Linking root trait with wood density and vitality of Scots pine breeds (*Pinus sylvestris*)

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Degree project/Independent project • 60 credits
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Department of Forest Ecology and Management
Forest Ecology and Sustainable Management (MSc)
Examensarbeten / SLU, Institutionen för skogens ekologi och skötsel, 2026:11
• ISSN 1654-1898
Umeå 2026

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Credits:	60 credits
Level:	A2E
Course title:	Master's thesis in Forestry Science
Course code:	EX1043
Programme/education:	Forest Ecology and Sustainable Management (MSc)
Course coordinating dept:	Department of Forest Ecology and Management
Place of publication:	Umeå
Year of publication:	2026
Cover picture:	Photo by Jenny Svennås-Gillner, SLU Media Bank
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Title of series:	Examensarbeten / SLU, Institutionen för skogens ekologi och skötsel
Part number:	2026:11
ISSN:	1654-1896
Keywords:	Collaboration gradian, fine root traits, plant-soil feedback, root economics spectrum, Scots pine (*Pinus sylvestris*), tree height, tree vitality, wood density

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Abstract

Roots, as a place for nutrient acquisition, are closely related to the growth of trees. In the root economics spectrum, fine roots have acquisitive traits or conservative traits, based on the trade-offs between enhancing growth rate by high nutrient uptake rate and metabolism, and enhancing defence and life span. Meanwhile, another gradient in the spectrum represents the nutrient source to the roots, either through a "do-it-yourself" strategy that increases the nutrient uptake by extending the soil exploration through longer roots, or through a "outsourcing" strategy that invests carbon to develop a mycorrhizal collaboration. For the purpose of linking the relationship between tree height growth, wood density, tree vitality (good or poor) and fine root traits, we collected and analysed 72 root samples (3 breeds × 3 blocks × 2 vitality classes × 4 replicates) from two Scots pine (*Pinus sylvestris*) breeds that were bred for height increment (HT1 & HT2) and one breed that were bred for purposes other than height (PL) from a 38-year-old stand. Through comparing root morphology traits including average diameter, specific root length, specific root area, root tissue density and root chemical traits including nitrogen content, carbon content, carbon-to-nitrogen ratio, we detected a trend of conservative strategy and observed lower wood density in the numerically highest breed, and discovered no significant differences in root traits between trees in good and poor vitality. We posit that, during the growth of trees, the roots traits might be considerably influenced by the environment, rather than a simple trade-off between acquisitive and conservative strategies. Unlike what is commonly believed, fast-growing trees don't necessarily have acquisitive root strategies, instead they tend to adjust the root traits according to the available resources in the environment, which might improve the defence and survive of trees.

Keywords: collaboration gradian, fine root traits, plant-soil feedback, root economics spectrum, Scots pine (*Pinus sylvestris*), tree height, tree vitality, wood density

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Abbreviations

Abbreviation	Description
AD	Average diameter
C	Carbon
CNRatio, C:N	Carbon-to-nitrogen ratio
N	Nitrogen
PCA	Principal component analysis
PSF	Plant-soil feedback
RES	Root economics spectrum
RTD	Root tissue density
SRA	Specific root area
SRL	Specific root length

1. Introduction

1.1 Swedish tree breeding programme

Tree breeding in modern forestry has various objectives, including increasing volume production, disease resistance or other desired characteristics (Ruotsalainen 2014). In particular, tree breeding programmes in Sweden have been ongoing since the mid-nineteenth century, where "plus trees" (trees in natural forests with superior characteristics) have been selected and crossed for desirable offsprings (Figure 1; Jansson et al. 2017). Scots pine (*Pinus sylvestris*) has been one of the main focal on tree breeding in Sweden since 1940s due to its large distribution and excellent adaptivity (Krakau et al. 2013; Jansson et al. 2017). These genetically improved Scots pine have significantly higher height, tree diameter, and volume relative to unimproved individuals (Jansson et al. 2017). In addition, because tree breeding tends to increase tree growth rate, the quality of the wood may also change (Zhang 1995). For example, a selection of Scots pine that increased height by 33% at 10 years old was expected to have decreased wood density by 1% at 33 years old (Hannrup et al. 2000). Besides changes in shape and functions, tree breeding will also bring changes in tissue morphology. For example, in the research of Leski et al. (2010), Scot pine seedlings of different genotypes showed significant differences in dry root weight. Building upon these, we know little about whether any changes in wood density with tree breeding are correlated with changes in other tissues. Despite increasing evidence of trait coordination across tissues, studies typically examine correlations in root and leaf tissues, whereas the coordination between stem and root traits remains poorly understood (Weemstra et al. 2016). Understanding tissue coordination could be useful to improve models where traits for only one tissue type are known.

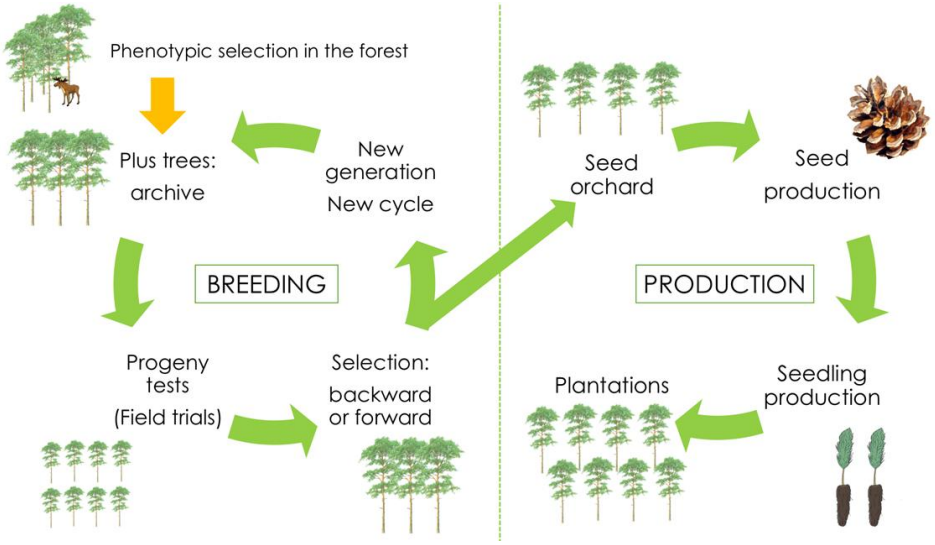

Figure 1. The process of plus-tree breeding. Before put into production, the desirable plus trees will go through generations of selection and breeding until they have stable properties. The studied breeds are the first offsprings of selected wild trees. [photography: Skogforsk].

1.2 Root economics spectrum

Fine roots (≤ 2 mm diameter or root orders 1–3) are the primary organs for nutrient uptake and play a key role in nutrient cycling (Roumet et al. 2016; Carmona et al. 2021). A substantial portion of carbon is allocated to root tissue to support its growth and function as well as supporting mycorrhizal fungal colonization for nutrient acquisition and stress resistance (Roumet et al. 2016; Brundrett & Tedersoo 2020). Therefore, the nutrient uptake capacity of fine roots is closely related to the growth of trees (Sanaei et al. 2025). Trees with fast growth are often associated with acquisitive fine root traits including high specific root length, small root average diameter, low root tissue density, and high nitrogen content (Comas & Eissenstat 2004; Sanaei et al. 2025). These traits are simultaneously related with roots of short life-span and low defence (Bergmann et al. 2020; Spitzer et al. 2022). By contrast, roots of high root tissue density, large diameter, low specific root length, and high carbon-to-nitrogen ratio represent a conservative strategy and are associated with high defence, long life-span yet low growth rate (Bergmann et al. 2020; Spitzer et al. 2022). The trade-off in fine roots between acquisitive and conservative strategies is observed in various tree species and thus forms the concept of root economics spectrum (RES) (Weemstra et al. 2016; Zheng et al. 2024). Root growth strategies vary among different species, and numerous root studies are based on multi-species data, whereas few studies have evaluated variation within single species (Kong et al. 2014; Rabearison et al. 2024).

1.3 Plant-soil feedback

In the management of forests, the vitality of trees is an important index of forest health and profitability (Calleja-Rodriguez et al. 2019). In Sweden, the death of a tree is usually the result of multiple disturbances, including but not limited to climate, pathogenic fungi, and pests (Calleja-Rodriguez et al. 2019). Trees in stress have been observed to have changes in fine root traits including smaller specific root length (SRL), fewer root tips, less C and N content (Repo et al. 2020; Hunziker et al. 2024).

During the growth of plants, the soil conditions, including nutrients and biota, will be altered and these effects will feed back on the growth and survival of plants, forming the different directions of plant-soil feedback (PSF) (Bennett & Klironomos 2019). Biotic disturbances will also alter the plant-soil feedback to be negative and further affect the vitality of trees (Štraus et al. 2024). Plant-soil feedback is the main driver of forest diversity and dynamics, yet as the main place for nutrient exchange in soil and biota, fine roots are rarely linked with vitality in field (Hunziker et al. 2024; Štraus et al. 2024).

1.4 Hypothesis

Here, we utilized a 38-year-old Scots pine tree breeding site in northern Sweden to determining the effects on tree breeding on stem and root traits and their coordination, as well as to evaluate the usefulness of root traits as predictors of tree vitality. We assessed the trait data among breeds, among traits and between tree vitality to test the following hypotheses:

1. Fine roots from trees bred to be taller will have more acquisitive traits relative to “Plus” trees, as a faster growth rate requires greater nutrient uptake capacity of roots, which is often supplied via acquisitive strategies (Comas et al. 2002; Comas & Eissenstat 2004; Bergmann et al. 2020).

2. Wood density will be lower in trees bred for height increment; root trait economic strategies will be coordinated with wood density such that conservative root traits will have positive correlation to wood density (Zhang 1995).

3. Fine root traits will predict tree vitality, which thicker roots (which tend to be associated with higher mycorrhizal colonization) and root with higher N being associated with more and less vital trees, respectively (Repo et al. 2020; Spitzer et al. 2022; Hunziker et al. 2024).

2. Methods

2.1 Study site

The study site is located in Flurkmark (64°02'N 20°13'E) in northern Sweden and approximately 155 m above sea level. The region has a short growing season from May to September, and is characterized by long, cold winters and short, mild summers (Kroon et al. 2019). The mean annual temperature is 4.6°C, with monthly averages from about -6°C in winter to 17°C in summer, and mean annual precipitation is about 595 mm (2015 – 2025) (SMHI 2026).

The site, cultivated in 1988 with a total area of 1.21 ha, was originally designed for studying the productivity of six Scots pine (*Pinus sylvestris*) breeds and one lodgepole pine (*Pinus contorta*) breed. There was no management in the site since cultivation except pine weevil treatment right after planting and a period of fencing (1994 – 2008). The site was divided into three blocks with trees planted at spacings of 1 × 1 m, 2 × 2 m, and 3 × 3 m due to initial experiment design to explore the intraspecific competition (Figure 2). Each tree breed was planted separately in individual plots within each block. Our study mainly focused on three breeds of Scots pine, labelled HT1, HT2, and PL. Among tree breeds, HT1 and HT2 are especially bred for larger height with two different sets of parents, while the control group (PL) is bred from parents that are generally considered to be superior, but height was not a target trait. In the survey when the site was 38-year-old, the breeds bred for height (HT1 & HT2) were observed to have slightly greater values in height than the control group (PL), with 0.03% higher in the average height, although the difference was not significant ($F_{2, 533} = 1.13$, $p = 0.32$), wherein HT2 showed the largest height to green crown (Figure S1; Table S2).

Figure 2. A Scots pine plot with 3 × 3 m spacing at the study site. [photography: Y. Wu].

2.2 Sample processing and analysis

2.2.1 Sampling

To test our hypothesis whether fine root traits will affect tree vitality, we developed a classification system based on the tree vitality classes adapted from the research of Coluzzi et al. (2020), and classified the trees accordingly through observation of the tree crown, branches, bark, and clues of pests and diseases (Table 1). In this study, we only focused on trees with very good vitality (Class 1) and very poor vitality (Class 4). In some plots, we could not find any trees in Class 4 and therefore turned to Class 3 (n = 10).

Table 1. Tree vitality classes based on Coluzzi et al. (2020). ND: Not Detected.

Vitality Class	Crown Dieback	Dead Branches	Pest and/or Disease	Bark Damage
1 (Good)	0%	ND	ND	ND
2 (Fair)	<20%	Some	Some	ND
3 (Poor)	21–50%	Substantial	Substantial	Some
4 (Very poor)	51–99%	Substantial	Substantial	Severe

In each block, trees from each breed were randomly selected and grouped by vitality (Class 1 or 4), with four trees per group, i.e. 3 breeds × 3 blocks × 2 vitality classes × 4 individuals = 72 trees. Trees at the edge of each plot were avoided as much as possible during selection to reduce possible edge effects. The

data for trees from Class 4 (n = 36) was only used when determining the correlation between root traits and tree vitality (Hypothesis 3), while only data for trees from Class 1 (n = 36) was used in the rest of the study (Hypothesis 1 & 2).

2.2.2 Root

Root samples were collected approximately 30 – 60 cm from the base of the selected trees mentioned above by coring (Ø10 cm) in the O-horizon in mid-July 2025 (Figure 3). The distance was relatively shorter to avoid collecting roots from the neighbouring trees, particularly in the plots with 1 × 1 m spacing. Cores were immediately sealed individually in plastic bags after collecting and transported to a walk-in cold room at the end of each field day. The samples were thereafter stored at 4 °C before further processing.

Figure 3. Collecting root sample with a cylinder core after removing the surface vegetation. The collection spot was about 30 cm away from the base of the tree. [photography: C. Spitzer].

The collected root samples were cleaned based on the process in the research of Spitzer et al. (2021). Briefly, root samples were washed in a 4 mm sieve placed above a 2 mm sieve and gently rinsed with water using a shower tap. Any roots that were washed into the 2 mm sieve were collected. We then placed all roots in a tray filled with water to separate Scots pine roots from roots and tissues of other species and removed any remaining soil or mycorrhizal fungus with tweezers (Figure 4; Figure 5). Fine roots were sampled (< 2 mm) using a ruler to determine diameter and immediately scanned in a transparent acrylic tray filled with distilled water using a flatbed scanner (Epson Expression 13000XL) in 16-bit Grayscale and 600 dpi resolution (York 2023). Roots were laid as flat as possible, without

overlapping or being placed near the edges of the acrylic tray. The scanned images were later processed with RhizoVisionExplorer (version 2.0.3) to obtain root morphological data using the following settings: analysis mode broken roots; 600 dpi; image thresholding level 150; filter non-root objects with maximum size 1 (York 2023). The data obtained included total root length (mm), average diameter (mm), volume (mm^3), and surface area (mm^2). After the scanning, the fresh weight of roots was recorded and subsequently dried at 70°C for 48 hours. After that, the dry weight of samples was recorded and used to calculate specific root length (SRL, total root length divided by dry weight; mm g^{-1}), specific root area (SRA, total root area divided by dry weight; mm^2 g^{-1}), and root tissue density (RTD, volume divided by dry weight; g mm^{-3}). The samples were then ground (Retch MM400 ball mill) and analysed for total carbon (C) and nitrogen (N) concentrations in 5 ± 0.5 mg ground roots (n = 71, including 1 sample with less amount and excluding 1 sample with no sufficient amount) by dry combustion using an elemental analyser (Flash EA 2000; Thermo Fisher Scientific, Bremen, Germany).

Figure 4. Cleaning the root samples. All trays were filled with water. Top-left included all the roots in the sample; top-right was the Scots pine roots with remaining soil and mycorrhizal fungus; bottom-left was the Scots pine roots after further cleaning. The remaining debris were carefully removed in water with tweezers (bottom-right). [photography: C. Spitzer].

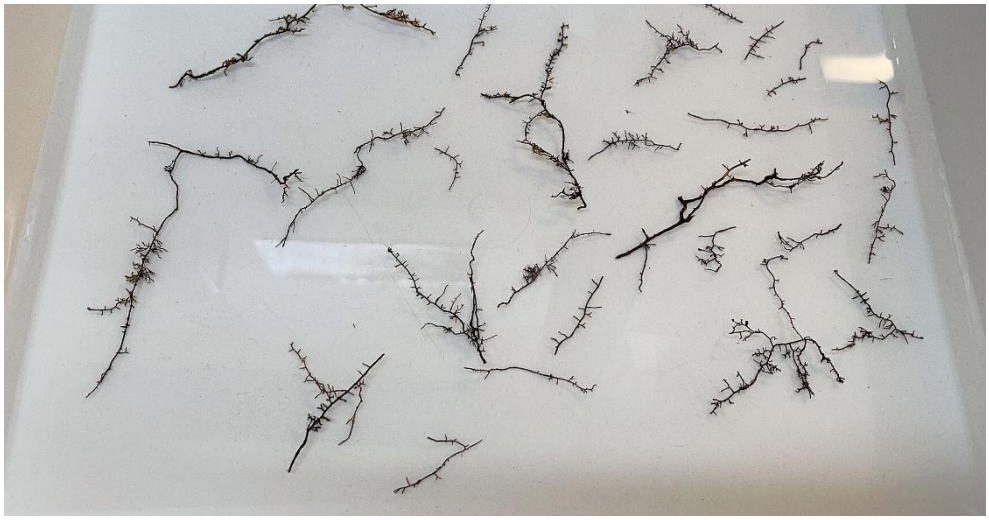

Figure 5. Cleaned fine roots in a tray filled with water. [photography: Y. Wu]

2.2.3 Soil core

We randomly collected soil samples in O-horizon with a 2-cm cylindrical soil corer from plots of three breeds in all three blocks (n = 9). The soil cores were sealed in plastic bags immediately after collection and moved to a walk-in cold room at the end of each field day. The cores were stored at 4 °C before further processing. The soil cores were sieved with a 4-mm sieve to remove plant tissues. After measuring wet weights, the soil samples were dried at 60 °C for 48 hours and then the dry weight was measured to obtain the moisture content (Table S1). After these, the dried soil samples were sealed in glass bottles and ground on a rolling mill for 48 hours. The ground soil samples were measured for carbon and nitrogen content by dry combustion using an elemental analyser (Flash EA 2000; Thermo Fisher Scientific, Bremen, Germany) (Table S1). Soil were homogenized, and then analyzed for carbon content (N), nitrogen content (N), carbon-to-nitrogen ratio (C:N), and moisture (betadisper, $F_{2, 6} = 0.4354$, $p = 0.6659$; PERMANOVA, $R^2 = 0.22$, $p = 0.47$).

2.2.4 Tree core

A tree core was taken at breast height (i.e. 1.3 m) from each selected tree with an increment borer and then stored in a paper straw. All the tree cores were then air dried 7 weeks. After the outer bark and cambium was removed, the remaining xylem of the tree cores was immersed in water for 48 hours. We measured wood density (ρ_{wood}) according to Archimedes' principle by recording the green mass of the samples (m_{green}) and their buoyancy (m_{water}) when immersed in water (Fedyukov et al. 2020). The difference between these values, divided by the density of water at the measurement temperature, was used to calculate the volume of each sample. The dry weight of the wood samples (m_{dry}) was

measured after the samples had dried in an oven at 60 °C for 48 hours. The density of the wood samples (ρ_{wood}) was then calculated using the following equation:

$$\rho_{wood} = \frac{m_{dry}}{(m_{green} - m_{water})/\rho_{water}}$$

Where:

ρ_{wood} is the density of target wood sample,
m_{dry} is the dry mass of the wood sample,
m_{green} is the green mass of the wood sample,
m_{water} is the buoyancy of the wood sample in water,
ρ_{water} is the density of water at the current temperature.

2.3 Statistical analysis

All statistical analysis was conducted with R (version 4.5.1). After confirming the multivariate homogeneity of root traits (betadisper), the traits were tested for differences in multivariate composition among groups using permutational multivariate analysis of variance (PERMANOVA) implemented in the *vegan* package (Oksanen et al. 2001). The multivariate distribution of the standardized dataset was analyzed and visualized in principal components analysis (PCA) with the *factoextra* package (Kassambara & Mundt 2016). The root traits were tested individual differences among groups with the analysis of variance (ANOVA) and conducted with a post-hoc Tukey's honestly significant difference (HSD). The results were visualized with package *multcompView* and *ggplot2* (Graves et al. 2006; Wickham et al. 2007). All the traits were tested block effect with package *lme4* and *lmerTest* (Bates et al. 2003; Kuznetsova et al. 2013). The correlation between traits was tested and visualized in Spearman's rank correlation.

3. Results

3.1 Root trait variations among tree breeds

The three breeds had significantly different multivariate dispersion in the studied root traits (betadisper, $F_{2, 32} = 2.12$, $p = 0.14$). In the principal component analysis (PCA), the first two principal component axes explained a total of 81.6% variance (Figure 6). The first axis accounted for 55.9% variance, mainly driven by higher specific root area (SRA), nitrogen content (N), and specific root length (SRL) on one hand (i.e. acquisitive strategy), and higher carbon-to-nitrogen ratio (C:N) (i.e. conservative strategy) on the other hand. The second axis accounted for 25.7% variance and was mainly driven by average diameter (AD) and root tissue density (RTD).

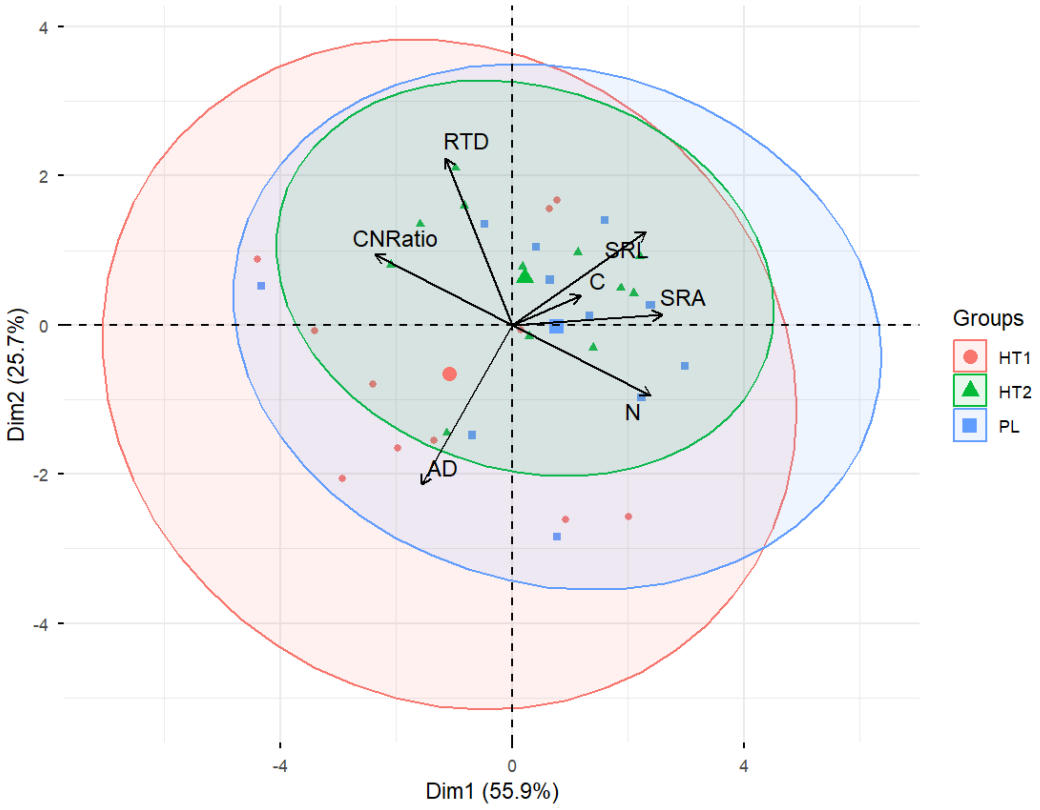

Figure 6. Principal component analysis (PCA) of fine root traits across tree breeds: two bred to be taller (HT1 & HT2) and the control (PL) which was not specifically bred for height increment although parents were had superior qualities. The ellipses represented the variation of root traits from their respective breeds in multivariate trait space, while the centroids represented their average multivariate trait composition. SRL, specific root length; AD, average diameter; RTD, root tissue density; SRA, specific root area; C, carbon content; N, nitrogen content; C:N, carbon-to-nitrogen ratio.

Multivariate trait composition differed significantly among breeds (PERMANOVA, $R^2 = 0.14$, $p = 0.02$). Pair-wise PERMANOVA revealed a significant difference between HT1 and HT2 ($R^2 = 0.15$, $p = 0.02$), and between HT1 and PL ($R^2 = 0.13$, $p = 0.04$), but no difference between HT2 and PL ($p = 0.35$). Further, statistically significant differences among breeds were only observed through one-way ANOVA in specific root length, average diameter, and C content (Table 2). Pair-wise post hoc analysis indicated that AD differed between HT1 and HT2, and was marginally insignificant between HT1 and PL, and that C differed between HT1 and HT2, and between HT1 and PL (Table 2; Figure 7). However, we found no pair-wise differences in SRL. In addition, SRA had marginally insignificant differences based on one-way ANOVAs ($p = 0.09$), which was primarily attributable to pair-wise difference between HT1 and PL ($p = 0.08$). For all other traits, there were no significant differences among breeds (Table 2; Figure 7). HT1 has significantly higher average diameter than PL, with HT2 as the medium, and lower C content than HT2 and PL. In addition, HT1 has marginally lower specific root length than HT2 and PL ($p < 0.1$), and lower specific root area than PL, with HT2 in the middle ($p < 0.1$).

Table 2. ANOVAs results comparing root traits among breeds, including two breeds that were bred for height (HT1 & HT2) and the control (PL) that was not specifically bred for height. SRL, specific root length; AD, average diameter; RTD, root tissue density; SRA, specific root area; C, carbon content; N, nitrogen content; C:N, carbon-to-nitrogen ratio.

Fine root traits	One-way ANOVA		Tukey's HSD Tests – adjusted p		
	F	p	HT1 – HT2	HT1 - PL	HT2 - PL
SRL (mm g^{-1})	3.49	**0.04**	0.08	0.06	0.99
AD (mm)	4.66	**0.02**	**0.02**	0.07	0.81
RTD (g mm^{-3})	0.65	0.53	0.60	1.00	0.58
SRA (mm^2 g^{-1})	2.63	0.09	0.28	0.08	0.76
C (%)	5.89	**< 0.01**	**< 0.01**	**0.04**	0.70
N (%)	1.75	0.19	0.92	0.20	0.35
C:N	0.97	0.39	0.96	0.40	0.55

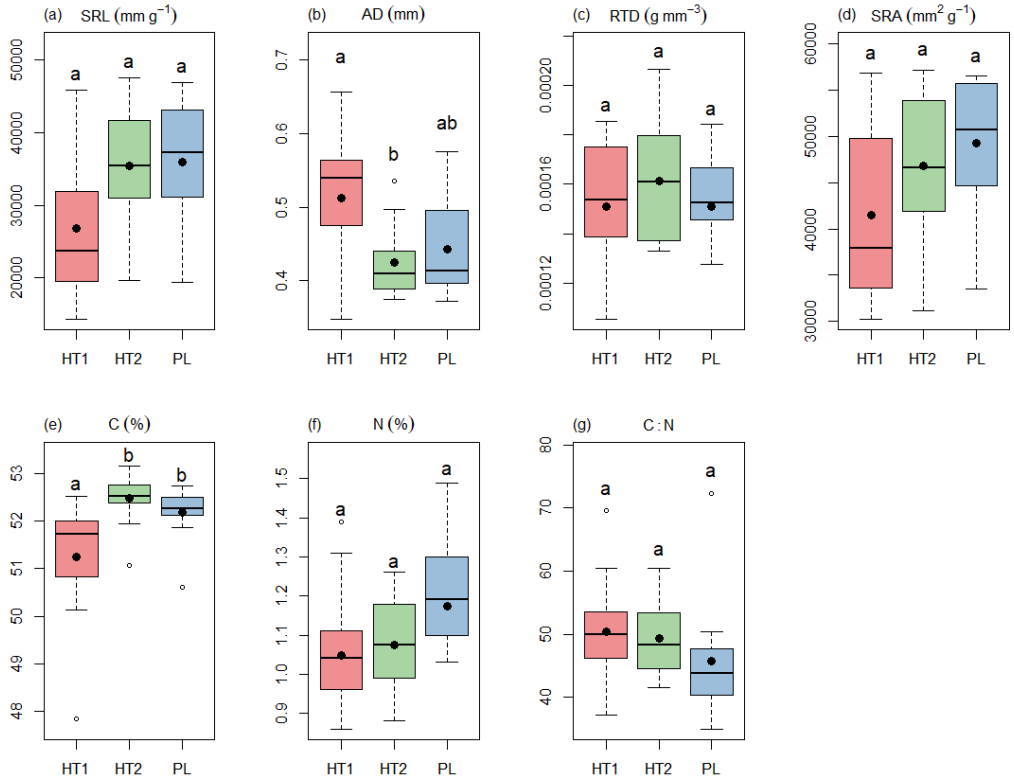

Figure 7. Boxplots showing differences in root traits among breeds with pair-wise differences labelled in letters ($p < 0.05$). Solid points in boxplots indicate mean values. HT1 & HT2 were bred for height and PL was the control. SRL, specific root length; AD, average diameter; RTD, root tissue density; SRA, specific root area; C, carbon content; N, nitrogen content; C:N, carbon-to-nitrogen ratio.

3.2 Correlations between wood density and root traits

Overall, the trees bred for height (HT1 & HT2) were observed to have 1.19% lower wood density than the control group (PL), though the difference is not significant ($F_{2, 32} = 1.02$, $p = 0.37$) (Figure S2).

The correlation analysis between wood density and root traits revealed that the wood density of PL showed a significantly positive relationship with carbon-to-nitrogen ratio (C:N), and negative relationship with nitrogen content (N) ($p < 0.05$; Figure 8). In terms of HT1 and HT2, none of the traits were significantly correlated with wood density. HT1 had little correlation with specific root length (SRL), specific root area (SRA) and C:N (spearman, $|\rho| < 0.1$), meanwhile HT2 had a positive correlation with SRA, SRL, carbon content (C), and N, and a negative correlation with average diameter (AD), C:N, and root tissue density (RTD). Notably, the wood density and trait correlations in HT2 and PL showed completely contrasting relationships.

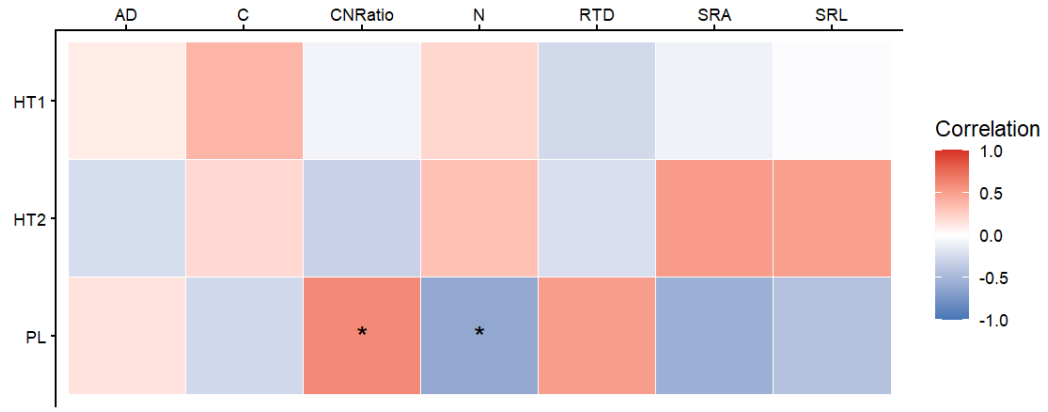

Figure 8. Heatmap of correlation between wood density and root traits among two breeds bred for height increment (HT1 & HT2) and the control (PL) with spearman correlation. The asterisks indicated significant correlation ($p < 0.05$). SRL, specific root length; AD, average diameter; RTD, root tissue density; SRA, specific root area; C, carbon content; N, nitrogen content; C:N, carbon-to-nitrogen ratio.

3.3 Root traits under different tree vitality

We also conducted principal component analysis (PCA) on root traits from trees of both good and bad vitality (Figure 9). The first two dimensions explain a total of 81.1% variance with PC1 and PC2 accounting for 53.2% and 27.9% variance respectively. There are no clear differences between root traits of trees with good and poor vitality, as the centroids of two ellipses are similar, and the ellipses distinctly overlap. Nonetheless, the orientation of the two ellipses suggests subtle differences in the direction of root traits variation between good and poor vitality. Moreover, the multivariate dispersion of root traits from trees of good and poor vitality was proved homogeneous (betadisper, $F_{1, 69} = 0.18$, $p = 0.67$). The multivariate trait composition test indicated no significant difference as well (PERMANOVA, $R^2 = 0.01$, $p = 0.77$), which was further confirmed by ANOVAs with individual traits (Figure S3; Table S4).

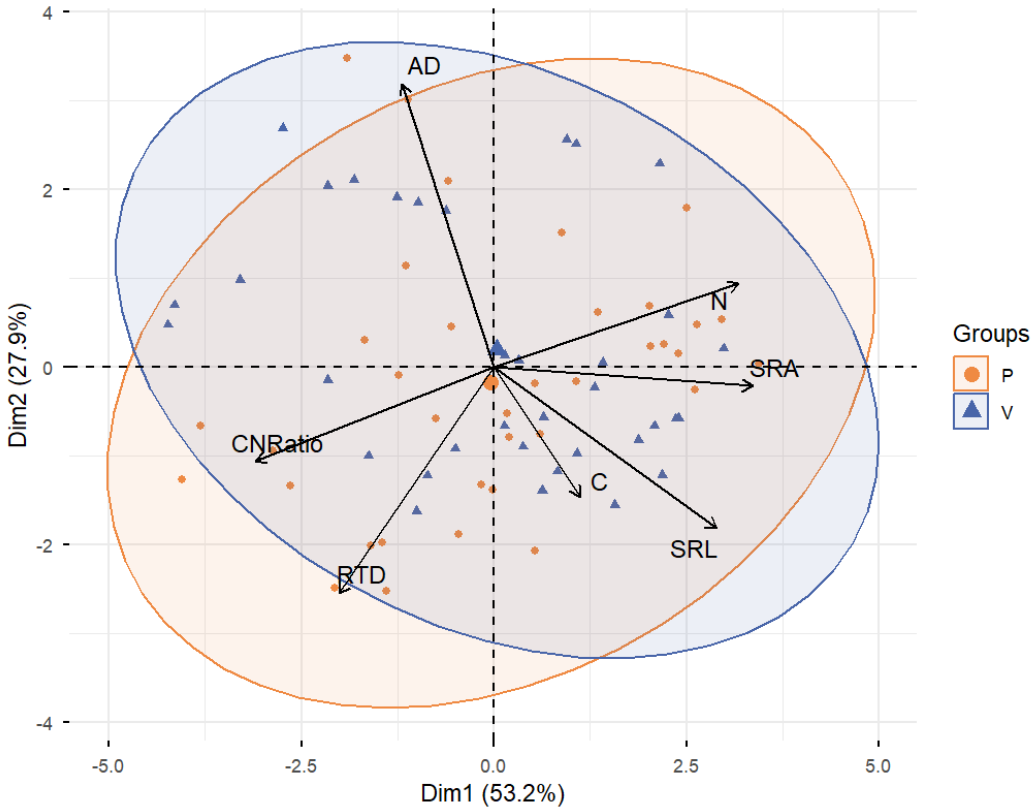

Figure 9. Principal component analysis (PCA) of fine root traits between good (V) and poor (P) vitality. SRL, specific root length; AD, average diameter; RTD, root tissue density; SRA, specific root area; C, carbon content; N, nitrogen content; C:N, carbon-to-nitrogen ratio.

In addition, several root traits have shown significant block effects when analysed between good and poor vitality, including specific root area ($p < 0.01$), specific root length ($p < 0.05$), root tissue density ($p < 0.05$), and C content ($p < 0.05$).

4. Discussion

Our study was aimed at linking root traits among tree height, wood density and tree vitality in three Scots pine breeds. We observed different root strategies among breeds, even if they were both bred for height increment (HT1 & HT2). In the breeding process, two breeds bred for height had the trend of decoupling the correlation between wood density and root traits. The tree vitality cannot be sufficiently explained by root traits, which was better affected by the environment in our study.

4.1 Relationship between tree growth and root traits

We found partial support for our first hypothesis, fine roots from tree breeds bred to be taller either had no differences to the control (i.e. HT2) or relatively more conservative root trait values (i.e. HT1). Fine roots of HT1 had higher average diameters (AD), which aligns with recent research evidence that point to high tree growth having stronger associations with higher average diameters (Weemstra et al. 2020; Rabearison et al. 2024). Although this study did not focus on tree growth, taller trees of the same age typically have faster growth rate and hence HT1 may be more productive, although such differences could not be detected in the height and volume production parameters for this breed. Although often considered a conservative trait, the higher average diameter observed in the breed bred for height increment (HT1) might represent a nutrient outsourcing by increasing mycorrhizal colonization to enhance soil nutrient uptake and thus enhance growth (Bergmann et al. 2020; Weemstra et al. 2020; 2021). Specific root length and average diameter are negatively correlated and represent opposing strategies for nutrient uptake along the collaboration gradient of the root economics space from self-supporting on the one hand to outsourcing to mycorrhizal fungi on the other hand (Bergmann et al. 2020). Higher specific root length is commonly considered as a typical acquisitive trait and positively correlated with higher growth rate, where longer and thinner roots increase the spatial extent of soil exploration and thus enhance the nutrient acquisition (Comas & Eissenstat 2004; Sanaei et al. 2025). However, some researchers pointed out that specific root length is more closely associated with soil environment, which might explain why all three breeds had no significant difference in specific root length (Weemstra et al. 2020; Rabearison et al. 2024).

Interestingly, although there were shifts for HT1 towards more conservative values along the “collaboration” gradient of the root economics space, roots had lower carbon content than the control, indicating relatively more acquisitive trait values. The significantly lower carbon content (C) observed in HT1 could be as a result of greater investment in mycorrhizal fungi, although this conjecture cannot

be confirmed in our study due to the lack of mycorrhizal observation (Colpaert et al. 1996; Weemstra et al. 2020). Another conjecture is that faster-growth breeds may invest less carbon in complex structures in roots, and allocate the carbon to aboveground tissues (Weemstra et al. 2020).

Meanwhile, we did not detect any significant differences for any of the key traits on the conservation gradient (i.e. root tissue density and root N content). It is likely that site conditions were suitable for growth of Scots pine and the homogenous soil conditions did not cause any changes in root traits, which can also explain the little difference in RTD among breeds (Kramer-Walter et al. 2016).

Kramer-Walter et al. (2016) pointed out that plants might have the capacity to construct roots in different trait combinations of specific root length and average diameter to enhance the adaptability in the surrounding environments. Simultaneously, we observed greater variability in specific root length and average diameter in the tallest breed (HT1). We therefore infer that this breed might effectively utilize this strategy to maximum its growth. At the same time, higher average diameter is proven to have positive relation with higher cortex fraction, which might enhance metabolic rate and pathogen resistance (Kramer-Walter et al. 2016; Bergmann et al. 2020). Similarly, root nitrogen content (N), which is considered to have positive relation with respiration, was detected numerically lower in the trees bred for height (HT1 & HT2), which might be because of a conservative strategy with long lifespan and low constructure cost (Chen et al. 2010; Paradiso et al. 2019; Rabearison et al. 2024).

Unfortunately, the breeds bred to be taller only had little height increment compared to the control, and the difference was not significant. This insignificance might be because of the effects from large family by replication interaction or genotype-by-environment interactions (Rweyongeza et al. 2003; Calleja-Rodriguez et al. 2019).

4.2 Linking wood density with root traits

We found no evidence that tree breeding and expected associated faster growth would result in lower wood density, although the mean values tended to be lower for HT1 and HT2 relative to the control (Figure S2). These finds are consistent with previous studies that have shown wood density of Scots pine will only slightly declines with growth rate (Hannrup et al. 2000).

Our study of correlation between wood density and root traits is aimed at linking correlation in tree growth with limited samples. Our hypothesis was partially supported in the control group (PL) where wood density had significantly positive correlation in carbon-to-nitrogen ratio (C:N), and significant negative correlation in nitrogen ratio (N) (Figure 8), which might be because low C:N and high N are commonly considered as acquisitive trait that related to high metabolic

rate rather than high constructural stabilization, and the conservative traits on the contrary may lead to a denser aboveground structure (Bergmann et al. 2020).

We observed different trends when linking root traits to wood density among breeds and detected a great number of root traits and wood density decoupled during the breeding for height increment in our study (Figure 8). The average density of wood is determined by the early wood and late wood proportion and their relative density (Louzada & Fonseca 2002). Previous studies have reported high heritability in the average wood density and early wood density, while the late wood density and proportion were more affected by environmental factors, which, for example, might be related to tree vigour and resilience under stress (Louzada & Fonseca 2002; Soro et al. 2022). Considering that the root traits present a multidimensional phenotype in enhancing adaptability, we speculate that wood density might be under the coordination of multiple genetic materials and therefore altered the correlation among root traits, or affected by other aspects such as environmental factors (Kramer-Walter et al. 2016).

4.3 The complexity in predicting tree vitality through root traits

We failed to find any evidence to support our third hypothesis that vitality is correlated with root traits. Overall, neither the root trait composition nor single root traits showed significant differences between trees of good and poor vitality. Only subtle differences were observed in the variance of traits. The significant block effects indicated the vitality of trees was more strongly affected by the environment in our studied site, most notably the difference in spacing.

4.3.1 The effect of plant-soil feedback (PSF) on tree vitality

We originally expected positive plant-soil feedback driven by a conservative root strategy in the trees of good vitality that preserves nutrients and enhances resistance in our studied site. The direction of plant-soil feedback is driven by the interaction of plant and soil microorganisms (Spitzer et al. 2022; Liu et al. 2025). For example, in previous studies, the growth of Scots pine is mainly positively associated with the nutrient acquisition of ectomycorrhizal fungi, forming a positive feedback of plant-soil feedback (PSF) (Štraus et al. 2024; Liu et al. 2025). Meanwhile, the colonization of ectomycorrhizal fungi is observed to have effect on root traits, particularly in increasing average diameter and decreasing specific root length (SRL) (Sun et al. 2010). However, we found no evidence that the root traits directly affected the direction of plant-soil feedback and thus the tree vitality. We conjecture that further research on the soil microorganism might reveal the biotic aspects on tree vitality.

4.3.2 Environmental effect on tree vitality

We detected significant block effects especially in specific root area (SRA), specific root length (SRL), root tissue density (RTD), and carbon content (C). We therefore speculate that the different spacing in three blocks might be the major contributing factor since no significant difference in the observed soil nutrients (C, N, C:N, moisture) was detected among block (Table S1). The mortality of Scots pine in harsh environments is considered a mix result of multiple aspects rather a single aspect, which is usually the combined influence of several factors including stress from climate, fungal infection, or pest (Calleja-Rodriguez et al. 2019). The stand density is proven to affect internally and externally. For example, small spacing might increase the mortality of trees through intraspecific competition, particularly the shade-intolerant species like Scots pine, or enhance the spread of pathogen through the closely distributed individuals, while large spacing might increase the risk of windthrown, and the fallen trees might further promote the spread of pathogens (Burdon et al. 1992; Beniušienė et al. 2025).

5. Conclusion

Our study indicates the complexity in fine root traits that affected the properties of trees. The numerically taller breed (HT1) exhibited more conservative traits characteristics rather than acquisitive traits which is contrary to the common expectation that fast-growing trees tend to adopt an acquisitive strategy, and had more variances in root traits. Similarly, more variant root traits were detected in trees of good vitality. We therefore infer that fast-growing and enhanced vitality might be a proof of trees' ability to adjust their traits in order to better utilize the available resources in the environment. However, our study is limited to the number of traits collected and the sample size, which limited our ability to further investigate these relationships. The study on fine root traits will help with a deeper understanding of the plant growth and the influence of the environment, in particular, the soil. Through analysing root traits in three Scots pine breeds from the Swedish tree breeding programme, we expect to provide new angles to the future breeding objectives in enhancing productivity and survival rate, especially considering the changing environment in the global scale.

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Popular science summary

Roots are the organ in trees that absorb nutrients and water, and most of this uptake takes place in the fine roots at the end of the root system. Based on their characteristics, fine roots can generally be divided into two functional types: long, thin, short-lived roots for rapid nutrient uptake, and short, thick, long-lasting roots for defence. Furthermore, for the purpose of obtaining more nutrients from the limited resources, trees develop a "outsourcing" collaboration with mycorrhizal fungi that trees provide the space in roots and nutrients to fungi, and the fungi return the nutrients that trees need. However, the growth of trees will change the soil nutrients and soil microorganism, which may promote or suppress the survive of trees.

Our study was aimed at answering these questions: whether fast-growing trees always have roots for rapid nutrient uptake to support their growth; and whether fine root traits can reflect tree vitality, since the root traits associated with fast growth may also make soil conditions less suitable for tree survival. Meanwhile, the fast growth may cause lower wood density. We expect to find the correlation between wood density and fine root traits.

We collected and analysed root samples from Scots pine in a 38-year-old forest in northern Sweden, including two breeds bred to be higher, and one breed bred for purpose other than height (the control). Unlike what we expected, the breeds bred to be taller either had more root traits for defence or showed no difference than the control. We infer that the breed bred to be taller developed a "outsourcing" relationship with mycorrhizal fungi, which Scots pine provide living place and carbon to mycorrhiza, while mycorrhiza provide nitrogen in return.

A previous study pointed out that the wood density of Scots pine will only decrease a little if it grows faster. We found the same trend in our study. In addition, we found trees with root traits for defence will have slower breathing metabolic rate. This suggests that these trees may firm their roots and trunk structures, instead of being eager to grow. However, the correlation between wood density and root traits was weaker in the breeds bred to be taller. We infer that the different parts of the trunk may have different inheritance and may be affected by the environment.

Unlike what we hypothesised, we did not find any differences in root traits between trees with good and poor vitality, but found the vitality was strongly affected by tree spacing. When the stand was initially designed for research, the trees here were planted in three different spacing: 3 × 3 m, 2 × 2 m, and 1 × 1 m. The small spacing might cause severe competition among trees, and make the pathogens spread easily, while the large spacing might increase the risk of windthrown, and the fallen trees would increase the number of pathogens. In

harsh environments like northern Sweden, the death of trees is often caused by multiple causes, rather than directly driven by root traits.

The study in root traits help better understanding the growth of plants and may play a guiding role in the future forest management activities such as breeding. In our study, we realized the complexity in understanding the underground traits of plants, and thus we expect to see more studies in the future to comprehensively explore this mystery tissue.

Appendix 1

Table S1. Soil nitrogen (N), carbon (C) and moisture content from plots of two breeds bred for height increment (HT1 & HT2) and one control breed (PL) in three blocks.

Block	Breed	N (%)	C (%)	C:N	Moisture (%)
	HT1	0.46	19.68	42.8	60.54
	HT2	0.45	18.78	41.7	49.36
1	PL	0.37	13.82	37.4	48.89
	HT1	0.47	22.81	48.5	61.74
	HT2	0.48	21.23	44.2	85.00
2	PL	0.46	16.60	36.1	63.64
	HT1	0.44	18.67	42.4	82.75
	HT2	0.38	15.56	40.9	61.06
3	PL	0.72	31.64	43.9	92.92

Appendix 2

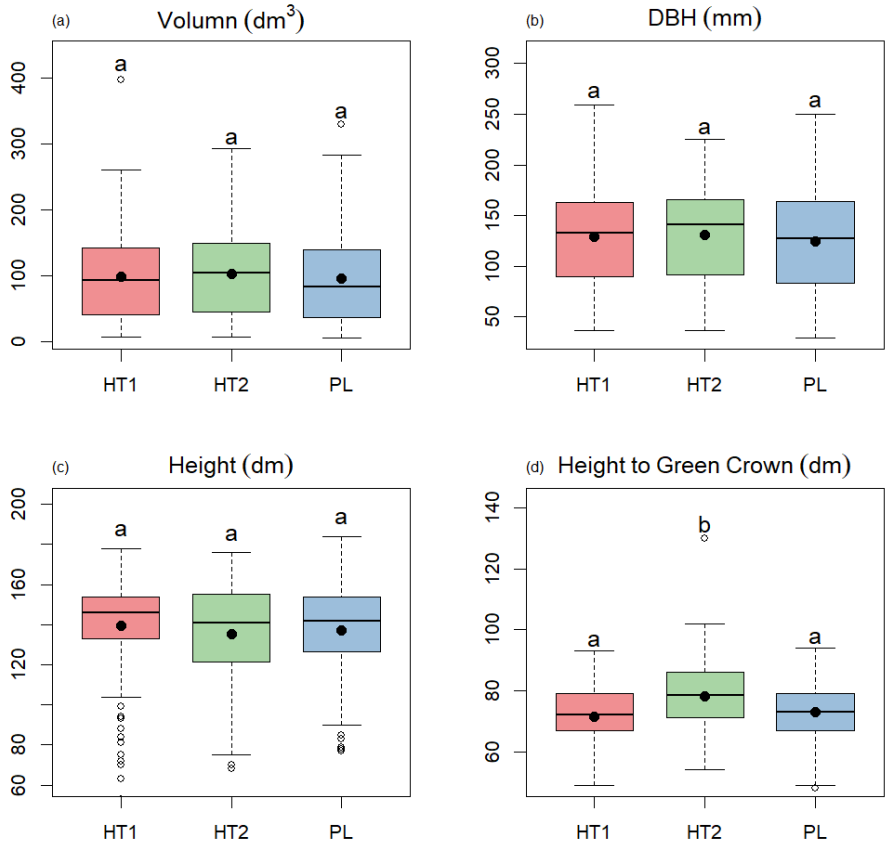

Figure S1. Boxplots of production data of three studied breeds when they were 36 years old, including total tree volume, diameter at breast height (DBH), total tree height, and height to green crown. Two of the breeds were bred for height (HT1, n = 269; HT2, n = 285), whereas the third breed was bred for other purposes other than height (PL, n = 288). The difference letters above each box indicate pairwise differences (p = 0.05). The solid points in each box indicate the mean value.

Appendix 3

Table S2. Production data of three studied breeds when they were 36 years old, including total tree volume, diameter at breast height (DBH), total tree height, and height to green crown. Two of the breeds were bred for height (HT1, n = 269; HT2, n = 285), whereas the third breed was bred for other purposes other than height (PL, n = 288).

		HT1	HT2	PL	F	p value
Volume (dm^3)	Mean	98.39	103.37	96.12	0.53	0.59
	SD	65.17	64.49	68.02		
DBH (mm)	Mean	128.79	130.85	124.76	0.83	0.44
	SD	130.85	46.54	48.34		
Height (dm)	Mean	139.31	135.51	137.37	1.13	0.32
	SD	23.89	25.52	23.59		
Height to Green Crown (dm)	Mean	71.52	78.15	72.89	20.48	**< 0.001**
	SD	10.68	10.76	8.62		

Appendix 4

Table S3. The average values and standard deviation (SD) of root traits among two breeds that were bred for height (HT1 & HT2) and the control (PL) that was not specifically bred for height. SRL, specific root length; AD, average diameter; RTD, root tissue density; SRA, specific root area; C, carbon content; N, nitrogen content; C:N, carbon-to-nitrogen ratio.

Fine root traits	HT1		HT2		PL	
	Mean	SD	Mean	SD	Mean	SD
SRL (mm g^{-1})	26787.20	10454.52	35352.50	8333.53	35884.75	8771.04
AD (mm)	0.51	0.09	0.42	0.05	0.44	0.07
RTD (g mm^{-3})	1.51e-4	2.75e-05	1.61e-4	2.41	1.51e-4	2.44e-05
SRA (mm^2 g^{-1})	41515.13	9341.31	46851.42	7745.26	49251.00	7631.37
C (%)	51.24	1.36	52.47	0.55	52.18	0.55
N (%)	1.05	0.19	1.08	0.12	1.18	0.20
C:N	50.34	9.13	49.39	5.99	45.81	9.41

Appendix 5

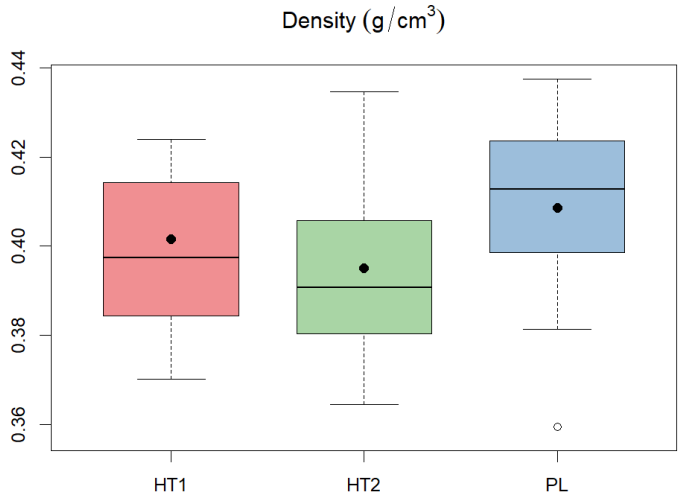

Figure S2. Boxplot of wood density among three breeds including two breeds bred for height (HT1 & HT2), and the control group that bred for purposes other than height (PL). The solid points in each box indicate the mean value. The lines inside each box indicate the median. The standard deviation for HT1, HT2, and PL is 0.03, 0.02, 0.02, respectively.

Appendix 6

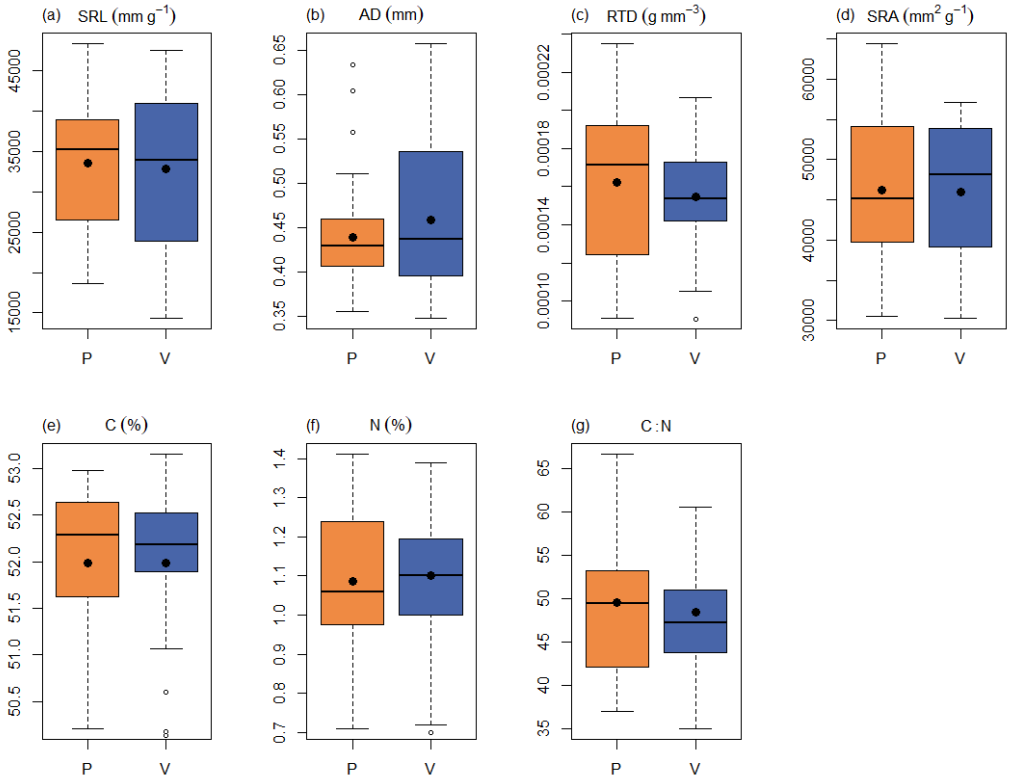

Figure S3. Boxplots of root traits from trees of good (V) and poor (P) vitality. The solid points in each box indicate the mean value. SRL, specific root length; AD, average diameter; RTD, root tissue density; SRA, specific root area; C, carbon content; N, nitrogen content; C:N, carbon-to-nitrogen ratio.

Appendix 7

Table S4. ANOVAs comparing root traits between good (V) and poor (P) vitality. SRL, specific root length; AD, average diameter; RTD, root tissue density; SRA, specific root area; C, carbon content; N, nitrogen content; C:N, carbon-to-nitrogen ratio.

Fine root traits	Vitality	Value		One-way ANOVA	
		Mean	SD	F	p
SRL (mm g^{-1})	P	33514.21	7574.79	0.10	0.75
	V	32843.03	9841.59		
AD (mm)	P	0.44	0.06	1.28	0.26
	V	0.46	0.08		
RTD (g mm^{-3})	P	1.62e-4	3.95e-05	1.00	0.32
	V	1.55e-4	2.50e-05		
SRA (mm^2 g^{-1})	P	46165.64	8739.53	0.01	0.94
	V	45997.01	8626.02		
C (%)	P	51.99	0.93	0.00	0.98
	V	51.99	1.01		
N (%)	P	1.09	0.20	0.13	0.72
	V	1.10	0.18		
C:N	P	49.57	9.69	0.27	0.61
	V	48.46	8.29		

Acknowledgement

I would like to express my sincere thanks to everyone who supported me during my master's program, academically and mentally. I would like to express my deepest gratitude to my supervisor Clydecia Spitzer for her tutoring in this thesis project and co-supervisor Michael Gundale for his comments and suggestions for improvement. In the meantime, I particularly appreciate the guidance and support from the forest vegetation ecology group during the lab work. Special thanks to Clydecia Spitzer and Morgan Karlsson for their support in sample collection. Without their support, this thesis would not have been complete.

I am grateful for the support from my family and friends back home. My family has been my steadfast support during my study. And I would like to especially thank Yi Ye for her constant encouragement during the program.

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