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Genotypic variations appear in fine root morphological traits of *Cryptomeria japonica* trees grown in a common garden

Ryo Nakahata[1,2] | **Wakana A. Azuma**[2,3] | **Tomoko Tanabe**[2,4] | **Kiyosada Kawai**[5] | **Tsutom Hiura**[6]

[1]Graduate School of Agricultural and Life Sciences, The University of Tokyo, Tokyo, Japan

[2]Graduate School of Agriculture, Kyoto University, Kyoto, Japan

[3]Graduate School of Agricultural Science, Kobe University, Kobe, Japan

[4]Graduate School of Global Environmental Studies, Kyoto University, Kyoto, Japan

[5]Japan International Research Center for Agricultural Sciences (JIRCAS), Tsukuba, Japan

[6]Department of Ecosystem Studies, The University of Tokyo, Tokyo, Japan

Correspondence
Ryo Nakahata, Graduate School of Agricultural and Life Sciences, The University of Tokyo, Tokyo 113-8657, Japan.
Email: ryo.nkht@gmail.com

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Abstract

Fine root morphological traits regulate the belowground resource acquisition strategies of trees. Therefore, investigating genotypic variations isolated from environmental variations within tree species helps in understanding how genotypic backgrounds affect intragenerational tree acclimation to the growing environment. Thus, this study aimed to clarify the effects of genotypic variations on the fine root morphology of three types of Japanese cedar (*Cryptomeria japonica*), which were derived from different provenances but were grown in a common garden. In the three geographically different provenances of *C. japonica* stands (Yanase, Yoshino, and Yaku), fine root morphological traits, such as root length and diameter and specific root length (SRL), were measured for each root up to the 4th branching order. Yaku cedar exhibited root traits distinct from the other provenances, such as growing longer and thinner roots in 1st root order to enhance root surface area. In addition, the SRL patterns with root orders and higher root tissue density suggested a resource conservation strategy. Yanase cedar demonstrated a significantly higher root branching ratio and specific root tips than the other provenances, indicating a strategy for investing resources in absorptive roots. Although Yoshino cedar had traits similar to those of Yanase cedar or intermediate between Yanase and Yaku cedars, high aboveground production may be achieved through nutrient acquisition with root exudates instead of absorptive root growth. Genotypic variations appeared in fine root morphological traits of *C. japonica* trees, even when grown in the same environments, implying distinct resource acquisition strategies characterized by each provenance.

KEYWORDS

Cryptomeria japonica, fine root morphology, genotypic variation, intraspecific variation, root branching order

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1 | INTRODUCTION

In forest ecosystems, belowground environmental conditions are generally more spatially heterogeneous and complicated compared with the aboveground environments, owing to multiple factors in various chemical materials, edaphic physical structures, and diverse microbiota compositions (Gallardo, 2003; Schoenholtz et al., 2000; Townsend et al., 2008). Therefore, perennial plants, which are anchored at a fixed position throughout their lifespan, change their resource acquisition strategies by regulating their root functional traits to adapt to each environment. Because of this adaptation, plants have belowground functional diversity with inter- and intraspecific variations, especially in the distal root systems (Ma et al., 2018; Weemstra et al., 2021).

Generally, roots less than 2 mm in diameter are referred to as fine roots (e.g., Pregitzer et al., 2002) and are further divided into absorptive and transport roots based on their physiological functions (McCormack et al., 2015). The functional heterogeneity within fine root systems appears as phenotypic variations in anatomical and morphological traits (Hishi, 2007; Hishi et al., 2017). Fine root length, diameter, and branching order, are closely related to physiological functions, such as absorptive and transport capacities, lifespan, and mycorrhizal colonization, at the individual root level (Hishi et al., 2017; McCormack et al., 2012, 2015) and they are sensitive to changing environments at the population level (Doi et al., 2017; Kramer-Walter et al., 2016; Ostonen et al., 2007; Wada et al., 2019). In general, the absorptive capacity and turnover rate (i.e., the inverse of lifespan) of individual roots increase with increasing specific root length (SRL: root length per root mass) and decreasing root tissue density (RTD: root mass per root volume) (Eissenstat, 1991; McCormack et al., 2012; Ostonen et al., 2007). Therefore, plant physiological characteristics and environmental adaptations can be evaluated by measuring root morphological traits (Guo et al., 2008; McCormack et al., 2015; Pregitzer et al., 2002). Furthermore, apart from pioneer roots that elongate during the initial phase of the root system development (Eissenstat & Achor, 1999; Nakahata, 2020; Zadworny & Eissenstat, 2011), root functional types are predetermined by root branching orders (Hishi, 2007; Hishi et al., 2017; Pregitzer et al., 2002; Tawa & Takeda, 2015). Thus, the evaluation of morphological traits for each root order in well-developed distal root systems is useful for identifying significant differences in adaptive root responses among plant individuals or populations.

In fine root morphological traits, inter- and intraspecific variations are caused by genotypic factors derived from evolutionary backgrounds (i.e., intergenerational adaptation) and environmental factors determined by the environmental circumstances where individuals grow (i.e., intragenerational acclimation). The evolutionary background of plants regulates their root morphological traits as a consequence of long-term natural selection spanning many generations (Guo et al., 2008; Ma et al., 2018). Nevertheless, even within the same species, fine root morphological traits change considerably with environmental conditions, possibly due to altitudinal or latitudinal gradients (Ostonen et al., 2007; Weemstra et al., 2021; Zadworny et al., 2016, 2017) and variations in soil chemical properties (Doi et al., 2017; Wada et al., 2019). Therefore, elucidating how the root morphological traits are predetermined by genotypic background, and how these root traits have plasticity in response to growing environments, is essential for understanding and predicting the response of trees and forest ecosystems to the environmental changes expected over the next several decades.

To date, interspecific variations in fine root morphological traits among different environments have been investigated using root order classification (Eissenstat et al., 2015; Pregitzer et al., 2002) and intraspecific variations of those have been conducted (Doi et al., 2017; Wada et al., 2019; Zadworny et al., 2016, 2017). The former often involves species variation caused by site-specific environments, making it difficult to distinguish trait variations based on genotypic or environmental factors. In contrast, the latter can reveal variations owing to environmental factors if the species is not genotypically differentiated. However, genotypic variations due to geographical differences are expected in the belowground and aboveground morphological traits of trees. Genotypic variations of aboveground parts within a single species have been recognized in foundation species distributed across broad regions: for example, Japanese beech (*Fagus crenata*) and cedar (*Cryptomeria japonica* D. Don) in the Japanese Archipelago (e.g., Azuma et al., 2023; Hiura, 1998; Osada et al., 2015), and European beech (*Fagus sylvatica*), Scots pine (*Pinus sylvestris*), and Norway spruce (*Picea abies*) in Europe (e.g., Benavides et al., 2021; Vilà-Cabrera et al., 2015).

C. japonica, an evergreen conifer, is broadly distributed across the Japanese Archipelago and comprises geographically differentiated or cultivated populations that exhibit various genotypic and phenotypic adaptations to the local environments (Hiura et al., 2021; Nishizono et al., 2014; Ohta & Hiura, 2023; Saito et al., 2023; Tsumura, 2023). Thus, *C. japonica* is one of the most suitable species for investigating genotypic variations in morphological traits based on broad geographic variations and cascading effects within a single species (Hiura, 2023). However, genotypic variations in the fine root morphological traits of a single

species remain unclear because it is difficult to separate the genotypic variations from trait variations owing to the growing environments. To quantify the effects of intraspecific genotypic variation in root morphological traits while ignoring environmental effects, it is required to verify the differences among trees with different genotypic backgrounds that have grown in a common environment. Therefore, the aim of this study was to clarify the influence of genotypic variations on the belowground resource acquisition strategy of three genotypes of Japanese cedars (*C. japonica*), which are derived from different provenances but grown in a common garden, by evaluating the distal root morphological traits for each root branching order.

Three similar-aged (ca. 50 years old) *C. japonica* stands, comprising cedars from the Yanase, Yoshino, or Yaku provenances, have already been investigated for aboveground growth and physiological characteristics in a common garden where this study was conducted (Azuma et al., 2023; Ohta et al., 2019). In exchange for physical resistance to inclement weather conditions in Yaku provenance (Kijidani et al., 2001; Nishi & Higashi, 1938; Numata, 1986), the growth characteristics and productivity (e.g., the annual stem growth rates and litterfall production) of Yaku cedar were significantly lower than those of Yanase and Yoshino cedars in this common garden. Moreover, Yaku cedar demonstrates higher sapwood density and shallower crown depth than the other two cedar provenances. These indicate slower tree growth and suggest a conservative strategy in allocating carbon resources to belowground parts. Although this conservative strategy of Yaku cedar expects thick root diameter that corresponds to low SRL (Weemstra et al., 2016), the low aboveground growth rate is possibly associated with thin root diameter (Hajek et al., 2013). If RTD is high as presumed by the aboveground sapwood density, thin root diameter can be justified even under the low SRL condition. Meanwhile, root nitrogen concentration, which increases with increasing SRL (Jia et al., 2013), and root exudation rate of low-molecular-mass organic acids (LMMOA) in Yoshino cedar was possibly higher than those in the other two cedar provenances (Ohta et al., 2019), indicating distinct root morphological traits and nutrient acquisition strategies compared with the Yanase cedar which exhibits similar growth characteristics (Azuma et al., 2023). Both increasing SRL and root exudation do not compete functionally with each other; rather, they may have a positive relationship that enhances absorptive functions (Gao et al., 2024). In contrast, Yanase cedar appears to maintain nutrient acquisition by enhancing absorptive root growth or root absorptive capacity (e.g., SRL) rather than relying on root exudation. This is evident in the early growing trees that construct a root system with higher SRL and more root tips (Comas & Eissenstat, 2004). Based on the findings of these studies, different belowground resource acquisition strategies for Yanase, Yoshino, and Yaku cedars were hypothesized as follows: (1) Yanase cedar has root morphological traits indicating resource consumptive strategy with short-lived absorptive root traits (e.g., high SRL) and high branching ratio to enhance nutrient acquisition. (2) Yoshino cedar has high SRL corresponding to the high root nitrogen concentration and employs a distinct foraging strategy, allocating resources to root exudation rather than to absorptive root growth. (3) Yaku cedar is relatively restricted in carbon resources and therefore have thin root diameter and long root lifespan (i.e., lower SRL, higher RTD or both) to enhance carbon use efficiency by increasing the root surface area per root volume and conserve resources for root turnover.

2 | MATERIALS AND METHODS

2.1 | Study site and plant materials

This study was conducted using three stands of Japanese cedars (*C. japonica*), which were derived from different provenances but were grown in a common garden in Wakayama Experimental Forest of Hokkaido University, Wakayama, Japan, at 33° 40′ N, 135° 40′ E. *C. japonica* is the principal species of temperate coniferous forests, which comprise a considerable proportion of the forest area in Japan (Forestry Agency, 2021). The elevation of the study site is ca. 240 m above sea level. The mean air temperature and annual precipitation are 14.7°C and 3564 mm, respectively, which were measured at the Nishikawa meteorological station (1985–2019; Japan Meteorological Agency; 33° 38′ N, 135° 43′ E) located ca. 5 km away from the study site. In this region with the high precipitation, the study site is covered with very thin and weakly developed mineral soil without horizon differentiation (Regosol, based on the World Reference Base) (Kanda et al., 2018). The common garden is located on a south-facing slope across which the soil color (gray), texture (silt and gravel), and depth (<10 cm) are uniform (Ohta et al., 2019). The slope has experienced significant erosion, exposing portions of the underlying bedrock composed of sandstones and mudstones.

Three stands comprised clonal cedars derived from different provenances of Yanase, Yoshino, and Yaku. These stands were established between 1967 and 1973, each covering an area of 0.1, 0.05, and 0.065 ha, respectively, with a density of ca. 2000 trees ha^{-1}. By 2015, the stand density of Yanase, Yoshino, and Yaku stands decreased to 1930, 2000, and 1831 trees ha^{-1}, respectively. As of 2018 when this study was conducted, the

stands were ca. 49, 46, and 52 years old, respectively. These stands were located on a south-facing slope within 50 m of each other and were not managed until the experimental field survey was conducted in 2016 (Ohta et al., 2019).

The native habitats of Yanase, Yoshino, and Yaku provenances are situated either in the Shikoku Island (33° 33′ N, 134° 05′ E), the central part of the Kii Peninsula (33° 53′ N, 135° 41′ E), and the Yakushima Island (30° 18′ N, 130° 30′ E) of the western Japan, respectively. These areas are covered by very thin soils, the basement rocks of which are sandstone and shale for Yanase provenance, sedimentary rocks for Yoshino provenance, and granite for Yaku provenance (Geological Survey of Japan, 2015). The mean air temperature and annual precipitation in Yanase, Yoshino, and Yaku provenances are 15.1°C and 4403 mm, 13.1°C and 1544 mm, and 19.6°C and 4568 mm, respectively (see Azuma et al., 2023). While our study site is geographically closer to Yoshino provenance, it shares climatic similarities with Yanase provenance. Notably, the native habitat of Yaku provenance is the southernmost natural habitat of Japanese cedar and the most unique environment. The soil in this area, derived from volcanic ash produced by the eruption about 7300 years ago, presents oligotrophic conditions (Geshi, 2009; Mukai et al., 2016).

The Yoshino and Yanase cedars had relatively high aboveground growth rates during the early growth stage (ca. <50 years old) than the Yaku cedar (Itaka et al., 2013; Nishizono et al., 2014; Takashima et al., 2009). Moreover, similar relative growth patterns were observed in each stand of the present common garden. In August 2015, mean tree height (±SD: standard deviation) and diameter at breast height (±SD) were 15.4 (±2.64) m and 19.2 (±5.00) cm, 18.3 (±2.10) m and 23.1 (±5.20) cm, and 10.9 (±1.96) m and 18.6 (±4.15) cm in Yanase, Yoshino, and Yaku plantations, respectively (Ohta et al., 2019). The chemical properties of fine roots and soil in the three stands were investigated in 2016 (Table S1). The soil properties had differentiated among stands, likely due to plant–soil interactions during stand growth (Ohta et al., 2019). Further details regarding the site, stand locations, and growth characteristics of each cedar provenance are mentioned in Ohta et al. (2019) and Azuma et al. (2023).

2.2 | Field survey for sampling of intact fine root systems in the common garden

Field surveys for root sampling in the common garden were conducted twice, consecutively in 2018 and 2019. In August 2018, three individuals were carefully selected from each of the three provenances. These individuals were selected from the central part of the plot and spaced at least 5 m apart from each other. They were specifically chosen for their typical growth characteristics and were assessed for aboveground growth and physiological characteristics (Azuma et al., 2023) and root morphological traits (this study). Subsequently, two distal root systems that included individual roots from 1st to 4th root orders were sampled from each selected individual tree as follows.

To sample intact living fine root systems of each individual tree, distal parts of the root systems were exposed at a depth of 5–10 cm in a soil organic layer, where fine roots concentrated enough and were not subjected to dry condition, within approximately 1 m of an individual stem. Fine roots of the target tree individuals were identified by carefully digging soil from the stem base along coarse roots toward the distal parts. Living fine roots were distinguished based on their integrity and color, following Vogt and Persson (1991). Exposed root systems were carefully sampled by detaching them from the soil and detangling other roots using hands and a pair of pruning scissors to ensure that intact root systems completely covered individual roots from 1st to greater than 4th root order without any loss. The sampled root systems were then carefully rinsed with pure water to remove the attached soil. Subsequently, they were wrapped with wet wipes and packed into plastic bags to prevent them from drying and maintain freshness. The samples were immediately placed in a refrigerator until the morphological analyses were performed.

Field root sampling was repeated for three different individuals for each stand in the same manner as in August 2019. Thus, 36 root systems (i.e., two root systems × three individuals × three plots × 2 years) were sampled and processed for the morphological analyses.

2.3 | Morphological analysis of distal root systems based on root order

Samples of root systems were cut into individual roots and separated according to 1st, 2nd, 3rd, and 4th root order classifications counted from the root tips (Pregitzer et al., 2002), using a pair of tweezers and a knife while observing the roots with a microscope (Doi et al., 2017). Roots greater than 4th root order were excluded from the analyses. After cutting and classifying, individual roots of each order were scanned using optical flatbed scanners (GT-X970; Seiko Epson Corp., Nagano, Japan) to measure the morphological traits.

Scanned images were analyzed to evaluate the mean root length (cm) and diameter (mm) and the number of

individual roots (no.) for each root order within a root system using WinRHIZO 2013 (Regent Instruments Inc., Quebec, Canada), a root image analysis software. Subsequently, samples were oven-dried to a constant mass at 65°C, and root mass (g) was weighed.

To further evaluate the morphological traits of the distal root systems, specific root length (SRL; m g^{-1}) and root tissue density (RTD; mg mm^{-3}) for each root order, root branching ratio (RBR; no. $no.^{-1}$) for each pair of consecutive root orders, specific root tip number (SRT; no. mg^{-1}), and specific root tip length (SRTL; cm g^{-1}) for each root system were calculated. SRL was determined as the root length per root mass. RTD was calculated as the root dry mass divided by the fresh root volume which was estimated based on root length and diameter assuming a cylindrical shape. RBR is defined as the individual root number of the $[n]$th root order per root number of the $[n+1]$th root order (Kong et al., 2014). SRT and SRTL were calculated by dividing the root tip number (i.e., the number of 1st order roots) and root tip length (i.e., the length of 1st order roots) by the total root mass from 1st to 4th order roots, respectively (Godbold et al., 2003; Hishi et al., 2017). The SRT and SRTL are indicators representing proportions of absorptive root number and length to the construction cost of a root system.

2.4 | Reconstruction of fine root systems using morphological traits by root branch orders

The schematic diagram of distal root systems from 1st to 4th root orders was constructed by referring to mean root length, diameter, and branching ratio for Yanase, Yoshino, and Yaku cedars, respectively. In the diagram, root length and diameter were assumed to be the same within each cedar type. Individual roots were colored with different thicknesses, representing significant differences in SRL verified by statistical analyses within each root system.

2.5 | Statistical analysis

Differences in the mean values of root length and diameter, SRL, and RTD among the three provenances (Yanase, Yoshino, and Yaku) were examined within each root order. In addition, differences among four root orders (1st, 2nd, 3rd, and 4th root orders) were tested within each provenance using the generalized linear mixed model (GLMM) with the restricted maximum-likelihood (REML) estimation method. Similarly, differences in the RBR among the provenances for each pair of root orders (1st to 2nd, 2nd to 3rd, and 3rd to 4th root order) and in the SRT and SRTL for whole root systems (from 1st to 4th root order) were examined using the same GLMM framework. In the GLMM, the effect of the fixed factor of provenances or root orders was tested as qualitative variables, assuming a normal error distribution of response variables, considering the identity link function, and including random variation of individual trees.

To verify the relationships between morphological traits and their consistency among provenances, correlations of root diameter either with root length, SRL, or RTD were evaluated using the GLMM with the REML estimation. Fixed effects of the logarithm of root diameter, tree provenance, and their interaction were analyzed, assuming a gamma distribution for response variables with the log link function and considering random variation of the individual trees.

Significant differences among provenances or root orders were determined based on if the P value was less than 0.05. These statistical calculations were performed using the R statistical software (version 3.5.0; R Development Core Team, 2018), and the GLMM estimation was implemented using the R package "lme4" (Bates et al., 2015).

3 | RESULTS

For 2nd, 3rd, and 4th root orders, means of individual root length were not significantly different among the three provenances (GLMM, $P > 0.48$; Figure 1a), whereas for 1st root order, the root length was higher in Yaku cedar than in the others ($P = 0.002$). The mean diameter of 1st order roots in Yaku cedar was significantly lower than that of the others ($P = 0.004$; Figure 1b), which is consistent with our 3rd hypothesis, although the differences were not significant among the provenances for 2nd and higher root order levels ($P > 0.15$). There were no significant differences in the SRL among the provenances for all root orders ($P > 0.07$; Figure 1c). Overall, the mean SRL of Yanase and Yoshino cedars varied largely between the 3rd and 4th root orders ($P < 0.001$), whereas the difference of SRL in Yaku cedar was not significant ($P = 0.056$). The SRL of Yaku cedar showed significant differences at 1st and 2nd root orders from 4th root order level ($P < 0.001$; Figure 1c). The RTD varied significantly with different root orders, exhibiting increasing trends with increasing root orders in each provenance (Figure 1d). Significant differences in the RTD among the three provenances were observed in 2nd and 3rd root orders, suggesting the RTD values of Yaku

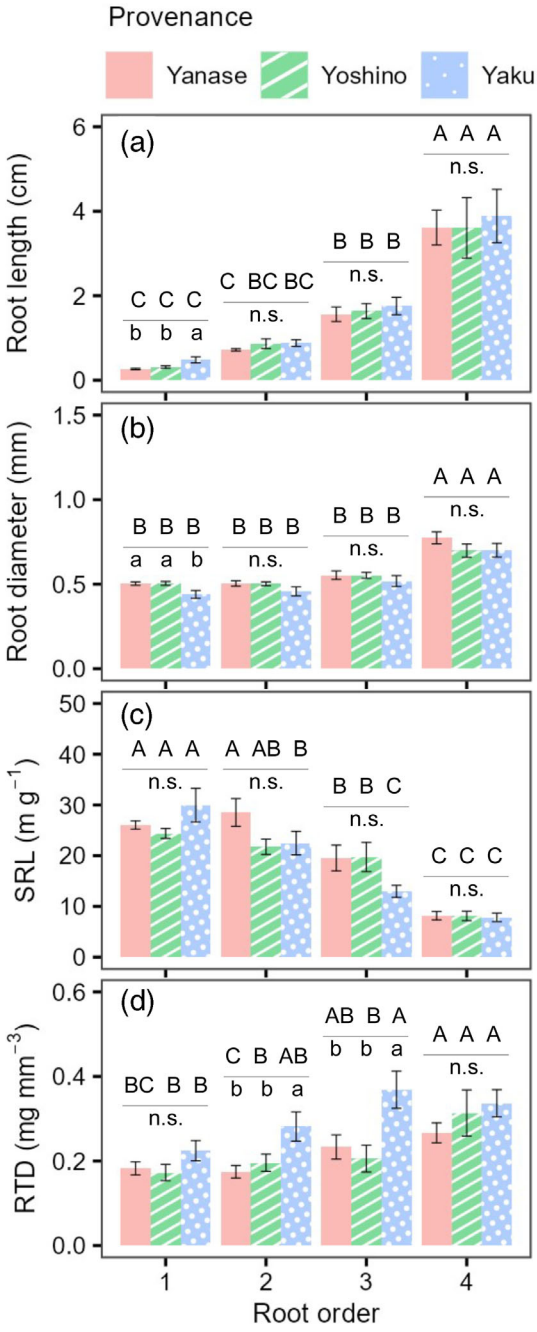


FIGURE 1 Mean values (±standard error, $n = 12$) in (a) root length, (b) root diameter, (c) specific root length (SRL), and (d) root tissue density (RTD) among root orders or tree provenances. Different capital or small letters indicate significant differences among the root orders or tree provenances, respectively (GLMM, $P < 0.05$), and n.s. denotes no significant difference.

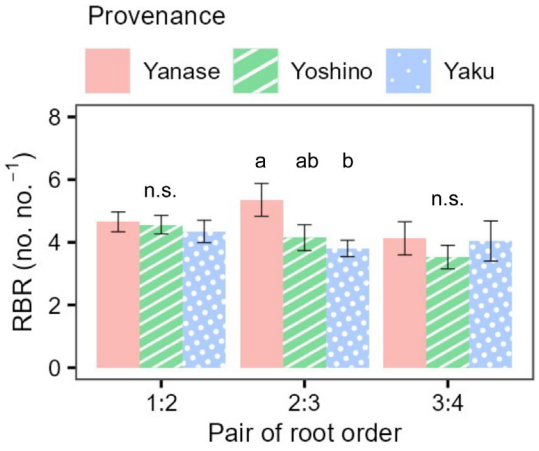


FIGURE 2 Mean values (±standard error, $n = 12$) in root branching ratio (RBR) among tree provenances for each pair of root orders. Different letters indicate significant differences among the tree provenances (GLMM, $P < 0.05$), and n.s. denotes no significant difference.

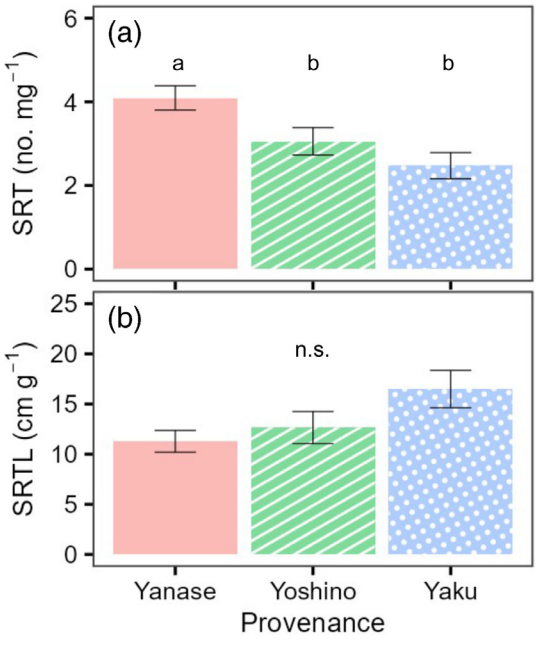


FIGURE 3 Mean values (±standard error, $n = 12$) in (a) specific root tips (SRT) and (b) specific root tip length (SRTL) among tree provenances. Different letters indicate significant differences among the tree provenances (GLMM, $P < 0.05$), and n.s. denotes no significant difference.

cedar were greater than those of the other two provenances ($P < 0.02$; Figure 1d).

The RBR between the 2nd and 3rd order roots was significantly higher in Yanase cedar than in the other two provenances (GLMM, $P = 0.02$; Figure 2), although no significant difference among the provenances was found in the other pairs of root orders ($P > 0.75$).

The SRT was the highest in Yanase cedar compared with the other provenances (GLMM, $P < 0.001$; Figure 3a), as the mean value of Yanase cedar was approximately twice that of Yaku cedar. There was no

significant difference in the SRTL among the three provenances ($P = 0.16$; Figure 3b), although the mean SRTL decreased in the following order: Yaku > Yoshino > Yanase cedars.

For all root orders, the relationships between individual root diameter and length indicated concave patterns in which the root length increased with increasing root diameter (Figure 4a). These relationships were consistent among the three provenances (GLMM, $P > 0.33$). In contrast, the SRL decreased exponentially with increasing root diameter (Figure 4b). Although the regression curves seem to differ among the provenances, the differences in slopes in the current GLMM were marginal and not significant between the Yanase and Yaku cedars ($P = 0.06$). Furthermore, the RTD did not demonstrate a significant relationship with the root diameter for any cedar provenance ($P > 0.27$; Figure 4c).

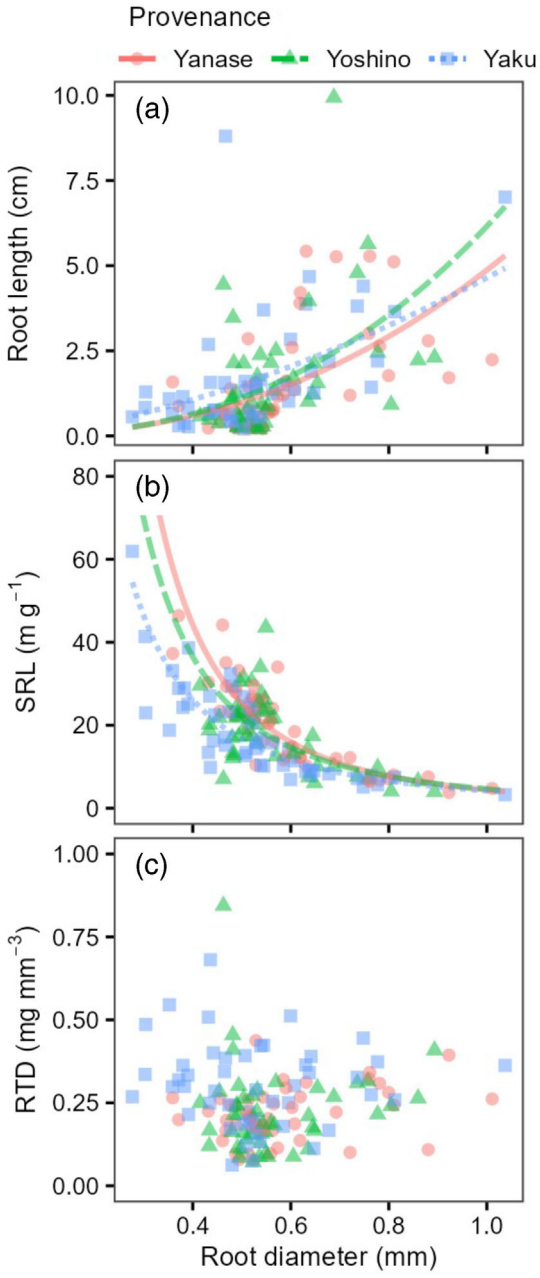


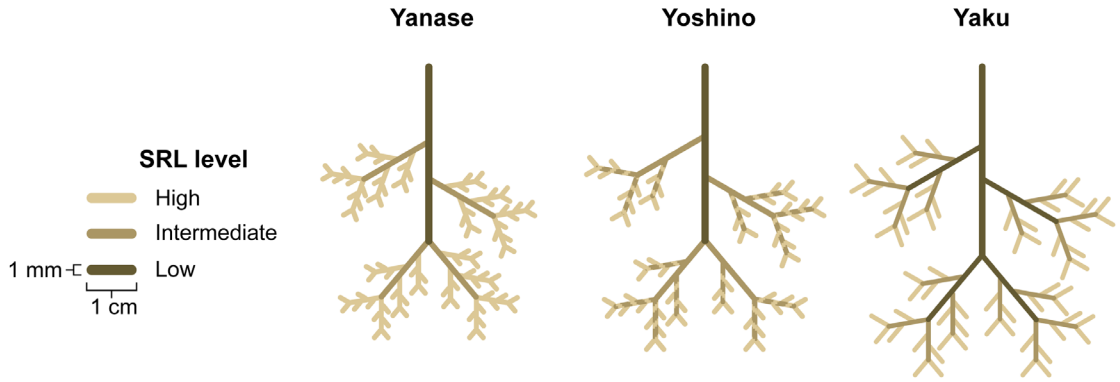
FIGURE 4 Relationships between root diameter and (a) root length, (b) specific root length (SRL), or (c) root tissue density (RTD) for each tree provenance. Symbols indicate the mean values within each root order, and lines represent significant regression curves ($P < 0.05$) for each provenance by the GLMM analyses. These regression curves were consistent among the three provenances ($P > 0.05$).

4 | DISCUSSION

This study is among the few that assessed intraspecific variations in fine root morphological traits mainly caused by different genotypic backgrounds, using three provenance types of *C. japonica* trees planted in a common garden. The study suggested that intragenerational tree acclimation to the growing environment, that includes soil chemical alteration by plant–soil interactions (Ohta et al., 2019), is possibly affected by genotypic backgrounds. Previous studies evaluating fine root morphological and anatomical traits of *C. japonica* have mainly focused on trait variations among root orders and their plasticity in response to environmental conditions and stand age (Hishi et al., 2017; Tawa & Takeda, 2015; Wada et al., 2019). Although fine root morphological traits have plasticity in response to growing environments (Doi et al., 2017; Wada et al., 2019; Zadworny et al., 2017), our common garden experiment suggests that intraspecific variations in fine root morphology can be determined not only by environmental conditions but also by genotypic differences in trees.

4.1 | Functional shift between absorptive and transport roots along root order

The SRL of Yanase and Yoshino cedars changed significantly at 3rd root order from that at 4th root order where transport roots were presumed, while the significant change from 4th root order appeared at 2nd root order in Yaku cedar. Root orders up to 2nd or 3rd levels are regarded as absorptive roots because they possess intact cortical cells, whereas root orders higher than them are considered transport roots (Freschet & Roumet, 2017; McCormack et al., 2015). Therefore, these results indicate that the root order in which root physiological functions shift largely between short-lived absorptive and long-lived transport roots differs among the provenances (Figure 5). The absorptive roots of Yaku cedar might be confined to more distal parts (1st and 2nd root orders) of the root system compared to Yanase and Yoshino cedars.



Aboveground productivity (Azuma et al. 2023)	High	High	Low
Root exudation rate (Ohta et al. 2019)	Low	High	Low
Foraging strategy	Resource consumptive for root growth	Resource consumptive for root exudate	Resource conservative

FIGURE 5 Schematic diagram of distal root systems from 1st to 4th root orders and summary of presumed foraging strategy for each cedar type (Yanase, Yoshino, and Yaku). The root diagram was constructed by referring to mean root length, diameter, and branching ratio from our results (Figures 1a, b and 2). Different root colors represent significant differences in specific root length (SRL) within each root system (c). Striped colors indicate no significant difference from just upper and lower root orders (e.g., 2nd order roots in Yoshino cedar). Aboveground productivity and root exudation rate in three cedar types were summarized from Ohta et al. (2019) and Azuma et al. (2023). Foraging strategy for each provenance was discussed in the Discussion section. The illustration was created by referring to Doi et al. (2017) and Wada et al. (2019).

In the previous studies, anatomical analyses of each root order for *C. japonica* demonstrated that high-absorptive primary roots without a cork cambium were found in 1st and 2nd order roots, while higher-order roots comprised almost of less-absorptive secondary roots with a cork cambium (Hishi et al., 2017; Tawa & Takeda, 2015), which corresponds with the changes in root functional types with root orders of Yaku cedar. Alternatively, the analyses for each diameter class suggested 0.6 mm as a rough boundary for distinguishing primary and secondary (i.e., absorptive and transport) roots in *C. japonica* (Tawa & Takeda, 2015), which is satisfied between 3rd and 4th root orders in Yanase and Yoshino cedars. Therefore, these previous reports do not prevent our interpretations that the proportions of absorptive roots can gradually change with root orders and those in 2nd and 3rd order roots might be affected by genotypic backgrounds.

4.2 | Possible mechanisms of resource conservative strategy in Yaku cedar

Tree height, canopy depth, and litterfall in the Yaku stand were lower than those in the other stands (Azuma et al., 2023; Ohta et al., 2019), thus possibly restricting the growth and productivity of Yaku cedars. Given that SRL is positively correlated with the turnover (i.e., inverse of lifespan) and respiration of individual roots (McCormack et al., 2012, 2015; Miyatani et al., 2018), Yaku cedar might conserve resources for root growth and maintenance costs by limiting the absorptive function only to lower-order roots in response to aboveground growth limitation. The relatively high RTD observed in 2nd and 3rd root orders of Yaku cedar (Figure 1d) provides additional evidence for its conservative (i.e., less absorptive) strategy, which is characterized by reduced absorptive capacity. This observation aligns with the high sapwood density found in the aboveground parts of the trees (Azuma et al., 2023), suggesting that wood anatomy can be strongly affected by genotypic backgrounds. In contrast to root length and SRL, which varied with root diameter, the RTD was not correlated (Figure 4). The positive link between root and stem tissue densities and the fact that higher values correspond with lower relative growth rates have also been reported in interspecific comparisons (Kramer-Walter et al., 2016).

Moreover, the conservative strategy of Yaku cedar, in terms of morphological traits, is implicated in 1st order roots, which were significantly longer and thinner than

those of Yanase and Yoshino cedars (Figure 1a, b). The longer and thinner roots have more efficient root absorption owing to the enhanced length and surface area of absorptive roots per unit of root volume. These results support our third hypothesis regarding the Yaku cedar strategy. However, contrary to our expectation, the SRL change with root diameter did not differ from the other provenances (Figure 4b). In addition, differences in the 1st order root morphology among the tree provenances might be related to mycorrhizal associations. Some *C. japonica* fine roots can form arbuscular mycorrhizas (AMs) primarily in the 1st root order (Hishi et al., 2017; Matsuda et al., 2021). As indicated that distal roots associated with mycorrhizal fungi become larger in diameter than those of non-infected roots (Eissenstat et al., 2015; Kong et al., 2014; Valverde-Barrantes et al., 2016), the 1st order roots of Yanase and Yoshino cedars, which were larger in diameter than those of Yaku cedar and other *C. japonica* stands (Wada et al., 2019), might have specific strategies for nutrient acquisition enhanced by AM colorizations.

As Yaku cedar has distinctly low aboveground productivity during the early growth stage in its native habitat (Itaka et al., 2013; Takashima et al., 2009) and in the common garden (Azuma et al., 2023; Ohta et al., 2019), fine root morphological traits of Yaku cedar were also differentiated from trees of other provenances, despite large differences in soil chemical properties between the present common garden and its unique native habitat on Yakushima Island where higher soil phosphorus contents are observed owing to volcanic ash (Mukai et al., 2016). Furthermore, Yaku cedar has a relatively long genetic distance from Yanase and Yoshino cedars, as indicated by phylogenetic analysis (Tsumura, 2023; Tsumura et al., 2020), and its native site is situated farthest from the study site compared to the other provenances in terms of climatic and geographical factors. These imply the limits of functional plasticity in response to varying growing environments and underscore the consistency of inherent characteristics determined by the genetic background.

4.3 | Possible mechanisms of resource consumptive strategies in Yanase and Yoshino cedar

Yanase and Yoshino cedars elongated short-lived absorptive roots (i.e., significant SRL change at a high root order and low RTD; Figure 1c, d) more than did Yaku cedar, likely to ensure relatively early maturation of tree biomass in their native habitats. This strategy corresponds to the relatively high aboveground production indicated by leaf litterfall (Ohta et al., 2019), enabling sufficient carbon resource supply to the belowground parts. Positive feedback mechanisms may exist in which high carbon resource allocation to roots promotes water and nutrient acquisition, further enhancing aboveground productivity. In Yanase cedar, the SRL in 2nd root order exhibited high values similar to those in 1st root order (Figure 1c), and the RBR between the 2nd and 3rd root orders was higher than that in the other provenances (Figure 2), resulting in high SRT also (Figure 3a). These results support our first hypothesis, indicating the possibility that Yanase cedar has a high absorption capacity, even in the 2nd root order, and invests the most resources in fine root growth and respiratory activities among the three provenances. *C. japonica* stands with high fine root biomass tends to have thicker roots (Hirano et al., 2017), which indicates Yanase cedar might invest more resource to fine root biomass growth than did Yaku cedar (Figure 1b). Inorganic nitrogen concentrations in the soil promote root elongation and branching (Giehl & von Wirén, 2014). Even though the same environments were assumed in the stand establishment, the edaphic conditions of each cedar stand have gradually changed over the years due to the positive feedback of plant–soil interactions, which fertilize soil nutrient conditions through litter supply and root exudation. Therefore, the high RBR of Yanase cedar might have been induced by the edaphic conditions derived from the positive feedback in its stand, which has the higher soil nitrate concentration compared with the Yoshino stand (Ohta et al., 2019).

Yoshino cedar demonstrated root morphological traits that were almost similar to Yanase cedar at the individual root level (e.g., root length and diameter) (Figure 1) and intermediate values at the whole root system level (e.g., RBR and SRT) (Figures 3 and 4) between the other two provenances. There were no remarkable characteristics of root morphology in Yoshino cedar. Nevertheless, the aboveground production such as litterfall production and relative growth rate of Yoshino cedar was equivalent to or better than that of Yanase cedar (Azuma et al., 2023; Ohta et al., 2019). Considering the contribution of the root exudation (Grayston et al., 1997), the high aboveground productivity of Yoshino cedar can be interpreted as a distinct resource acquisition strategy, which is consistent with the second hypothesis of this study. Ohta et al. (2019) investigated soil and root chemical properties and root exudation of LMMOA in the same stands of Yanase, Yoshino, and Yaku cedars and revealed that the root exudation rates of LMMOA from distal root systems were higher in Yoshino cedar than in Yanase and Yaku cedars. Although there is a concern that the exudation of LMMOA is a part of total root exudation, high root exudation can enhance soil microbial activity and further

accelerate the mineralization of organic nitrogen and other nutrient availability (Dakora & Phillips, 2002). Hence, Yoshino cedar might compensate for nutrient acquisition that succeeds in high aboveground productivity by investing carbon resources in root exudation presumably instead of producing roots with absorptive morphological traits compared with Yanase cedar. Although total carbon invested in root exudates remains unknown, Ohta et al. (2019) discussed that Yoshino cedar improves nutrient conditions in the rhizosphere by using root exudates of LMMOA, thereby resulting in higher nitrogen concentrations in the fine roots than the other cedar types. Thus, there might be positive feedback effects on tree growth through alterations in soil environments via supplies of litter and root exudates. Even if planted trees alter soil environments with their plant–soil interactions, differences in soil chemical properties among cedar stands (Ohta et al., 2019) are expected to cause intraspecific variations in fine root morphology in *C. japonica*, as indicated by Wada et al. (2019), who reported that root diameter increases and SRL decreases with increasing soil NH_4^+, carbon, and nitrogen. In our study site, the similar relationships between fine root traits and soil properties may emerge as a consequence of the long-term plant–soil interactions in the future, though differences of these chemical properties remain unknown or marginal (Ohta et al., 2019).

4.4 | Conclusions and future directions

This study emphasizes the significance of fine root morphological traits as potential indicators of genotypic variations. It suggests that local adaptation, owing to geographical characteristics, can be integrated into resource acquisition strategies by altering root morphological and soil chemical characteristics. Even under similar stand initial conditions in the same common garden, Yanase, Yoshino, and Yaku cedars possibly have different resource acquisition strategies based on their genotypic backgrounds, which were reflected in their root morphological traits (Figure 5), exudate dynamics, and soil chemical properties altered by plant–soil interactions (Ohta et al., 2019). Although this study demonstrated the influence of genotypic factors on intraspecific variation in root morphological traits of *C. japonica* trees grown in a common garden, further investigation is required at this site to prove resource use strategies in belowground parts by estimating fine root production and biomass, and in their native habitats to understand the extent of regulation of root morphological traits by genotypic and environmental factors. The quantitative evaluation of intraspecific variations in functional traits, either due to genotypic background or plasticity in response to growing environments, will provide new insight to understand the limits of tree responses to changing environments.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ORCID

Ryo Nakahata https://orcid.org/0000-0001-9967-3763
Wakana A. Azuma https://orcid.org/0000-0002-4254-719X
Tomoko Tanabe https://orcid.org/0000-0003-0696-8680
Kiyosada Kawai https://orcid.org/0000-0001-8224-0515
Tsutom Hiura https://orcid.org/0000-0002-6735-1935

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SUPPORTING INFORMATION

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