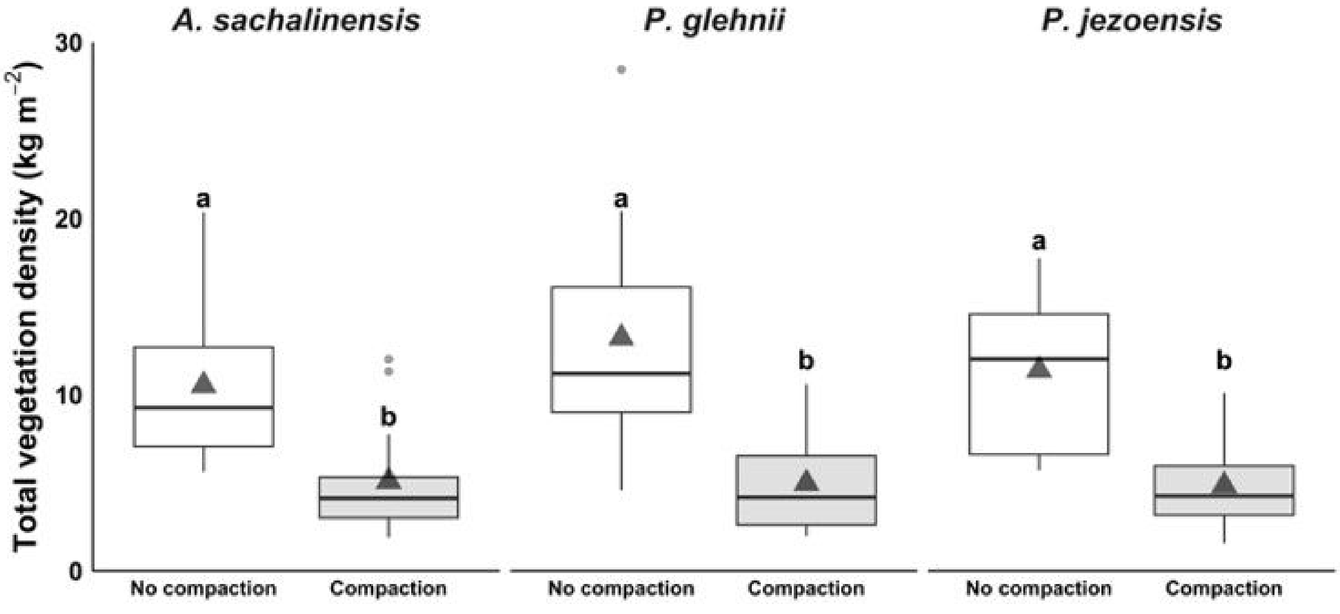

Figure 2

Variation of total vegetation density in 2021 between soil compaction and species difference. White and grey boxplot denote the values of no soil compaction and soil compaction and triangles denote mean values. Different letters denote significant differences among the six combinations of species and compaction treatment (Tukey, $p < 0.05$).

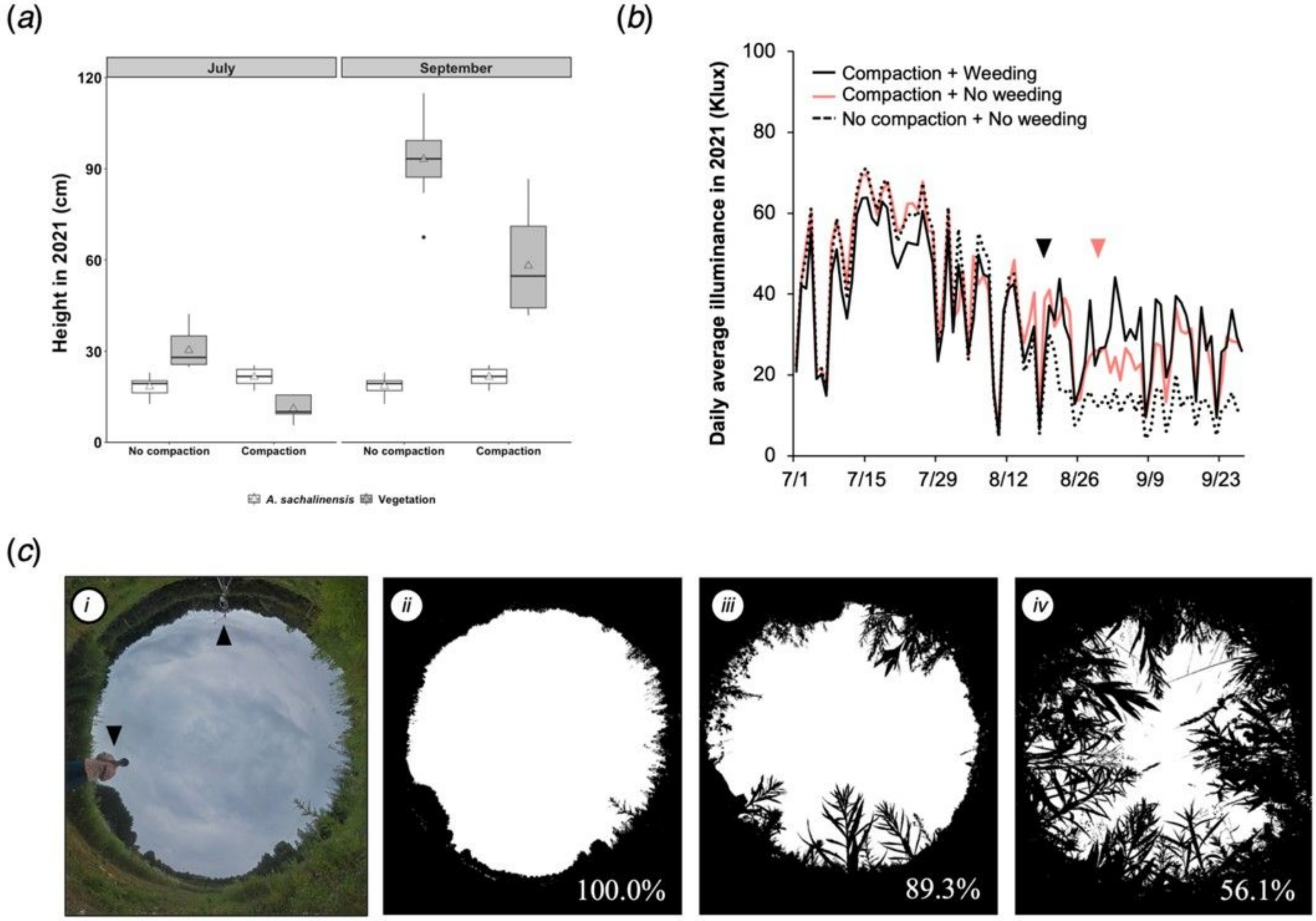

Figure 3

(a) The height of *Abies sachalinensis* seedling and the representative height of vegetation plants in July and September 2021. White boxes denote the height of *A. sachalinensis* seedlings and grey boxes denote the height of vegetation. Triangles denote mean values. (b) Variation of daily average of illuminance 20 cm above the ground between treatments except for no soil compaction and weeding. The black triangles indicate the start of cover in the non-compaction block without weeding, and the pink triangles indicate the start of cover in the soil compaction block without weeding. (c) All-sky photos in compaction and weeding treatment in September 2021. (i) and (ii) show the weeding block without any competitive vegetation. (i) is the image before conversion to black and white and (ii) is the photo after conversion, where the artificial obstructions in images are denoted by arrows in (i). (iii) shows the soil compaction block without weeding treatments, and (iv) shows the no compaction block without weeding treatment. The numbers in the lower right denote the relative open rate to (ii).

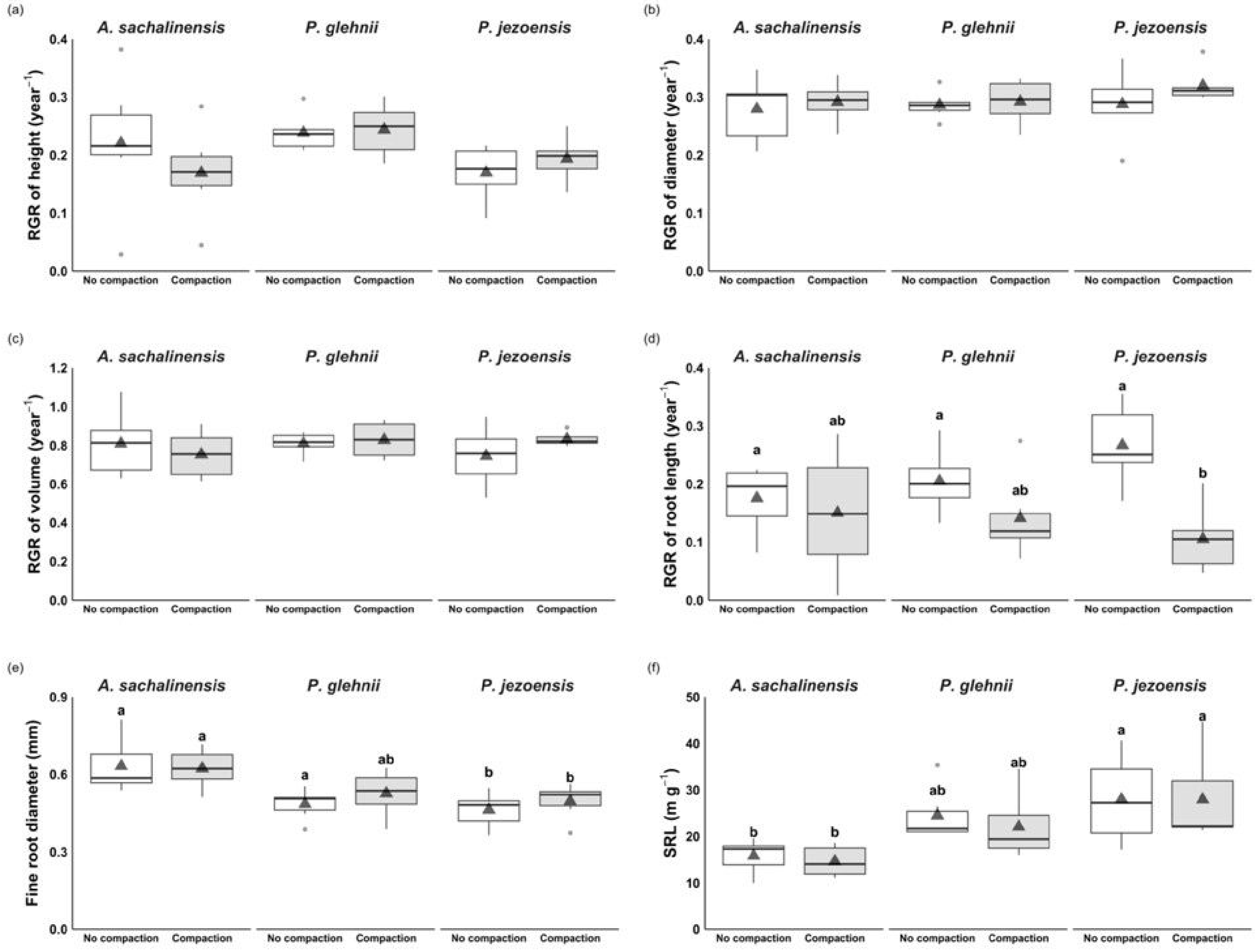

Figure 4

Variation of above- and belowground traits between soil compaction and species difference under weeding conditions. White and grey boxplot denote the values of no soil compaction and soil compaction and triangles denote mean values. Different letters denote significant differences among the six combinations of species and compaction treatment (Tukey, $p < 0.05$).

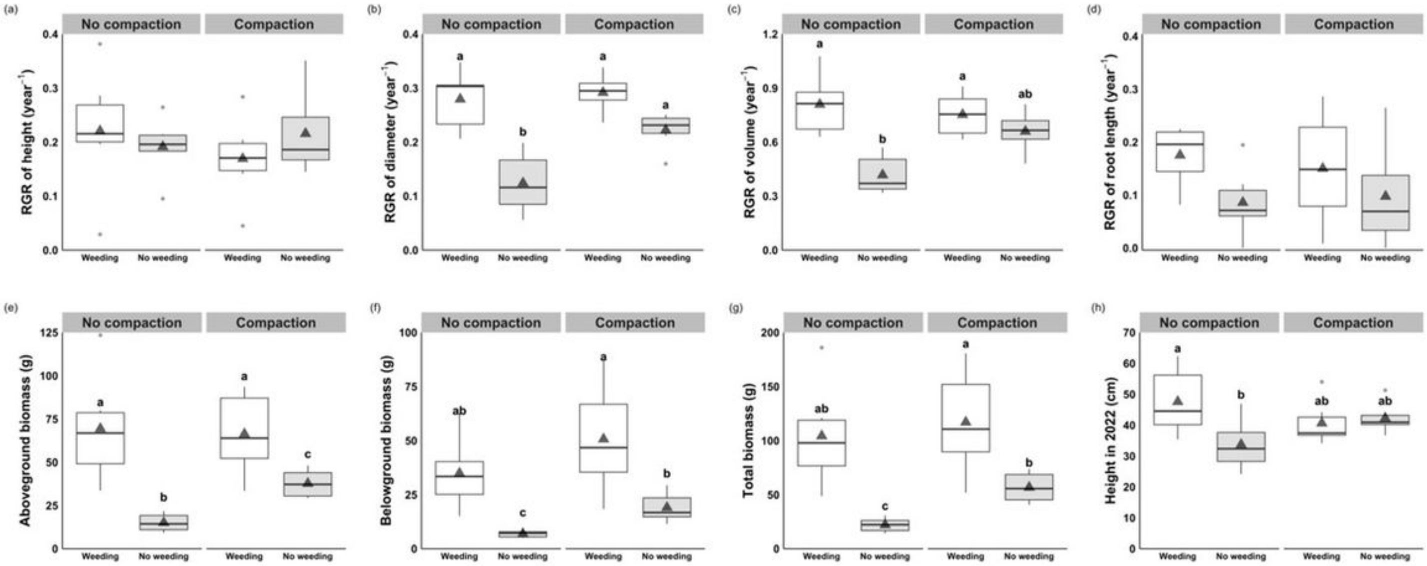

Figure 5

Variation of growth performance of *Abies sachalinensis* seedings between soil compaction and weeding treatments. White and grey boxplot denote the values of weeding treatment and no weeding treatment. Triangles denote mean values. Different letters denote significant differences among the six combinations of species and compaction treatment (Tukey, $p < 0.05$).

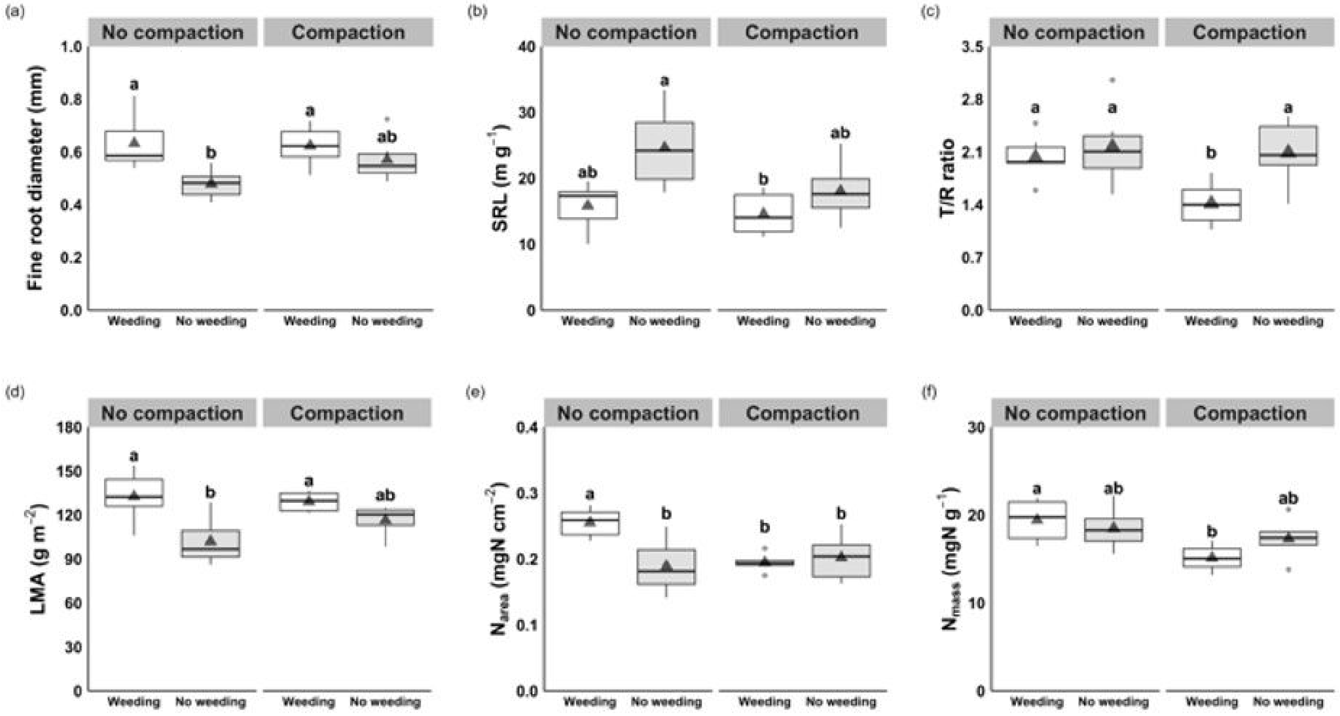

Figure 6

Variation of fine roots, T/R ratio, and needle leaves traits of *Abies sachalinensis*seedings between soil compaction and weeding treatments. White and grey boxplot denote the values of weeding treatment and no weeding treatment. Triangles denote mean values. Different letters denote significant differences among the six combinations of species and compaction treatment (Tukey, $p < 0.05$).

Supplementary Files

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