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Nutrient and Water Acquisition Strategies of Oil Palm Fine Roots Enriched with Crops Species

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ABSTRACT

Fine roots (≤2 mm diameter) are a plant organ that plays a major role in nutrient and water acquisition from the soil and a parameter for understanding belowground changes. Fine root traits can determine the plant's strategies in maximizing resource acquisition for productivity with an acquisitive strategy or maximizing resource investment with a conservative strategy. In this study, enrichment planting was carried out in oil palm plantations through a combination of oil palm and tree crops. It is necessary to determine whether enrichment planting can impact the nutrient and water acquisition of oil palm fine roots. Therefore, this study aimed to determine the nutrient and water acquisition strategies of oil palm fine roots enriched with crop species by analyzing differences in morphological traits through fine root inventory. The enrichment planting treatments were R0 (plot of oil palm without enrichment crop), R1 (plot of oil palm with one crop), R2 (plot of oil palm with two crops), R3 (plot of oil palm with three crops), and R6 (plot of oil palm with six crops/multispecies). The results showed that enrichment planting in oil palm plantations can be practiced with two and three crop species, as in plots R2 and R3, which support a conservative strategy with high RTD (root tissue density) and low SRL (specific root length) and SRA (specific root area) in oil palm fine roots. In contrast, high species diversity in plot R6 triggered a shift to an acquisitive strategy with high SRL and SRA and low RTD.

1. Introduction

Roots, especially fine roots, are plant parts that play an important role in resource acquisition from the soil. Fine roots are active and sensitive to changes in the soil environment (Zhu *et al.* 2021). Variations in fine root traits can represent plant adaptation strategies under a wide range of environmental conditions (Ma *et al.* 2024). Resource acquisition strategies by fine roots are described in the root economic spectrum (RES) theory, which explains the trade-off between resource acquisition and conservation based on root traits (Chen *et al.* 2021; Zhou *et al.* 2024). Roots will maximize resource uptake and productivity with an acquisitive strategy characterized by high specific root length (SRL) and specific root area (SRA), thin root diameter, low root tissue density (RTD), and relatively short lifespan. Conversely, roots will maximize resource investment and plant longevity with a conservative strategy characterized by thick root diameter, low SRL and SRA, high RTD, and relatively long lifespan (Reich 2014; McCormack and Iversen 2019; Hogan *et al.* 2020; de la Riva *et al.* 2021).

The acquisition of nutrients and water from the soil in plants is carried out by fine roots with a diameter of ≤ 2 mm (McCormack *et al.* 2015). Fine roots are differentiated into fine root diameter classes (<0.5 mm, <1 mm, <2 mm, and 1-2 mm) (Ostonen *et al.* 2007). The

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finest roots (diameter <0.5) are assumed to be the most active roots in nutrient absorption (Ostonen *et al.* 2007; Weemstra *et al.* 2017). Fine roots function to absorb nutrients and water from the soil for transport to the crown (Gao *et al.* 2021a). Fine root traits vary depending on plant species and environmental factors (Cornejo *et al.* 2020). Fine roots are used to determine nutrient and water acquisition strategies and the competitive ability of plant species in an ecosystem (Isaac and Borden 2019).

Research on fine roots, especially in oil palm plants, was conducted in oil palm plantations in Jambi Province. Oil palm is a plant that is generally cultivated with a monoculture planting system. However, this study implemented enrichment planting in oil palm plantations, which involved planting multiple tree species on the same land. Oil palm planting in the study area has been carried out since 2006, and enrichment planting began in December 2013 (Teuscher *et al.* 2016). Enrichment planting is a cultivation method with land utilization through planting native species to increase economic and ecological value (Paquette *et al.* 2009; Teuscher *et al.* 2016; Lindh *et al.* 2024). Economic benefits can provide sustainable income from crop yield rotation and ecological benefits from increased crop diversity (Marshall *et al.* 2022).

Oil palm is combined with several types of fruit and wood crops, including *Parkia speciosa* (Stink bean), *Archidendron pauciflorum* (Jengkol), *Durio ziberthinus* (Durian), *Dyera polyphylla* (Jelutong), *Peronema canescens* (Sungkai), and *Shorea leprosula* (meranti). The six types of crops used for enrichment have economic value and play a role in ecological functions. Stink bean and Jengkol are legume crops that can fertilize the soil (Manar *et al.* 2023). Durian has a large root length and good root branching that can be useful in maintaining soil structure and the flow of nutrients and water in the soil (Masri *et al.* 1998). Meranti from the family Dipterocarpaceae has roots associated with ectomycorrhizae that are beneficial for ecosystem restoration (Omon 2002). Jelutong is a local crop commonly used by communities for peatland rehabilitation (Tata *et al.* 2016), and Sungkai is used for reforestation activities that can increase land productivity (Wahyudi *et al.* 2012). The combination of trees with cultivated crops can increase land productivity, carbon sequestration, nutrient cycling, and soil water retention (Norrlin *et al.* 2020). This is closely related to the role of the roots of each crop, especially fine roots.

Research on nutrient and water acquisition strategies by fine roots has been reported by McCormack and Iversen (2019), who observed variations in fine root traits that determine soil resource acquisition strategies. However, research on nutrient and water acquisition strategies of oil palm fine roots enriched with other crop species has not been conducted. Therefore, it is necessary to conduct research to analyze the impact of enrichment planting on the nutrient and water acquisition strategies of oil palm fine roots. The method that can be used is fine root inventory. Fine roots are collected using a soil corer by taking fine roots at a certain soil depth. Fine roots are scanned with a root scanner and then analyzed using WinRhizo to obtain morphological data (fine root length (FRL), root length per area (RLA), specific root length (SRL), specific root area (SRA), root tissue density (RTD), and fine root diameter) (Li *et al.* 2022; Kotowska *et al.* 2022). In addition, fine roots are dried and weighed for biomass and necromass as indicators of soil fertility and ecosystem changes (Cornejo *et al.* 2020). Oil palm enriched with tree crops allows for changes in the nutrient and water acquisition strategies of fine roots. Therefore, the objectives of this study are (1) to analyze differences in oil palm fine root traits on land enriched with other crop species; (2) to determine the type of nutrient and water acquisition strategy (acquisitive or conservative) by oil palm fine roots on a variety of tree species for enrichment; and (3) to determine the appropriate combination of species for enrichment in oil palm plantations.

2. Materials and Methods

This research was conducted from August 2022 to June 2023. Sampling was carried out in the permanent plot of CRC990-EFForTS located in the oil palm plantation of PT Humusindo (01.95° S and 103.25° E, 47±11 m a.s.l.), Bungku Village, Bajubang District, Batanghari Regency, Jambi Province (Figure 1). The climate in the area is humid tropical with moderate to high rainfall intensity (Tables 1 and 2). Loamy Acrisol is the dominant soil type in the region (Allen *et al.* 2015), with soil texture consisting of fractions of silt (40.5±8.3%), sand (29.9±12.6%) and clay (29.5±8.3%), and a soil bulk density of 1.09±0.1 g/cm^3 (Teuscher *et al.* 2016).

2.1. Materials

The research materials were oil palm fine roots and the fine roots of surrounding trees, including *Parkia speciosa* (Stink bean), *Archidendron pauciflorum* (Jengkol), *Durio zibethinus* (Durian), *Dyera polyphylla*

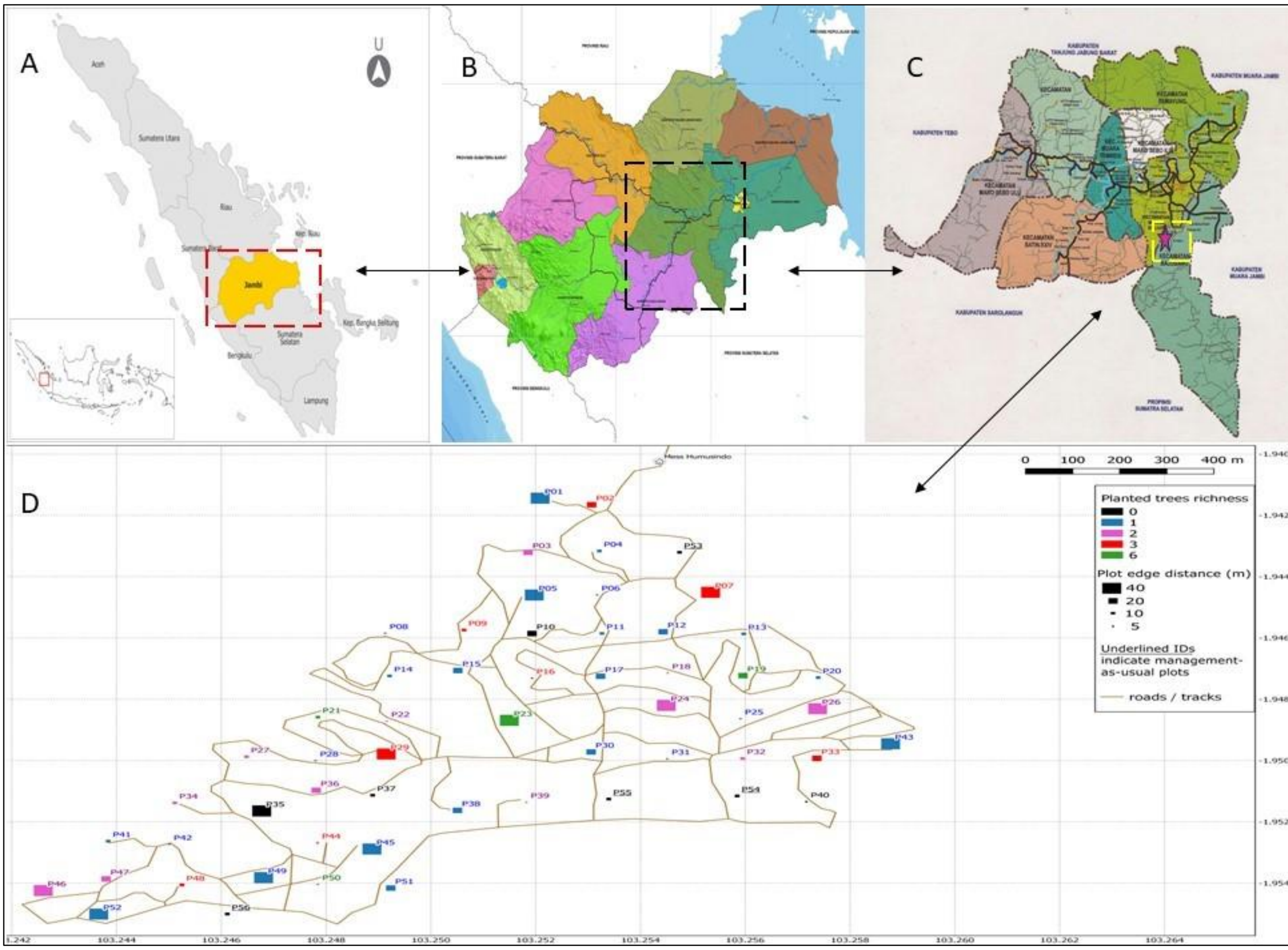

Figure 1. Map of the study area. (A) Sumatra, (B) Jambi Province, (C) Batanghari Regency. The star symbol indicates the location of PT Humusindo in Bungku Village, and (D) Enrichment planting plots at PT Humusindo with colored boxes indicating crop diversity and plot size

Table 1. Climate variables at the study site in 2021-2022. Values given are mean ± standard deviation

Variable	Mean ± SD	
	2021	2022
Humidity (%)	91±12	89±14
Temperature (°C)	27±4	27±4
Soil Humidity (%)	44±4	42±7
Soil Temperature (°C)	32±2	32±2

Table 2. Rainfall in Jambi Province in 2021-2022

Month	Rainfall (mm)	
	2021	2022
January	183.0	294.1
February	28.1	225.2
March	411.2	431.1
April	437.5	206.6
May	320.7	268.5
June	169.7	227.5
July	273.9	135.9
August	164.0	307.9
September	343.8	175.1
October	294.1	505.6
November	348.9	316.2
December	251.4	243.9

Source: Muaro Jambi Climatology Station

(Jelutong), *Peronema canescens* (Sungkai), *Shorea leprosula* (Meranti), and several wild plants. The tools used in this research include a soil corer, sieve, root scanner, WinRhizo software, petri dish, tweezers, caliper, scales, and oven.

2.2. Methods

This study used the fine root inventory method using a soil corer. There were 56 observation plots with different levels of species diversity and plot sizes. Plots were treated with enrichment planting through the combination of oil palm and trees at the level of crop species diversity (R0, R1, R2, R3, and R6). The R0 is an oil palm plot without enrichment crops (monoculture), R1 is an oil palm plot with one crop species, R2 is an oil palm plot with two crop species, R3 is an oil palm plot with three crop species, and R6 is an oil palm plot with six crop species/multispecies. The control plot (Rctl) was a conventionally managed monoculture oil palm plot.

Plantation management included fertilizer application (230 kg N (Urea), 196 kg P (Triple Superphosphate and rock phosphate), 142 kg K (KCl), 54 kg Mg (Kieserite and Dolomite), and 0.79 kg B (Borax), per ha per year and added S ($(NH_4)2SO_4$), Si (Zeolite), and (Ca). In addition, regular weeding is done, and herbicides are rarely used, only when there is a shortage of workers (Teucher *et al.* 2016).

Plots planted with enrichment species were fertilized in the planting holes before tree planting with synthetic (19 kg N, 8 kg P, 6 kg K, and 3 kg Mg) and organic (11 kg N, 7 kg P, 10 kg K, 4 kg Mg, and 20 kg Ca) fertilizers, only in plots (R1, R2, R3, and R6). In contrast, plots without enrichment species (R0) were not fertilized. The application of fertilizers, herbicides, and pesticides was stopped after the enrichment trees were planted. Weeding was done in the enrichment plots (R0, R1, R2, R3, and R6). However, plots R1, R2, R3, and R6 were stopped after 2 years of tree planting. Any trees that died were replaced during the first year after planting (Teucher *et al.* 2016). In addition, some oil palms were removed before planting more enrichment trees (Figure 2). The distance between oil palm plants is 9 m (Zemp *et al.* 2023), while the distance between enrichment trees is ± 2 m. The enrichment plots (R0, R1, R2, R3, and R6) had plot sizes of 5 m × 5 m, 10 m × 10 m, 20 m × 20 m, and 40 m × 40 m, while all Rctl plots had a size of 10 m × 10 m. Particularly for the 5 m × 5 m plots, there was no removal of oil palms because there were no oil palms inside the plots but outside the plots. Then, plots measuring 10 m × 10 m, 20 m × 20 m, and 40 m × 40 m were each made into sampling plots of size (5 m × 5 m) for a total of 43 plots (Figure 2) (Table 3).

2.2.1. Fine Root Sampling

Fine root sampling was conducted by establishing a sampling pattern at five points, four in the corner and one in the center, at soil depths of 0-10 cm and 10-30

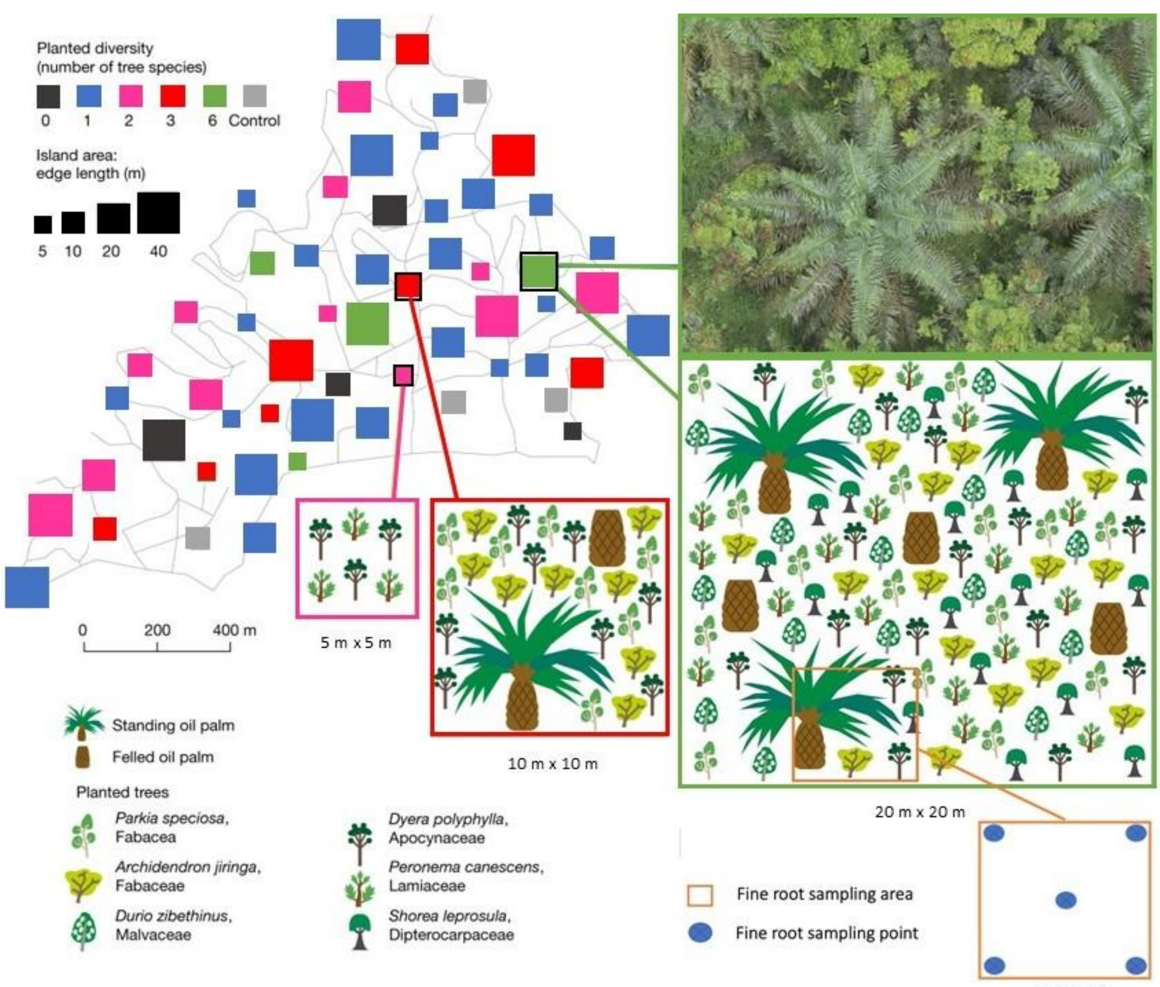

Figure 2. Oil palm enrichment plots with tree species at different species diversity levels and plot sizes (modified from Zemp *et al.* (2023))

Table 3. List of enrichment species combinations in oil palm plantations

Plot codes and colors	Oil palm enrichment species	Total number of plots	Plot size (m^2)
R1	Stink bean	4	40 × 40, 20 × 20, 10 × 10, 5 × 5
	Jengkol	4	40 × 40, 20 × 20, 10 × 10, 5 × 5
	Durian	4	40 × 40, 20 × 20, 10 × 10, 5 × 5
	Sungkai	4	40 × 40, 20 × 20, 10 × 10, 5 × 5
	Meranti	4	40 × 40, 20 × 20, 10 × 10, 5 × 5
	Jelutong	4	40 × 40, 20 × 20, 10 × 10, 5 × 5
R2	Stink bean, jengkol	1	40 × 40
	Stink bean, durian	1	5 × 5
	Stink bean, sungkai	1	10 × 10
	Stink bean, meranti	1	20 × 20
	jengkol, meranti	1	5 × 5
	jengkol, jelutong	1	10 × 10
	jengkol, sungkai	1	20 × 20
	durian, jelutong	1	20 × 20
	durian, sungkai	1	40 × 40
	durian, meranti	1	10 × 10
	sungkai, jelutong	1	5 × 5
	meranti, jelutong	1	40 × 40
R3	Stink bean, durian, meranti	1	20 × 20
	Stink bean, sungkai, meranti	1	40 × 40
	Stink bean, jengkol, jelutong	1	10 × 10
	Stink bean, durian, jelutong	1	5 × 5
	jengkol, durian, jelutong	1	40 × 40
	jengkol, sungkai, jelutong	1	20 × 20
	jengkol, sungkai, meranti	1	5 × 5
	durian, sungkai, meranti	1	10 × 10
R6	multispecies (6 species)	4	40 × 40, 20 × 20, 10 × 10, 5 × 5
R0	multispecies (6 species)	4	10 × 10

The total number of plots is 56. The color box on the plot code indicates the level of species diversity, as in Figure 2

cm in a sampling plot measuring 5 m × 5 m (Figure 2). The original 5 m × 5 m plot did not have a dedicated sampling plot, so samples were taken on the plot itself. Fine root samples were taken using a soil corer with a diameter of 3 cm. The distance between the sampling point and the crop was about 1-2 m. The soil samples obtained were put into separate plastic bags according to the depth of the soil.

2.2.2. Fine Root Washing

The soil samples were soaked in water to separate the roots. The roots were washed separately according to depth using a sieve with a pore diameter of 1.25 mm so that only the soil was washed away and the roots remained in the sieve. The roots were transferred into a plastic bowl using tweezers. All fine roots taken that had a diameter of ≤ 2 mm were put into a petri dish filled with water (Kotowska *et al.* 2022).

2.2.3. Fine Root Categorization

Fine roots were separated from the soil and then grouped into three categories, namely oil palm, tree, and herb fine roots, based on the fine root characteristics of each plant type. Each fine root was placed in a petri dish with filter paper. The fine roots were separated between live and dead roots using tweezers and a magnifying glass (Kotowska *et al.* 2022). Live fine roots have a stronger structure and bright color and are not easily broken, while dead fine roots are more fragile, dark in color, and easily broken (Pransiska *et al.* 2016). Furthermore, live fine roots were observed to obtain data on the morphological traits of fine roots.

2.2.4. Observation of Fine Root Morphological Traits

Fine root morphology was observed using a root scanner. The fine roots observed were live fine roots. The root scanner box is given water, then the fine roots are placed in the root scanner box until all the fine roots are submerged in water. The fine roots are spread in the scanner box so that they do not pile up on each other. Next, the fine roots were scanned, and the scanned images were analyzed using WinRhizo Pro 2020a software (Regent Instruments Inc.), which can automatically detect root morphology data. The analysis results obtained fine root data, including fine root length (FRL), root length per area (RLA), specific root length (SRL, fine root length per dry weight of live fine roots), specific root area (SRA, fine root surface area per dry weight of live fine roots), fine root diameter, and root tissue density (RTD, dry weight of live fine roots per volume).

Fine root morphological traits such as SRL, SRA, diameter, and RTD are used to determine nutrient and water acquisition strategies and responses to various environmental conditions (Addo-Danso *et al.* 2019; Fort and Freschet 2020; Gao *et al.* 2023). SRL and SRA are parameters to measure uptake and resource allocation to determine the total surface area and soil volume explored by fine roots (Addo-Danso *et al.* 2019; de la Riva *et al.* 2021; Zhu *et al.* 2021). RTD is a root trait often used as a key trait in the root economic spectrum (RES) that is positively correlated with root lifespan and nutrient absorption rate. In contrast, root diameter indicates resource conservation that is positively correlated with root lifespan (Kong *et al.* 2019).

2.2.5. Measurement of Fine Root Biomass and Necromass

Live and dead fine roots were weighed to determine the wet weight. After weighing, the fine roots were put in an envelope and dried in an oven at 70°C until they reached a constant dry weight to obtain data on biomass (live fine roots) and necromass (dead fine roots) (Ostonen *et al.* 2005).

2.3. Data Analysis

Data were analyzed using R software version 4.3.0. Fine root morphology data at different depth levels and species diversity were log-transformed to obtain data differences. Fine root biomass and necromass were transformed by square root transformation. Data were tested by ANOVA and followed by DMRT (Duncan Multiple Range Test) post hoc test (sig $< \alpha = 0.05$) to see differences between treatments. Analysis of differences in fine root traits in each treatment was observed using the ggplot2 package. Furthermore, a correlation test was conducted between morphological traits, biomass, and fine root necromas using principal components analysis (PCA) using the Prcomp function.

3. Results

3.1. Fine Root Morphology

3.1.1. FRL (Fine Root Length) and RLA (Root Length per Area)

FRL and RLA in all observed plots had a similar pattern (Figure 3). The FRL and RLA of oil palms in the Rctl plots were the longest at two soil depths compared to the enrichment plots. There was a decrease in the FRL and RLA of oil palms and trees in the enrichment plots (R0, R1, R2, R3, and R6) at a soil depth of 30 cm, indicating an impediment to the vertical distribution of fine roots at deeper soil depths. The FRL and RLA of the Rctl plots were significantly different in the DMRT test ($p>0.05$) from the enrichment plots at 30 cm soil depth, except for the R1 plot (Table 4).

3.1.2. SRL (Specific Root Length) and SRA (Specific Root Area)

The SRL and SRA values in this study showed a similar pattern (Figure 4). In general, the SRL and SRA of tree fine roots were higher than those of oil palm. The SRL and SRA values of oil palm fine roots in each plot at two soil depths did not differ significantly from the DMRT test ($p>0.05$) (Table 4). These results indicate that oil palm fine roots do not significantly explore resources to a depth of 30 cm.

3.1.3. Fine Root Diameter and Root Tissue Density (RTD)

The diameter of oil palm fine roots was larger than that of trees (Figure 5A), while the RTD of oil palm fine roots was lower than that of trees (Figure 5B). The diameter of oil palm fine roots in Rctl plots with enrichment plots did not differ significantly from the results of the DMRT test ($p>0.05$) at all soil depths, indicating that the diameter of oil palm fine roots was not influenced by enrichment planting. The RTD of oil palm at a depth of 10 cm was highest in R3, which was 0.45±0.05 and significantly different from the RTD in the enrichment plots R0 (0.33±0.01), R1 (0.32±0.01) and R6 (0.32±0.06) (Table 4). High RTD is positively associated

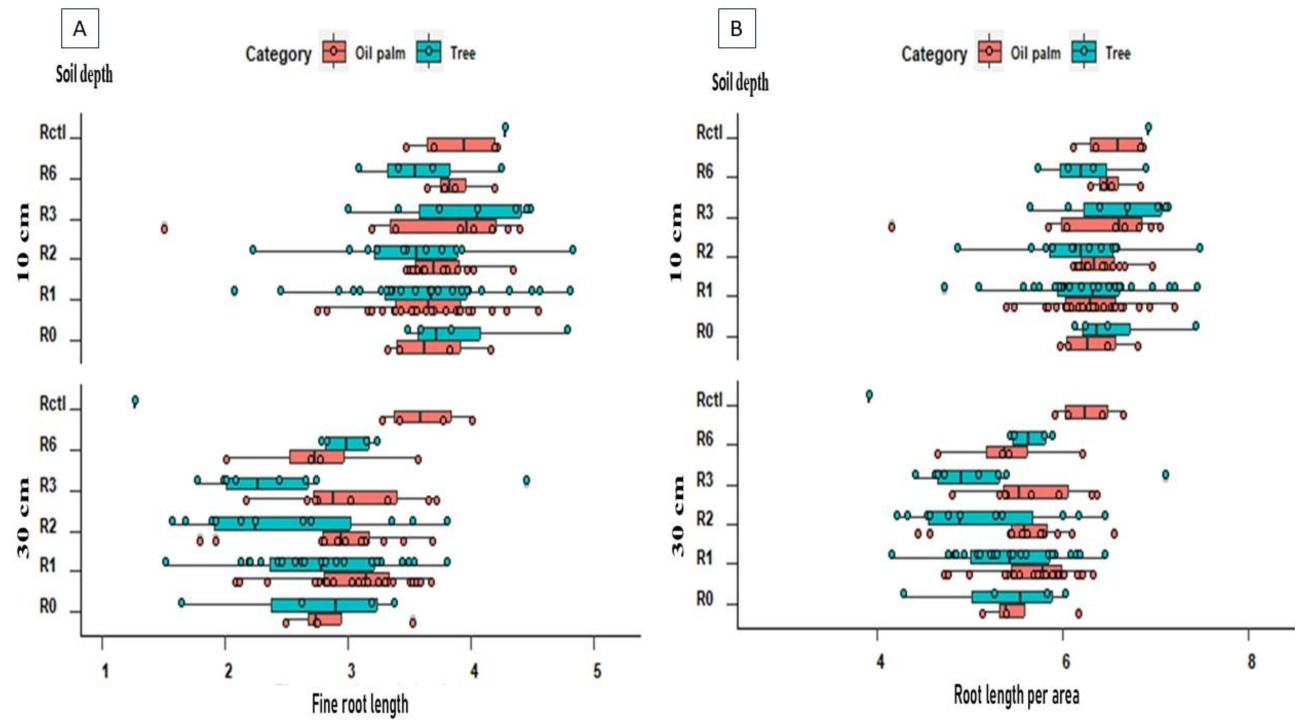

Figure 3. Distribution of mean values of fine root length (A) and root length per area (B) in each plot at different species diversity (log-transformed values). Rctl (oil palm control plot with management), R1 (plot of oil palm with one crop), R2 (plot of oil palm with two crops), R3 (plot of oil palm with three crops), R6 (plot of oil palm with six crops/multispecies), and R0 (oil palm plot without management). Each chart was organized by depth (0-10 cm and 10-30 cm). The colors in the boxplots differentiate between crop types: oil palm (red) and trees (blue)

Table 4. Mean values of oil palm fine root morphology at different levels of species diversity

Plot code	FRL (cm)	RLA ($m\ m^2$)	SRL ($m\ g^{-1}$)	SRA ($cm^2\ g^{-1}$)	Diameter (mm)	RTD ($g\ cm^{-3}$)
			Soil depth 10 (cm)			
R0	3.67±0.19	6.32±0.19	2.35±0.06	5.21±0.05	0.45±0.01	0.33±0.01^{b}
R1	3.63±0.08	6.28±0.08	2.61±0.07	5.38±0.05	0.42±0.01	0.32±0.01^{b}
R2	3.75±0.07	6.40±0.07	2.49±0.06	5.25±0.05	0.41±0.01	0.39±0.02^{ab}
R3	3.60±0.33	6.25±0.33	2.39±0.12	5.18±0.08	0.42±0.01	0.45±0.05^{a}
R6	3.87±0.11	6.52±0.11	2.65±0.18	5.46±0.17	0.42±0.01	0.32±0.06^{b}
Rctl	3.88±0.18	6.53±0.18	2.64±0.29	5.38±0.30	0.40±0.01	0.41±0.06^{ab}
			Soil depth 30 (cm)			
R0	2.87±0.22^{b}	5.52±0.22^{b}	2.75±0.48	5.61±0.42	0.45±0.024	0.31±0.01
R1	3.05±0.09^{ab}	5.69±0.08^{ab}	2.54±0.05	5.37±0.03	0.44±0.01	0.30±0.01
R2	2.89±0.15^{b}	5.56±0.16^{b}	2.37±0.08	5.24±0.04	0.46±0.014	0.34±0.02
R3	3.00±0.18^{b}	5.65±0.18^{b}	2.37±0.12	5.24±0.08	0.46±0.02	0.32±0.01
R6	2.75±0.31^{b}	5.40±0.31^{b}	2.42±0.09	5.22±0.04	0.44±0.024	0.33±0.01
Rctl	3.61±0.16^{a}	6.26±0.16^{a}	2.45±0.13	5.28±0.07	0.43±0.02	0.33±0.02

All data were log-transformed to simplify analysis and produce a normal distribution of data. Mean ± standard error of FRL (fine root length), RLA (root length per area), SRL (specific root length), SRA (specific root area), fine root diameter, and RTD (root tissue density) at 10 and 30 cm soil depth with different species diversity. R0 (oil palm plot without management), R1 (plot of oil palm with one crop), R2 (plot of oil palm with two crops), R3 (plot of oil palm with three crops), R6 (plot of oil palm with six crops/multispecies), and Rctl (oil palm control plot with management). Numbers followed by different letters in the same column mean significantly different based on the DMRT test ($\alpha = 0.05$)

with conservative crop strategies. The RTD of oil palm at 30 cm soil depth was not significantly different from the DMRT test ($p>0.05$) between each plot.

3.2. Fine Root Biomass and Necromass

Oil palm fine roots have higher biomass and necromass than tree fine roots (Figure 6). The biomass

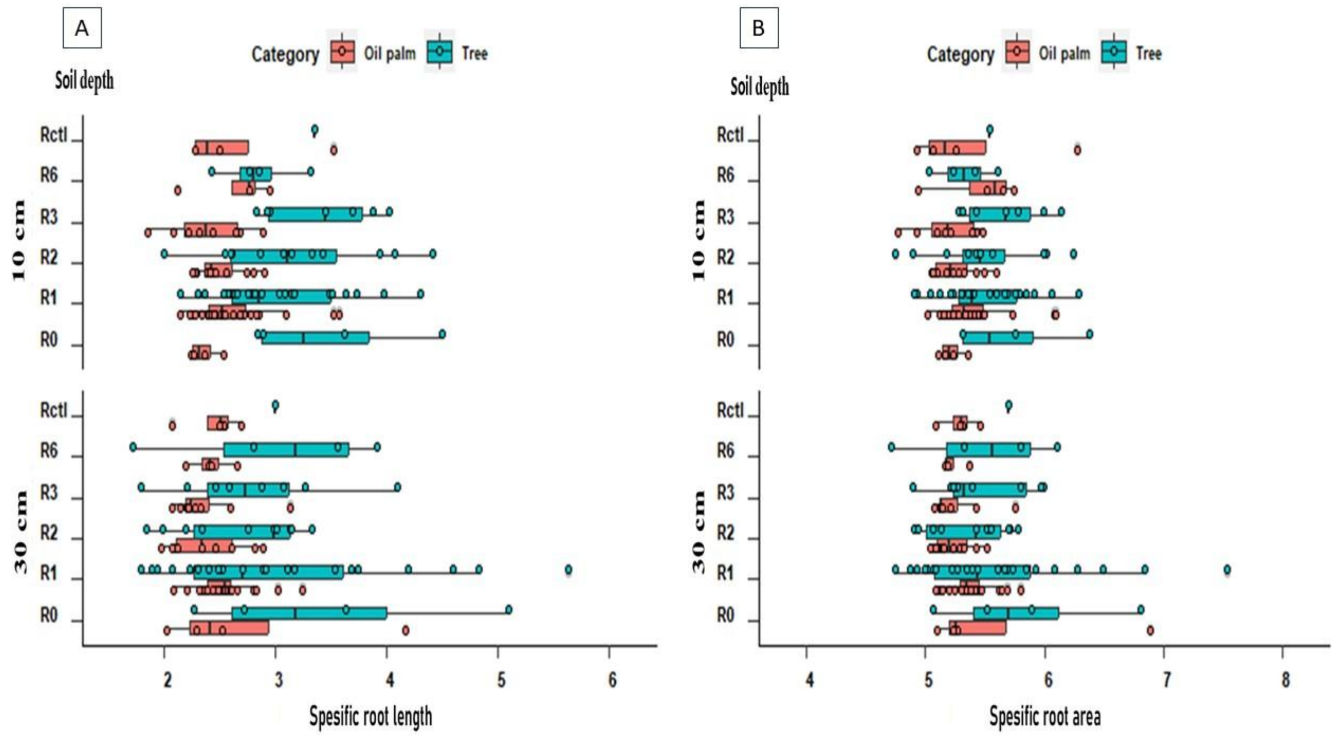

Figure 4. Distribution of mean values of specific root length (A) and specific root area (B) in each plot at different species diversity (log-transformed values). Rctl (oil palm control plot with management), R1 (plot of oil palm with one crop), R2 (plot of oil palm with two crops), R3 (plot of oil palm with three crops), R6 (plot of oil palm with six crops/multispecies), and R0 (oil palm plot without management). Each chart was organized by depth (0-10 cm and 10-30 cm). The colors in the boxplots differentiate between crop types: oil palm (red) and trees (blue)

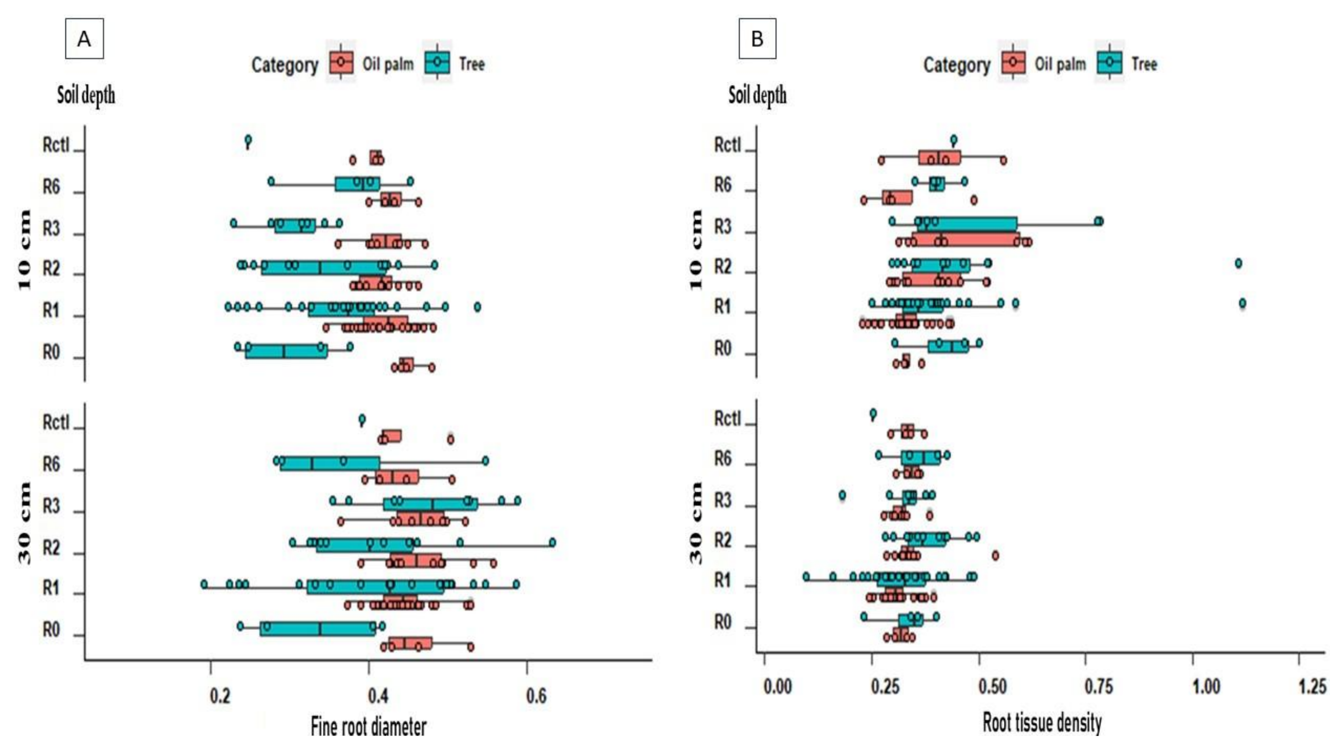

Figure 5. Distribution of mean values of fine root diameter (A) and root tissue density (B) in each plot at different species diversity (log-transformed values). Rctl (oil palm control plot with management), R1 (plot of oil palm with one crop), R2 (plot of oil palm with two crops), R3 (plot of oil palm with three crops), R6 (plot of oil palm with six crops/multispecies), and R0 (oil palm plot without management). Each chart was organized by depth (0-10 cm and 10-30 cm). The colors in the boxplots differentiate between crop types: oil palm (red) and trees (blue)

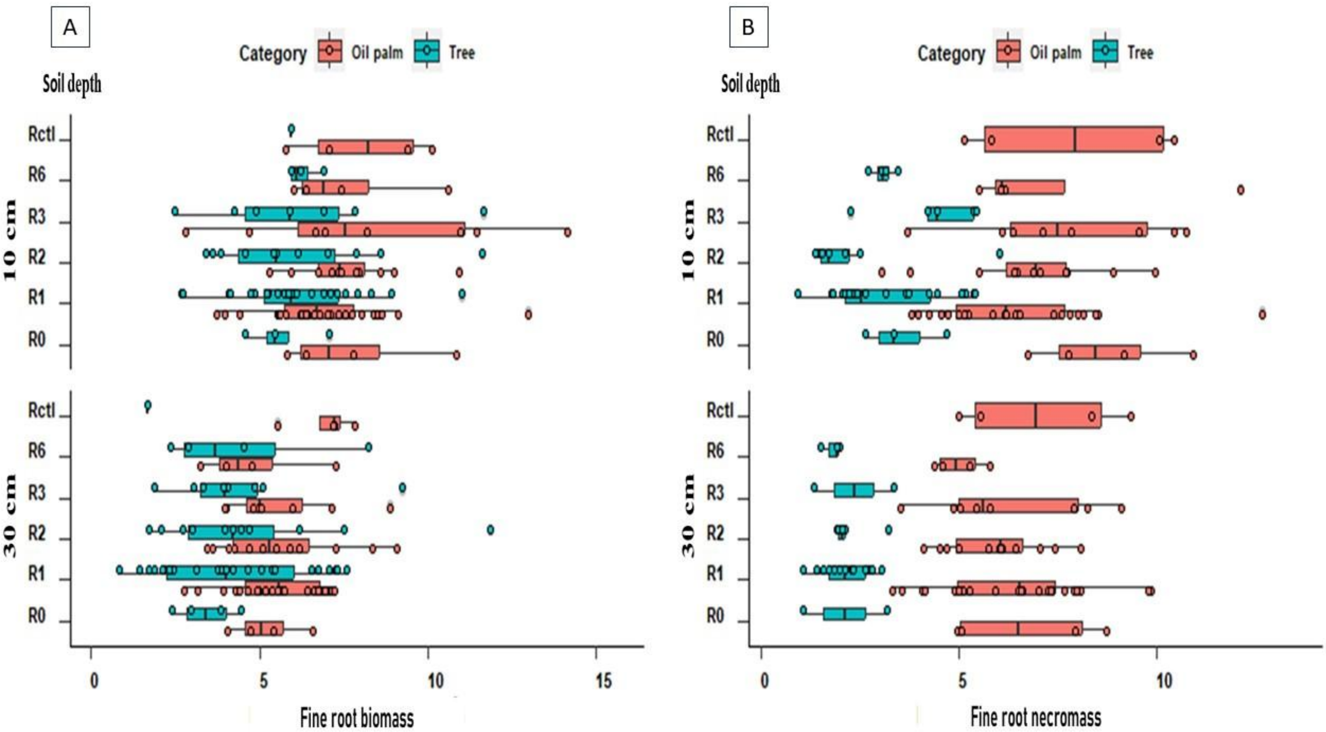

Figure 6. Distribution of mean values of fine root biomass (A) and fine root necromass (B) in each plot at different species diversity (values transformed into square root). Rctl (oil palm control plot with management), R1 (plot of oil palm with one crop), R2 (plot of oil palm with two crops), R3 (plot of oil palm with three crops), R6 (plot of oil palm with six crops/multispecies), and R0 (oil palm plot without management). Each chart was organized by depth (0-10 cm and 10-30 cm). The colors in the boxplots differentiate between crop types: oil palm (red) and trees (blue)

and necromass of fine roots at a depth of 10 cm were not significantly different between plots based on the DMRT test results (p>0.05). Still, at a depth of 30 cm, there was a decrease in biomass and necromass of fine roots in plot R6, which was significantly different from the plot in Rctl (Figure 6 and Table 5). These results indicate that enrichment planting with high crop diversity in plot R6 can reduce the biomass and necromass content of oil palm fine roots.

3.3. Relationship Between Morphology, Biomass, and Necromass of Oil Palm Fine Roots in Enrichment Plantations

Oil palm fine roots at 10 cm soil depth in plot R2 clustered on all fine root traits in PC1 (dim1: 54.8%) and PC2 (dim2: 20.4%), indicating that plot R2 had a more stable root system. The root traits RTD, diameter, and necromass in PC1 were positively correlated at 10 cm depth but negatively correlated with the SRL and SRA of plot R6 (Figure 7A). The same positive correlation also existed for the root traits RTD, diameter, and necromass in PC1 at a depth of 30 cm. Still, they were negatively correlated with SRL and SRA and not correlated with FRL and RLA of the Rctl plot (Figure 7B).

Table 5. Mean values of biomass and necromass of oil palm fine roots at different levels of species diversity

Plot code	Fine root biomass (g m^{-2}) at soil depths		Fine root necromass (g m^{-2}) at soil depths	
	10 cm	30 cm	10 cm	30 cm
R0	7.70±1.12	5.19±0.54^{ab}	8.65±0.90	6.67±0.97^{ab}
R1	6.90±0.40	5.52±0.26^{ab}	6.43±0.40	6.30±0.36^{ab}
R2	7.65±0.42	5.62±0.52^{ab}	6.71±0.56	5.94±0.35^{ab}
R3	8.23±1.33	5.60±0.59^{ab}	7.74±0.85	6.25±0.69^{ab}
R6	7.59±1.04	4.82±0.87^{b}	7.47±1.56	5.01±0.31^{b}
Rctl	8.08±1.00	6.94±0.48^{a}	7.87±1.38	7.06±1.05^{a}

Data were transformed into square roots to simplify analysis and produce normal data distribution. Mean ± standard error of FRL (fine root length), RLA (root length per area), SRL (specific root length), SRA (specific root area), fine root diameter, and RTD (root tissue density) at soil depths of 10 and 30 cm with different species diversity. R0 (oil palm plot without management), R1 (plot of oil palm with one crop), R2 (plot of oil palm with two crops), R3 (plot of oil palm with three crops), R6 (plot of oil palm with six crops/multispecies), and Rctl (oil palm control plot with management). Numbers followed by different letters in the same column mean significantly different based on the DMRT test (α = 0.05)

4. Discussion

Enrichment planting was carried out in oil palm plantations with different levels of crop species diversity, resulting in diverse fine root morphological traits. FRL

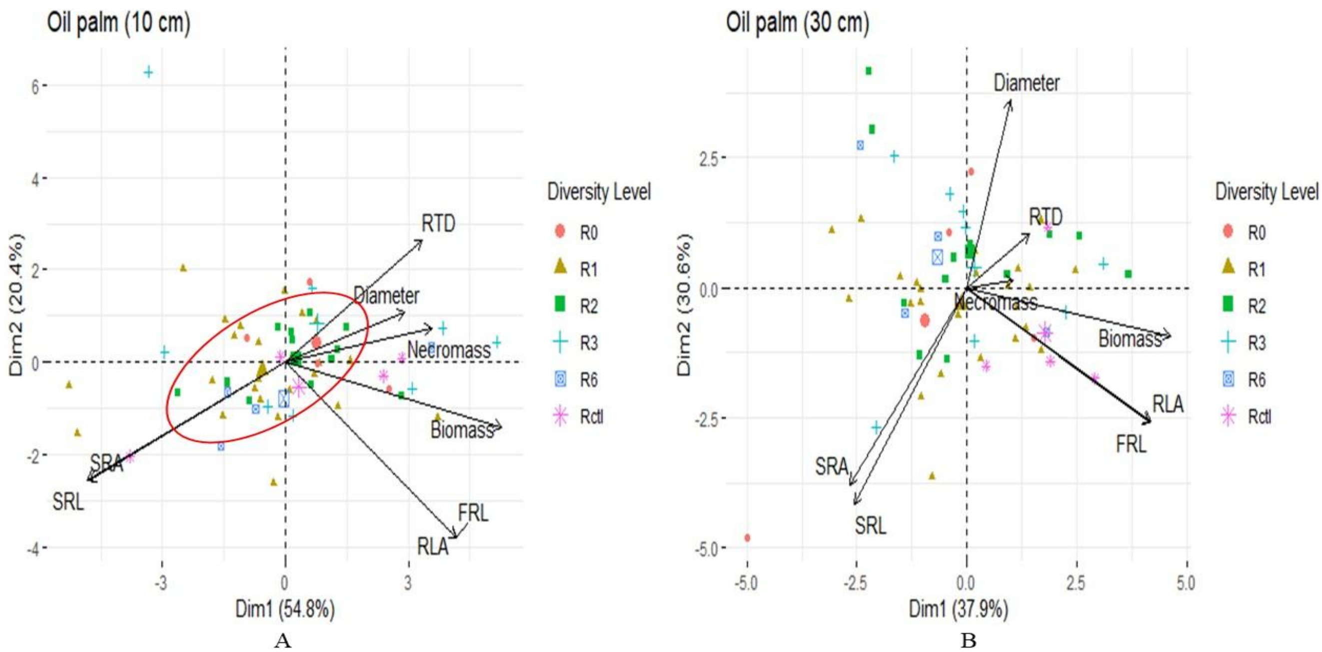

Figure 7. Relationship between morphology, biomass, and necromass of oil palm fine roots in enrichment plots at soil depths of 10 cm (A) and 30 cm (B). R0 (oil palm plot without management), R1 (oil palm plot with one crop), R2 (oil palm plot with two crops), R3 (oil palm plot with three crops), R6 (oil palm plot with six crops/multispecies), and Rctl (oil palm control plot with management). Root traits analyzed were FRL (fine root length), RLA (root length per area), SRL (specific root length), SRA (specific root area), fine root diameter, and RTD (root tissue density). The red circle in Figure (7A) shows the grouping of each root character variable in the R2 plot

(fine root length) and RLA (root length per area) in the Rctl plot had high fine root lengths at two soil depths. The Rctl plot was a monoculture oil palm plot with land management, indicating no interspecies competition and adequate nutrient content from fertilization, so there were no obstacles in the vertical distribution of fine roots to 30 cm soil depth. The enrichment plots (R0, R1, R2, R3, and R6) showed a decrease in FRL and RLA at 30 cm soil depth, but the fine roots of oil palm plot R1 were not significantly different from those of plot Rctl (Table 4). This may be due to less interspecies competition in single-species enrichment. Stunted fine root growth may be due to interspecies competition for soil resources (Gao *et al.* 2021b), as well as allelopathic effects from other species (Schenk 2006). In addition, soil structure and texture, as well as nutrient and water content, can cause the vertical distribution of fine roots to decrease (Hu *et al.* 2023). The dominant soil at the study site is acrisol loam, with soil texture consisting of high fractions of dust, sand, and clay, warm air, and soil temperature/humidity with high rainfall (Tables 1 and 2). This can make the soil structure compact with small soil pores, which can cause the growth of fine roots to be slow, especially at deeper soil depths.

The morphological traits of SRL (specific root length) and SRA (specific root area) generally showed that the fine roots of trees were higher than those of oil palms in the two soil depths. This result is similar to the research of Kotowska *et al.* (2022), which found that tree fine roots have higher SRL than oil palm fine roots. Species genotype factors still play a major role in root traits; in this case, tree roots have a longer root architecture. However, fine root traits can change depending on influencing environmental factors (Corneo *et al.* 2018; Cornejo *et al.* 2020). In addition, the SRL and SRA of oil palms in all plots did not differ significantly across the two soil depths. According to Wang *et al.* (2022), if the availability of nutrients and water in the soil is fulfilled for plants, there is no significant effect on the nature of fine roots in seeking more resources. Fine roots have high SRL and SRA to maximize nutrient and water uptake, whereas the SRL and SRA of fine roots are low when nutrients and water are adequate (Addo-Danso *et al.* 2019). However, oil palm fine roots at 10 cm depth showed potential acquisitive traits in plot R6, as it had the highest SRL and SRA values compared to other plots (Table 4). This result supports the low RTD (root tissue density) data of oil palm roots in plot R6 at 10 cm depth (Table 4). There were differences in RTD between enrichment plots but not significantly different from the Rctl plot at a depth of 10 cm. RTD was highest in plot R3, followed by plot R2. The RTD value in Plot R3 was significantly different from the low RTD in Plots R0, R1, and R6 (Table 4). The low RTD in plots R0 and R1 is thought to be due to the small diversity not being able to support the resource needs of the crops, while the high crop diversity in plot R6 is thought to trigger competition between species in the struggle for resources.

Crop diversity can increase beneficial soil microbes in the decomposition process, providing more nutrients in the soil (Han *et al.* 2021). Increased litter produced by more crop species can provide a more diverse food source for decomposer organisms, thus accelerating nutrient cycling (Giweta 2020). However, high species diversity can increase pathogenic microbes (Burrill *et al.* 2023) that damage root cells and thus reduce root tissue density (RTD) (Liu *et al.* 2024), but further research is needed on how much species diversity is affected by increased pathogenic microbes. In addition, RTD is influenced by high species density (Valverde-Barrantes *et al.* 2021). Plant densities with high species diversity can trigger competition for nutrients and water, leading to limited nutrient and water availability, which impacts root allocation to acquisitive strategies (Wang *et al.* 2021). Therefore, enrichment plots with six crop species (R6) are considered to experience a change in strategy from conservative to acquisitive characterized by high SRL and SRA and low RTD based on the RES (Root Economic Spectrum) perspective (Reich 2014; Addo-Danso *et al.* 2019). These results imply that high crop species diversity in fields with high crop density leads to rooting competition that can modify root architecture.

Another root trait observed was fine root diameter. Oil palm fine root diameter did not differ significantly between monoculture and enrichment plots at the two soil depths. However, in general, oil palm fine roots have larger root diameters with lower RTD when compared to trees (Figure 5). This result is closely related to the characteristics of the crop species that show structural tissue differences between trees as dicotyledons and oil palms as monocotyledons. The fine roots of oil palm have a large root diameter but low tissue density (RTD) because oil palm roots have large and small xylem vessels that dominate the cross-section of the root diameter (Nisa *et al.* 2024). Some plant species with large root diameters do not increase resource investment in structural tissues as expected from a RES perspective (Valverde-Barrantes and Blackwood 2016). Therefore, large root diameter is not associated with high RTD (Kong *et al.* 2019). Thus, in this study, oil palm fine root diameter was not influenced by oil palm enrichment, so the strategy of nutrient acquisition by fine roots cannot be seen from fine root diameter data alone.

Enrichment planting in oil palm plantations is expected to support conservative nutrient and water acquisition strategies that can increase the stability and efficiency of resource use. Overall, based on the observed fine root morphological traits, plots R2, R3, and Rctl showed a conservative strategy characterized by low SRL and SRA and high RTD. Plots R0 and R1 showed inconsistent root morphological traits characterizing a resource acquisition strategy with low SRL, SRA, and RTD. The R6 plot showed a change in strategy to acquisitive, characterized by high SRL and SRA and low RTD. In addition, analysis of fine root biomass and necromass is required in this study to understand the impact of stand changes in different land conditions (Verma *et al.* 2021).

The fine root biomass of oil palms and trees is higher at soil depths of 10 cm than 30 cm. The top layer of soil contains more nutrients and water and decreases with increasing soil depth (Jaloviar *et al.* 2009; Pransiska *et al.* 2016). Therefore, a soil depth of 10 cm encourages root growth and high nutrient and water absorption, resulting in more fine root biomass. There was no significant difference in fine root biomass at 10 cm depth between plots, indicating that enrichment planting can fulfill the nutrient and water requirements of oil palms. In the Rctl plot, fine root biomass was high at both soil depths because the Rctl plot is a plot with maximum oil palm management, so the high fine root biomass content was obtained from regular fertilization. The enrichment plots had high fine root biomass from enrichment trees and other plants growing around the oil palms. High plant diversity can increase soil fertility and plant biomass (Furey and Tilman 2021) and stimulate the growth of decomposer microbial populations in the soil (Lange *et al.* 2015). According to Zhao *et al.* (2022), enrichment planting can enrich beneficial microbial communities and increase nitrogen content, especially when planted with legumes, such as the enrichment of stink bean and jengkol trees in the oil palm plantation in this study. However, fine root biomass decreased at 30 cm depth, especially in plot R6, which was significantly different from plot Rctl (Table 5). Competition for nutrients and water between oil palm fine roots and trees at deeper soil depths and the large number of crops living in the same field allows interspecies competition for space between crops for nutrients and water (Craine and Dybzinski 2013). This result is also supported by the decrease in oil palm fine root necromass in plot R6 at 30 cm depth.

Oil palm fine root necromass is more abundant than that of trees. This is related to the anatomical structure of oil palm fine roots, which are monocotyledonous plants that do not experience radial growth as in trees, as in dicotyledonous plants (Page 2016). Hence, oil palm fine roots have low tissue density and die easily. Necromass functions as a pool of C and N in the soil, but the decomposition rate of each crop's fine roots can be different (Saha *et al.* 2023). Based on research by Pransiska *et al.* (2016), necromass in oil palm plantations is twice as high as in forests, but the rate of necromass decomposition is higher in forests. This is because the soil in the forest has high activity and a variety of microbes and decomposer organisms (Rivas *et al.* 2023), resulting in the same total organic matter as oil palm plantations. Therefore, oil palms in enrichment plots can have high organic matter because they obtain nutrients from the decomposition of tree fine root necromass. However, the production of necromass and fine root biomass of oil palm decreased at a depth of 30 cm at a high crop diversity in plot R6 (Table 5). This phenomenon may be related to the low availability of nutrients in plot R6 at a depth of 30 cm caused by interspecies competition for resources. According to Pan *et al.* (2022), biomass and necromass are influenced by the availability of nutrients in the soil. The existence of competition between crops and the dominance of certain species that are stronger in absorbing nutrients and water (Ayma-Romay *et al.* 2021) causes the availability of resources in the soil to be increasingly limited for other species. These results support the results of research on the morphological traits of fine roots, which show a change in the resource acquisition strategy that is more acquisitive in enrichment planting with six crop species. Thus, the low biomass and necromass content in plot R6 is also supported by the morphological traits of high SRL and SRA and low RTD, which indicate that plot R6 implements an acquisitive nutrient and water acquisition strategy.

PCA analysis was conducted in this study to determine the relationship between oil palm enrichment and fine root traits. Oil palm fine roots at 10 cm depth in plot R2 clustered in all fine root traits, showing strong relationships (Figure 7A). This is thought to be because plot R2 with two crop species enrichment showed a more stable root system than other plots with less or more diversity, allowing each fine root trait to be expressed. In contrast, plot R6 clustered on SRL and SRA traits, suggesting changes in oil palm fine roots based on these root traits. High SRL and SRA are characterized as acquisitive traits (Cornejo *et al.* 2020), which were found in plot R6. Meanwhile, oil palm fine roots at 30 cm depth showed Rctl plots clustered on FRL and RLA traits. This indicates a higher distribution of oil palm fine roots in the Rctl plot than in the other plots. In contrast, fine roots in the other plots (R0, R1, R2, R3, and R6) did not cluster around specific root traits, suggesting that oil palm fine roots at deeper soil depths cannot indicate the crop's fine root traits and resource acquisition strategies. Therefore, nutrient and water acquisition strategies by oil palm roots can only be observed at 10 cm soil depth, which is a fertile soil layer. Makita *et al.* (2011) stated that the high nutrient content of fine roots in the 0-10 cm soil layer allows fine roots to show the ability to acquire resources through the plasticity of fine roots in response to available resources.

This study concluded that enrichment planting in oil palm plantations causes changes in the traits of oil palm fine roots. Plot R0 and plot R1 showed low SRL, SRA, and RTD traits. Plot R2, R3, and Rctl with low SRL/SRA and high RTD while plotting R6 with high SRL/SRA and low RTD. Results showed that enrichment plots (R0 and R1) had inconsistent fine root traits characterizing nutrient and water acquisition strategies. Meanwhile, enrichment plots (R2, R3, and Rctl) supported conservative nutrient and water acquisition strategies that could increase stability and resource use efficiency. In contrast, the enrichment plot with six crop species (R6) showed fine root traits that underwent a shift in nutrient and water acquisition strategy to acquisitive. The high crop diversity in the plot (R6) triggered interspecies competition, which led to limited nutrient and water availability, and thus, the fine roots exhibited acquisitive behavior. From these results, enrichment planting in oil palm plantations can be practiced with two and three crop species, as in plots R2 and R3.

The limitation of this study is that there was no analysis of the chemical content of fine roots and soil in each plot, so the types of nutrients contained cannot be described in more detail. In addition, further research is needed to analyze the effect of plant diversity with plant density on the resource acquisition strategy by fine roots, as well as to identify the fine roots of tree species that are most influential in enriching oil palm crops. This will be used to determine the optimal level of diversity and crop spacing to minimize nutrient and water acquisition competition between crop species.

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