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Xylem Vessels Traits of Oil Palm Roots Influenced by Root Diameter and Soil Hydrological Regime

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ABSTRACT

Oil palm has been widely studied regarding growth and development, water use, productivity, and other economically relevant functions. However, not much is known about the hydraulic conductivity of oil palm root systems and how xylem vessels perform their function to transport water from roots to shoots so far. This information is needed to describe oil palm strategies to maintain water status, especially in oil palms that grow under various soil hydrological regimes. To investigate the root hydraulic performance, we measured mean xylem vessel diameter (D), vessel density (VD), vessel lumen area (A_{lumen}), and potential hydraulic conductivity (Kp) for oil palm root samples in seasonally flooded riparian and well-drained sites at Harapan Jambi Forest. The result showed that D, A_{lumen}, and Kp increased with increasing root diameter at both plantation types. On the contrary, VD significantly decreased with increasing root diameter. Potential hydraulic conductivity (Kp) in riparian sites was smaller than in well-drained sites and significantly different in root diameter >2-5 and >5-10 mm and related to both plantation types. The low potential hydraulic conductivity of root xylem vessels and the narrowing of xylem vessel lumen that occurs in oil palm roots in the seasonally flooded riparian sites were presumed as adaptation mechanisms to maintain water supply from the roots to the shoot in oil palm plants in these sites.

1. Introduction

Oil palm (*Elaeis guineensis* Jacq., Arecaceae) is one of the highest-yielding plants. It causes economic benefits but is related to high forest conversion rates, land-use change, and thus ecological cost (Clough *et al.* 2016). Some oil palm cultivation areas are subjected to environmental stresses, such as drought or waterlogging events. One of Indonesia's extensive oil palm plantations is in Harapan Forest, Jambi Province. Some oil palm plantations in Jambi are located in riparian and well-drained sites on mineral soils; therefore, during the rainy season, oil palms in the riparian sites are prone to waterlogging (Hardanto *et al.* 2017; Waite *et al.* 2019). Waterlogging poses a problem for oil palm plantations, causing significant decreases in physiological activity, vegetative growth, and yields (da Ponte *et al.* 2019). Some studies confirm that the responses of oil palm are related to water stress (Legros *et al.* 2009) or the effects of nutrients on plant growth, physiological features, and the productivity of oil palm (Kreuzwieser and Rennenberg 2014; da Ponte *et al.* 2019). Therefore, others evidence is needed to determine how oil palms respond and adapt to such conditions (Sun *et al.* 2011).

Roots play an important role in plants. They provide a anchor, uptake of water and nutrients, and photosynthate storage (Brunner *et al.* 2015; Logsdon 2015). Based on their diameter, roots are differentiated into fine roots, coarse roots, and anchor roots. Fine roots are less than 2 mm in diameter and mainly absorb water and serve ephemeral roles in foraging for belowground resources, i.e., nutrients (Guo *et al.* 2008), while coarse roots are solid and sturdy textured roots responsible for transporting and delivering water and nutrients to the shoots and also support the tree structurally and have

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great importance for long term nutrient budgets in the soil (Hellsten *et al.* 2013). Coarse roots act as an anchor roots are more than 5-10 mm in diameter, strengthening plants' establishment and supporting the aboveground biomass (Waldron 1977).

Water and minerals are taken from the soil and transported to the shoots through the xylem, passing in thousands of interconnected conduit networks caused by the water potential gradient created by transpiration in the leaves (Jansen *et al.* 2018). The xylem vessels play a role important in water transport from the root to the canopy. Hydraulic conductivity shows the driving force of the xylem in transporting water from root to shoot. The potential hydraulic conductivity per sapwood area (Kp; kg m^{-1} MPa^{-1} s^{-1}) derived from the composition and size of conduits can describe the ability and efficiency of the xylem to transport water. Potential hydraulic conductivity measures how much a specific xylem area can transport at a certain time and pressure. The amount of water needed in a plant can be estimated using sap flux measurement or transpiration. Atmospheric conditions set the transpiration rate, and on a short time scale, it is regulated by stomata. Hydraulic conductivity can be used to proxy for how much water a plant can transpire (Kotowska *et al.* 2020). The anatomical characteristics of xylem vessels determine the hydraulic conductivity depending on the number, total area, and diameter of the xylem vessels (Schuldt *et al.* 2013).

When in a waterlogged period, the xylem's driving force will be different in xylem vessels and different from those not in waterlogged soil. The total area and number of xylem vessels determine the efficiency of water transport (hydraulic conductivity) (Pinto *et al.* 2012). Xylem vessel dimensions can influence not only water transport efficiency but may have at least some influence on how much the plant can lower its water potential to keep the transpiration demand without the risk of hydraulic failure; for example, Waite *et al.* (2019) reported that the risk of hydraulic failure in oil palm leaves can be reduced by controlling the environment so that embolism and damage to the xylem vessels do not occur . Although increasing attention has been given to tree roots' role in the adaptation to unfavourable environments, this issue is far from being unravelled (David *et al.* 2013). The xylem anatomical and hydraulic properties of fine and coarse roots were less intensive than stem and branches (Kirfel *et al.* 2017), especially in oil palm roots, which is still limited.

Oil palm plantations in riparian sites prone to waterlogging periodically can be expected to undergo physiological adjustments, such as in their hydraulic conductivity, than oil palm plantations in a well-drained sites. The hydraulic conductivity of oil palm root xylem and their adaptation to riparian areas are poorly understood. Oil palms growing in riparian sites are presumed to have adapted to face waterlogging conditions. Therefore, the water supply that needs to be maintained in the shoots can still be optimally fulfilled. This study aims to analyze the influences of the differences in root diameter and plantation types (riparian and well-drained) on the hydraulic conductivity of oil palm root xylem in Jambi and to predict the adaptation form of oil palm in riparian sites.

2. Materials and Methods

2.1. Study Sites and Macroclimate Conditions

The study sites were located in oil palm plantations in well-drained and riparian sites located in the Province of Jambi in the lowlands of eastern Sumatera, Indonesia. The study was carried out on 8 plots of 50 m × 50 m, where HO stands for oil palm well-drained sites (consist four plots, namely HO1, HO2, HO3, HO4), whereas HOR for riparian oil palm sites (consist four plots, namely HOR1, HOR2, HOR3, and HOR4) (Table 1). Unlike well-drained sites, riparian

Table 1. Plot coordinates for each oil palm plantation in well-drained (HO) and riparian (HOR) sites

Plot code	Coordinate		C-org (%)	N-Total (%)	C/N	Texture (%)		
						Sand	Silt	Loam
HO1	S 01°54'35.6"	E 103°15'58.3"	1.19	0.23	5.28	74.18	15.02	10.80
HO2	S 01°53'00.7"	E 103°16'03.6"	1.23	0.17	7.06	71.49	21.92	6.59
HO3	S 01°51'28.4"	E 103°18'27.4"	1.86	0.23	8.21	78.96	18.33	2.71
HO4	S 01°47'12.7"	E 103°16'14.0"	1.89	0.21	9.08	77.43	22.37	0.21
HOR1	S 01°54'07.7"	E 103°22'53.3"	2.29	0.27	8.36	70.46	26.74	2.80
HOR2	S 01°52'40.5"	E 103°21'23.0"	4.55	0.48	9.54	15.50	50.44	34.05
HOR3	S 01°51'40.2"	E 103°18'20.2"	2.63	0.32	8.19	24.24	44.51	31.26
HOR4	S 01°42'39.5"	E 103°17'31.1"	2.86	0.31	9.21	15.13	46.00	38.87

site were periodically flooded at least once a year. It is because the lowland rivers of Jambi Province show strong seasonal fluctuations between the dry and the wet season. Consequently, large areas in the province's lowlands are inundated during the rainy season (Merten *et al.* 2020). The HO and HOR soil is classified as Acrisol with sandy loam and clay loam texture, respectively (FAO-classification). The average soil moisture in the well-drained and riparian sites was 30.7 vol.% and 38.8 vol.%, respectively, in 2016-2017. The climate is tropical, with 2881.9 mm yr^{-1} and 2552 mm yr^{-1} precipitation in 2016 and 2017, a mean daily relative humidity of 91.3 % in well-drained and 89.9% in the riparian area.

2.2. Experimental Design for Root Sampling

For each site type determined four replicate plots with the 13-20 years old oil palm tree. The root samples were collected at 50 m × 50 m plots in homogeneous riparian and well-drained oil palm plantation sites From each plot, three oil palm trees were determined. Three holes were dug in 20-30 cm soil depth at 100 cm distance from each oil palm tree, and three root samples were collected from each < 2 mm, 2-5 mm, and 5-10 mm diameters. In total, 144 oil palm root samples were collected. The root samples were cleaned from soil residues and immediately stored in 70% alcohol to prevent microbial growth.

2.3. Xylem Vessel's Anatomy and Root Hydraulic Conductivity

The root samples were sectioned in 10 µm-thin cross-sections using a sliding microtome (G.S.L.1, WSL Bismendorf, Switzerland) and stained using a mixture of 0.65% alcian blue and 0.35% safranin (w/v) in 3 minutes. We processed and analyzed images of each cross-section sample with a stereo-microscope with an automatic stage equipped with a digital camera (SteREOV20, Carl Zeiss Micro Imaging GmbH, Göttingen, Germany).

The samples were analyzed using Adobe Photoshop CS5 (Adobe System Inc., USA), where tylosis, which occasionally occludes the xylem vessels, was manually cleaned, and ImageJ for analyzing the diameter and number of all xylem vessels in the cross-sections by the automated particle analysis-function and calculating the xylem areas. Xylem vessel diameters (D, µm) were calculated from major (a) and minor (b) vessel radii according to $Di = ((32 \times (a \times b)^3)/(a^2 + b^2))^{1/4}$ (White 1991), and vessel density (VD, n mm^{-2}) and the vessel lumen area (A_{lumen} in percentage) were obtained. We further calculated the potential hydraulic conductivity (K_p, kg m^{-1} MPa^{-1} s^{-1}) of a wood segment based on the Hagen-Poiseuille's law as K_p, $Kp = (((\pi \times \sum r^4) / 8\eta) \times \rho) / A_{xylem}$, where r is vessel radius, Kp: hydraulic conductivity, kg m^{-1} MPa^{-1} s^{-1}), η: the water viscosity (1,002 × 10^{-9} MPa s), ρ: the density of water (998.2 kg m^{-3}), and A_{xylem}: the analyzed sapwood area (μm^2) (Kotowska *et al.* 2015; Kirfel *et al.* 2017).

2.4. Statistical Analysis

Statistical analysis was performed using R software version 3.6.1 (packages: lme4, ggplot2 (Wickham 2016), ggpubr (Kassambara 2020). Linear mixed-effects models were used to test the influence of root diameter and the plantation types on hydraulic anatomy (D, VD, A_{lumen}, and Kp), which are root diameter and plantation types as the fixed effect and plot as the random effect. The Pearson correlation was used to show the relationship between root hydraulic conductivity (Kp) to xylem vessel diameter (D), vessel lumen area (A_{lumen}), and vessel density (VD). R^2 conditional (for fixed and random effect) and R^2 marginal (for fixed) effects were calculated in this study (Nakagawa and Schielzeth 2013). The Satterthwaite test then estimated the differences between root diameter classes and plantation types for all hydraulic traits. Non-normally distributed data were log-transformed.

3. Results

The results of LME models of all root diameter classes and the plantation type showed a significant influence of root diameter on some of the studied xylem anatomical and hydraulic traits. Mean vessel diameter (D) and vessel lumen area (A_{lumen}) were influenced by the interaction between the area and root diameter ($p<0.001$, Table 2), inversely vessel density (VD) was influenced by the differences in root diameter ($p<0.001$, r^2: 0.564, Table 3). Xylem vessel anatomical dimensions varied distinctly across the root diameter and sites (Table 4). The widest vessels were observed in the roots with the largest diameters located in a well-drained sites (mean vessel diameter (D) = 61.08 µm). In comparison, much narrower vessels occurred in the riparian site's xylem of the smallest root diameter (D = 21.49 µm). Xylem vessel diameter in the well-drained sites was larger than in the riparian sites ($p<0.001$, r^2: 0.797, Figure 1, Table 5).

Table 2. The relationship between area types and root diameter to oil palm's xylem vessel diameter and root lumen area. Given are mean values ± SD for each diameter and plantation type

Root diameter/plantation (mm)	Well-Drained		Well-Drained	
	D (μm)	A_{lumen} (mm^{-2})	D (μm)	A_{lumen} (mm^{-2})
<2	22.60±7.5	0.12±0.07	21.49±6.7	0.15±0.13
2-5	4.85±9.3***	1.00±0.41***	40.63±7.4	0.72±0.32
5-10	61.08±7.7***	2.60±0.83***	52.23±3.9***	2.05±0.86***

Asterisk (*) in the same column indicates significantly different (t-test result - Satterthwaite's method) *** P<0.001

Table 3. The relationship between root diameter to xylem vessel density of oil palm's root. Given are mean values ± SD for each diameter and plantation type

Root diameter (mm)	VD (n mm-2)
< 2	465.11±259.1***
2-5	125.91±40.17***
5-10	72.59±8.85***

Asterisk (*) in the same column indicates significantly different (t-test result - Satterthwaite's method) *** P<0.001

Table 4. Mixed effect models on the influence of site (riparian vs. non-riparian) and root diameter class and their interaction on Kp, VD, d, and Alumen. Given are values (number in parentheses give SE of the estimates) and t-value for the fixed effect and SD for the random effect. Fixed effects were plantation sites (riparian/non-riparian) and root diameter class, with the plot as the random effect

Coefficient	Kp (kg m^{-1} MPa^{-1} s^{-1})	t-value	VD (n mm^{-2})	t-value	d (μm)	t-value	A_{lumen} (μm)	t-value
Intercept (root diam. 0-2 mm)	63.97 (46.08)	1.38	437.68*** (38.97)	11.23	22.6*** (1.79)	12.6	841.4** (256.7)	0.005
Root diam. 2-5 mm	298.26*** (36.3)	8.20	-316.98*** (42.07)	-7.5	22.2*** (2.02)	11.01	2541*** (272.1)	308e-16
Root diam. 5-10 mm)	604.4*** (36.3)	16.66	-375.04*** (42.07)	-8.9	38.5*** (2.021)	19.04	5611.9*** (272.1)	<2e-16
Sites: root diam. 0-2 mm	10.7 (65.2)	0.15	54.86 (55.1)	0.99	-1.107 (2.5)	-0.4	-75.8 (363.01)	0.84
Sites: root diam. 2-5 mm	-105.4* (51.3)	-2.05	-44.4 (59.5)	-0.75	-3.11 (2.86)	-1.09	-593.8 (384.8)	0.13
Sites: root diam. 5-10 mm)	-226.2*** (51.3)	-4-41	-34.95 (59.5)	-0.59	-7.66** (2.9)	-2.7	-1973.3 *** (384.8)	1.02e-06
Number of plot	8		8		8		8	
SD residual	125.75		145.75		2.183		942.5	
SD Plot	76.55		50.34		7.001		339.8	
Observation	144		144		144		144	

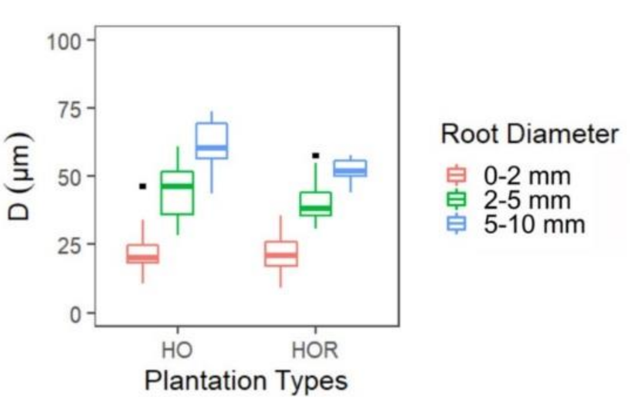

Figure 1. Vessel diameter (D) of oil palm's root at different diameters in riparian (HOR) and well-drained (HO) sites with four replications from each site type. D has a significant effect on root diameter and plantation types, but it is only found in 5≤d<10 mm root's diameter

Table 5. The R^2 marginal and R^2 conditional based on the results of the linear mixed effect model analysis for each anatomical and hydraulic trait of the oil palm root xylem

Coefficient	R^2 marginal	R2 conditional
Kp (kg m^{-1} MPa^{-1} s^{-1})	0.595	0.666
VD (n mm^{-2})	0.564	0.610
D (μm)	0.797	0.816
A_{lumen} (μm)	0.268	0.293

The xylem vessel density decreased exponentially with increasing vessel diameter. The xylem vessel density in each oil palm root diameter was higher in the riparian sites than in the well-drained sites (p<0.001, Figure 2). The xylem vessel density of narrow vessels on small-diameter roots was densely

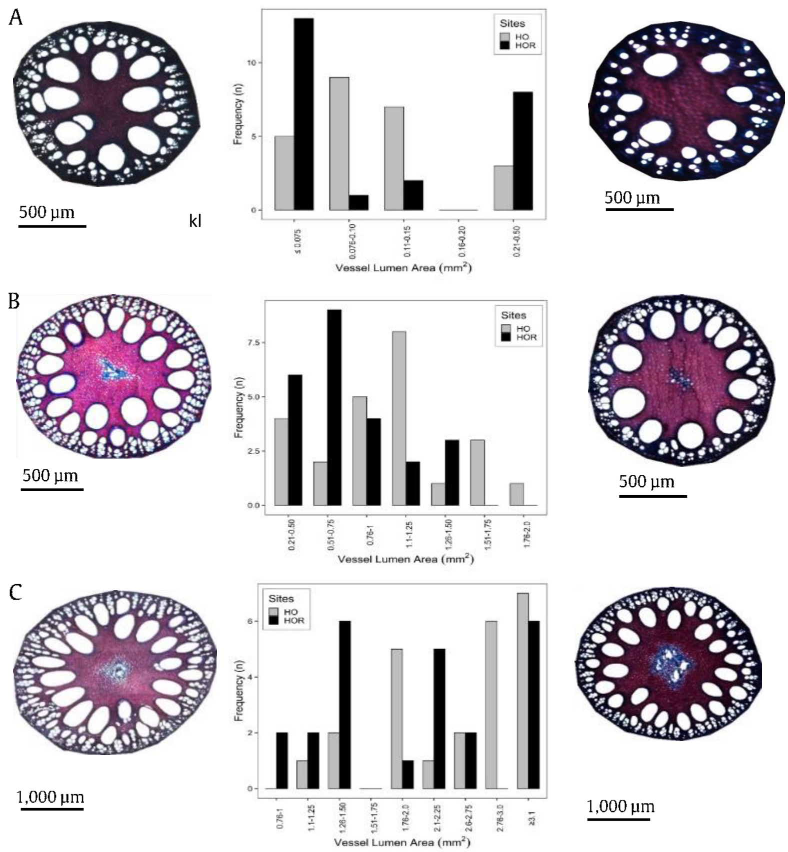

Figure 2. Classification of vessel lumen area of oil palm's root xylem vessels in riparian (right) and well-drained (left) sites with four replications from each site type. Root's diameter: (A) <2 mm, (B) 2≤d<5 mm, and (C) 5≤d<10 mm

packed in 465.11 mm^{-2}. The vessel density was also remarkably high in small-diameter roots compared to large-diameter roots. Similar trends in D were also found in the A_{lumen} of oil palm roots, as A_{lumen} increased with the increase in root diameter. The results showed that Alumen in well-drained sites was larger than in riparian sites ($p<0.001$, r^2: 0.268, Figure 3, Table 4). In each root diameter class, we found that A_{lumen} showed a different distribution pattern in riparian and well-drained sites ($p<0.05$, Figure 3). In root diameter <2 mm, the smallest distribution of A_{lumen} was ≤ 0.075 mm^2, and the frequency was dominated by oil palm root xylem in the riparian sites. While the largest distribution ranged from 0.21-0.5 mm^2, and the frequency was dominated by oil palm root xylem in the riparian sites. In root diameter 2 ≤ d < 5 mm, the smallest distribution of A_{lumen} ranged from 0.21-0.5 mm^2, and the frequency was dominated by oil palm root xylem in the riparian sites. While the largest distribution was 1.76-2.00 mm^2, and the frequency was dominated by oil palm root xylem in the well-drained sites. The smallest distribution of A_{lumen} in root diameter 5 ≤ d < 10 mm ranged from 0.76-1.00 mm^2, and the frequency was dominated by oil palm root xylem in the riparian sites. While the largest distribution of A_{lumen} was ≥3.1 mm^2, it was dominated by oil palm root xylem in the well-drained sites.

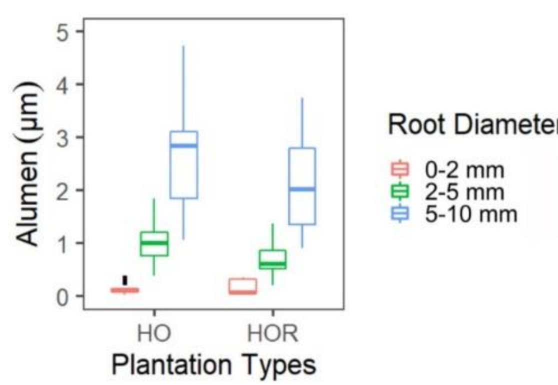

Figure 3. Vessel lumen area (A_{lumen}) of oil palm's root at different diameters in riparian (HOR) and well-drained (HO) sites with four replications from each site type. A_{lumen} has a significant effect on root diameter and plantation types, but it is only found in 5≤d<10 mm root's diameter

When focusing on hydraulic properties, we found a similar pattern in potential hydraulic conductivity (Kp), where potential hydraulic conductivity was the highest in the larger root's diameter on the well-drained sites ($p<0.001$). Potential hydraulic conductivity in oil palm root systems was influenced by the interaction between root diameter and the site ($p<0.001$), except in root diameter at <2 mm. The Kp in the well-drained sites on each diameter class is higher than in the riparian sites (Figure 4). Based on

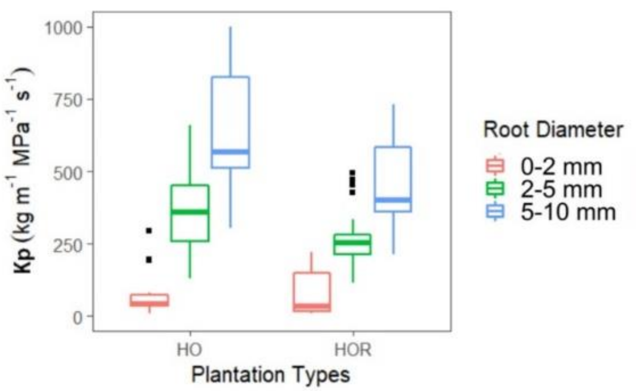

Figure 4. Potential hydraulic conductivity (Kp) of oil palm's root at different diameters in riparian (HOR) and well-drained (HO) sites with four replications from each site type. Kp significantly affects root diameter and plantation types but is not found in <2 mm root's diameter

the regression analysis, Kp increased with D and A_{lumen} and showed a positive correlation with Kp ($p<0.001$, $R^2 = 0.71$ and $p<0.001$, $R^2 = 0.32$, respectively, Figure 5). In contrast, Kp showed a negative correlation with VD and showed a relationship with Kp ($p<0.001$, $R^2 = 0.39$, Figure 5).

4. Discussion

Different xylem anatomical designs represent a functional adaptation to variations in water availability, among other environmental factors (Kirfel *et al.* 2017). Our study showed that xylem vessel density (VD) in oil palm root xylem decreased with increasing root diameters; on the other side, the area types did not influence it. The highest vessel density was found in < 2 mm root diameter. These results align with Kirfel *et al.* (2017), in which VD in mature beech trees' fine to medium-sized roots significantly decreases with increasing root diameter. The VD of oil palm root xylem in riparian sites in our study was greater than in well-drained sites and contradicted with Waite *et al.* (2019), who found that VD in oil palm fronds was higher in a well-drained sites. These differences assume that the decrease of VD in oil palm roots xylem in riparian is the oil palm roots strategy to limit water uptake during water-saturated conditions.

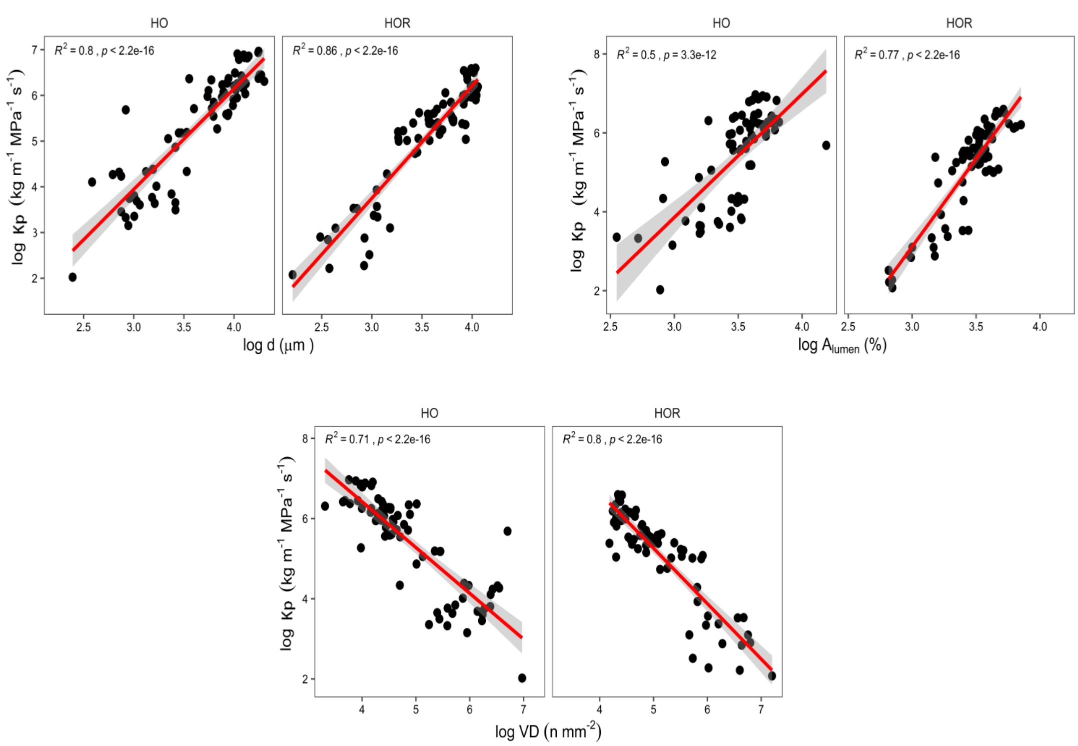

Figure 5. The relationship between D, A_{lumen}, and VD on Kp of oil palm's root in riparian and non-riparian sites. Red lines are regression curves of linear models, and grey areas show 95% confidence intervals

The conductivity of a given diameter conduit can also vary (Kim *et al.* 2014). We could confirm that vessel diameter and hydraulic conductivity increase with increasing root diameters depending on root diameter and the site types. Since the increased root diameter, we found a significant increase in mean xylem vessel diameter (D) and vessel lumen area (A_{lumen}). As observed in other studies, this result demonstrates that the xylem vessel's diameter increases with root diameter and affects root hydraulic conductivity (McCulloh *et al.* 2011). Several studies stated that as the root's diameter gets wider, so does the xylem's diameter. It is caused by the cell that constructs the plant's organ getting larger (Kirfel *et al.* 2017). Several studies have stated that plants with large diameter xylem vessels have a large hydraulic conductivity of xylem vessels, but are more at risk of cavitation than small diameter xylem vessels (Pockman and Sperry 2000).

Another study by Rewald *et al.* (2011) showed that coarse roots have a wider xylem vessel diameter than fine roots with a narrower root diameter in olive plants. If we compared these observations to Waite *et al.* (2019), the oil palm roots had a wider xylem vessel diameter than the oil palm frond. A previous study on hydraulic anatomical properties in trees confirms that xylem vessel sizes are the largest in roots and basipetal taper to the branches (Kotowska *et al.* 2015). Xylem vessel diameter in the xylem generally decreases from roots to shoots, as it has been postulated as the basic principle of hydraulic tree architecture (Anfodillo *et al.* 2013). Consistent with these predictions, it has commonly been observed that the largest vessels along the water flow path are found in the roots of trees from the temperate or Mediterranean environment (Domec *et al.* 2009). Xylem anatomy determines hydraulic safety (Jansen and Nardini 2014). Furthermore, the morphology and thickness of pit membranes between xylem vessels have been suggested to influence hydraulic resistance and vulnerability to embolism in plants (Jansen *et al.* 2009). These pit membranes of water-conducting cells in the xylem can differ in their structural characteristics across different organs within a tree (Kotowska *et al.* 2020).

The highest vessel diameters of oil palm roots xylem were found in well-drained sites in 5-10 mm diameter roots. Oil palm roots from well-drained sites also showed higher lumen area (A_{lumen}) in the xylem than roots from riparian sites. Our results showed that the largest A_{lumen} dominates the oil palm root xylem in the well-drained sites, while the smallest A_{lumen} dominates the riparian sites. Contrary to this evidence, and according to Waite *et al.* (2019), xylem vessel diameters in oil palm fronds were higher in riparian sites than in well-drained sites. Therefore, we assumed that the narrowing of the xylem vessel diameter and the smaller lumen area of oil palm roots in riparian sites was caused by the lower evaporative demand and, on average, higher soil moisture in the riparian sites. It can be expected that this is a strategy of oil palm roots to adjust the water supply from the roots to the canopy (Brunner *et al.* 2015).

Changes in plant morphology and physiology can be affected by changes in the environment, including changes in xylem vessel size and density. There is little doubt that the large diameter of the vessels, as in the palms, results from increased conductivity (Tyree and Zimmermann 2002). However, wide vessels are potentially more metabolizable than narrow vessels, as demonstrated by the change in xylem vessel diameter in the growth ring (Hargravei *et al.* 1994). In the xylem vessels of palm frounds re wide and surrounded by parenchyma cells with thick cell walls presumably these parenchyma cells protect the xylem vessels from vulnerable due to high conductivity (Tyree and Zimmermann 2002; Carlquist 2012).

The adjustment to climatic variability in plant is controlled at the xylem vessels level by acclimation the xylem vessel's hydraulic properties (Tyree and Zimmermann 2002) as the size, density, and other variables of the vessels. Within the same plants, larger vessels allow more efficient water flow but are simultaneously more prone to failure if plants are exposed to drought stress. The risk failure can be reduced by reducing the proportion of hydraulically efficient vessels, reinforcing vessel walls or interconduit pits aperture, refilling embolized vessels, increasing redundancy through independent modular pathways (Pittermann *et al.* 2006a, 2006b; Chave *et al.* 2006; Choat *et al.* 2008; Schenk *et al.* 2008; Martinez-Cabrera *et al.* 2009; Hacke and Jansen 2009; Salleo *et al.* 2009).

We could confirm that the potential hydraulic conductivity (Kp) of oil palm roots depended on root diameter and the type of site. We found that the Kp of oil palm roots in the well-drained sites was higher than in the riparian sites, as the increase of root diameters increases Kp. According to the Hagen–Poiseuille law, a slight increase in mean xylem vessel diameter causes an exponential increase in potential hydraulic conductivity (Kirfel *et al.* 2017). The highest Kp in oil palm roots was found in 5-10 mm diameter roots, and the lowest was found in fine roots < 2 mm. The increase of Kp with root diameter was closely related to the xylem vessel diameter and vessel lumen area, and it had a consistent trend across root diameter classes. These results suggest that under our study sites' conditions, adjusting xylem vessel anatomy with root diameter and area types might be crucial for enhancing hydraulic efficiency and allowing sufficient water supply to the shoot. Greater xylem vessel diameter accompanied by high conductivities for rapid water transport usually lead to an elevated risk of xylem embolism and hence xylem dysfunction (Williams *et al.* 2001).

As a monocot, oil palms (Arecaceae) belong to an interesting family concerning the co-occurrence of vessels and tracheid and not having monocot cambia (Carlquist 2012). Further, oil palm roots do not develop secondary diameter growth. They do not have a monocot cambium, meaning they have developed a series of xylem strategies different from those of the arboreal monocots with monocot cambia. Our evidence showed that morphologically oil palm roots seem to have huge xylem vessels in the center and packages of a smaller vessel towards the cortex. Compared with monocots such as rice (*Oryza sativa*), whose mature roots show a different morphological appearance in transverse sections. The vascular tissues are organized in a central vascular cylinder surrounded by the endodermis and embedded in the cortex. The xylem forms a solid central core with a ridge-like projection extending toward the periphery of the vascular cylinder (Scarpella and Meijer 2004).

Plantation types can develop complementary adaptive strategies to water availability through hydraulic regulation (Liu *et al.* 2019). Our results showed that high Kp in oil palm roots occurs in well-drained sites with enough water availability. At the same time, Kp is lower in the riparian sites with a high-water availability. Oil palms in the riparian sites, which are flooded at least once a year, must maintain water availability up to the oil palm's canopy. Plants will adapt to unfavorable environmental conditions for survival. Therefore, oil palm is presumed to have an adaptation mechanism through the root xylem vessels' hydraulic conductivity and the narrowing of the xylem vessel lumen in the roots of oil palm in the riparian siteswell. When plants pose waterlogging, the water uptake is often substantially reduced; consequently, it has a low hydraulic conductivity (Yan *et al.* 2015). It also changes leaf water potential, stomatal closure, etc (Atkinson *et al.* 2008). Waterlogging would reduce gaseous oxygen concentrations in soils and lead to hypoxic or anoxic conditions (Wittmann and Pfanz 2014). Additionally, Drew (1997) stated that long-term waterlogging would decrease water uptake capacities because roots have a crucial organ for plants' water absorption to maintain their water status.

In our sites, the soil texture on well-drained sites was dominated by sand, while in the riparian sites, it was dominated by silt and clay. Among the various soil structural porosity, the sand fraction has large particles, so the soil has a large porosity. The clay fraction has small particles, so the soil with a small fraction has a small porosity. The role and growth of roots in the soil is controlled by the quality and character of the soil and the type of root growth (Bodner *et al.* 2014). The physical properties of the soil significantly affect the penetration of plant roots. The soil texture in the riparian sites has a low sand fraction but a high clay and silt fraction; therefore, the soil will become compact due to the waterlogged period, which can cause root growth to slow down due to the small and dense gaps or pores in the soil. In addition to the plant hydraulic conductivity, Carminati (2013) reported that the root-soil interface's resistance has been supposed to affect root water uptake.

This study concludes that characteristics of xylem vessels of oil palm roots, including diameter, lumen area, and potential hydraulic conductivity, increase with increasing root diameter. Potential hydraulic conductivity, diameter, and lumen area of xylem vessels were affected by the interaction between root diameter and site type. Potential hydraulic conductivity in the riparian sites is lower than in non-riparian sites at root diameters >2-5 and >5-10 mm. The adaptation mechanism in oil palm is thought to reduce root hydraulic conductivity and narrow the xylem vessel lumen of oil palm roots in the riparian sites.

Overall, based on our evidence in this study, we suggest that riparian sites may be less suitable for planting oil palm, as riparian sites have an important role in ecological functions as buffer zone between streams and upland plantations. Further studies of hydraulic conductivity in oil palm's stem and leaf and the embolism mechanisms of oil palm in both riparian and well-drained sites are needed. Further studies aim to know whether there are similar or different hydraulic conductivity values in the xylem's stem with the xylem's roots in the riparian and well-drained sites and have a particular insight into the mechanism in water uptake and transport in oil palm.

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