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Comparison of root system architecture and developmental processes among clones of *Cryptomeria japonica* D. Don

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Research Article

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Abstract

Breeding for traits that enhance growth, pest resistance, and environmental adaptability is essential for sessile plants, particularly in the context of climate change. The root system architecture (RSA) of trees plays a critical role in slope stabilization. Root traits undergo complex morphological changes to adapt to soil conditions, but due to their inaccessibility, understanding of tree RSA lags behind that of herbaceous species. Consequently, it remains unclear whether tree RSA can be improved through breeding. In the present study, we excavated the entire root systems of three 10-year-old Japanese cedar clones-nine individuals in total—to assess intraspecific variation in root system traits, which is key to breeding improvement. We counted the primary roots emerging from the trunk and measured the cross-sectional area (CSA) of roots at 30 cm, 60 cm, and 90 cm from the trunk to analyze root system structure. Additionally, we estimated root system development using growth ring analysis of root samples. While no clear differences were observed among clones in root development processes, we did find variation in the number of primary roots and root direction. These findings suggest that Japanese cedar breeding, which has been traditionally focused on above-ground traits, can be extended to include below-ground characteristics, aiming to develop forests optimized for both growth and slope stabilization.

I. Introduction

Trees, being perennial and large, remain sessile in the field for decades, are enduring various environmental stresses (Gardiner et al. 2016; Grossnickle 2005; Kozlowski and Davies 1975). Their roots not only sense organisms such as soil microbes and neighboring plants but also develop in response to water, nutrients, slopes, and physical barriers like rocks, resulting in highly complex structures (Anten and Chen 2021; Bao et al. 2014; Chiatante et al. 2003; Colombi et al. 2023; Koevoets et al. 2016; Ryan et al. 2016). Roots provide structural support (Nicoll and Ray 1996), and this function is especially important in trees, contributing to the stabilization of mountain slopes (Stokes et al. 2009). Tree roots are considered the only natural structures capable of stabilizing slopes (Tsukamoto 1991). Vertically oriented roots(Danjon and Reubens 2007) typically penetrate to the bedrock, resulting in a “pile effect” that stabilizes the tree and enhances shear resistance in failure zones (Tsukamoto 1987). In contrast, horizontally extending roots (Danjon and Reubens 2007) interlock with roots of neighboring roots, generating a "net effect" that restrains soil and sand movement, particularly along potential landslide edges (Tsukamoto 1987; Vergani et al. 2017).

Regarding slope stabilization, tree root systems are reported to enhance soil shear strength (Stokes et al. 2009). Soil reinforcement by roots is commonly expressed as an increase in cohesion within the Mohr-Coulomb failure criterion (Schmidt et al. 2001). Abe (1997) presented a practical model for this by formulating root pull-out resistance. Moreover, Lee et al. (2019) and Giadrossich et al. (2020) have clarified the relationship between root thickness and pull-out resistance, showing that the total root CSA within the potential failure zone plays a key role in slope stabilization.

Roots have been described as “The Hidden Half” (Danjon et al. 2013a), and observing their morphology directly remains challenging (Danjon and Reubens 2007; Ohashi et al. 2019; Todo et al. 2021). Woody plants growing in environments with periodic fluctuations form growth rings (Larson 1994). Trees typically produce earlywood, composed of large cells with thin walls at the beginning of the growing season, and latewood, composed of small cells with thick walls toward the end. When the formation of growth rings follows an annual cycle, they are referred to as annual rings (Arx and Dietz 2005), which are often used for age estimation. Growth rings also form in roots, and a study on a 300-year-old tree showed that ring width variations were generally consistent between the

trunk and roots (Schulman 1945), suggesting that growth ring analysis of root wood may provide retrospective insights into root development.

Japanese cedar (*Cryptomeria japonica* D.Don) is an evergreen conifer in the Cupressaceae family and an economically important tree species. Breeding programs for Japanese cedar have been underway since the 1950s (Hoshi et al. 2013). Currently, second-generation elite trees are being selected (Takahashi et al. 2023). Breeding efforts have primarily focused on growth (Hiraoka et al. 2019; Yasuda et al. 2021), wood quality (Fukatsu et al. 2007; Takahashi et al. 2021; Yasuda et al. 2021), trunk straightness (Kurinobu and Chigira 2000), and male flowering traits (Saito and Akashi 1998; Tamaki and Kurinobu 2012; Tsubomura et al. 2012). However, as in *Pinus radiata* in New Zealand (Jayawickrama and Carson 2000) and *Pinus taeda* in the United States(Isik and McKeand 2019), root system traits have not yet been targeted for breeding in Japanese cedar.

Fukuda et al. (2018) reported clonal differences in the morphological traits of the root systems of Japanese cedar cuttings at the seedling stage. In the present study, we hypothesized that the underground root system of Japanese cedar could also serve as a potential breeding target and aimed to clarify clonal differences in root system architecture at the young stage. Previous research has indicated that trees grown on slopes develop root systems structurally different from those on flat land (Danjon et al. 2013b). Therefore, we excavated the entire root systems of nine 10-year-old individuals representing three cuttings from three Japanese cedar clones, all planted on a slope. The root systems were visualized in 3D using image analysis, and quantitative trait values were obtained by measuring the number of primary roots, root thickness relative to distance from the trunk, and the number of growth rings. These measurements aimed to determine whether the root traits vary among clones. Additionally, dendrochronological techniques were used to analyze growth rings in the roots to assess the clonal differences in root system development.

II. Methods

1.Research site and materials

The study was conducted in the prefectural experimental forest for Japanese cedar cuttings in Aira City, Kagoshima Prefecture (location: 31°45'05.3"N, 130°30'56.9"E; average temperature during the growing season: 19.1°C; average precipitation during the growing season: 2,672 mm year $^{-1}$). The soil at the site is basaltic andesite with a neutral pH, making it well-suited for Japanese cedar cultivation. Trees were planted in February 2013 at a density of 2,500 per hectare. Of the 35 clones established at the site, three Japanese cedar cutting clones, Kagoshima1gou, Kyuuiku2-33, and Kyuuiku2-160, were randomly selected as study materials. Kagoshima1gou is a first-generation elite clone, whereas Kyuuiku2-160 and Kyuuiku2-33 are second-generation elite clones. Planting at the site was generally randomized, with no clustering of clones (Supplementary Fig. 1). In November 2023, after 11 growing seasons, tree height and DBH (measured at 120 cm above ground level) were measured for all nine individuals (three from each clone). The above-ground parts were then felled at ground level. The slope of the growing area was measured three times using a laser rangefinder (Nikon, Forestry Pro J), from the base to the top of the slope, spanning the target individuals. The entire root system was manually excavated several times using shovels and crowbars between November 2023 and May 2024 (Supplementary Fig. 2). Average tree height and DBH were highest in Kyuuiku2-33, followed by Kyuuiku2-160 and Kagoshima 1gou (Table 1). Compared with Kagoshima 1gou, a first-generation elite clone, the second-generation elite clones Kyuuiku2-160 and Kyuuiku2-33 exhibited better above-ground growth. A strong correlation(r = 0.78) was observed between the dry weight of the underground part, including the root base, and the volume estimated from above-ground traits(Hosoi et al. 2010). Kyuuiku2-160 not only exhibited significantly lower values for above-ground traits than all other individuals but also had markedly inferior underground

characteristics. This was likely due to the presence of a large rock directly beneath the tree (data not shown), which appeared to hinder root system development (Table 1).

2. Research Methodology

The underground root systems were transported to the laboratory, where fine roots less than 2 mm in diameter and small roots measuring 2-5 mm were excised. Subsequent analyses focused on the root systems of individual trees, comprising medium-sized roots or larger, as defined by (Ohashi et al. 2019). Roots emerging directly from the trunk were defined as primary roots. To aid in spatial analysis, the bases of primary roots were marked with yellow tape; roots growing 30 cm from the trunk were marked with green tape, those at 60 cm with orange tape, and those at 90 cm with blue tape (Supplementary Fig. 3). Roots were categorized by growth angle: roots extending 0–30 degrees from the ground plane were considered horizontal, those at 30–60 degrees were oblique, and those at 60–90 degrees were vertical. The radially growing root systems were photographed from directly above and divided into four directional sectors, starting at the top of the slope and proceeding clockwise at 90-degree intervals: right of the contour line, downslope, and left of the contour line. Position data for all roots at the green, orange, and blue tape markers were recorded in terms of rooting direction and slope orientation. It is important to note that root trajectories are not perfectly linear during development and often become curved (Stokes et al. 2009). Therefore, in the present study, root position data were recorded separately at each distance, and position information may vary along the same root depending on the measurement point.

To perform 3D reconstruction using SfM-MVS, the root system was inverted and securely fixed to prevent movement. Photographs were taken from a distance of approximately 2 meters, capturing 360-degree images at 5-degree intervals around the root system, ensuring that reference markers essential for 3D reconstruction were visible within the camera's field of view. Photographs were taken at four height levels: eye level (150 cm), chest (120 cm), waist (90 cm), and knees (60 cm), yielding 288 photographs per individual. JPG files were imported into MetaShape Professional (AgiSoft, Version 1.7.3). The relative positions of the images were determined using reference markers. A sparse point cloud was generated using the aligned images, followed by the creation of a dense point cloud using a reliability threshold ranging from 5–7 to 255 (maximum) depending on the individual. The source data were set to depth map, highest quality, and high polygon count to construct the 3D mesh. Reconstruction was carried out according to this procedure(Supplementary movies).

The thickness of the root at the green, orange, and blue markers was measured in two orthogonal directions using an electronic caliper, and the average value was used as the root thickness. Root segments were obtained using a saw at three distances from the trunk: 30–60 cm, 60–90 cm, and beyond 90 cm. The number of growth rings on the cut surfaces was counted under a magnifying glass. In the present study, only clearly visible and continuous rings were considered growth rings.

3.Statistical analysis

All analyses were conducted using R (2025.05.1+513). The ggplot package was used for plotting graphs, and the stats, car, and multcomp packages were used for statistical modeling. Tukey's HSD multiple comparison test was used to assess clonal differences in the number of primary roots and the cross-sectional area (CSA) of the roots. The above-ground volume was calculated using a stem volume estimation program (developed by the Forestry

and Forest Products Research Institute) based on tree species, site, tree height, and diameter at breast height. For CSA, the root was treated as a complete circle, and the radius (r) was calculated as half the root thickness and was determined using this formula.

$$CSA = \pi r^2$$

Because the variance and mean of growth ring numbers were approximately equal, a Poisson distribution was assumed, with the log as the link function. A generalized linear model (GLM) was then used to examine the relationship between root thickness and growth ring number. To assess the unevenness of root thickening, CSAs of all roots were measured at the 60 cm point and then arranged in descending order. The number of roots or their positional data was recorded until the cumulative total exceeded 50%.

To estimate past CSA from root sections, the wood area of each growth ring was measured using cross-sectional images. Analyses were performed using ImageJ. Regions of interest (ROIs) along the outline of each growth ring were manually defined using the Polygon Selection tool. The wood area of each ring was calculated by generating two ROIs corresponding to its outer and inner circumferences. The areas were measured using the Analyze > Measure function, and the wood area was obtained by subtracting the inner area from the outer area. All ROIs were measured at the same scale, with actual length per pixel calibrated beforehand, and the resulting values (cm²) were used for analysis. To assess the cumulative contribution of each individual to root thickness bias, a nonlinear regression model fitting was fitted using the nlsLM function from the minpack.lm package in R. The cumulative contribution rate was fitted to the following exponential saturation model:

$$y = a(1 - e^{-bx})$$

Here, y denotes the cumulative contribution rate, x the selection rank, and a and b the estimated parameters. Initial values were set as a = 100 and b = 0.1, and the model was fitted for each individual.

III. Results

1. SfM-MVS imaging and clonal differences in root architecture traits

Three-dimensional images were reconstructed from point cloud data of nine individuals, with three individuals representing each of the three clones (Fig. 1). In *Kagoshima1gou*, horizontal roots predominated, many extending downward along the slope. In Kyuuiku2-160, vertical roots were primarily observed, although one individual lacked them (see above). In Kyuuiku2-33, horizontal roots were predominant, with roots growing both upward and downward along the slope.

The number of primary roots emerging directly from the trunk was 7.0 (± 1.7) for Kagoshima1gou, 8.7 (± 1.5) for Kyuuiku2-160, and 23.7 (± 7.5) for Kyuuiku2-33 (Table 1; Fig. 2). A statistically significant difference was observed between Kyuuiku2-33 and the other two clones (Tukey-adjusted $p < 0.05$).

At 30 cm from the trunk, the total root CSA was 147.2 ± 17.2 cm^2 for Kagoshima1gou, 170.3 ± 82.2 cm^2 for Kyuuiku2-160, and 240.5 ± 12.0 cm^2 for Kyuuiku2-33 (Fig. 3a; Tukey-adjusted $p > 0.05$). At 60 cm, the total root CSA was 60.2 (± 8.1) cm² for Kagoshima1gou, 92.5 (± 53.5) cm^2 for Kyuuiku2-160, and 92.4 (± 39.1) cm^2 for Kyuuiku2-33 (Fig. 3a; Tukey-adjusted $p > 0.05$). At 90 cm, the total CSA was 13.4 (± 5.8) cm^2 for Kagoshima1gou, 35.5 (± 27.6) cm^2 for Kyuuiku2-160, and 25.9 (± 18.9) cm^2 for Kyuuiku2-33 (Fig. 3a; Tukey-adjusted $p > 0.05$). The number of roots at

each distance from the trunk was 24.3 (± 0.6) at 30 cm, 35.7 (± 10.2) at 60 cm, and 24.0 (± 5.3) at 90 cm for Kagoshima1gou; 23.7 (± 9.5) at 30 cm, 35.3 (± 24.7) at 60 cm, and 29.0 (± 26.2) at 90 cm for Kyuuiku2-160; and 68.7 (± 14.8) at 30 cm, 107.3 (± 9.5) at 60 cm, and 41.0 (± 31.0) at 90 cm for Kyuuiku2-33 (Table 1). With respect to CSA, Kyuuiku2-160 and Kyuuiku2-33 exhibited comparable values. Although Kyuuiku2-33 tended to produce more roots, individual roots were thinner (Fig. 3b).

When the CSA was calculated by root direction at a distance of 60 cm from the trunk, the horizontal roots of Kagoshima1gou measured 43.8 (± 20.4) cm^2, the oblique roots 20.6 (± 14.1) cm^2, and the vertical roots 8.0 cm^2. For Kyuuiku2-160, the horizontal roots were 23.5 (± 10.3) cm^2, oblique roots 55.4 (± 8.1) cm^2, and vertical roots 59.9 (± 7.9) cm^2. For Kyuuiku2-33, the horizontal roots measured 44.9 (± 19.4) cm^2, oblique roots 31.2 (± 22.1) cm^2, and vertical roots 16.3 (± 22.4) cm^2 (Fig. 4a). As observed visually(Fig. 1), most roots were horizontal in Kagoshima1gou, vertical in Kyuuiku2-160, and horizontal in Kyuuiku2-33. The CSA at 60 cm from the trunk was 2.9 (± 2.3) cm^2 upslope, 15.0 (± 10.4) cm^2 to the right of the contour line, 41.6 (± 18.5) cm^2 downslope, and 9.9 (± 11.1) cm^2 to the left of the contour line for Kagosghima1gou. The upslope area was 24.7 (± 2.0) cm^2, 11.4 (± 5.1) cm^2 to the right of the contour line, 59.1 (± 49.6) cm^2 downslope, and 1.7 (± 0.4) cm^2 to the left of the contour linefFor Kyuuiku2-160. The upslope area was 20.7 (± 7.4) cm^2, 15.4 (± 19.4) cm^2 to the right of the contour line, 44.9 (± 25.5) cm^2 downslope, and 11.4 (± 1.1) cm^2 to the left of the contour line for Kyuuiku2-33 (Fig. 4b). For all three clones, the roots on the lower slope were the most numerous.

2. Estimated clonal differences in root system developmental process

The number of measured cut sections is shown in Table 1. The number of roots increased from 30 to 60 cm due to branching. However, not all roots extended to the 90 cm point; thus, the number decreased from 60 to 90 cm. In the present study using 10-year-old trees, no cut sections had more than 10 growth rings, and the number of growth rings either remained constant or declined from 30 cm to 60 cm and from 60 cm to 90 cm. The distribution of growth ring numbers was generally consistent across all three clones (Fig. 5a). Medium-sized roots thicker than 5 mm were examined, whereas fine and smaller roots (2–5 mm in diameter) were excluded. As a result, few roots had only one growth ring, and the distribution formed a right-skewed bell curve. There was no significant difference in the relationship between distance from the trunk and number of growth rings among clones (Fig. 5b; Tukey-adjusted $p > 0.05$). Regarding the relationship between CSA and number of growth rings for each clone

Kagoshima1gou: $\mathrm{GR} = 2.33\ln(D) - 1.89$

Kyuuiku2-160: $\mathrm{GR} = 2.53\ln(D) - 2.38$

Kyuuiku2-33:

where GR is growth ring and D is the diameter of the root (Fig. 5c).

The results of the three clones were combined, and

Average root development speed (m year $^{-1}$) = $0.3/(GR_{n} - GR_{n+30})$, where n = 30, 60.

Based on this formula, the root elongation rate of Japanese cedar was estimated to be 0.20 m year^{-1} between 30 and 60 cm and 0.64 m year^{-1} between 60 cm and 90 cm. Compared with the results of 0.44 m year^{-1} for radiata pine (*P. radiata* D. Don) and 0.25 m year^{-1} for kanuka (*Kunzea ericoides* A. Rich.) (Alex et al. 1999), the present study showed slower growth near the base and faster growth at the tip. When root development was analyzed by slope orientation and rooting direction, no clear differences were observed among clones in nearly all orientations and directions (Fig. 6; Tukey-adjusted).

Estimation of past CSA from root cross-sections showed that roots reached 60 cm from trunk approximately 5 years after planting (Fig. 7). Thereafter, annual root wood growth increased steadily until the 11th year examined in the present study. The results order was Kyuuiku 2-160 > Kyuuiku 2-33 > Kagoshima1gou, with Kagoshima1gou showing the lowest annual and cumulative growth.

IV. Discussion

1. Potential in root system breeding for Japanese cedar

Root system traits are known to be highly responsive to environmental factors (Stokes et al. 2009), although some studies suggest they are also influenced by genetic factors (Hamada et al. 2012; Kitomi et al. 2020). In the present study, differences between clones were observed in two traits -number of primary roots and root direction- indicating the potential for breeding the root system in Japanese cedar. Japanese cedar is typically classified as an oblique root-type tree (Karizumi 2010). Among the three clones examined in the present study, one exhibited predominantly vertical roots, whereas the other two exhibited mainly horizontal roots. Karizumi (2010) excavated roots from relatively flat terrain, but the root system architecture of Japanese cedar may vary in afforestation sites located on slopes; thus, further investigation is required to assess the environmental responsiveness of Japanese cedar roots. Since most coarse roots in 10-year-old Japanese cedar trees did not extend to 90 cm, the detailed analysis conducted at the 60 cm depth in the present study is considered reasonably valid. However, factors such as stand age and tree density (Genet et al. 2008; Temgoua et al. 2016) must be considered when selecting the reference point for trait evaluation. A statistically significant difference was observed in the number of primary roots among Kagoshima1gou, Kyuuiku2-160, and Kyuuiku2-33 (Fig. 3). In the present study, even in individual □ of Kyuuiku2-160, which exhibited significantly lower trait values within the clone because of the rock, the number of primary roots remained within the range typical of the clone. This result suggests that the number of primary roots is a trait more strongly influenced by genetic factors than by environmental conditions.

However, our conclusions are based on a limited number of trees at a single experimental site. Thus, the observed clonal differences may partly reflect site-specific environmental interactions. Expanding the analysis to diverse soil types and sites is essential to confirm the generalizability of these findings.

2. Estimation of root system developmental process

As shown in Figure 5c, the number of growth rings in relatively thin roots—particularly those less than 25 mm in diameter—varied widely, ranging from 1 to 9 even at the same CSA. When comparing the positions of these roots, most were located downslope and horizontally in Kagoshima1gou, downslope and obliquely in Kyuuiku2-160, and downslope and horizontally in Kyuuiku2-33 (Table 2). Furthermore, when examining the ratio of individual root

thickness to the total at the 60 cm point, it became evident that root enlargement was not uniform. A small number of roots (on average, about 10% of the total) accounted for more than 50% of the total CSA (Fig. 8). These thick roots were mostly positioned downslope and horizontally in Kagoshima1gou, downslope and vertically in Kyuuiku2-160, and downslope and horizontally in Kyuuiku2-33 (Table 3). These findings indicate that many roots developed downslope and that some roots subsequently thickened, resulting in a diverse root architecture ranging from thin to thick roots. Chiatante et al. (2003) studied five broad-leaved tree species and found that they effectively positioned their roots for self-loading, developing bilateral fan-shaped root systems at both the top and bottom of the slope. Mullen et al. (2005) reported that *Arabidopsis thaliana* produces more roots on the lower part of the slope, and Guo et al. (2024) reported that when camphor trees (*Cinnamomum camphora*) were subjected to downward pulling in a specific direction, roots on the opposite side of the pull became enlarged. Although these results differ from those of the present study, the root response when the direction of pulling is considered analogous to slope direction may be linked to differences in reaction wood formation between angiosperms and gymnosperms.

Past CSA estimation indicated that the ranking of above-ground traits did not align with that of below-ground wood growth (Fig. 7). Although no significant differences were detected, fluctuations in the annual root wood growth rankings suggest the presence of clonal variation in root development. The calculated root elongation rate was not uniform, suggesting it undergoes a complex developmental process. Acquiring underground space is a key survival strategy (Grossnickle 2005; Nakahata 2020), and vigorous above-ground growth is considered to result from rapid and extensive root system development. The interannual correlation for the above-ground traits of Japanese cedar was 0.81 for tree height and 0.86 for DBH (Hiraoka et al. 2019), whereas the corresponding value for root system development was 0.71 in this study. This indicates that heterogeneous soil conditions and competition more strongly influence root systems, leading to a more complex growth process. Future larger-scale analyses, particularly of 20–30-year-old Japanese cedar trees, should provide deeper insights into underground development strategies.

V. Conclusion

In the present study, the entire root systems of nine 10-year-old Japanese cedar trees were excavated. The number and thickness of roots were measured at three points 30 cm, 60 cm, and 90 cm and the root system architecture was clarified in detail. As a result, differences in the number of primary roots and root direction were observed between clones, suggesting the potential for breeding and improving the Japanese cedar root system. The presence of clones with both horizontal and vertical root directions under identical environmental conditions may enhance the slope stabilization function of an entire stand when these clones are planted in combination. In recent years, frequent slope collapses caused by heavy rainfall likely due to climate change have been reported. Root system breeding is therefore expected to contribute to the development of forests that are more resilient to climate change.

Although no clear differences among clones were detected in root development based on growth rings, the results showed subtle variations, highlighting the need for further investigation. The thickness of roots developing on the downslope side varied, even with the same number of growth rings, and selective thickening of roots was observed in response to slope-induced load stress.

The present study was conducted in a single experimental site under specific soil and topographic conditions, and only three trees per clone were analyzed. Therefore, these findings should be considered preliminary. Future research based on the results of the present study should include multiple sites with contrasting soil types and topographies as well as a larger sample size across developmental stages, to more clearly separate environmental and genetic influences. Controlled-environment experiments would further strengthen the physiological interpretation of root development.

Abbreviations

CSA, Cross-sectional Area; RSA, Root system architecture; GR, Growth ring; DBH, Diameter at breast height; SfM-MVS, Structure from Motion and Multi-View Stereo

Declarations

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Author's contribution

Conceptualization: TY, AW

Project administration: TY, AW

Analysis and methodology: TY, AW

Writing - original draft preparation: TY

Writing – review and editing: AW

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Conflict of interest

There are no conflicts of interest to disclose in the present study

Data availability statement

The datasets generated during and analysed during the presemt study are available from the corresponding author on reasonable request

References

Abe K (1997) Research on evaluation methods for slope failure prevention function of tree root systems[in Japanese]. Bull For & For Prod Res Inst 373: 105-181.

Alex W, Chris P, Michael M (1999) Root strength, growth, and rates of decay: root reinforcement changes of two tree species and their contribution to slope stability. Plant and Soil 217: 39-47.

Anten NPR, Chen BJW (2021) Detect thy family: Mechanisms, ecology and agricultural aspects of kin recognition in plants. Plant Cell Environ 44: 1059-1071. doi: 10.1111/pce.14011.

Arx Gv, Dietz H (2005) Automated Image Analysis of Annual Rings in the Roots of Perennial Forbs. International Journal of Plant Sciences 166: 723-732. doi: 10.1086/431230.

Bao Y, Aggarwal P, Robbins NE, 2nd, Sturrock CJ, Thompson MC, Tan HQ, Tham C, Duan L, Rodriguez PL, Vernoux T, Mooney SJ, Bennett MJ, Dinneny JR (2014) Plant roots use a patterning mechanism to position lateral root branches toward available water. Proc Natl Acad Sci U S A 111: 9319-9324. doi: 10.1073/pnas.1400966111.

Chiatante D, Scippa SG, Di Iorio A, Sarnataro M (2003) The Influence of Steep Slopes on Root System Development. Journal of Plant Growth Regulation 21: 247-260. doi: 10.1007/s00344-003-0012-0.

Colombi T, Eitelberg L, Kolb E, Legue V, Bogeat-Triboulot MB (2023) Genotypic differences in systemic root responses to mechanical obstacles. Physiol Plant 175: e14094. doi: 10.1111/ppl.14094.

Danjon F, F., Stokes A, Bakker MR, M. R. (2013a) Root systems of woody plants. Plant Roots : The Hidden Half. CRC Press, Boca Raton (united states).

Danjon F, Khuder H, Stokes A (2013b) Deep phenotyping of coarse root architecture in R. pseudoacacia reveals that tree root system plasticity is confined within its architectural model. PLoS One 8: e83548. doi: 10.1371/journal.pone.0083548.

Danjon F, Reubens B (2007) Assessing and analyzing 3D architecture of woody root systems, a review of methods and applications in tree and soil stability, resource acquisition and allocation. Plant and Soil 303: 1-34. doi: 10.1007/s11104-007-9470-7.

Fukatsu E, Higashihara T, Nakada R (2007) Analysis of variation and heritability of wood density in families by controlled mating in Cryptomeria japonica[in Japanese]. Kanto J For Res 58: 83-86.

Fukuda Y, Hiraoka Y, Ohira M, Takahashi M, Iki T, Miura M, Kurita M, Watanabe A (2018) Genetic Variation of Root Traits of Cuttings and Their Relation to Early Shoot Growth in Cryptomeria japonica. J Jpn For Soc 100: 218-223. doi: 10.4005/jjfs.100.218.

Gardiner B, Berry P, Moulia B (2016) Review: Wind impacts on plant growth, mechanics and damage. Plant Sci 245: 94-118. doi: 10.1016/j.plantsci.2016.01.006.

Genet M, Kokutse N, Stokes A, Fourcaud T, Cai X, Ji J, Mickovski S (2008) Root reinforcement in plantations of Cryptomeria japonica D. Don: effect of tree age and stand structure on slope stability. Forest Ecology and Management 256: 1517-1526. doi: 10.1016/j.foreco.2008.05.050.

Giadrossich F, Schwarz M, Marden M, Marrosu R, Phillips C (2020) Minimum representative root distribution sampling for calculating slope stability in Pinus radiata D.Don plantations in New Zealand. New Zealand Journal of Forestry Science 50. doi: 10.33494/nzjfs502020x68x.

Grossnickle SC (2005) Importance of root growth in overcoming planting stress. New Forests 30: 273-294. doi: 10.1007/s11056-004-8303-2.

Guo C, Hu Y, Qin J, Wu D, Leng H, Wang H (2024) Adaptive strategies in architecture and allocation for the asymmetric growth of camphor tree (Cinnamomum camphora L.). Sci Rep 14: 22604. doi: 10.1038/s41598-024-72732-1.

Hamada A, Nitta M, Nasuda S, Kato K, Fujita M, Matsunaka H, Okumoto Y (2012) Novel QTLs for growth angle of seminal roots in wheat (Triticum aestivum L.). Plant and Soil 354: 395-405. doi: 10.1007/s11104-011-1075-5.

Hiraoka Y, Miura M, Fukatsu E, Iki T, Yamanobe T, Kurita M, Isoda K, Kubota M, Takahashi M (2019) Time trends of genetic parameters and genetic gains and optimum selection age for growth traits in sugi (Cryptomeria japonica)

based on progeny tests conducted throughout Japan. Journal of Forest Research 24: 303-312. doi: 10.1080/13416979.2019.1661068.

Hoshi H, Kuramoto N, Hiraoka Y (2013) Promotion of breeding through the use of elite trees in the future[in Japanese]. Forest Genetics and Tree Breeding 2: 132-135. doi: 10.32135/fgtb.2.4_132.

Hosoi K, Mitsuda Y, Iehara T (2010) Differences between the present stem volume tables and the values of the volume equations, and their correction. Jpn J For Plann 44: 23-39. doi: 10.20659/jjfp.44.2_23.

Isik F, McKeand SE (2019) Fourth cycle breeding and testing strategy for Pinus taeda in the NC State University Cooperative Tree Improvement Program. Tree Genetics & Genomes 15. doi: 10.1007/s11295-019-1377-y.

Jayawickrama K, Carson M (2000) A breeding strategy for the New Zealand radiata pine breeding cooperative. Silvae Genet 49: 82-90.

Karizumi N (2010) The latest tree root diagram[in Japanese]. Seibundo Shinkosha.

Kitomi Y, Hanzawa E, Kuya N, Inoue H, Hara N, Kawai S, Kanno N, Endo M, Sugimoto K, Yamazaki T, Sakamoto S, Sentoku N, Wu J, Kanno H, Mitsuda N, Toriyama K, Sato T, Uga Y (2020) Root angle modifications by the DRO1 homolog improve rice yields in saline paddy fields. Proc Natl Acad Sci U S A 117: 21242-21250. doi: 10.1073/pnas.2005911117.

Koevoets IT, Venema JH, Elzenga JT, Testerink C (2016) Roots Withstanding their Environment: Exploiting Root System Architecture Responses to Abiotic Stress to Improve Crop Tolerance. Front Plant Sci 7: 1335. doi: 10.3389/fpls.2016.01335.

Kozlowski TT, Davies WJ (1975) Control of Water Balance in Transplanted Trees. Arboriculture & Urban Forestry (AUF) 1: 1-10. doi: 10.48044/jauf.1975.001.

Kurinobu S, Chigira O (2000) Second-generation plus tree selection by local foresters in controlled pollinated progenies of the first-generation plus trees of sugi (Cryptomeria japonica) (III) - estimates of genetic parameters on growth and form traits in three genetic tests at 30 years of age. Bulletin of the National Forest Tree Breeding Center 17: 177-188.

Larson PR (1994) The Vascular Cambium Development and Structure. Springer Series in Wood Science.

Lee J-T, Yen L-Z, Lee M-J (2019) Wind affects the growth, root anchorage and tensile strength of Australian pine (Casuarina equisetifolia) seedlings. Journal of Forest Research 24: 219-229. doi: 10.1080/13416979.2019.1624306.

Mullen JL, Wolverton C, Hangarter RP (2005) Apical control, gravitropic signaling, and the growth of lateral roots in Arabidopsis. Advances in Space Research 36: 1211-1217. doi: 10.1016/j.asr.2005.03.1031212.

Nakahata R (2020) Pioneer root invasion and fibrous root development into disturbed soil space observed with a flatbed scanner method. Trees 34: 731-743. doi: 10.1007/s00468-020-01953-4.

Nicoll BC, Ray D (1996) Adaptive growth of tree root systems in response to wind action and site conditions. Tree Physiology 16: 891-898.

Ohashi M, Ikeno H, Sekihara K, Tanikawa T, Dannoura M, Yamase K, Todo C, Tomita T, Hirano Y (2019) Reconstruction of root systems in Cryptomeria japonica using root point coordinates and diameters. Planta 249: 445-455. doi:

10.1007/s00425-018-3011-x.

Ryan PR, Delhaize E, Watt M, Richardson AE (2016) Plant roots: understanding structure and function in an ocean of complexity. Annals of Botany 118: 555-559. doi: 10.1093/aob/mcw192.

Saito H, Akashi H (1998) Selection effects by male strobili characteristics in Sugi (Cryptomeria japonica D Don)[in Japanese]. Nichirinron 109: 359-362.

Schmidt KM, Roering JJ, Stock JD, Dietrich WE, Montgomery DR, Schaub T (2001) The variability of root cohesion as an influence on shallow landslide susceptibility in the Oregon Coast Range. Canadian Geotechnical Journal 38: 995-1024. doi: 10.1139/t01-031.

Schulman E (1945) Root Growth-Rings and Chroniology. Tree-Ring Bulletin 12: 2-5.

Stokes A, Atger C, Bengough AG, Fourcaud T, Sidle RC (2009) Desirable plant root traits for protecting natural and engineered slopes against landslides. Plant and Soil 324: 1-30. doi: 10.1007/s11104-009-0159-y.

Takahashi M, Miura M, Fukatsu E, Hiraoka Y, Kurita M (2023) Research and project activities for breeding of Cryptomeria japonica D. Don in Japan. Journal of Forest Research 28: 83-97. doi: 10.1080/13416979.2023.2172794.

Takahashi Y, Ishiguri F, Aiso H, Takashima Y, Hiraoka Y, Iki T, Ohshima J, Iizuka K, Yokota S (2021) Inheritance of static bending properties and classification of load-deflection curves in Cryptomeria japonica. Holzforschung 75: 105-113. doi: 10.1515/hf-2019-0316.

Tamaki S, Kurinobu S (2012) Prediction of pollen reduction using selected less pollen variety of Sugi (Cryptomeria japonica) propagated by clonal cuttings and open pollinated progenies from clonal seed orchards. Bulletin of the Forestry and Forest Products Research Institute, Ibaraki 425: 197-205.

Temgoua AGT, Kokutse NK, Kavazović Z (2016) Influence of forest stands and root morphologies on hillslope stability. Ecological Engineering 95: 622-634. doi: 10.1016/j.ecoleng.2016.06.073.

Todo C, Ikeno H, Yamase K, Tanikawa T, Ohashi M, Dannoura M, Kimura T, Hirano Y (2021) Reconstruction of Conifer Root Systems Mapped with Point Cloud Data Obtained by 3D Laser Scanning Compared with Manual Measurement. Forests 12. doi: 10.3390/f12081117.

Tsubomura M, Fukatsu E, Nakada R, Fukuda Y (2012) Inheritance of male flower production in Cryptomeria japonica (sugi) estimated from analysis of a diallel mating test. Annals of Forest Science 69: 867-875. doi: 10.1007/s13595-012-0223-2.

Tsukamoto Y (1987) Research on the effect of tree root systems on deterring collapse[in Japanese]. Bulletin of the Experiment Forests, Tokyo University of Agriculture and Technology.

Tsukamoto Y (1991) How useful are forests in preventing landslides?[in Japanese]. Japanese Forestry Society 3: 45-51. doi: 10.11519/jjsk.3.0_45.

Vergani C, Giadrossich F, Buckley P, Conedera M, Pividori M, Salbitano F, Rauch HS, Lovreglio R, Schwarz M (2017) Root reinforcement dynamics of European coppice woodlands and their effect on shallow landslides: A review. Earth-Science Reviews 167: 88-102. doi: 10.1016/j.earscirev.2017.02.002.

Yasuda Y, Iki T, Takashima Y, Takahashi M, Hiraoka Y, Mishima K (2021) Genetic gains in wood property can be achieved by indirect selection and nondestructive measurements in full-sib families of Japanese cedar (Cryptomeria japonica. D. Don) plus tree clones. Annals of Forest Science 78. doi: 10.1007/s13595-021-01064-1.

Tables

Table 1 Basic data

Clone	TreeID	Slope (˚)	Height (m.cm)	DBH (cm)	Stem volume (m3)	Dry weight of below ground (kg)	Number of primary root	Number of root - Average CSA (cm2) - Average number of growth ring		
								30cm	60cm	90cm
Kagoshima1gou	1	11	7.10	11.2	0.04	3.78	8	24 - 5.40 - 5.33	43 - 1.19 - 3.12	30 - 0.22 - 1.60
	2	33	6.99	10.5	0.03	4.83	5	24 - 6.12 - 4.42	24 - 2.64 - 3.88	20 - 0.82 - 2.50
	3	33	6.42	11.1	0.03	5.64	8	25 - 6.56 - 4.68	40 - 1.65 - 2.88	22 - 0.77 - 2.41
Kyuuiku2-160	1	11	8.35	14.4	0.07	7.71	10	27 - 8.49 - 5.33	42 - 2.86 - 3.67	22 - 2.55 - 4.22
	2	11	5.88	8.05	0.02	2.85	7	13 - 5.88 - 4.92	8 - 3.85 - 3.25	7 - 0.58 - 3.00
	3	39	8.38	13.7	0.06	7.99	9	31 - 6.61- 4.29	56 - 2.27 - 2.79	58 - 0.80 - 2.38
Kyuuiku2-33	1	11	9.22	14.6	0.08	9.70	24	85 - 2.68 - 4.20	100 - 0.48 - 2.70	10 - 0.44 - 3.10
	2	35	8.83	14.5	0.08	9.23	16	56 - 4.49 - 4.77	118 - 1.04 - 3.07	72 - 0.46 - 2.26
	3	39	8.33	14.5	0.07	11.6	31	65 - 3.73 - 4.52	104 - 1.02 - 3.42	41 - 0.98 - 3.59

Table 2 List of roots with a diameter of 25 mm or less and a growth ring count of 5 or more at 60 cm

Clone	Slope orientation	Rooting direcrtion	Count
Kagoshima1gou	Top	Horizontal	0
	Top	Oblique	2
	Top	Vertical	4
	Right	Horizontal	1
	Right	Oblique	2
	Right	Vertical	0
	Bottom	Horizontal	17
	Bottom	Oblique	4
	Bottom	Vertical	1
	Left	Horizontal	9
	Left	Oblique	1
	Left	Vertical	2
Kyuuiku2-160	Top	Horizontal	1
	Top	Oblique	10
	Top	Vertical	2
	Right	Horizontal	0
	Right	Oblique	4
	Right	Vertical	0
	Bottom	Horizontal	4
	Bottom	Oblique	14
	Bottom	Vertical	4
	Left	Horizontal	3
	Left	Oblique	0
	Left	Vertical	1
Kyuuiku2-33	Top	Horizontal	19
	Top	Oblique	10
	Top	Vertical	0
	Right	Horizontal	9
	Right	Oblique	0
	Right	Vertical	6
	Bottom	Horizontal	40
	Bottom	Oblique	32

	Bottom	Vertical	7
	Left	Horizontal	15
	Left	Oblique	10
	Left	Vertical	0

Table 3 List of roots in descending order of diameter at 60 cm until the cumulative total accounts for 50%

Clone	Slope orientation	Rooting direcrtion	Count
Kagoshima1gou	Up	Horizontal	0
	Up	Oblique	0
	Up	Vertical	0
	Right	Horizontal	0
	Right	Oblique	1
	Right	Vertical	0
	Down	Horizontal	8
	Down	Oblique	1
	Down	Vertical	0
	Left	Horizontal	1
	Left	Oblique	0
	Left	Vertical	0
Kyuuiku2-160	Up	Horizontal	2
	Up	Oblique	1
	Up	Vertical	1
	Right	Horizontal	0
	Right	Oblique	0
	Right	Vertical	0
	Down	Horizontal	0
	Down	Oblique	1
	Down	Vertical	3
	Left	Horizontal	0
	Left	Oblique	1
	Left	Vertical	0
Kyuuiku2-33	Up	Horizontal	8
	Up	Oblique	3
	Up	Vertical	2
	Right	Horizontal	5
	Right	Oblique	1
	Right	Vertical	0
	Down	Horizontal	15
	Down	Oblique	4

	Down	Vertical	0
	Left	Horizontal	1
	Left	Oblique	0
	Left	Vertical	3

Figures

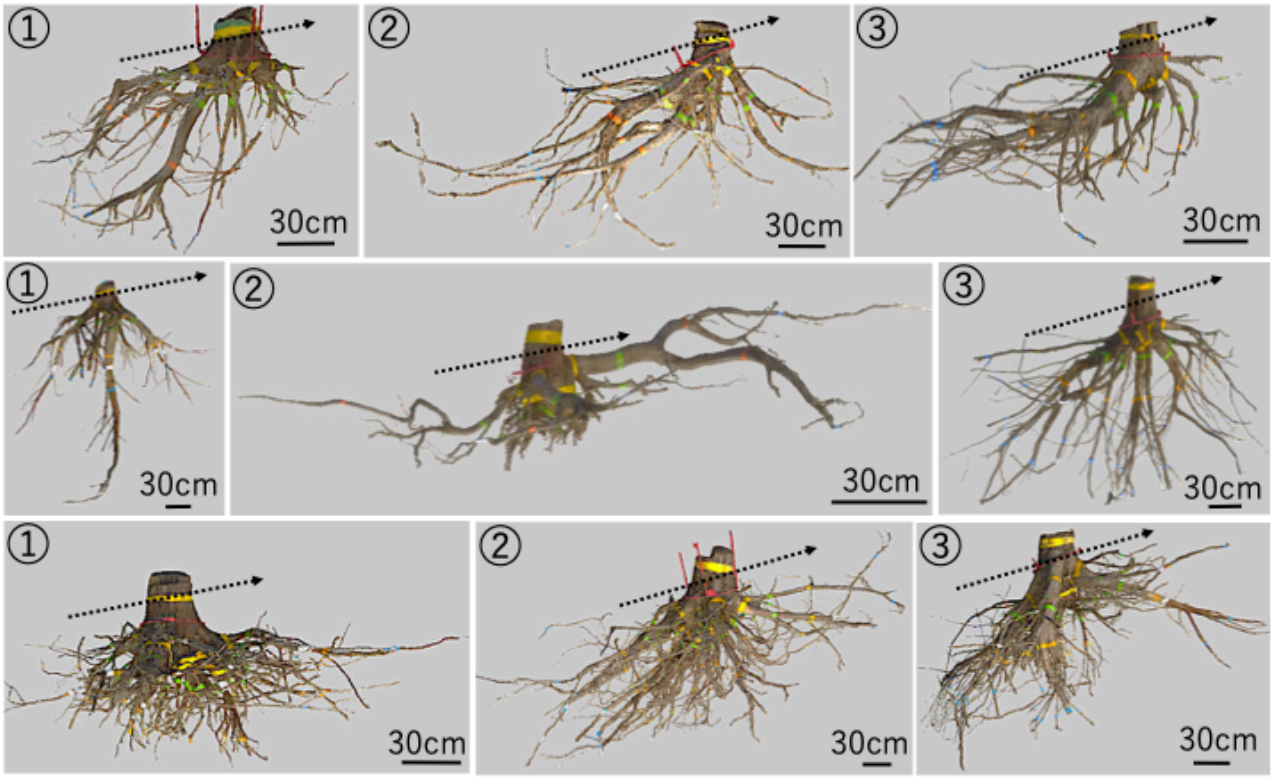


Figure 1

3D images of individual objects created by SfM-MVS

The top row shows Kagoshima1 gou, the middle row shows Kyuuiku2-160, and the bottom row shows Kyuuiku2-33

The dashed line represents the ground surface, and the arrows indicate the top of the slope

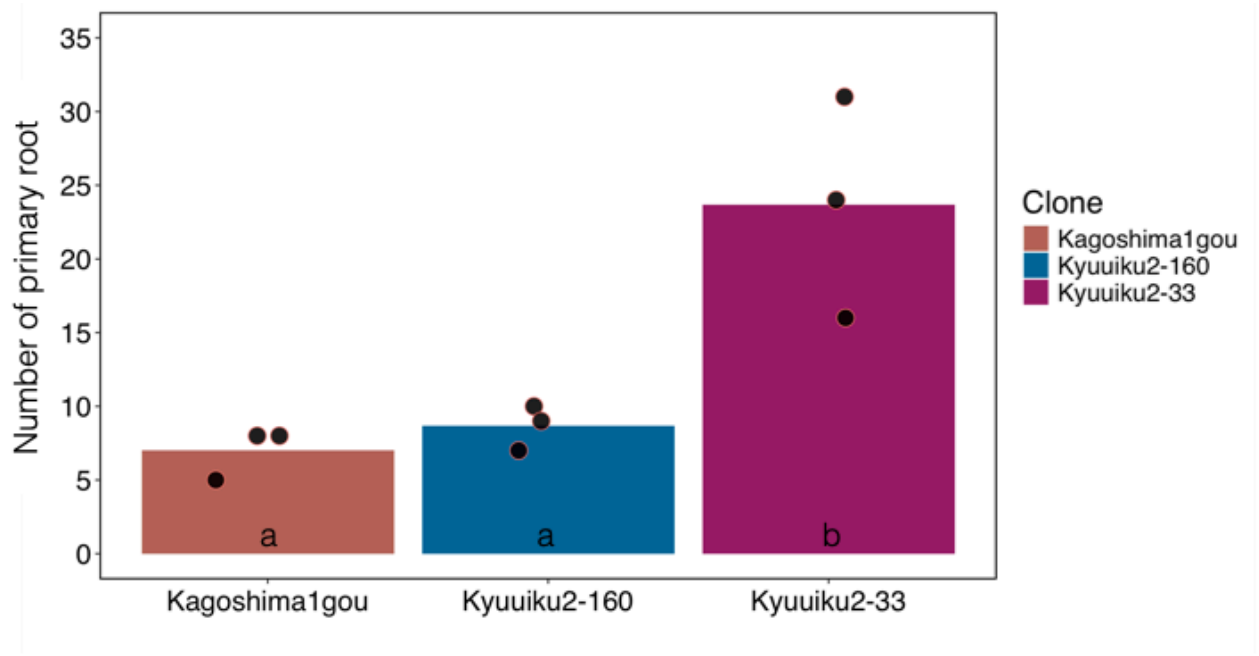


Figure 2

Comparison of the number of primary roots per clone

Each point represents data for each individual. Each bar shows the average value for each clone. Different letters indicate significant differences according to Tukey's test at 5% error probability

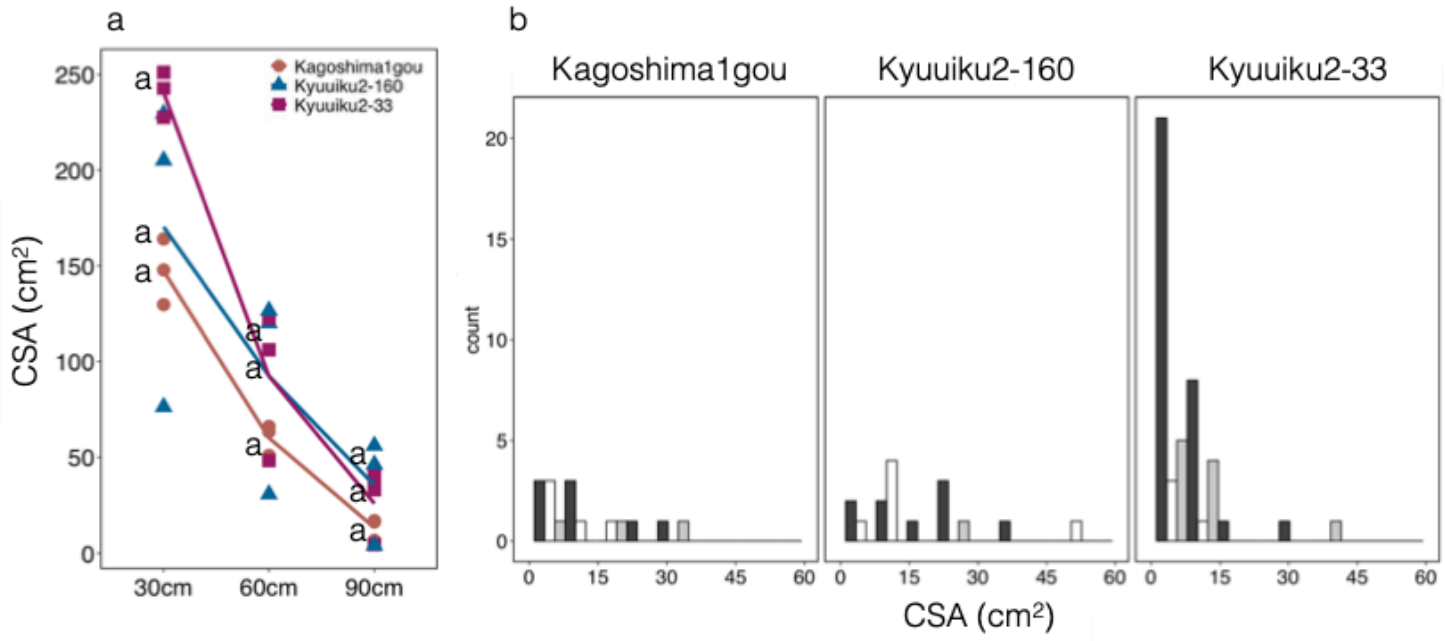


Figure 3

Clonal differences in CSA

a. Changes in CSA according to distance from the trunk.Each point represents data for each individual. Average values within each clone are connected by line. Different letters indicate significant differences according to Tukey's

test at 5% error probability

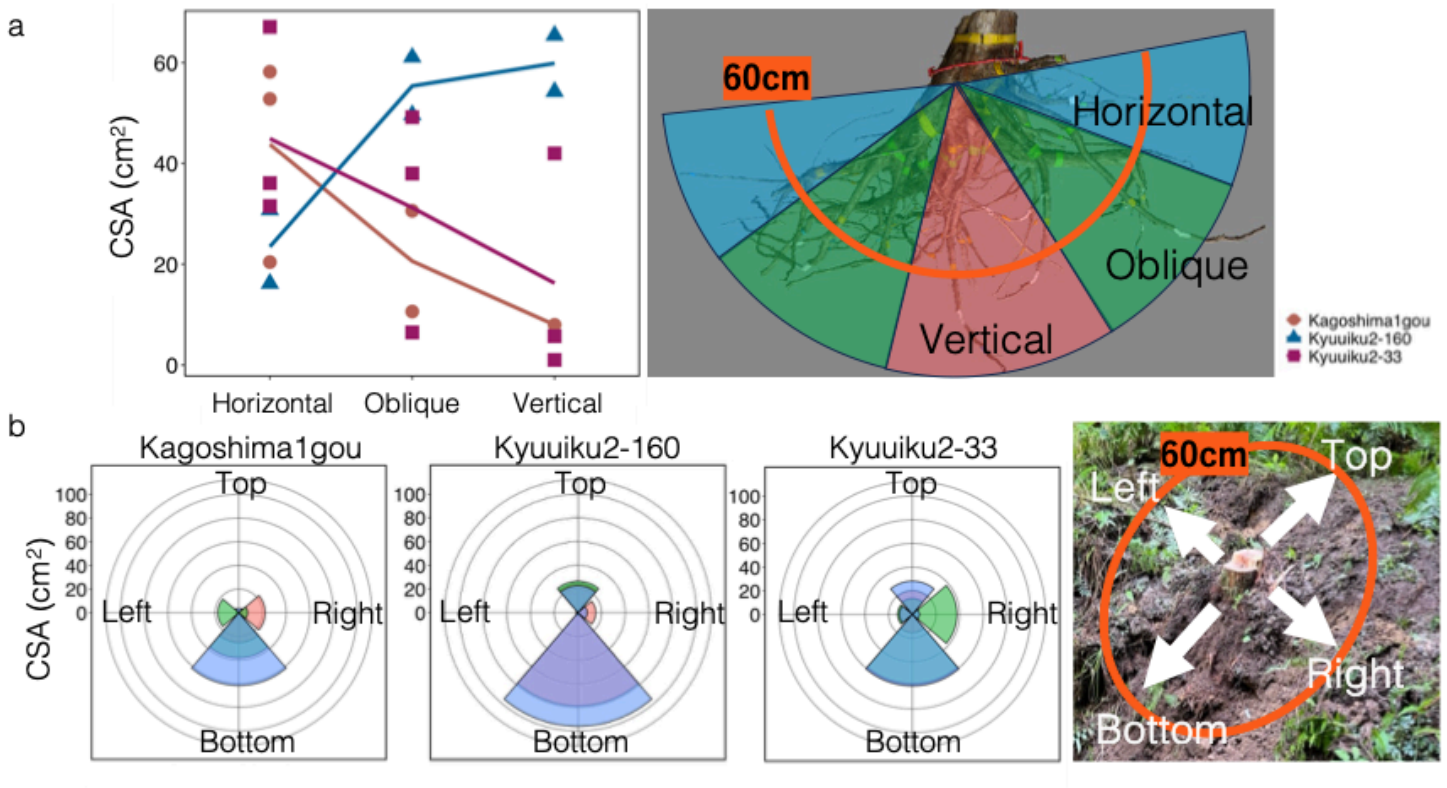


Figure 4

CSA at 60 cm by root direction(a) and slope orientation(b)

a. Each point represents data for each individual. Average values within each clone are connected by line

b. CSA at the top of the slope, the right of the contour line, the bottom of the slope, and the left of the contour line are represented as fan segments. Data for each individual is shown in a different color in each figure.

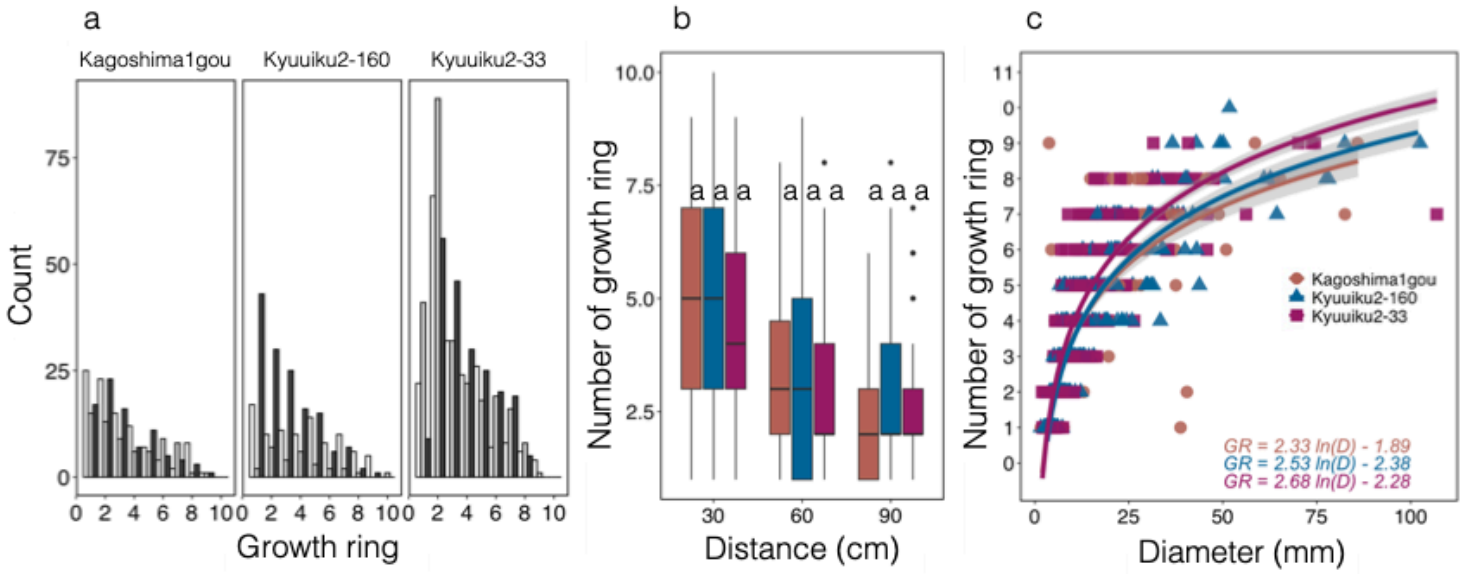


Figure 5

Growth ring data

a. Histogram of the number of growth rings in individual roots at 60 cm

b. Comparison of the number of growth rings between clones by distance from the trunk. Different letters indicate significant differences according to Tukey's test at 5% error probability

c. Relationship between root thickness and number of growth rings for each clone

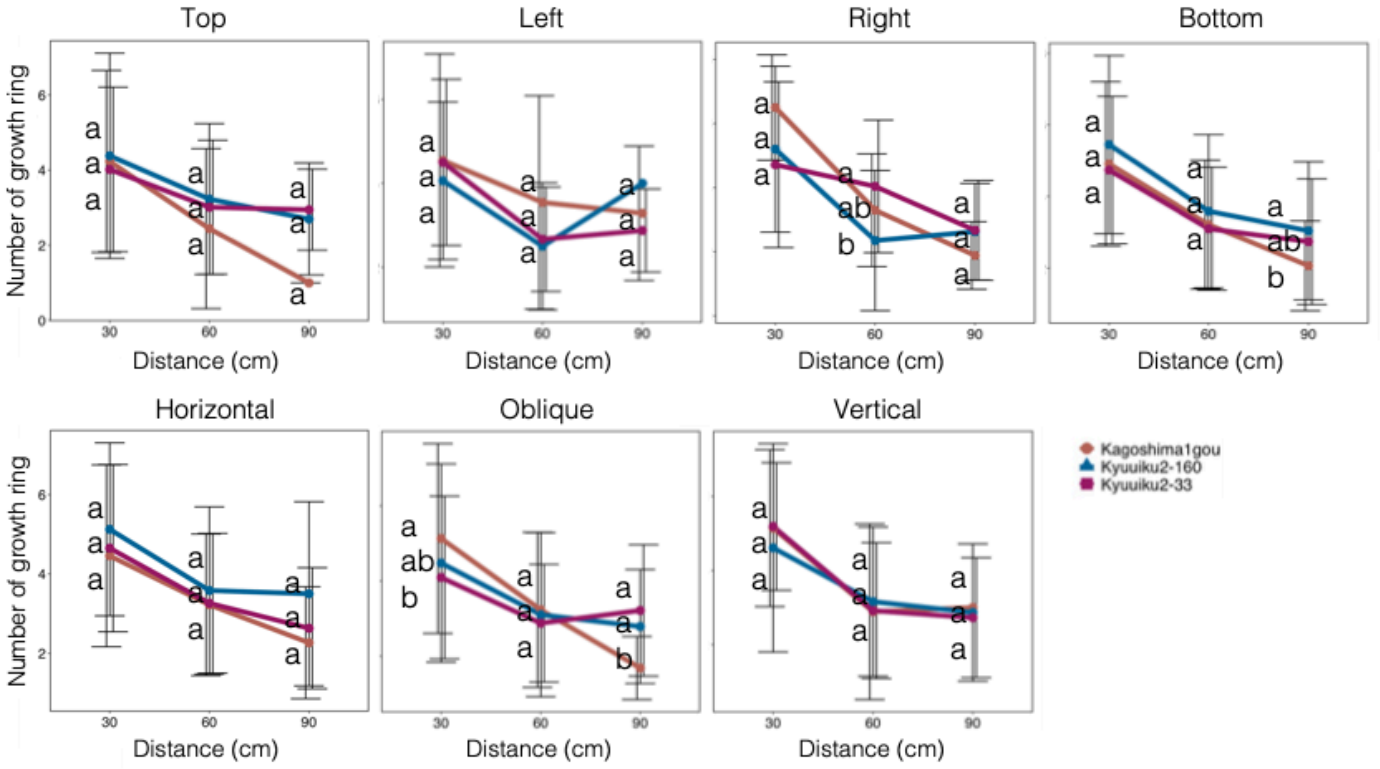


Figure 6

Number of growth ring by slope direction and root direction according to distance from the trunk

Average values within each clone are connected by lines. Error bars represent standard deviation

Different letters indicate significant differences according to Tukey's test at 5% error probability

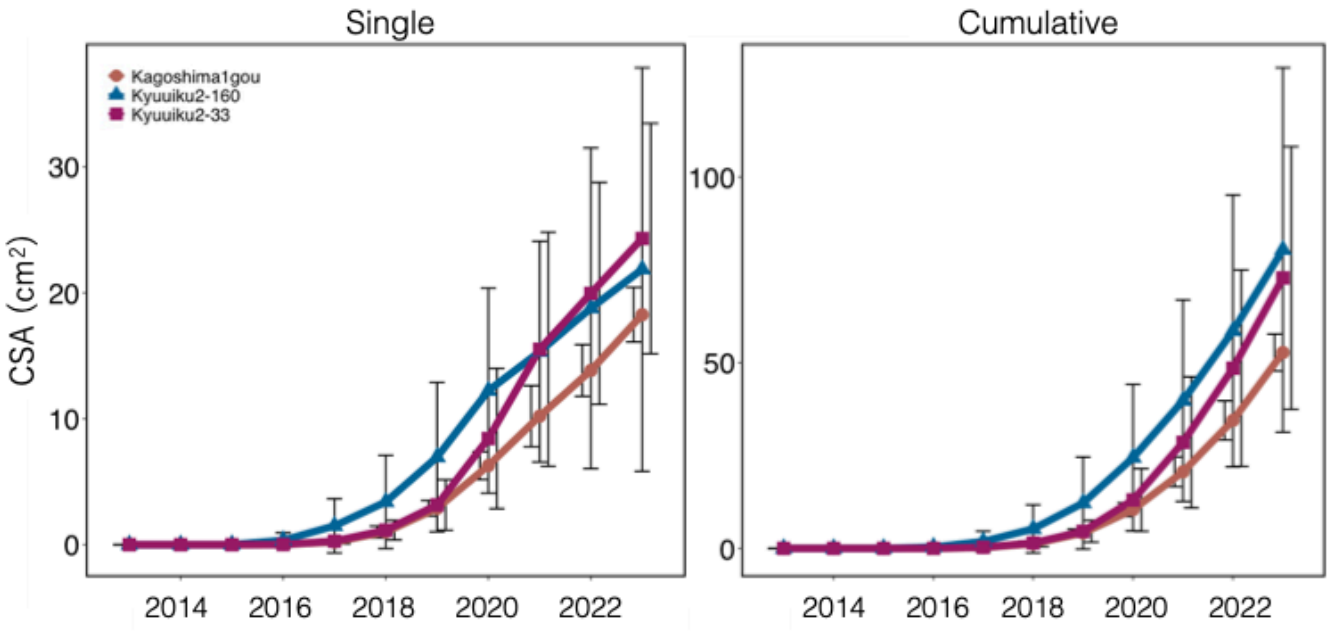


Figure 7

CSA growth timec ourse for root at 60cm from trunk

left: single year

right: cumulative

Average values within each clone are connected by lines. Error bars represent standard deviation

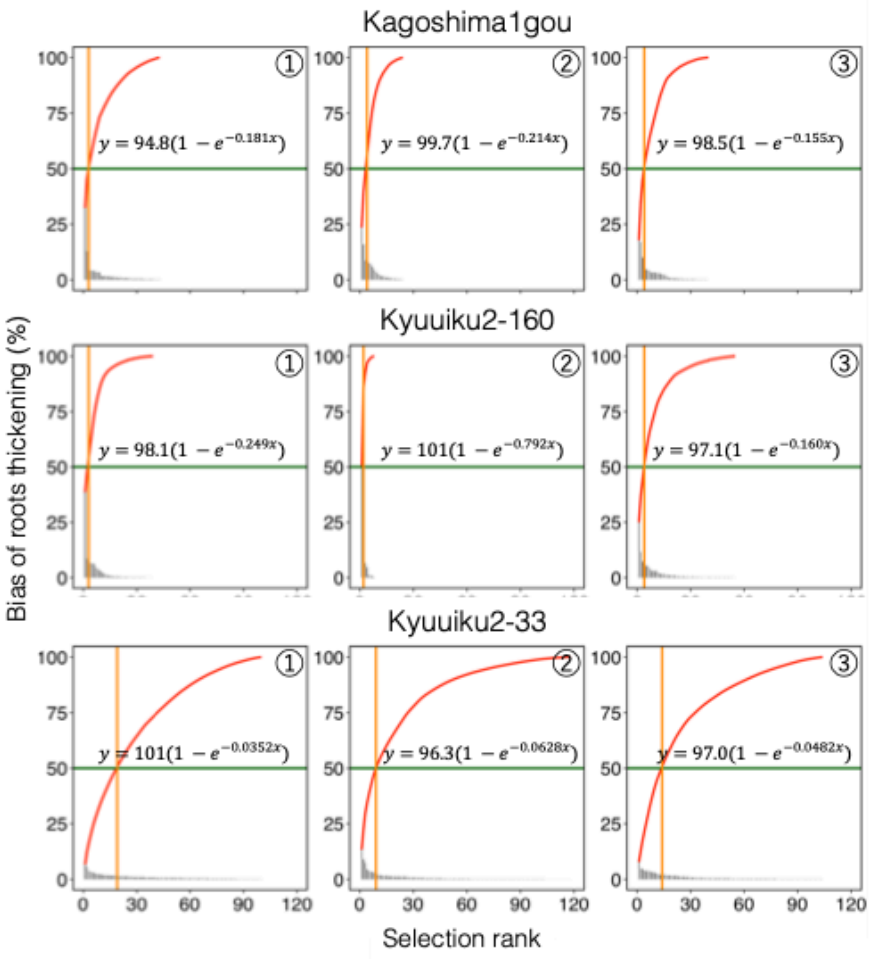


Figure 8

Bias of roots thickening

The CSA of each individual is arranged in descending order. The cumulative percentage of the total is shown in red. The green line indicates 50%, and the orange line marks the root where the cumulative CSA exceeds 50%.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- CJRootPlantAndSoilTYAWSIKagoshima1gou2.mp4
- CJRootPlantAndSoilTYAWSIKagoshima1gou2.mp4
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