Morphological responses of shoots and fine roots to weed control in *Abies sachalinensis* and *Picea jezoensis* seedlings

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A mechanistic understanding of how morphological traits of seedlings are relevant to their functions against competition is the basis for managing vegetation in plantations. This study evaluated the growth responses and functional traits of shoots and fine roots in seedlings of boreal silvicultural species to manual weed control. Aboveground morphological traits reflecting competitive ability, including the total number of shoots per individual, length and weight per current shoot, area and weight per current leaf, and their ratio were evaluated. The fine roots were classified as pioneer roots or fibrous roots and were evaluated for diameter and specific root length (SRL). Compared with *Picea jezoensis*, *Abies sachalinensis* has superior competitive ability by reducing the total number of shoots by approximately 40%, preserving shoot length, and increasing specific leaf area by approximately 30% under competition. This finding is partly inconsistent with conventional strategies against shade, and *A. sachalinensis* is tolerant and partly avoidant of competing vegetation compared with *P. jezoensis*. The lack of interspecies differences in growth responses to weed control indicates that individual growth cannot be explained by aboveground responses alone. Thinner and higher SRL of fibrous roots in competing conditions were observed only in *A. sachalinensis*. However, thinner and higher SRL of pioneer roots in competing conditions were observed in both species. Altogether, these results highlighted that the fine root system widely adopts an avoidance strategy against competition regardless of aboveground competitive strategies. Because soil resources can be depleted, the preemptive strategy to access soil space against competition is responsible.

Keywords: word; competition; C/F ratio; specific branch length; pioneer root; fibrous root

Introduction

As a practical forestry issue, competition from vegetation has a serious effect on the growth and development of planted seedlings (Minogue et al. 1991, Balandier et al. 2006). A better understanding of seedling responses to competition is particularly important for optimizing costly vegetation management (e.g., clear underbrush) in conifer plantations (Masaki et al. 2017). Relatively few studies have evaluated the impacts of nonchemical vegetation management on the belowground traits of tree seedlings (e.g., Lockaby et al. 1988, Curt et al. 2005). This is because root surveys are time-consuming, and postplanting soil management is not preferable (Minogue et al. 1991, Ricard et al. 2003). In herbaceous plants, experimental studies have evaluated the effects of above- and belowground competition on survival and growth separately to establish general principles of competition (Kiær et al. 2013, Schmid et al. 2015, Semchenko et al. 2018). In plantations, however, conifer seedlings are larger just after planting but grow more slowly than competing vegetation surrounding the planted seedlings. Even in these specific situations, the above- and belowground responses to vegetation management may provide novel clues for understanding the ecological strategies of conifer seedlings against competition (Lieffers et al. 1993, Curt et al. 2005).

The morphological responses of plant organs can be a proxy indicating resistance strategies against competition, i.e., competitive ability (Kiær et al. 2013, Semchenko et al. 2018). For example, shoot length and specific leaf area often increase under aboveground competition in a given species. In a single shoot, the relatively greater biomass allocation to nonphotosynthetic organs (C) relative to photosynthetic organs (F) is the functional index (C/F ratio), which indicates a strategy to avoid rather than tolerate light competition, and vice versa (Kuroiwa et al. 1964). These contrasting

64 strategies have been widely observed among different functional types of plant species,
65 highlighting the importance of diverse abilities to minimize negative impacts from
66 competitors (Novoplansky 2009, Reich 2014).

67 The morphological traits reflect multiple functions in fine roots with a diameter
68 of less than 2 mm (Freschet et al. 2021). Thus, the belowground competitive ability
69 requires the evaluation of functional traits of fine roots that are not limited to size,
70 biomass, or allocation (Kramer-Walter et al. 2016, Semchenko et al. 2018). The ability
71 to develop longer and thinner roots is relevant to strategies for the early acquisition of
72 soil resources (Ostonen et al. 2007). In contrast, superior longevity and transport
73 efficiency, which are based on root diameter and tissue density, are important for
74 tolerance to competition (Kramer-Walter et al. 2016). However, not all roots may
75 respond in the same way because of their different levels of plasticity by functional type
76 (de Kroon & Visser 2003). In particular, fine roots develop at the optimal cost because
77 the soil resources are heterogeneous (Begon et al. 2006). In this context, the
78 classification of fine roots as pioneer roots or fibrous roots may be useful because they
79 are developed for specific functions, such as exploring soil spaces or acquiring
80 resources, respectively (Zadworny & Eissenstat 2011, Sell et al. 2022). While previous
81 studies have evaluated the competitive ability of fine roots on the basis of the
82 relationship between root functional traits and competing vegetation conditions (e.g.,
83 Curt et al. 2005, Beyer et al. 2013, Semchenko et al. 2018), few studies have evaluated
84 the abilities of pioneer and fibrous roots.

85 This study compared the morphological responses of shoots and fine roots to
86 weed control between boreal conifer species, i.e., *Abies sachalinensis* (Sakhalin fir) and
87 *Picea jezoensis* (Ezo spruce). In this study, weed control is defined as the manual
88 removal of weeds without the use of chemicals such as herbicides. Both target species

89 are widely distributed, often regenerate on fallen logs under the canopy, and are used
90 for plantations in Hokkaido, a northern island of Japan. A relatively higher survival rate
91 under low light conditions was observed in *A. sachalinensis* than *P. jezoensis* (Iijima et
92 al. 2009). Previous studies revealed that a relatively lower C/F ratio and number of
93 branches in *A. sachalinensis* than in *P. jezoensis*, suggesting that *A. sachalinensis* has a
94 tolerance strategy against shaded conditions, whereas *P. jezoensis* has an avoidance
95 strategy; however, these findings are based only on aboveground responses to shade
96 treatment or crown cover (Sato 1990, Fujimoto & Shimada 1991). A recent study
97 reported that fine roots were relatively thicker in *A. sachalinensis* than in *P. jezoensis*
98 under weed control and that the fine roots of *A. sachalinensis* were thinner and had a
99 greater specific root length under competition (Sugai et al. 2024a). However, the
100 responses of *P. jezoensis* to weed control and the interspecific differences between *A.*
101 *sachalinensis* and *P. jezoensis* have not been verified.
102 By comparing the morphological responses of shoots and fine roots to weed
103 control between two species with different competitive strategies, this study aims to
104 obtain ecological insights into above- and belowground competitive abilities. In
105 addition to delving deeper into previously reported aboveground strategies (i.e., *A.*
106 *sachalinensis* with a tolerance strategy and *P. jezoensis* with an avoidance strategy)
107 (Fujimoto & Shimada 1991), the following hypotheses were tested on the basis of the
108 relationship between fine root morphology and functions (Kiær et al. 2013): if
109 morphological responses to competition are specific to the root functional type
110 regardless of the species, fibrous roots may become thinner and longer, and pioneer
111 roots may become thicker and shorter to facilitate each function against competition.
112 However, if the responses are specific to the species regardless of the root functional
113 type, the fine roots of *A. sachalinensis* may become shorter and thicker whereas the fine

roots of *P. jezoensis* may become thinner and longer to promote species-specific strategies against competition (Fig. 1).

Material and Methods

The experimental site was the nursery at the Hokkaido Research Institute, Forestry and Forest Products Research Institute (FFPRI) (42°59′N, 141°23′E, 153.0 m a.s.l.). The nursery has clay soil with a dark brown color, which would be classified as dark brown forest soil (B_D, Mashimo 1997). The study area is located in a boreal cool temperate climate, with an average annual temperature of about 7.5°C and a total annual precipitation of 952 mm (Mizoguchi and Yamanoi 2015). In April 2021, the soil of the nursery was plow entirely, and three 12 m × 3 m rectangles were established 5 m apart. The rectangle was divided into four 2 m × 3 m plots with a separation of 1 m (12 plots in total). Within each rectangle, the plots were alternately divided into plots with and without weed control (WC) (Total of six plots in each treatment). Two five-year-old seedlings of *Abies sachalinensis* and *Picea jezoensis* were transplanted in May 2021 and cultivated until November 2022 (3 rectangles × 4 plots × 2 plants = 24 seedlings in each species) (Fig. S1). Seeds of each species were originated from multiple mother trees in the Hokkaido Research Institute in FFPRI, where they were cultivated in a nursery just until transplanting. In each plot, six planting points were set, with a distance of 1 m between adjacent points and 0.5 m from the edge of the plot. Among these six points, two points were randomly selected for each species. Transplanting was conducted via a commercial shovel (AD-574, Aida godo factory Co., Ltd, Niigata, Japan), and a hole approximately 0.1 m wide and 0.2 m deep was created. One seedling was planted in a hole and the root collar was set at almost ground level. The space was then filled with the soil from each hole, and the seedlings were irrigated with tap water. The major weed species observed during the experimental period were *Phleum pratense*, *Equisetum*

arvense, *Erigeron annuus*, *Barbarea vulgaris*, *Anthoxanthum odoratum*, *Taraxacum officinale*, *Cirsium aomorense*, and *Artemisia montana* (Takahashi et al. 2000). In the plots with WC, all the aboveground parts of the weeds in each plot were manually removed. To avoid damaging the roots of the seedlings, the belowground parts were not modified in this treatment. This treatment was conducted once each month from July to September 2021 and 2022.

Growth and biomass analysis

In early July 2021, late September 2021 and late November 2022, the height and the root collar diameter of all planted seedlings were measured with a ruler and an electronic caliper (CDN-P20, Mitutoyo Corporation, Kanagawa, Japan), respectively. The root collar diameter was measured in two perpendicular directions and the average was calculated. The relative growth rates of height and root collar diameter were calculated via the following equation:

$$RGR = \frac{ln\, V_2 - ln\, V_1}{D_2 - D_1}$$

Where *RGR* denote the relative growth rate, V_1 and V_2 denote values in the initial and the final size measurement, D_1 and D_2 denote dates of initial and final size measurement, respectively. In the studied species, the height growth during the year was almost complete by July (Fujimura & Sakagami 1981). On the other hand, the spring growth of evergreen conifers largely depends on the current carbon gain of needles formed in the previous year (Hansen & Beck 1994). Thus, the period for calculating the RGR for height was set from September 2021 to November 2022. The annual values of each RGR were calculated by multiplying the obtained values by 365 (cm cm^{-1} $year^{-1}$).

The seedlings were harvested in late November 2022, when the roots of both species almost ceased growing (Satoh 1995). Until this time, none of the cultivated seedlings died. One healthy seedling of each species was selected from each plot (Total 12 plants in each species), all the aboveground parts were collected at first, then all the belowground parts were collected. The sampling process for the belowground parts was described in the below section. After the subsequent morphological measurements, all the aboveground parts were dried in an oven, and the dry mass (g $plant^{-1}$) was measured. The belowground parts were also dried in an oven after the morphological measurements, and the dry mass (g $plant^{-1}$) was measured, where the woody roots with a diameter greater than 2 mm and other fine roots were separated via an electronic caliper (CDN-P20, Mitutoyo Corporation, Kanagawa, Japan). The fine root ratio (%) was calculated as the biomass proportion of fine roots in all belowground parts. The ratio of total belowground biomass (Root, R) to total aboveground biomass (Shoot, S) was calculated as the R/S ratio.

Aboveground morphological traits

The method for measuring the morphological traits is summarized in Fig. S2. First, the number of all shoots directly branching from the stem (no. $plant^{-1}$) was counted for each individual. The best-growing, intact current-year shoot branching from the uppermost part of the main stem was subsequently collected. The shoot length (cm) and base diameter (mm) were measured via a ruler and an electronic caliper (CDN-P20, Mitutoyo Co., Kanagawa, Japan), respectively. The base diameter was measured in two perpendicular directions, and the average value was obtained. The ratio of length to average base diameter (cm mm^{-1}) was calculated for each shoot. Then, 20 current leaves were first collected from the center of each shoot. The projected images of these leaves

were acquired with a handy scanner (MSC10, King jim Co., Tokyo, Japan), the total projected area was evaluated via free image analysis software (ImageJ, National Institutes of Health, Maryland, USA), and then, these leaves were dried in an oven, and the dry mass was measured. Next, the shoots were dried in an oven, and the dry mass was measured. The dried shoot was further divided into remaining leaves as photosynthetic organs and a branch as nonphotosynthetic organ, and the dry mass of each branch was measured. The dry mass of all the leaves in the shoot was the sum of the mass of the 20 leaves and the mass of the shoot including the remaining leaves minus the mass of a branch. The projected area and mass of 20 leaves were used to calculate the average area per leaf (LA, $mm^2\ leaf^{-1}$), the average mass per leaf (LM), and the ratio of leaf area to dry mass (SLA, $cm^2\ g^{-1}$). The total mass of leaves in a shoot, LA, and LM were used to calculate the total area and number of leaves in a shoot (no. $shoot^{-1}$). The ratio of the length to the mass in a branch was calculated as the specific branch length ($cm\ g^{-1}$). The dry masses of all the leaves and a branch were used to calculate the C/F ratio. The C/F ratio has been widely used as a proxy for biomass allocation between photosynthetic organs (i.e., leaf dry mass, F) and nonphotosynthetic organs (i.e., branch dry mass, C). Note that these abbreviations originated from Moji & Saeki (1953), and they are probably abbreviations of Latin notations. Specifically, F may denote *Folium*, i.e., leaf, and C may denote *Corpora*, i.e., bodies involved branches and a stem (Sugai, personal communication). The relatively higher C/F ratio often suggests a strategy to avoid light competition, while a lower C/F ratio indicates a strategy to tolerate it (Kuroiwa et al. 1964, Fujimoto & Shimada 1991).

Root sampling and belowground morphological traits

After the aboveground parts were collected, the belowground parts were excavated within a 0.5 m square and 0.4 m deep. As destructive whole-root excavating often requires a great deal of labor and time, a certain spatial extent (0.5 m square or 1.0 m square) considering sample size and individual body size has been suggested (Tanaka 1999). The above range was determined as the space in which to collect as many roots of individual plant species as possible using shovels in this study. To avoid drying and to fluff the adhering soil around roots, the belowground parts were soaked in buckets of tap water until the following measurements were taken. After being transported to the laboratory, the soil and organic matter attached to the collected belowground parts were carefully removed via tap water and tweezers. Next, the number of all pioneer roots (no. $plant^{-1}$) was counted for each individual. In general, pioneer roots are well developed, relatively longer and thicker roots, which make the framework of a root system as skeletal roots (Fig. S3). On the other hand, fibrous roots, or feeder roots, are relatively shorter and thinner roots, and have superior absorptive functions with shorter root life span (Zadworny & Eissenstat 2011, Sell et al. 2022, Sugai et al. 2024b). Based on these studies, the pioneer root was defined as a fine root with a notable white color, a relatively large diameter, and a unique shape that is relatively long from the root crown to the lateral root-branching zone in this study. Note that pioneer roots were visually identified within a fine root system based on the above definition without quantitative criteria. Then, two fine root systems, including one pioneer root and several fibrous roots, respectively, were collected. When an individual has only one pioneer root in all fine root systems, the fine root system containing one pioneer root and the fine root system without a pioneer root were used for subsequent measurements. After sorting one or two pioneer roots and 10 to 15 fibrous roots from the collected fine root systems, the fine soil and organic matter adhering to their surface were removed. These roots

were carefully arranged without overlap in an acrylic case filled with tap water, and scanned to obtain a projected image of the roots (GTX-900, Seiko Epson Corporation, Nagano, Japan). The average diameter (mm), total root length, and total root volume of the projected roots were measured for each root type via a root morphometry application (WINRHIZO Pro 2021, Regent Instruments Inc., Quebec, Canada). The dry mass of these roots was measured after drying at 55 °C for seven days, and the specific root length (SRL, i.e., the ratio of the dry mass to the projected root length, m g^{-1}) and the root volume density (RTD, i.e., the ratio of the total projected root volume to the dry weight, g cm^{-3}) were calculated.

Belowground competitive conditions

In November 2022, before the seedlings were harvested, three surface soil samples were collected with 100 ml metal cores (DIK-1801, Daiki Rika Kogyo Co., Ltd., Saitama, Japan) for quantifying the belowground competitive conditions with reference to previous methods (Tanaka 1999, Achat et al. 2008). The sampling points in each plot were randomly selected from a distance of 20 cm from each seedling. In fact, Achat et al. (2008) evaluated that the belowground competition conditions, i.e., the spatial distribution of roots of competing vegetation, showing that a distinctly reduced pattern in the vertical distribution at 120 cm depth, but no clear distribution pattern in the horizontal distribution at least 100 cm width. Therefore, the sampling locations in this study could reflect the belowground competitive conditions, at least in the surface soil. The surface organic matter, including the aboveground parts of the competing vegetation, was carefully removed just before sampling. After the cores were dried in an oven, the dry mass of the collected soil was determined. The dried soil samples were then loosened with tap water on a 2 mm mesh sieve (ISO3310, Tokyo screen Co.,

263 Tokyo, Japan) and separated into fine soil exiting the sieve, gravel on the sieve, and
264 organic matter, including plant roots. The roots in the organic matter were classified as
265 seedling roots or competing vegetation roots on basis of their color and texture. The
266 vegetation roots and gravel were collected and dried in an oven, after which the dry
267 mass was measured. Then, their content (g g^{-1}) was calculated as the ratio to the mass of
268 dry soil in the core. Note that the variation in these weight-based calculated values
269 showed the same pattern as the variation in content per volume or area based on the
270 used core. The fine soil mass was calculated by subtracting the mass of gravel and
271 organic matter from the mass of the solid phase, and the bulk density (g cm^{-3}) was
272 determined as the mass of fine soil to the core volume (Ugawa et al. 2012). The values
273 for each parameter obtained at the three sites were averaged and used as representative
274 values for the belowground conditions of each plot.
275
276 **Statistical analysis**
277 All the statistical analyses were conducted with free statistical analysis software
278 (R version 4.4.0, R core team 2024). As the current experiment was a split-plot design,
279 the following models were constructed (Mizuguti 2011):
280
281 $$Y_{ijk} = \mu + V_i + \varepsilon_{ij} + S_k + V_i \times S_k + \omega_{ijk}$$
282
283 where Y_{ijk} denotes the evaluated plant traits in i-th treatment of V, j-th species of S, and
284 k-th level of individual at a whole-plant level (i.e., the RGR for the height, the RGR for
285 the root collar diameter, the above-, and belowground biomass, the fine root ratio, the
286 T/R ratio, the number of total shoots and pioneer roots) at a shoot level (i.e., the total
287 dry mass, the total leaf area, the total leaf number, the shoot length, the ratio of length to

base diameter, the specific branch density, the C/F ratio, LA, SLA), and a root tip level (i.e., the average diameter, SRL, RTD); μ denotes the overall mean; V_i denotes the fixed effects of the i-th treatment (WC or NWC); ε_{ij} denotes the error of the whole plot; S_k denotes the fixed effects of the j-th species (*Abies* or *Picea*); and ω_{ijk} denotes the error of the split plot. The effects of WC, species differences, and its interaction on these traits were evaluated by ANOVA using the *car* package with these generalized linear models (Fox & Weisberg 2018). Trait values, except for count data (i.e., the number of total shoots and pioneer roots), were log-transformed and used in this analysis. The relevant code developed during this study is available on the following link (https://rpubs.com/tetsuto_sugai/ANOVA_SPD). A Gaussian and Poisson distributions were assumed for log-transformed values and count data, respectively. To reveal the differences caused by WC and species, a multiple comparison test was performed via the *multcomp* package (Hothorn et al. 2008). The effects of WC on belowground conditions (i.e., the vegetation roots, the gravel, and the bulk density) were evaluated via Welch's t test. Based on the previous studies (Curt et al. 2005, Beyer et al. 2013, Semchenko et al. 2018) and the hypotheses of this study (Fig. 1), the belowground competitive ability of each root type was evaluated with Pearson's correlation analysis between the morphological parameters and vegetation roots and the relationship between root mean diameter and SRL. To visualize the rate of change of one variable parameter relative to the rate of change of another variable one in the correlation analysis, log-transformed values were also used. In addition, the effects of vegetation root biomass, root functional types, and its interaction on root morphological traits were evaluated by ANOVA using the same processes as above. This study adopted a significance level of 5% for these analyses.

313 **Results**

314 **Responses to weed control at individual level**

315 The significant effects of weed control (WC) were observed in the RGR for the
316 root collar diameter (RCD) (Table 1, $P<0.01$), the total dry mass of the above-
317 ($P<0.01$), and belowground parts ($P<0.01$), the dry mass of woody roots and fine roots
318 ($P<0.05$), the fine root ratio ($P<0.05$), and the number of pioneer roots ($P<0.05$).
319 Significant species differences ($P<0.001$) and interactions with WC ($P<0.01$) were
320 detected only in the number of total shoots. The RGR for RCD, the total dry mass of
321 above-, and belowground parts, and the dry mass of woody roots and fine roots were
322 increased by WC in both species (Table 2, $P<0.05$). The fine root ratio was decreased
323 only in *P. jezoensis* by WC ($P<0.05$). The number of total shoots was significantly
324 greater in *P. jezoensis* than in *A. sachalinensis* regardless of the treatment, but WC
325 significantly increased the number of total shoots only in *A. sachalinensis* ($P<0.05$).
326 The number of pioneer roots in both species increased with WC but was significantly
327 lower in *P. jezoensis* than in *A. sachalinensis* without WC. ($P<0.05$)
328

329 **Responses to weed control at a shoot level**

330 Weed control had significant effects on the total dry mass of a branch (Table 1,
331 $P<0.05$), the total leaf number, the C/F ratio ($P<0.001$), and the specific branch length
332 ($P<0.01$). Many functional traits, such as the total leaf area ($P<0.001$), shoot length
333 ($P<0.01$), length/base diameter ratio ($P<0.05$), C/F ratio ($P<0.05$), specific branch
334 length ($P<0.05$), leaf area ($P<0.001$), and SLA ($P<0.001$), significantly differ across
335 species. The C/F ratio ($P<0.001$) and SLA ($P<0.05$) had interaction effects with WC.
336 The results of multiple comparison tests were almost consistent with the results of the
337 ANOVA above. For example, WC significantly increased the dry mass of a branch in

both species (Fig. 2A, $P<0.05$), the total leaf area in a shoot (Fig. 2C, $P<0.05$) and the average area of a leaf (Fig. 2H, $P<0.05$) in *A. sachalinensis*. The shoot length and specific branch length of *A. sachalinensis* were significantly greater than those of *P. jezoensis* without WC (Fig. 2D and G, $P<0.05$), whereas no variation in WC was detected. The degree of the reduction in the C/F ratio caused by WC in *P. jezoensis* (61%) was significantly greater than that in *A. sachalinensis* (38%) (Fig. 2F, $P<0.05$). The degree of increases in the specific branch length did not differ across species (approximately 2.9 times greater in *P. jezoensis*, and 2.8 times greater in *A. sachalinensis*). The reduction in SLA caused by WC was observed only in *A. sachalinensis* (Fig. 2I, $P<0.05$).

Belowground competitive conditions

The vegetation roots were nearly halved in the WC treatment (Table 3, $P<0.01$). Although the bulk density was significantly increased by WC ($P<0.05$), its degree was relatively small compared with that of the vegetation roots. There was no significant change in the gravel content among the treatments.

Responses to weed control at a root level

Weed control had a significant effects only on the SRL of pioneer roots (Table 1, $P<0.05$). Species differences were found in the average diameter of pioneer ($P<0.001$) and fibrous roots ($P<0.05$), the SRL of pioneer ($P<0.01$) and fibrous roots ($P<0.05$), and the RTD of pioneer roots ($P<0.01$). In fibrous roots, the interaction effects between WC and species differences were observed in the average diameter ($P<0.01$) and the SRL ($P<0.01$). An increase in the average diameter (Fig. 3A, $P<0.05$) and a reduction in the SRL (Fig. 3C, $P<0.05$) caused by WC were observed in the

363 pioneer roots of each species. The relatively greater average diameter (Fig. 3A, $P<0.05$),
364 lower SRL (Fig. 3C, $P<0.05$), and greater RTD (Fig. 3E, $P<0.05$) of pioneer roots in *A.*
365 *sachalinensis* than in those in *P. jezoensis* were found only without WC. Conversely,
366 the relatively greater average diameter (Fig. 3B, $P<0.05$) and lower SRL (Fig. 3D,
367 $P<0.05$) of fibrous roots in *A. sachalinensis* than those in *P. jezoensis* were observed
368 only with WC.
369
370 **Correlations between root morphological traits and vegetation roots**
371 Significant correlations between the vegetation roots and the morphological
372 traits of each root type were observed only in *A. sachalinensis* (Table 4). For both root
373 types, the correlations with the average root diameter were significantly negative
374 ($P<0.05$). In addition, the relationship between average root diameter and vegetation
375 roots significantly varied depending on root types (Table 5, $P<0.05$), and the average
376 diameter of pioneer root could significantly respond to vegetation roots more than that
377 of fibrous roots in *A. sachalinensis* (Fig. 4). The correlation coefficient with the SRL
378 was relatively greater in pioneer roots ($r=0.85$, $P<0.001$) than in fibrous roots ($r=0.61$,
379 $P<0.05$) in *A. sachalinensis* (Table. 4).
380
381 **Discussion**
382 **Aboveground responses to weed control**
383 A significant improvement in growth under WC was observed in terms of the
384 root collar diameter rather than height in both species (Table 2). This was in accordance
385 with previous studies and it was associated with the seasonal growth pattern of planted
386 seedlings (Balandier et al. 2006). The height growth is often concentrated in early
387 spring, shortly after competing vegetation begins to grow, whereas diameter growth

388 continues throughout the season (e.g., Fujimura & Sakagami 1981, Hansen & Beck
389 1994). In addition, seedlings are generally exposed to open light conditions immediately
390 after planting and then encounter closed conditions as competition follows in
391 plantations (Balandier et al. 2006). In this study, the R/S ratio did not vary with WC in
392 either species (Table 2). As the same results were often observed in other studies
393 (Lockaby et al. 1988, Curt et al. 2005), whether competition changes the R/S ratio may
394 still be debatable. The R/S ratio is a common index reflecting the optimal balance for
395 efficiently acquiring resources, and a low R/S ratio is expected under shaded conditions
396 (Balandier et al. 2006, Asefa et al. 2022). For example, Kimata (1973) reported that the
397 completely shaded conditions caused by shielding reduced the R/S ratio of *A.*
398 *sachalinensis* seedlings by approximately half. Notably, the shade experiments did not
399 directly manipulate the soil resource conditions. In general, functional traits that
400 determine the ability to acquire a resource adjust in response to its availability, resulting
401 in the mitigation of growth and survival constraints. However, the adjustment of these
402 traits to the availability of multiple resources has been overlooked to date, and it is
403 possible that the biomass allocation may not change when both light and soil nutrient
404 resource availability are simultaneously limited (Freschet et al. 2015). Indeed,
405 morphological balance (e.g., the ratio of total root length to total leaf area) reflected the
406 functional response to resource availability rather than the R/S ratio (Freschet et al.
407 2015). Specifically, even if the quantitative balance of resource allocation does not
408 change between above- and belowground, morphological acclimation to how the
409 allocated resources are used may be relevant to growing and surviving against
410 competition. In addition, the effects of WC on the fine root ratio were significant, and a
411 greater fine root ratio was detected without WC, although no significant changes were
412 detected in *A. sachalinensis* (Table 2). These results were consistent with the responses

of broadleaf tree (*Fagus sylvatica*) seedlings to competition (Curt et al. 2005), indicating that biomass allocation within a root system may also be associated with resistance to competition.

The decreasing number of total shoots in *A. sachalinensis* reflected the significant impacts of shade without WC (Table 2). In addition, the degree of reduction in the total shoot number was significantly greater in *A. sachalinensis* more than in *P. jezoensis* (Table 2). These responses were consistent with a previous study (Fujimoto & Shimada 1991). At the shoot level, *A. sachalinensis* presented a lower C/F ratio than *P. jezoensis*, although there was no significant species difference under competition (Fig. 2F). Nevertheless, the shoot length was significantly greater in *A. sachalinensis* than *P. jezoensis* under competitive conditions (Fig. 2D). In fact, *A. sachalinensis* maintained the higher specific branch length than *P. jezoensis* (Fig. 2G). Specifically, *A. sachalinensis* would adopt the competitive strategies that maintain the length of a branch at the expense of its number, which is realized by improving branch form efficiency. On the other hand, *P. jezoensis* would adopt the strategies that prioritize the number of branches rather than their length (Table 2, Fig. 2D). The relatively short branch length under competition in *P. jezoensis* was due to the lower specific branch length (Fig. 2G). In addition, *P. jezoensis* was not able to modify the relatively lower SLA against competition (Fig. 2I). Since this was not consistent with the responses of other *Picea* sp. to variable light conditions (e.g., Grassi & Bagnaresi 2001, Day et al. 2014), the present leaf morphological response to competition may have also been induced by stimuli other than light. (e.g., soil resources). If individual leaf morphology and its form efficiency do not acclimate to competition, it would be difficult to maintain overall carbon gain. The low C/F ratio indicates a strategy that tolerates competition by increasing carbon gain relative to the respiration of nonphotosynthetic organs, while it is

438 inferior to avoiding competition (Kuroiwa et al. 1964). Thus, the formation of branches
439 of short length may squander the opportunity to avoid symmetrical competition with
440 vegetation (Nomoto & Yokoi 1981).
441
442 **Belowground responses to weed control**
443 This study revealed that both pioneer roots and fibrous roots significantly
444 responded to WC in *A. sachalinensis*. In *P. jezoensis*, significant responses to WC were
445 recognized only in pioneer roots. Our results did not support both hypotheses (Fig.1);
446 rather, the transitions of increased root mean diameter and decreased SRL due to weed
447 control were common in this study (Fig. 5), highlighting that the consistent avoidance
448 strategy for competition independent of root functional type- or species-specific
449 strategies. If strategies for the early acquisition of soil resources are relevant to longer
450 and thinner fine roots (Ostonen et al. 2007), the responses of decreasing diameter and
451 increasing SRL are expected against competition (Fig. 1). The thinner and greater SRL
452 of pioneer roots under no weed control also raises the question of whether the collected
453 pioneer roots were mature. At least in *A. sachalinensis*, the average diameter in late
454 autumn (i.e., November) was evidently lower than that immediately after the snow
455 melted (i.e., April), and the SRL was more than twice as large (Sugai et al. 2024b).
456 Although the present conditions of competition as well as soil varied with the study site
457 of Sugai et al. (2024b), competition may postpone the maturation period of these thinner
458 and longer fine roots as pioneer roots. In fact, this study was able to significantly induce
459 a twofold difference in the biomass of vegetation roots (Table 3). Although the
460 vegetation roots detected in WC may reflect their growth approximately 2 months after
461 the last weeding, the fall season is generally the final stage of root growth of boreal
462 herbaceous plants, and its competitive impacts could be weak (Steinaker et al. 2010).

463 The lack of significant correlations between pioneer root morphology and vegetation
464 roots indicated that indirect factors other than the biomass of competing vegetation may
465 induce morphological changes, at least in *P. jezoensis* (Table 4), such as the allelopathic
466 effect of root exudates (Bi et al. 2022). A recent study reported that root exudates
467 experimentally isolated from *Pinus sylvestris* reduced or increased the root length and
468 biomass of Chinese desert vegetation. This finding indicates that competition varies
469 markedly with the functional type of vegetation (Balandier et al. 2006). Particularly in
470 plantations in Hokkaido, planted seedlings are often covered by dwarf bamboo, and
471 studies regarding their impacts and management practices have progressed extensively
472 (e.g., Yoshida et al. 2023). Given that the impacts of weeds on the root morphology of
473 planted seedlings can vary among their species and combinations (Balandier et al.
474 2006), competing vegetation may also have the potential to induce morphological
475 changes in the roots of planted seedlings. In this study, however, the facilitative effects
476 of coexistence with unmanaged weeds were not detected, at least in terms of growth or
477 biomass (Table 2). Thus, the significant correlations between average root diameter and
478 vegetation roots reflect the variation in belowground competitive ability among tree
479 species as well as among root types (Beyer et al. 2013, Semchenko et al. 2018).
480 It should be noted that the present study did not clarify the mechanisms by
481 which the fibrous roots of *P. jezoensis* did not respond to competition. The root
482 elongation of *P. glehnii* seedlings stopped in the middle of November (Satoh 1995), and
483 the current SRL and RTD values were similar to those of the mature fine roots of *P.*
484 *abies* (Ostonen et al. 2007). These studies indicated that the present fibrous roots were
485 not immature. Given that the relatively thick fibrous roots of *A. sachalinensis*
486 significantly decreased in response to competition, the thin fibrous roots of *P. jezoensis*
487 under WC may not have been thinner. Similarly, very fine roots less than 0.5 mm in

488 diameter are widely observed in woody species (Majidi et al. 2008, Makita et al. 2011).
489 Compared with that of fine roots 0.5–1.0 mm in diameter, the SRL of very fine roots in
490 *P. abies* did not respond to thinning residue input, which could improve soil resource
491 availability (Majidi et al. 2008). Given that the functions of fine roots are relevant to
492 their anatomical traits (e.g., Masumoto et al. 2022), there is still room to evaluate
493 whether nonsignificant changes in fibrous root diameter are responsible for competition.
494 However, the fibrous roots of *P. jezoensis* may prioritize their quantitative responses
495 over their morphological responses (Table 2). As discussed above, these findings are
496 consisted with previous studies (Freschet et al. 2015). On the basis of a study of 12
497 herbaceous species grown under factorial combinations of high/low light and fertilizer
498 treatments, Freschet et al. (2015) reported that the adjustment of root biomass allocation
499 would be more important than the adjustment of SRL in regulating the relative length of
500 root plants that explore the soil. More interestingly, quantitative changes in the organs
501 (i.e., resource allocation) rather than qualitative changes (i.e., morphological
502 modifications) in response to competitive conditions were also observed in the shoots of
503 *P. jezoensis*. Although the mechanism underlying the lack of morphological change is
504 still unclear and the integrated competitive strategies between above- and belowground
505 over the scope of this study, it may be important for *Picea* sp. with very fine fibrous
506 roots to change the distribution of resources within the fine root system against
507 competition.
508
509 **Implication based on interspecific variation**
510 It has reported that *P. jezoensis* adopts an avoidance strategy under the canopies
511 of mature trees, i.e., competitive conditions for light, and *A. sachalinensis* adopts a
512 tolerance strategy (Fujimoto & Shimada 1991). However, this study revealed that *A.*

513 *sachalinensis* maintained branch length under competition, which may avoid
514 competition. Moreover, *A. sachalinensis* developed shoots with low C/F, suggesting
515 that morphological tolerance strategy was also adopted. The interspecific variation in
516 aboveground morphological responses to competition may be associated with
517 differences in shade tolerance and regeneration processes. As both *A. sachalinensis* and
518 *P. jezoensis* often rely on regeneration on fallen logs, they can avoid biotic impacts,
519 such as competition and pathogens originating from the soil, but are often present under
520 the canopy, i.e., shaded conditions. Iijima et al. (2009) reported that *A. sachalinensis*
521 has a relatively higher survival rate under low light conditions than *P. jezoensis*, and
522 that *A. sachalinensis* can also regenerate on the forest floor. The seedlings regenerating
523 on the forest floor should encounter competition sooner than those regenerating on
524 fallen logs. Thus, *A. sachalinensis* may have developed strategies against competition
525 more than *P. jezoensis*.
526 Nevertheless, no differences in growth or biomass responses to WC were
527 detected across the species in this study (Table 2). Thus, the question arises as to
528 whether *P. jezoensis* has a disadvantageous morphology against competition. This may
529 be associated with greater dependence on the conditions of complete freedom from
530 competition, such as gap formation and after disturbance (Nishimura et al. 2010,
531 Takahashi et al. 2019). In general, *Picea* sp. is a more long-lived tree species compared
532 to *Abies* sp. (Takahashi 1996, Day et al 2014). Takahashi (1996) reported that *Picea*. sp.
533 may show a passive aboveground morphological response to competitive conditions. In
534 fact, severe shade treatment killed only *P. jezoensis* seedlings, and not *A. sachalinensis*
535 seedlings (Ishizuka & Sugai 2021). However, the mortality of *A. sachalinensis*
536 seedlings increases immediately after exposure to canopy opening (Tsunoda et al.
537 2024). In particular, canopy opening in winter can cause severe photoinhibition and

538 growth suppression in *A. sachalinensis* seedlings (Kitao et al. 2018). Given the greater
539 density of needles on branches in *Picea* sp. than in *Abies* sp., the densification of short
540 branches under shaded conditions may help maintain the survival rate by preventing the
541 sudden intense light stresses produced by gaps from shining down on the entire shoot.
542 In addition, liberation from competition increases the photosynthetic rates of *P. glauca*,
543 and their foliage can rapidly acclimate to open conditions (Lieffers et al. 1993).
544 Although whether these responses are common in *A. sachalinensis* is unclear, *Picea* sp.
545 may have superior growth abilities for the conditions after overcoming competition.
546 Even though aboveground competitive strategies significantly differ between
547 species, the fine roots of both species presented similar responses in terms of their
548 morphological traits. Although the number of pioneer roots was significantly lower in
549 *P. jezoensis* (Table 2), the relative number of pioneer roots per belowground biomass
550 was greater in *A. sachalinensis* even without WC (data not shown). Thus, at the
551 individual scale, it was unclear which species presented the significant functional
552 suppression of pioneer roots. However, the consistent responses among species, at least
553 in the pioneer roots (Fig. 5), suggest that the belowground competitive strategy does not
554 always correspond to the aboveground strategy (Asefa et al. 2022). In general,
555 compared with resources in the atmosphere (e.g., light, CO_2), soil resources (e.g., water,
556 nutrients) are distributed unevenly and are often depleted. The preemptive strategy to
557 access unexplored soil space should provide an advantage in the subsequent competition
558 (Begon et al. 2006, Cabal et al. 2024). Thus, even in pioneer roots, it may be plausible
559 to get thinner and longer against competition to early access the available rhizosphere.
560 On the other hand, it should also be noted that multiple traits, which did not marginally
561 meet the set significance level (Table 2), may reflect interspecific difference in other
562 competitive strategies. This is relevant to the split-plot design. Given that the design is

563 generally not sensitive to detect interaction effects (Mizuguti 2011), it is important to
564 adopt an optimal experimental design to elucidate the complex mechanisms of plant
565 coexistence.
566
567 **Conclusion**
568 This study revealed that weed control (WC) significantly modified the above-,
569 and belowground morphological traits of planted boreal coniferous seedlings. Both
570 target species, *A. sachalinensis* and *P. jezoensis*, adopted species-specific aboveground
571 strategies against competition. The results suggested that tolerance and partial
572 avoidance of aboveground competition were recognized simultaneously in *A.*
573 *sachalinensis* seedlings. This is empirical evidence that competition strategies cannot be
574 completely divided into two categories, i.e., tolerance or avoidance, at least when they
575 are based on shoot morphological traits. In contrast, the belowground morphological
576 responses to WC consistently demonstrated an avoidance strategy regardless of the
577 species. The response of pioneer roots to WC highlighted the general importance of
578 preempting soil space even among species with different aboveground competitive
579 strategies. These results confirm the remarkable plasticity of fine root systems in
580 response to weed control. Given that root morphology is relevant to multiple functions,
581 merely removing the aboveground parts of weeds could uniformly affect the
582 belowground ecological functions in plantations. At an individual scale, fine roots have
583 critical roles in survival and growth, especially in the early stages of trees. Also, fine
584 roots are generally more vulnerable to environmental stresses such as drought and low
585 temperatures than shoots. Therefore, in the novel plantation management under climate
586 change, it will be important to guide roots to grow under optimal conditions in space
587 and time by biotic and abiotic environmental modifications, including weed control.

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592 **Declaration of interest statement**

593 The authors declare that they have no conflict of interest.

594 **Data availability**

595 The data developed during the current study is available from the corresponding author
596 on reasonable request.

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779 Table 1. Summary of ANOVA results (n = 6) for the traits between weed control (WC), species (S), and its interaction (WC×S). *F*: *f* value; *P*: *P* value.
780 RCD: root collar diameter. SRL: specific root length; RTD: root tissue density.
781

			Weed control (WC)		Species (S)		WC × S	
Level	Trait		*F*	*P*	*F*	*P*	*F*	*P*
Individual	RGR	Height	0.89	0.39	3.54	0.07	0.29	0.60
		RCD	18.48	<0.01	0.90	0.35	0.70	0.41
	Total dry mass	Aboveground	28.18	<0.01	1.88	0.19	0.01	0.92
		Belowground	33.91	<0.01	1.72	0.20	0.06	0.81
		Woody root	50.00	<0.05	1.01	0.33	0.31	0.59
		Fine root (< 2mm)	19.39	<0.05	2.31	0.14	0.02	0.89
		Fine root ratio	25.27	<0.05	0.14	0.71	1.06	0.32
		R/S ratio	0.17	0.69	0.01	0.92	0.05	0.82
	Morphology	Shoots	1.88	0.23	102.65	<0.001	13.34	<0.01
		Pioneer roots	4.88	<0.05	3.04	0.10	1.28	0.27
Shoot	Dry mass	Branch	12.86	<0.05	0.05	0.82	3.12	0.09
		Leaves	2.30	0.19	3.84	0.06	0.09	0.76
	Total leaf number		6.87	<0.05	1.48	0.24	0.42	0.52
	Total leaf area		3.01	0.14	46.52	<0.001	1.83	0.19
	Shoot length		2.67	0.16	10.05	<0.01	3.71	0.07
	Length/Base diameter ratio		2.02	0.21	5.02	<0.05	0.33	0.57
	C/F ratio		65.22	<0.001	6.13	<0.05	17.56	0.00
	Specific branch length		17.68	<0.01	7.73	<0.05	0.08	0.80
	Leaf area		0.20	0.68	86.43	<0.001	0.47	0.50
	SLA		1.13	0.34	45.49	<0.001	4.83	<0.05
Root	Pioneer root	Average diameter	5.27	0.07	15.81	<0.001	3.13	0.09
		SRL	9.60	<0.05	12.55	<0.01	3.30	0.08
		RTD	2.22	0.20	10.96	<0.01	2.11	0.16
	Fibrous root	Average diameter	0.22	0.66	6.12	<0.05	10.99	<0.01
		SRL	0.75	0.43	7.13	<0.05	12.71	<0.01
		RTD	0.76	0.42	0.33	0.57	1.69	0.21

782

Table 2. The average and standard error values in growth, biomass, and morphological traits at individual level (n = 6). The different letters denote significant differences between species and weed control treatment (P<0.05). WC: weed control; NWC: no weed control; RCD: root collar diameter. The part of data regarding RGR and above-, and belowground dry mass are from Sugai et al. (2024a).

			Picea jezoensis		*Abies sachalinensis*	
Trait		Unit	NWC	WC	NWC	WC
RGR	Height	cm $cm^{-1}year^{-1}$	0.13 ± 0.02 a	0.19 ± 0.02 ab	0.19 ± 0.019 ab	0.29 ± 0.03 b
	RCD	mm $mm^{-1}year^{-1}$	0.09 ± 0.01 a	0.29 ± 0.02 b	0.12 ± 0.021 a	0.28 ± 0.02 b
Dry mass	Aboveground	g $plant^{-1}$	23.13 ± 5.37 a	97.61 ± 11.36 b	15.07 ± 1.952 a	69.41 ± 11.77 b
	Belowground	g $plant^{-1}$	10.22 ± 1.71 a	49.40 ± 5.24 b	6.92 ± 0.619 a	34.87 ± 6.16 b
	Woody root	g $plant^{-1}$	3.85 ± 0.85 a	27.97 ± 3.64 b	2.42 ± 0.283 a	17.17 ± 3.78 b
	Fine root (< 2mm)	g $plant^{-1}$	6.37 ± 0.91 a	21.43 ± 1.79 b	4.50 ± 0.371 a	17.70 ± 2.64 b
	Fine root ratio	%	63.53 ± 2.47 a	44.61 ± 2.40 b	65.44 ± 1.728 a	52.37 ± 3.34 ab
	R/S ratio	g g^{-1}	0.47 ± 0.04 a	0.52 ± 0.04 a	0.48 ± 0.04 a	0.50 ± 0.03 a
Morphology	Shoots	no. $plant^{-1}$	44.83 ± 3.19 ab	53.17 ± 2.07 a	21.00 ± 1.434 c	35.83 ± 2.13 b
	Pioneer roots	no. $plant^{-1}$	3.17 ± 1.21 a	19.67 ± 2.81 b	7.67 ± 2.663 c	25.00 ± 2.90 b

Table 3. Belowground competitive condition and soil properties in no weed control and weed control, and results of Welch's *t* test (n = 6). *T*: *t* value; *: $P < 0.05$; **: $P < 0.01$.

	Bulk density (g cm^{-3})	Vegetation roots (mg g^{-1})	Gravel (mg g^{-1})
No weed control	0.84 ± 0.01	1.12 ± 0.13	146.32 ± 5.00
Weed control	0.91 ± 0.01	0.52 ± 0.94	146.33 ± 0.02
T	-3.36*	4.02**	0.00

Table 4. Summary of correlation coefficients between the vegetation roots and the morphological traits of pioneer roots and fibrous roots (n = 12). SRL: specific root length; RTD: root tissue density; *: P <0.05; ***: P <0.001.

	Pioneer root		Fibrous root	
	Picea jezoensis	*Abies sachalinensis*	*Picea jezoensis*	*Abies sachalinensis*
Average diameter	-0.41	-0.68*	-0.03	-0.70*
SRL	0.37	0.85***	0.00	0.61*
RTD	-0.25	0.01	-0.03	-0.12

Table 5. Summary of ANOVA results (n = 6) for the traits between vegetation roots (V), root functional type (R), and its interaction (V×R). *F*: *f* value; *P*: *P* value. SRL: specific root length; RTD: root tissue density. *: $P < 0.05$; **: $P < 0.01$.; ***: $P < 0.001$.

Species	Trait		Vegetation roots (V)	Root type (R)	V × R
Abies sachalinensis	Average diameter	*F*	0.88	17.39	4.88
		P	0.36	<0.001***	<0.05*
	SRL	*F*	9.99	4.59	0.05
		P	<0.01**	<0.05*	0.83
	RTD	*F*	0.25	1.74	0.13
		P	0.62	0.2	0.72
Picea jezoensis	Average diameter	*F*	0.00	27.83	1.93
		P	0.98	<0.001***	0.18
	SRL	*F*	0.00	17.36	0.11
		P	0.99	<0.001***	0.75
	RTD	*F*	0.01	3.67	0.12
		P	0.92	0.07	0.73

812 Figure captions:

813 Fig. 1: Conceptual scheme of the relationship between fine root morphology and
814 strategy against competition. The ability to grow thinner and longer fine roots is
815 associated with superior resource acquiring in the avoidance strategy against
816 competition, whereas thicker and high tissue density of fine roots is relevant to efficient
817 resource transporting in the tolerant strategy. Besides, fine roots can be functionally
818 classified into relatively shorter and thinner fibrous roots with superior absorptive
819 functions and well developed, longer and thicker pioneer roots with transport functions.
820 The first hypothesis (H1) is that the morphological responses of fine roots are specific
821 to root functional types, facilitating the function specific to each root type. If this is the
822 case regardless of species, it suggests that the competitive strategies may be
823 independent between above and belowground. The second hypothesis (H2) is that the
824 fine root responses are specific to species, and morphological changes occur according
825 to the competitive strategy adopted by each species. If this is true, it suggests that the
826 common competitive strategy may be adopted above and belowground. The arrows
827 denote the direction of the response to the competition. Solid line: fibrous roots, dotted
828 line: pioneer roots, black line: *A. sachalinensis*, and gray line: *P. jezoensis*.

829 Fig. 2: Shoot functional traits between weed control and species (n = 6), including the
830 dry mass (A-C), morphology (D, E, H), and the ratio of dry mass and/or morphology (F,
831 G, I). Different color bars, except for those in A, denote different treatments. Different
832 letters denote significant differences between weed control and species (P<0.05). In the
833 panel A, different color bars denote different organs. Different capital and lowercase
834 letters denote significant differences in leaf and branch dry mass between weed control
835 and species, respectively. WC: weed control; NWC: no weed control.

836 Fig. 3: Variation in functional trait responses of pioneer roots (A, C, E) and fibrous
837 roots (B, D, F) between weed control and species (n = 6). Different color bars denote
838 different treatments. Different letters denote significant differences between weed
839 control and species (P<0.05). WC: weed control; NWC: no weed control.

840 Fig. 4: Relationship between average fine root diameter and vegetation root mass in
841 each species (n=12). Note that both parameters are logarithmized. Black points with
842 long-dash regression lines and grey points with dotted regression lines denote the values

of pioneer roots and fibrous roots, respectively. R^2 denotes the coefficient of determination (**: P <0.01).

Fig. 5: Relationship between average fine root diameter and specific root length in each species and each root type (n=12). Note that both parameters are logarithmized. Square points with dotted regression lines and triangle points with long-dash regression lines denote the values of fibrous roots and pioneer roots, respectively. White and black points denote the values at no weed control (NWC) and at weed control (WC), respectively. R^2 denotes the coefficient of determination (***: P <0.001).