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Shifting Root Strategies: Impacts of Forest Conversion on Fine Root Traits in Monoculture Systems

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ABSTRACT

The intensification of land-use from natural forests to monoculture systems such as rubber and oil palm plantations alters soil structure and resource availability, thereby affecting fine root acquisition strategies. This study assessed the impact of land-use intensification on fine root morphology, water content, and acquisition strategies across different land-use types. Fine root samples were collected from four systems: natural forest, jungle rubber, rubber, and oil palm plantations (five plots per system). Fine roots were classified into absorptive (first–third order) and transportive (fourth–fifth order), and traits were analyzed using WinRHIZO Pro 2020a. The results showed a decline in absorptive root length along the intensification gradient, with oil palm significantly shorter than forest and jungle rubber. In contrast, root length per area (RLA) was higher in the forest than in rubber plantations. Absorptive root tip length was significantly greater in oil palm compared to rubber. Transportive root length also declined, with significant differences only between oil palm and jungle rubber. Fine root diameter (FRD) and root tissue density (RTD) tended to increase, while specific root length (SRL) and specific root area (SRA) tended to decrease in absorptive roots. In transportive roots, SRL was inconsistent, and SRA remained stable. Water content tended to decrease in absorptive roots but remained relatively stable in transportive roots.

1. Introduction

Forests are complex natural ecosystems that play a crucial role in maintaining environmental stability, capturing CO_2, storing water, and supporting biodiversity (Bastin *et al.* 2019; Harris *et al.* 2021; Alam *et al.* 2023). Forest root systems also serve as indicators of soil fertility and ecosystem stability (Abe *et al.* 2021; Staszel-Szlachta *et al.* 2024). However, forests in Indonesia continue to decline due to land conversion into plantations, agriculture, and settlements. Land-use change not only fragments habitats and reduces biodiversity (Margono *et al.* 2014) but also degrades soil quality by lowering organic carbon and nutrient availability (Widyati *et al.* 2022). The intensification of land use into rubber and oil palm monocultures drives deforestation and land-cover change (Gaveau *et al.* 2016; Setiawan *et al.* 2016), alters soil nutrient and soil organic matter (Allen *et al.* 2015; Widyati *et al.* 2022), and modifies fine-root dynamics (Violita *et al.* 2016).

Fine roots (diameter ≤ 2 mm) have traditionally been regarded as uniform in their absorption function (Jackson *et al.* 1997). Still, a new approach classifies them based on their specific functions, namely absorptive and transportive roots (McCormack *et al.* 2015). Absorptive roots play a role in the acquisition of water and nutrients, often associated with mycorrhizae, while transportive roots support the transportation and

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temporary storage of resources (Wang *et al.* 2021; Li *et al.* 2023). According to the Root Economic Spectrum (RES), fine root resource acquisition strategies can be divided into two types: acquisitive and conservative (Weemstra *et al.* 2016). Acquisitive roots express traits such as high specific root length (SRL), large specific root area (SRA), low tissue density, thin diameters, and short lifespan, traits associated with rapid exploration and turnover, while conservative strategies emphasize persistence and resource efficiency, with thicker roots, lower SRL and SRA, denser tissues, and longer lifespan (Reich 2014; Maracahipes *et al.* 2018; McCormack and Iversen 2019; Hogan *et al.* 2020; de la Riva *et al.* 2021). These patterns offer important insights into how plants optimize belowground allocation in response to environmental constraints.

Several studies have shown that forest conversion influences fine root characteristics. Pransiska *et al.* (2016) reported that land-use intensification to jungle rubber, rubber plantations, and oil palm affects root biomass, root morphology, and soil organic matter content. Pierik *et al.* (2021) also found that rooting strategies shift toward more conservative traits in upland environments compared to lowland areas.

Information regarding fine root strategies in resource acquisition across converted tropical land-use systems in Indonesia remains limited. Kotowska *et al.* (2022) highlighted that shifts from conservative to acquisitive land-use strategies in forests are not always consistent. To advance understanding of this pattern, this study investigated four land-use types representing a gradient of land-use intensification from natural systems to monocultures: forest (natural forest vegetation), jungle rubber (rubber trees grown among forest vegetation as an agroforestry transition), rubber plantations (monoculture rubber), and oil palm plantations (monoculture oil palm). The objectives of this study are: (1) to assess the impact of land-use intensification on fine root morphology and water content, and (2) to analyze the types of fine root acquisition strategies in converted tropical land-use systems.

2. Materials and Methods

2.1. Study Site and Land-Use Systems

This study was conducted between August 2022 and June 2023 in two lowland tropical rainforest regions in Jambi Province, Sumatra, Indonesia: Harapan (02°11′24″S, 103°20′24″E) and Bukit Duabelas (01°56′24″S to 02°08′24″S, 102°34′48″E to 102°50′60″E), ranging in elevation from 40 to 100 m above sea level (Kotowska *et al.* 2022). The region has a mean annual air temperature of 26.7±0.2°C and annual precipitation of 2,235±385 mm (mean ± SD; Drescher *et al.* 2016). In the Harapan region, the dominant soil type was classified as sandy loamy Acrisol, whereas in Bukit Duabelas it was clayey Acrisol (Kotowska *et al.* 2022). These sites are part of the long-term ecological research network under the CRC990/EFForTS (Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems) project.

Four land-use types were selected to represent a gradient of land-use intensification: (1) natural forest, (2) jungle rubber (traditional agroforestry system), (3) rubber plantations (Hevea brasiliensis), and (4) oil palm plantations (Elaeis guineensis) (Figure 1). Permanent 50 × 50 m plots were established in each system across both landscapes. In total, twenty plots (five plots per land-use system) were included in the study. Due to the availability and condition of long-term research plots during fieldwork, not all land-use systems were equally represented across both landscapes. Rubber trees ranged from 15–40 years old in jungle rubber and 7–16 years in monocultures, while oil palm trees were 8–15 years old. Plantation systems were intensively managed: oil palm plots received annual inputs of 150–300 kg ha^{-1} of NPK, KCl, and/or urea fertilizers, while rubber monocultures received 100–200 kg ha^{-1} per year, applied in two doses (Allen *et al.* 2015; Euler *et al.* 2016; Kotowska *et al.* 2022).

2.2. Fine Root Sampling and Classification

Fine roots with diameters ≤ 2 mm were collected using the root-tracing method. Target trees were selected based on stem tagging records, with a minimum diameter at breast height (dbh) of ≥ 10 cm. A total of 59 individuals were sampled to represent dominant species and capture the diversity of each land-use system. Tree selection was guided by vegetation inventory data, prioritizing species with the highest frequency of occurrence, ensuring that sampled individuals reflected the representative community within each system. Root samples were collected from three to five dominant trees per plot in forest and jungle rubber systems, depending on tree availability and condition. In jungle rubber, sampling included both dominant forest trees and one Hevea brasiliensis per plot to represent its mixed community composition, reflecting the characteristics of a traditional mixed-species agroforestry system. In rubber and oil palm plantations, which were more homogeneous,

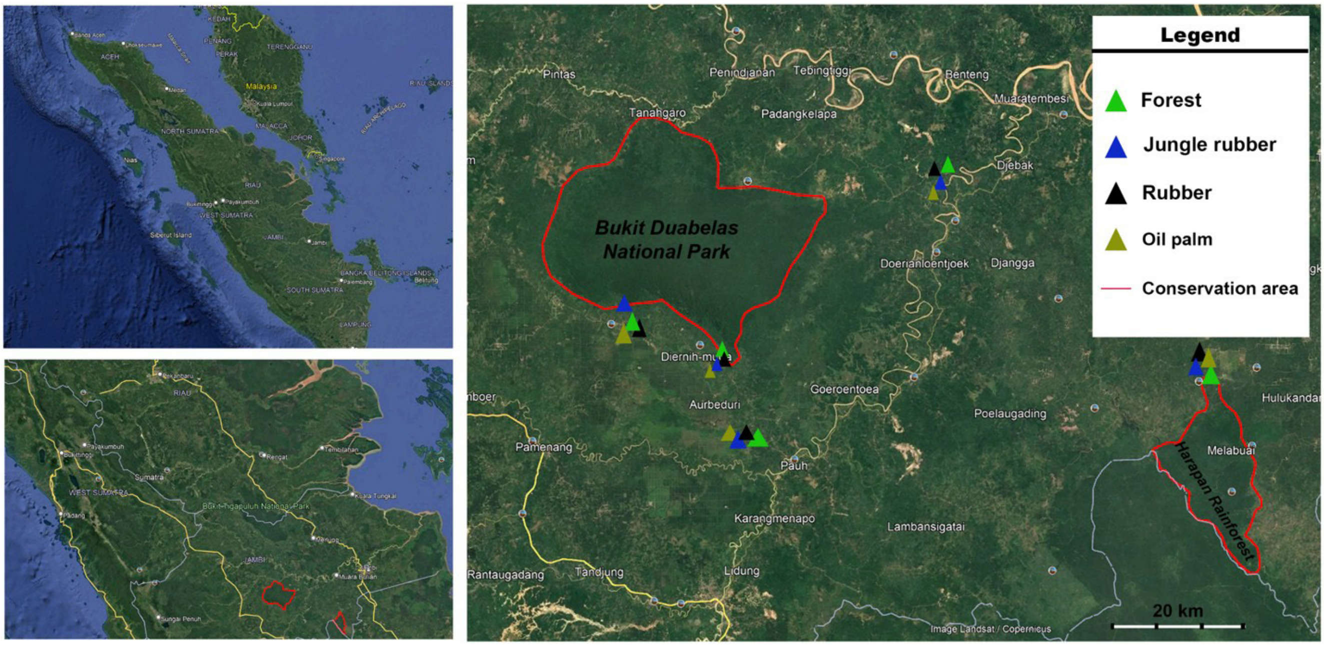

Figure 1. Maps of the research location

samples were collected from one representative tree per plot, either Hevea brasiliensis or Elaeis guineensis. Thus, the higher number of sampled trees in forest and jungle rubber reflects their greater structural and compositional heterogeneity. In contrast, in the structurally homogeneous monoculture plantations, a single representative tree per 50 × 50 m plot was sufficient to characterize stand-level fine root traits while avoiding unnecessary pseudoreplication within plots.

Tracing began at the starting point, identified as a fine root segment (2 mm diameter) directly connected to the main root at the tree base. Fine roots were carefully traced to their terminal tips through manual soil excavation with simple hand tools, such as a small shovel or garden fork. Only intact root segments with complete branching were collected. If the traced root was broken or incomplete, the tracing process was repeated on another side of the same tree until an undamaged segment with full branching was obtained. Collected root segments were cut with scissors, placed in labelled plastic bags, and transported to the laboratory. In the laboratory, roots were washed over a 1.25 mm sieve under running water until free of adhering soil. When compact soil particles were present, roots were soaked in deionized water, then rinsed. Clean roots were stored in Petri dishes filled with deionized water to maintain freshness prior to classification.

Root classification was based on branching order following McCormack *et al.* (2015). First to third order roots were categorized as absorptive, while fourth and fifth order roots were classified as transportive.

2.3. Root Trait Measurements

Root segments were spread in a transparent tray filled with water and scanned using a root scanner. Scanned images were analyzed using WinRHIZO Pro 2020a software (Regent Instruments Inc.) to quantify morphological traits, including root segment length, surface area, root diameter, and tip root. Functional traits were measured separately for absorptive and transportive roots, including:

- Root length (cm)
- Root length per area (RLA; cm m^{-2})
- Tip length (cm)
- Specific root length (SRL; m g^{-1})
- Specific root area (SRA; cm2 g^{-1})
- Fine root diameter (FRD; mm)
- Root tissue density (RTD; g cm^{-3})
- Water content (%), calculated as:

$$\frac{\text{wet weight - dry weight}}{\text{wet weight}} \times 100\%$$

Samples were oven-dried at 70°C until a constant dry weight was achieved.

2.4. Statistical Analysis

Statistical analyses were conducted using RStudio software (version 2024.12.1-563). All data were transformed using a square-root transformation. Model assumptions were verified using both visual diagnostics and formal tests. Normality was visually inspected using Q–Q plots, and further tested with the Shapiro–Wilk test. Homogeneity of variances (homoscedasticity) was assessed using residuals versus fitted plots and formally tested with Levene's test. Linear Mixed-Effects Models (LMM) were used to test the effect of land-use system (forest, jungle rubber, rubber, oil palm) on fine root traits. Land-use was included as a fixed effect, and plot identity as a random effect. Because the two study landscapes (Harapan and Bukit Duabelas) differ in soil type and not all land-use systems were equally represented across them, we additionally tested models including landscape as a random intercept. Results were consistent across model structures, indicating that our inferences on land-use patterns are robust to model specification. Models were fitted using the lme4 package (Bates *et al.* 2015), and fixed-effect significance was assessed with the lmerTest package (Kuznetsova *et al.* 2017). Pairwise comparisons were conducted using Tukey's HSD test based on estimated marginal means with the emmeans (Lenth *et al.* 2023) and multcompView (Graves *et al.* 2019) packages. Principal Component Analysis (PCA) was applied to community-level trait means to examine multivariate relationships among morphological traits and water content, using the prcomp function.

3. Results

3.1. Fine Root Morphological Variation and Water Content Across Land-Use Systems

3.1.1. Length and Root Length per Area (RLA)

Absorptive root length declined significantly with increasing land-use intensity. Fine roots in oil palm plantations (2.13±0.11 cm) were significantly shorter than those in the forest (2.74±0.12 cm) and jungle rubber (2.73±0.12 cm). At the same time, no significant difference was found between forest and jungle rubber ($p>0.05$) (Figure 2A). Transportive root length also showed a significant decline with land-use intensification, with roots in oil palm (1.62±0.11 cm) being significantly shorter than in jungle rubber (1.97±0.08 cm) ($p<0.05$). No other pairwise differences were significant. Root length per area (RLA) also decreased significantly, with forest (0.10±0.01 cm m^{-2}) showing higher values than rubber plantations (0.08±0.00 cm m^{-2}) ($p<0.05$). In contrast, transportive root RLA did not differ significantly across land-use systems ($p>0.05$) (Figure 2B).

3.1.2. Fine Root Tip Length

Fine root tip length was significantly greater in oil palm (1.89±0.15 cm) than in rubber plantations (1.29±0.07 cm) ($p<0.05$), while no significant differences were observed among the other land-use types.

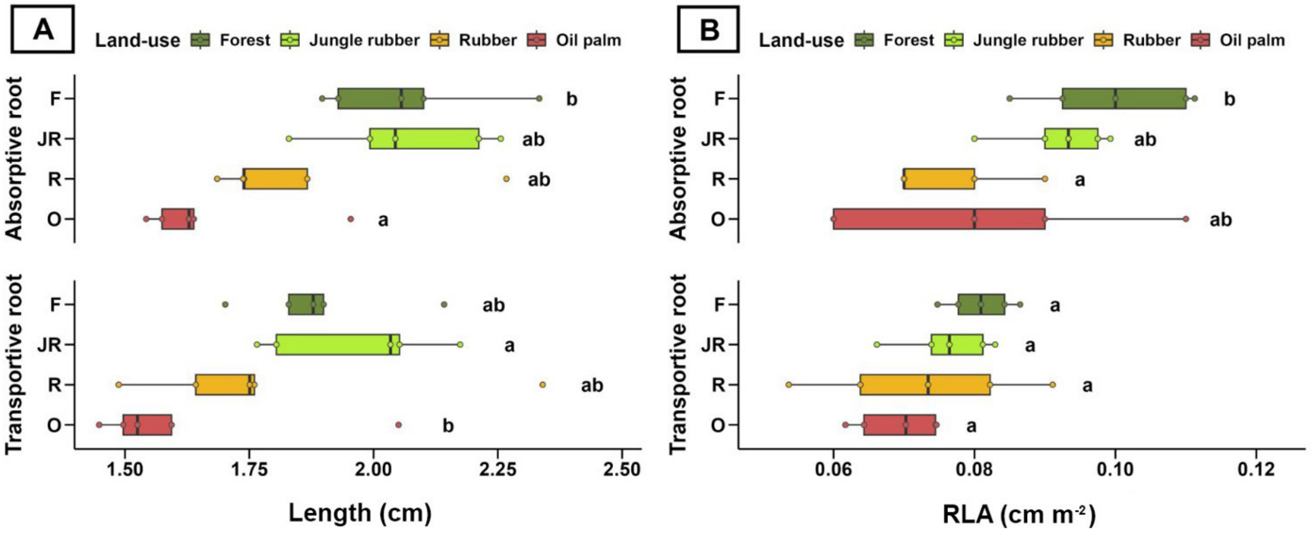

Figure 2. Mean fine root length (A) and root length per area (RLA) (B) comparing absorptive and transportive roots across four land-use systems: forest (F), jungle rubber (JR), rubber (R), and oil palm (O). Different letters above each boxplot indicate significant differences among land-use types ($p<0.05$; Tukey's HSD test following linear mixed models). Data were square-root transformed

Transportive root tip length did not differ significantly across the four systems (Figure 3).

3.1.3 Specific Root Length (SRL) and Specific Root Area (SRA)

In general, specific root length (SRL) and specific root area (SRA) of absorptive roots tended to decrease from natural forest to intensively managed agricultural systems (Figure 4A). By contrast, SRL in transportive roots did not show a consistent trend among land-use types, while SRA remained relatively stable across all systems (Figure 4B). Nevertheless, differences in SRL and SRA among the four land-use systems were not statistically significant for either absorptive or transportive roots (p>0.05).

3.1.4. Fine Root Diameter (FRD) and Root Tissue Density (RTD)

Fine root diameter (FRD) and root tissue density (RTD) of absorptive fine roots tended to increase along the intensification gradient. In contrast, in transportive roots, both traits showed a decreasing trend (Figure 5A and B). However, there were no significant differences in FRD or RTD among the land-use types for either root category (p>0.05).

3.1.5. Water Content

The water content of the absorptive roots tended to decrease with the intensification of land-use, while the transportive roots were relatively stable (Figure 6). However, these differences were not statistically significant (p>0.05).

3.2. Principal Component Analysis of the Morphology of Fine Root Traits and Water Content

PCA revealed the dominant axes of root trait differentiation, with the first two components capturing the principal gradients of variation. In absorptive roots, PC1 (47.7%) and PC2 (30.2%) explained 77.9% of the total variance (Figure 7A). The negative side of PC1 was driven by acquisitive traits, including specific root area (SRA, –0.477), specific root length (SRL, –0.419), root length (–0.402), and water content (–0.388). In contrast, the positive side was characterized by conservative traits, such as root tissue density (RTD, +0.368) and

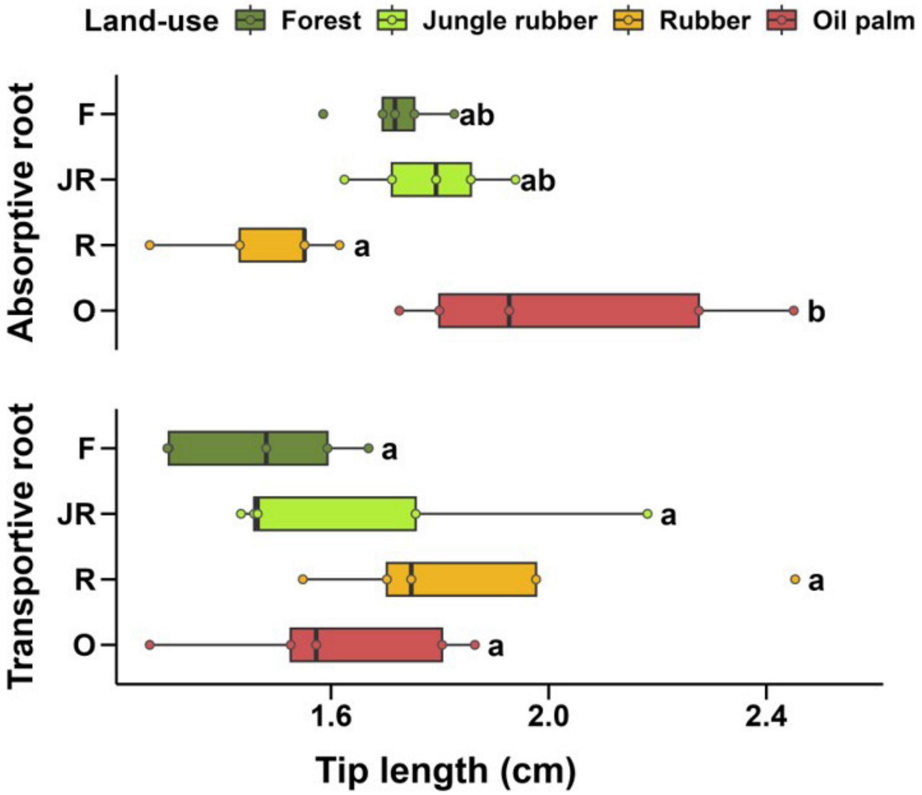

Figure 3. Mean fine root tip length comparing absorptive and transportive roots across four land-use systems: forest (F), jungle rubber (JR), rubber (R), and oil palm (O). Different letters above each boxplot indicate significant differences among land-use types ($p < 0.05$; Tukey's HSD test following linear mixed models). Data were square-root transformed.

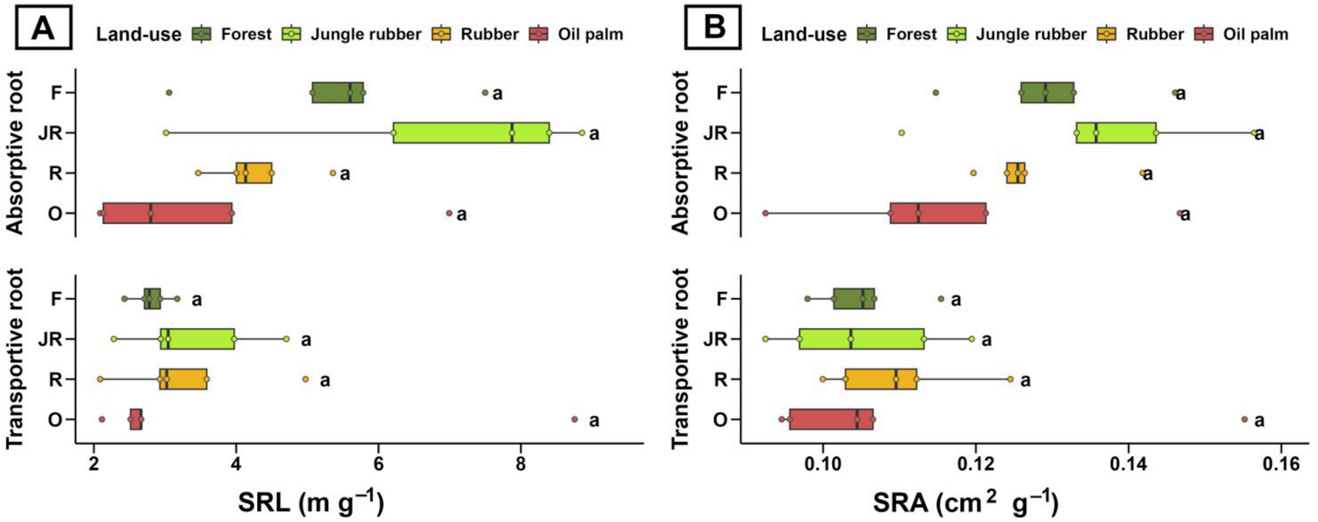

Figure 4. Mean specific root length (SRL) (A) and specific root area (SRA) comparing absorptive and transportive roots across four land-use systems: forest (F), jungle rubber (JR), rubber (R), and oil palm (O). Different letters above each boxplot indicate significant differences among land-use types (p<0.05; Tukey's HSD test following linear mixed models). Data were square-root transformed

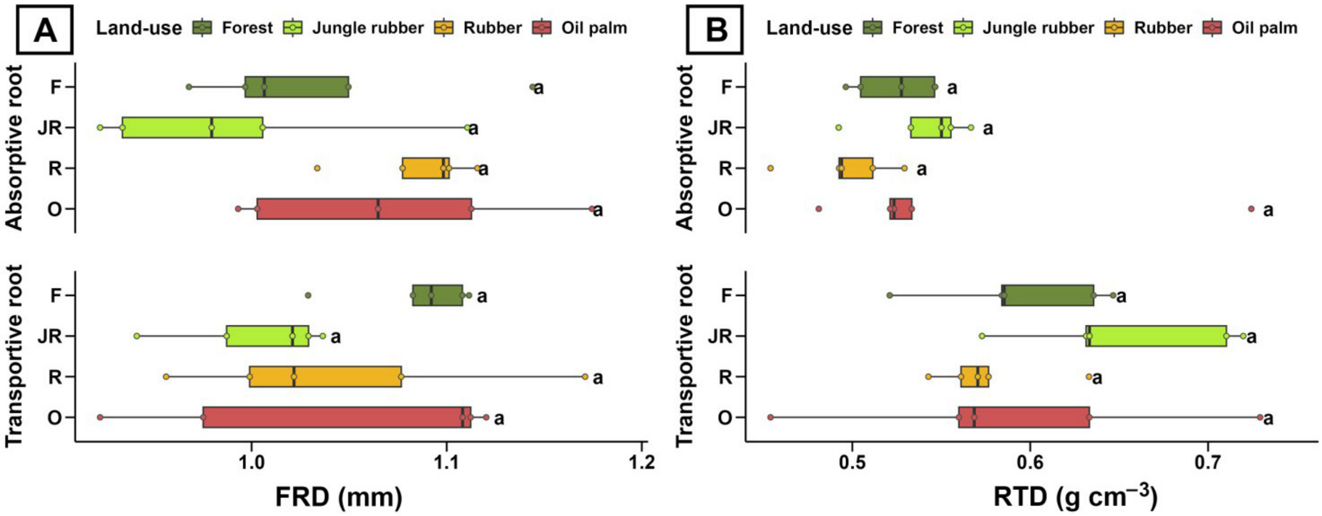

Figure 5. Mean fine root diameter (FRD) (A) and root tissue density (RTD) (B) comparing absorptive and transportive roots across four land-use systems: forest (F), jungle rubber (JR), rubber (R), and oil palm (O). Different letters above each boxplot indicate significant differences among land-use types (p<0.05; Tukey's HSD test following linear mixed models). Data were square-root transformed

fine root diameter (FRD, +0.223). Along PC2, FRD (+0.560) and water content (+0.388) loaded positively, whereas tip length (–0.456) and RTD (–0.382) loaded negatively. In the ordination space, forest and jungle rubber clustered toward the acquisitive side of PC1, with jungle rubber positioned slightly closer to the center but still overlapping with forest. Rubber plantations shifted toward the conservative quadrant associated with FRD, while oil palm plots grouped on the positive side of PC1 with FRD and RTD, showing broad dispersion and therefore higher within-system variability.

For transportive roots, PC1 (42.0%) and PC2 (26.5%) explained 68.5% of the total variance (Figure 7B). Length-related traits such as SRL (+0.511), SRA (+0.505), and root length (+0.365) loaded positively on PC1, whereas FRD (–0.349) and RTD (–0.343) were associated with the negative side. PC2 further separated water content (+0.368) and FRD (+0.381) on the positive axis from RTD (–0.482) and root length per area (RLA, –0.466) on the negative axis. Unlike absorptive roots, transportive roots did not exhibit a clear separation among land-use systems. Forest and jungle

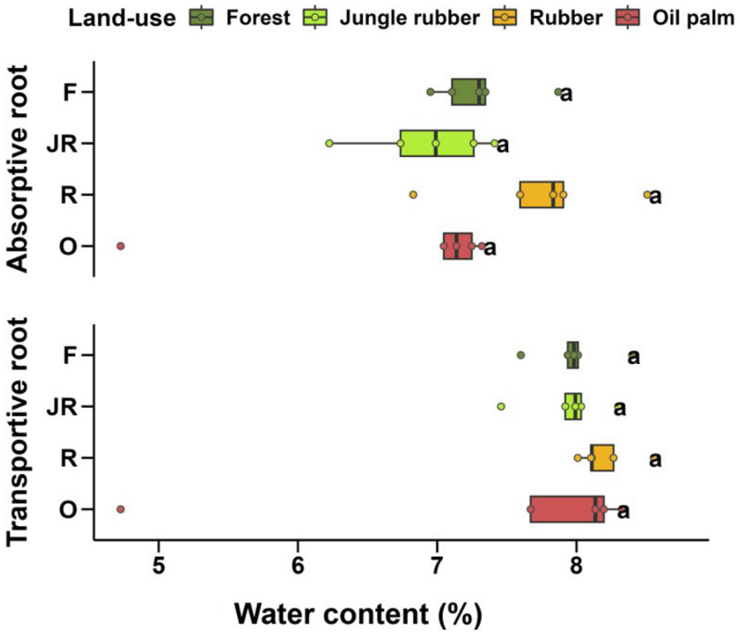

Figure 6. Mean water content comparing absorptive and transportive roots across four land-use systems: forest (F), jungle rubber (JR), rubber (R), and oil palm (O). Different letters above each boxplot indicate significant differences among land-use types ($p<0.05$; Tukey's HSD test following linear mixed models). Data were square-root transformed

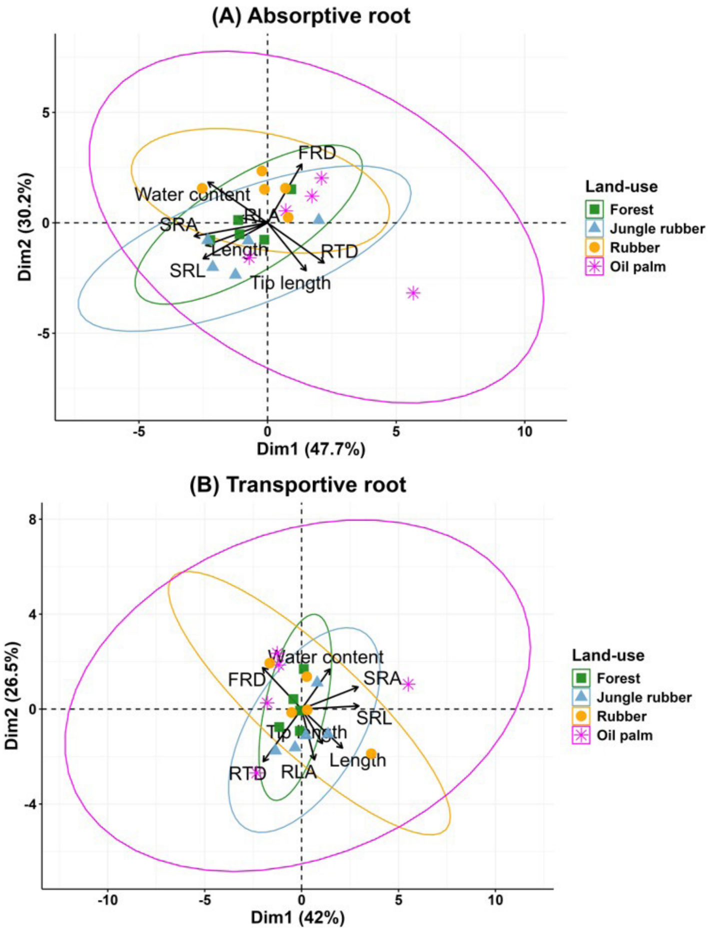

Figure 7. Principal component analysis (PCA) biplots of community-level mean fine root morphological traits and water content for (A) absorptive roots and (B) transportive roots across four land-use systems (Forest, Jungle rubber, Rubber, and Oil palm). The first two principal components (PC1 and PC2) explain 77.9% of the total variance (A) and 68.5% of the total variance (B), respectively. Arrows indicate the direction and strength of each root trait variable

rubber overlapped, clustering toward RTD and RLA, while rubber and oil palm samples were more widely dispersed across the ordination space without forming distinct groups.

4. Discussion

Land-use intensification from forest to jungle rubber, then to rubber and oil palm plantations, leads to significant environmental changes that affect fine root morphology and function. Root length in both absorptive and transportive classes declined along the land-use intensification gradient. In absorptive roots, oil palm plots had significantly shorter fine roots than forest and jungle rubber ($p<0.05$), whereas forest and jungle rubber did not differ. Root length per area (RLA) showed a similar decline, with higher values in forest than in rubber ($p<0.05$), while RLA of transportive roots did not differ among systems. These patterns mirror the decline in total fine root length following forest conversion reported by Saputra *et al.* 2020 and the drop in root length density across the forest plantation gradient documented by Sahner *et al.* (2015). Such morphological shifts likely reflect soil structural degradation, declines in soil organic carbon stocks following conversion (Guillaume *et al.* 2016), and elevated nutrient leaching under intensified land use (Kurniawan *et al.* 2018). Similar adaptive shifts in root morphology have been documented along other environmental gradients, such as elevation (Cornejo *et al.* 2020).

Transportive root length also declined under more intensive management, with jungle rubber showing significantly longer transportive roots than oil palm ($p<0.05$). Interestingly, in our dataset, the mean transportive root length in jungle rubber was comparable to, and in some cases slightly exceeded, that of natural forest. This pattern may be explained by the mixed-species composition of jungle rubber, where rubber trees (*Hevea brasiliensis*) co-occur with remnant and secondary forest species (Pransiska *et al.* 2016; Kotowska *et al.* 2022; Penot 2024). Such mixtures can create more heterogeneous belowground resource distributions and intensify root competition, leading to greater variability in root traits at the community level (Mommer *et al.* 2012; Rajaniemi 2022). As a result, the relatively high transportive root length observed in jungle rubber plots likely reflects community-level responses to species mixing rather than a simple effect of land-use intensity. The greater root length observed in less intensive systems may reflect increased belowground competition and the need to explore larger soil volumes to obtain limited water and nutrients (Meinen *et al.* 2009). In contrast, the compacted soils and slower decomposition in oil palm plantations likely inhibit root elongation (Guillaume *et al.* 2016; Violita *et al.* 2016; Lynch 2019), prompting plants to develop shorter fine roots as an energy-saving strategy, while maintaining their uptake capacity (Kong *et al.* 2014).

Fine root tip length also responded to land-use intensification. Oil palm produced longer absorptive root tips than rubber with a significant difference ($p<0.05$). Oil palm roots are suspected to lack root hairs, which rely on meristematic and elongation zone activity to expand their absorptive surface (Intara *et al.* 2018). Thin-walled parenchyma, slow lignification, and the abundance of fine roots with xylem diameters <2 mm further promote root tip extension in oil palm (Sim and Zaharah 2014; Intara *et al.* 2018). In contrast, earlier lignification in the apical zone of rubber roots may restrict root elongation, resulting in shorter root tips (Maeght *et al.* 2015).

Other fine root traits showed less pronounced differences among systems. Specific root length (SRL) of absorptive roots in jungle rubber tended to be higher than in natural forest and showed the widest range of values. However, mean SRL did not differ significantly among land-use types. This pattern is consistent with the mixed-species composition of jungle rubber, where rubber trees co-occur with remnant and secondary forest species that often express more acquisitive fine root traits (Caplan *et al.* 2019; Wambsganss *et al.* 2021; Rajaniemi 2022). Along the intensification gradient, SRL and specific root area (SRA) of absorptive roots tended to decline with increasing land-use intensity, broadly aligning with previous findings (Pransiska *et al.* 2016; Kotowska *et al.* 2022). Fine roots with high SRL reflect efficient uptake of water and nutrients in ecosystems with high plant diversity (Wambsganss *et al.* 2021). By contrast, in transportive roots, SRL did not show a consistent trend among systems, and SRA remained relatively stable, which may reflect adaptation of transport tissues to limited resource availability (Kong *et al.* 2019). However, these differences were not statistically significant, suggesting that plants with sufficient resource supply may maintain relatively stable root morphologies despite land-use intensification (Addo-Danso *et al.* 2019). Increases in fine root diameter (FRD) and root tissue density (RTD) of absorptive roots along the intensity gradient, though not statistically significant, may indicate adaptation to drier, nutrient-poor soils, where thicker, denser roots are longer-lived and more efficient at resource uptake (Kong *et al.* 2019).

Fine root water content tended to decrease in absorptive roots, whereas transportive roots remained relatively stable, and neither pattern was statistically significant. Water content reflects the capacity for turgor regulation and water transport efficiency (Ievinsh 2023). The humid microclimate and dense soil cover in primary forests help maintain fine root water content (De Frenne *et al.* 2021). In contrast, oil palm plantations with higher transpiration rates and uneven water supply may exhibit reduced root water-holding capacity (Akram *et al.* 2022). Water content did not differ significantly among land-use types, and this overall stability is expected under the humid conditions of the study region, where plants can maintain similar fine root hydration even when their root lengths differ.
Although community-mean FRD and RTD did not differ among land-use types, forests and jungle rubber tended to maintain longer absorptive and transportive roots than rubber and oil palm. This pattern suggests that tissue-level structural traits within the <2 mm fine root class are relatively conserved. In contrast, spatial deployment traits, such as root length and soil exploration, remain more plastic and responsive to the competitive and compositional context of the plant community (Valverde-Barrantes *et al.* 2015; Sun *et al.* 2017). In diverse forest and jungle rubber stands, the coexistence of multiple tree species with more acquisitive strategies likely promotes complementary belowground foraging, as species differ in fine root deployment rather than tissue structure, with several species investing in long, highly branched fine roots at similar diameters to exploit heterogeneous nutrient and water patches more completely (Brassard *et al.* 2011; Eissenstat *et al.* 2015; McCormack *et al.* 2015). By contrast, rubber and oil palm monocultures are dominated by a narrower set of conservative root strategies, producing shorter fine root systems despite similar average diameter and tissue density (Sahner *et al.* 2015; Pransiska *et al.* 2016; Kotowska *et al.* 2022; Tonra *et al.* 2025).

PCA revealed contrasting multivariate patterns in absorptive and transportive fine roots along the land-use gradient from forest to monoculture systems of rubber and oil palm. In absorptive roots, the first two axes captured a clear gradient from acquisitive to conservative strategies (Figure 7A). Traits linked to high specific root length and specific root area, longer fine roots, and higher tissue hydration aligned with the acquisitive end. This combination reflects thinner, longer, and more hydrated roots that enhance soil exploration and rapid, efficient uptake of water and nutrients (Valverde-Barrantes *et al.* 2017; Zhu *et al.* 2021; Valverde-Barrantes 2022). In contrast, fine root diameter and root tissue density indicated investment in denser, longer-lived tissues that emphasize structural resilience and extended tissue lifespan (McCormack *et al.* 2015; Hou *et al.* 2024).

In the ordination space, forests and jungle rubber tended to cluster toward the acquisitive quadrant, consistent with greater uptake efficiency, whereas rubber and oil palm shifted toward the conservative quadrant characterized by thicker and denser roots (McCormack *et al.* 2015; Weemstra *et al.* 2020). Jungle rubber remained close to forests, suggesting that this agroforestry system retains forest-like uptake strategies. Group ellipses partially overlapped, and several univariate contrasts were not significant; therefore, the PCA patterns are interpreted as descriptive gradients rather than inferential evidence of group separation.

For transportive roots, the main axes were opposed to elongation-related traits, such as specific root length, specific root area, and root length. In contrast, tissue density and fine root diameter were opposed to diameter metrics. Water content varied along a secondary dimension (Figure 7B). Unlike the absorptive compartment, land-use groups broadly overlapped in the transportive compartment, indicating weaker separation among systems. This configuration aligns with the hydraulic efficiency-to-safety continuum. In general, larger diameters and higher water content are thought to be associated with greater axial conductivity, whereas denser, more lignified tissues reinforce structural integrity, stabilising transport under stress (Hafner *et al.* 2019; Reyt *et al.* 2021; Sha *et al.* 2024). In our study, FRD and water content did not differ significantly among land-use types, so this axis is interpreted as a conceptual hydraulic-efficiency-to-safety continuum rather than as a direct contrast among groups. Accordingly, the PCA of transportive roots aligns less clearly with the canonical Root Economics Spectrum. Instead, it reflects multidimensional variation constrained by conduction and support roles, which yields comparatively conservative tissue properties and a more limited response to land-use conversion (McCormack *et al.* 2015; Sanaei *et al.* 2025).

Overall, these results highlight the nuanced responses of fine root morphology and function to land-use intensification in tropical landscapes. Land-use intensification has the potential to shift root strategy from acquisitive to conservative, particularly in absorptive roots. The shift in morphological characteristics of transportive roots is less clearly visible because the primary function of those roots is primarily to function as transport channels and temporary storage of resources, not for the acquisition of water and nutrients.

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