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ABSTRACT

Background and aims: This study aimed to characterize the functional root traits of 4-contrasting oil palm progenies grown under different fertilization regimes, and identify the most relevant root traits associated with nutrient uptake efficiency.

Methods: Four 8-year-old oil palm progenies differing in potassium (K) and magnesium (Mg) uptake efficiencies were studied in a split-plot trial in Nigeria. Fertilization treatments combined three K-levels (0, 1.5, 3.0 kg KCl $palm^{-1}$ $year^{-1}$; 60% K_2O) with three Mg-levels (0, 0.75, 1.5 kg Kieserite $palm^{-1}$ $year^{-1}$; 27% MgO). Root biomass, diameter (D), length, surface, volume, and specific root length (SRL) were measured.

Results: Total root biomass did not differ significantly among progenies (mean = 5.23 ± 0.37 Mg ha^{-1}), but lateral and vertical root distributions revealed distinct rooting strategies within progenies for optimal mineral uptake. Effects of fertilizers applied radially close to the palm trees were observed mainly in the topsoil (0-20 cm) at 1.5-3.5m from the application zone, where root traits differed significantly among progenies. The most productive progeny, with the highest K and Mg contents, exhibited finer roots with higher-SRL and smaller-D, making it the most efficient material for mineral uptake.

Conclusion: Differences in root morphology and spatial distribution among oil palm progenies reflect specific adaptation strategies influencing nutrient acquisition. Identifying traits such as higher-SRL and finer root diameter can guide breeders for quick selection of progenies with efficient nutrient uptake and higher yield potential. This study presents a practical framework for enhancing oil palm productivity through root trait-based breeding under field conditions.

Keywords: Oil palm, root biomass, root traits, mineral uptake efficiency, potassium, magnesium

Introduction

Oil palm (*Elaeis guineensis* Jacq.) has a fascicular root system (Corley and Tinker 2016; Jourdan 1995) which represents a thick horizontal filter carpet that captures nutrients applied to the soil as fertilizers. The oil palm root system is horizontally and vertically well developed in the soil (Dassou *et al.* 2021), and its fine roots are in perpetual renewal (Jourdan and Rey 1997a,b). It plays a fundamental role in water and nutrient uptake, even at great depth, at least until a depth of 8 m (Valverde-Barrantes *et al.* 2017; Nodichao *et al.* 2011; Nelson *et al.* 2006). A plant's nutrient uptake capacity depends on the availability of nutrients in the soil (edaphic medium), the mineral status of its root system, the plant species or genotype, and the sink strength of its aerial organs, which varies over the seasons (Lynch 1995; Legros *et al.* 2006; Dassou *et al.* 2025).

The oil palm root system architecture, structured in primary, secondary and fine (tertiary and quaternary) roots (Jourdan and Rey 1997a,b), exhibits the specific roles of each root type (Atger 1992). The proximal part of primary roots, closest to the trunk, are mostly involved in the anchorage of the palm tree at the vicinity of the trunk (Ennos 2000) and represents the place where carbon reserves of the root system are mainly stored (Syahrinudin *et al.* 2005; Legros *et al.* 2006). All primary and secondary roots are considered as pipes of raw sap, where water, nutrients, carbohydrates and metabolites are transported between the soil beneath and around the palm tree and the photosynthetic seat in leaves (Legros *et al.* 2006; Ahmad and Maathius 2014; Lamade *et al.* 2014). By contrast, the fine roots mainly perform hydromineral uptake (Lopèz-Bucio *et al.* 2002; Nodichao *et al.* 2008).

According to Jourdan and Rey (1997a,b), water and nutrients are also absorbed by the apex of all root types having a creamy white colour resulting from unsuberized rhizodermic root cells and lack of Casparian strips in the endodermis that facilitates water and mineral passage to the vascular cylinder (Jourdan 1995; Jourdan *et al.* 2000). Therefore, a mineral arrangement is

usually observed with a certain gradient along the roots (Kheong *et al.* 2010). Some of the nutrients absorbed by the oil palm trees are directly absorbed in their ionic forms such as the monovalent potassium (K^+) cation and the divalent magnesium (Mg^{2+}) cation (Doğan and Akinci 2011). Since oil palm is predominantly grown on highly weathered tropical soils with low soil nutrient reserves (Paramananthan 2000), these nutrients are typically supplied by fertilizers. Potassium (K) is one of the main nutrients required by oil palm (Dassou *et al.* 2025; Dassou *et al.* 2022a,c). It plays a crucial role in crop growth, production and alleviation of the effect of some environmental stress (Dubos *et al.* 2010; Dassou *et al.* 2022a,c). However, there is potassium deficiency in many tropical soils (Firmano *et al.* 2020).

Unlike magnesium (Mg), K is characterized by high mobility in the soil and plants at all levels; i.e., within individual cells and neighboring tissues as well as in long-distance transport (Marschner 1995). Potassium is also the most abundant cation in plant cytoplasm (Ciríaco da Silva *et al.* 2011), notably in oil palm (Ng *et al.* 1968; Teoh and Chew 1988; Ollivier *et al.* 2017, and Dassou *et al.* 2022b, 2025). In oil palm progenies exhibiting different crude palm oil (CPO) yields, different leaflet concentrations with variable uptake efficiencies were observed for potassium and magnesium (Dassou *et al.* 2022a,b; Dassou *et al.* 2025). We then hypothesized that differences in nutrient uptake efficiency can be explained by differences in root characteristics. Hence, the first objective of this study was to characterize root traits that discriminate oil palm progenies in K and Mg uptake.

Traditionally, fertilizers are usually applied in a circle around the oil palm trees, approximatively at 1 m from the trunk, at mature age. However, it is not clear which parts of the root system and which root traits are affected by fertilizer applications.

Root biomass is the most frequently used parameter to characterize plants root development and its distribution within the soil (Jourdan 1995; Jourdan and Rey 1997a,b; Levillain *et al.* 2011; Nodichao *et al.* 2011 and Dassou *et al.* 2021). It has been shown that oil palm root

biomass differs according to age and genetic origin (Ruer 1968; Cornaire *et al.* 1994; Jourdan 1995; Jourdan and Rey 1997a,b; Nodichao *et al.* 2011; Dassou *et al.* 2021). Several researchers have also concluded that root biomass increases with increasing soil humidity and fertility (Djègui 1995; Aholoukpè 2016; Dassou *et al.* 2021).

According to Rengel and Damon (2008) and Nodichao *et al.* (2011), oil palm progenies that have higher mineral uptake capacity must also have a greater root surface area in contact with the soil which increases mineral uptake at the root-soil interface.

Root length and volume are also used to characterize oil palm progenies' tolerance to water stress. Oil palms with long roots have the capacity to absorb more water and nutrients from a larger soil volume and lower soil depths (Nodichao 2008; Nodichao *et al.* 2011).

Another key parameter is the specific root length (SRL) which indicates the amount of root length produced per unit of root biomass (Eissenstat 1991; Eissenstat *et al.* 2000). Plants with high SRL have a greater capacity for nutrient and water uptake per unit of root dry mass, as they produce more root length for a given root dry-mass investment. However, they are generally considered to have shorter root lifespan than low-SRL plants (Salahuddin *et al.* 2018; Maurice *et al.* 2010). According to the latter authors, high SRL can result from having a low root diameter or low tissue density, each of which is independently associated with different root traits (Eissenstat *et al.* 2015). In water-deficit environments, palms with higher SRL are able to access and absorb more water and minerals from deeper soil layers in the soil profile, enhancing water and mineral use efficiency during crop maturation, and ultimately improving yield compared to low SRL palms. The growth speed of deep roots in wetter soil profiles can also enhance water uptake when moisture is sufficient at depth (Comas *et al.* 2013). Despite substantial advances in understanding plant belowground components, the complex relationships between root traits and the functioning of the oil palm root system remain an active area of research.

Theoretically, an efficient root system should enhance soil exploration and increase the plant's ability to capture more nutrients by making soil nutrients available to the plant (particularly the more mobile ones), with limited root biomass investment, thereby reducing the carbon cost associated with root development.

The present article aims to compare root traits and root distribution patterns of four different oil palm progenies that have contrasting K and Mg uptake efficiencies and to assess their respective responses to the K and Mg fertilizers applications. This study will also help to identify root system structure, root functional and structural traits that could explain fertilizer applications and would reveal the root traits that allow selection of oil palm progenies that take up nutrients more efficiently.

To achieve these aims, we assume that the most efficient oil palm progeny in nutrient uptake exhibits larger fine root biomass (RB) and higher specific root length (SRL). Additionally, we will verify if the zone where fertilizers are applied in oil palm plantations is also the zone where oil palm root traits exhibit significant differences between progenies.

Materials and methods

Geographic situation, ecological and soil of the study area

The study was carried out at Ologbo (Presco Plc oil palm plantation) located at Benin City (Edo State) in Nigeria. As presented in (Dassou *et al*. 2022a), precipitation in the study area has a monomodal distribution, with a dry season from November to March, a rainy season from April to October and an average annual rainfall of 2069 mm between 1996 and 2021 (Bonneau and Impens 2022). The average annual temperature of the same area varied between 20.3 °C and 33.7 °C and the average annual radiation during the same period was 13.78 MJ m^{-2} d^{-1}. The height above sea level was 20 m. The soils of the study site are very uniform and belong to the ferralitic type (Ferralsols or Oxisols according to FAO soil classification, resp.).

The soil is deep (more than 15 m), very sandy in the topsoil, with a gradual increase in clay content with soil depth and a low level of chemical fertility (Dassou *et al.* 2022a,c; Table 1).

Germplasm studied and fertilizer management

Four *Tenera* crosses of different oil palm (*Elaeis guineensis* Jacq.) progenies from two different genetic origins (C1, C2 and C3 from *Deli* x *La Me* origin and C4 from *Deli* x *Yangambi* origin) and previously tested in Indonesian genetic block (Ollivier *et al.* 2017) were selected for this study (Table 2). They have shown various ranges of potassium (3.35, 3.81, 3.86 and 3.31 kg of K $palm^{-1}$ for progenies C1, C2, C3 and C4, respectively) and magnesium (0.42, 0.46, 0.54, 0.45 kg of Mg $palm^{-1}$ for progenies C1, C2, C3 and C4, respectively) uptake efficiencies (Dassou *et al*. 2025).

Experimental design

The experiment was conducted on the same trial described by Dassou *et al.* (2022a,b,c; 2025). It consisted of a factorial trial design, with 3 levels (0, 1.5, 3.0 kg $palm^{-1}$ $year^{-1}$) of potassium chloride (KCl) and 3 levels (0, 0.75, 1.5 kg $palm^{-1}$ $year^{-1}$) of kieserite ($MgSO_4$) fertilizer applications, respectively (K x Mg) as main factor (Fertilizer application scheme is presented in Table 3). Each of the nine main factors considered as random effect, was split into 4 subplots corresponding to each of the 4 different *Tenera* oil palm progenies obtained from the two oil palm origins and with 6 replicates, making a total of 1,944 useful palms in the trial. Within each fertilized plot, the palms in each subplot were surrounded by border palms in all directions (45 border palms per fertilizer plot, i.e. a total of 2,430 border palms for all 54 fertilized plots) with some additional border palms planted along the sides of the road to protect the palms under study and their main border palms from attacks by rodents, as the trial is located

near a forest. Palms were seven years old and planted 9 m apart in a staggered, equilateral triangle design at a planting density of 143 palms ha^{-1}.

To compare progenies in terms of K and Mg uptake capacity, this study focused on five fertilizer treatment combinations (K0Mg1, K1Mg1, K2Mg1, K1Mg0 and K1Mg2), as proposed by Dassou *et al.* (2025), while considering budgetary constraints and the need to reduce labor time in root sampling and conditioning (Dassou *et al.* 2021). The experimental design maintains statistical validity with these five combinations of fertilizers as the response curves for a fertilizer must have approximately the same shape whatever the level of the other fertilizer and to be approximately parallel to each other. Combinations K0Mg1, K1Mg1 and K2Mg1 enable the drawing of the K response curve with the average level of magnesium (Mg1), while combinations K1Mg0, K1Mg1 and K1Mg2 allow the drawing of the Mg response curve with the average level of potassium (K1). Thus, only one palm was selected from each subplot of each of the 5 fertilizer treatments mentioned above and in 3 replicates, making a total of 60 palms that were sampled for root biomass assessment.

Measured variables

Root biomass

Root sampling method

Four teams were organized to achieve root sampling at the same time in the field on all four selected oil palm progenies belonging to each main fertilizer plot and were moving together from one main (fertilizer) plot to another. Oil palm progenies' roots were sampled by using the most accurate and efficient root sampling method called "simplified Voronoi method" (Dassou *et al.* 2021). According to the layout of the twelve right-angle triangles (Full Voronoi trenches, Fig. 1_a) inside the hexagonal Voronoi space, only one, among four, Voronoi trench was considered under the "footpath zone" (Fig. 1_b). It permits to discard the windrow area, where

204 big forest tree trunks and fronds were placed, and to only select homogenous zones (Aholoukpè
205 *et al.* 2016) for the root biomass assessment. Only the central oil palm tree, which has a size
206 comparable to that of its six immediate neighbors of the same age (meaning that no trees had
207 been replaced) was selected in each subplot. Three root types studied by Dassou *et al.* (2021)
208 were sampled: primary roots (R1), secondary roots (R2) and fine roots (RF). Roots were
209 sampled according to sampling zones (Fig. 1_c,d) with distances from the oil palm trunk (Z0:
210 under the oil palm stem, between its center and its periphery = 30° acute angle section, Z1: from
211 the oil palm stem base up to 1 m from the stem, Z2 = Z2S (Z2 Simplified) + Z2C (Z2
212 Complementary): between 1 and 2.5 m from the oil palm stem, along the simplified strip of 70
213 cm and Z3 = Z3S (Z3 Simplified) + Z3C (Z3 Complementary): between 2.5 and 4.5 m from
214 the center of the stem, always following the simplified strip of 70 cm), sampling horizons (H1:
215 0 – 20 cm, H2: 20 – 50 cm and H3: 50 – 100 cm), root types (R1, R2 and RF), oil palm progenies
216 (C1, C2, C3 and C4) and fertilizer treatments (K0Mg1, K1Mg1, K2Mg1, K1Mg0 and K1Mg2).
217 In Z2 and Z3, only Z2S and Z3S were sampled according to the simplified Voronoi Method.
218 The oil palm rooting profile was not limited to a depth of 1 m (Nodichao *et al.* 2011). However,
219 in this study, we limited root sampling to a depth of 1 m to save labor time for budgetary
220 reasons.

221

222 Root processing

223 After collection, the roots were cleaned and sorted into three living root classes
224 according to topological order, typology and diameter (Jourdan and Rey 1997a,b): first order
225 roots emerging on the root bole under the palm tree, named primary roots (R1) with diameter >
226 5 mm; ramifications of R1, named secondary roots (R2), with a diameter range between 2 and
227 5 mm; all ramifications of R2 (tertiary and quaternary roots), named here after fine roots (RF=
228 R3+ R4), with diameter < 2 mm. Dead roots were separated from living ones and were

discarded. Consequently, only living roots were considered in total root biomass estimations following Dassou *et al.* (2021).

For each root type, the total fresh weight of the sampled was recorded and a sub-sample (aliquot), was weighed. The aliquot was dried in the oven at 80 °C for 48 h to estimate its dry weight following Dassou *et al.* (2021). Sample dry matter weight was then calculated according to each root types, sampling zones and sampling horizons.

Root biomass assessment

According to Dassou *et al.* (2021), root biomass obtained from simplified Voronoi (SV) method was extrapolated over the complete Voronoi (CV) sampling volume (Z2S to Z2 and Z3S to Z3, Fig. 1_d).

Z2S = 64% Z2 (Eq. 1)

Z3S = 34% Z3 (Eq. 2)

With Z2S and Z3S, the respective sampling volumes in the simplified Voronoi,

And, Z2 and Z3, the respective sampling volumes in the complete Voronoi.

Thus, hypothesizing that root biomass in the 12 Voronoi triangles are homogenous with similar root density (especially for fine roots) in both footpath and windrow areas, the root biomass (RB) of each tree was assessed using equation 3:

RB_{tree} (Kg) $= [RB_{CV-footpath\ zone}$ (Kg) x 12] (Eq. 3; Dassou *et al.* 2021)

Root biomass was expressed in Mg ha^{-1} based on the planting density (143 palms ha^{-1}), we used equation 4:

$RB_{plantation}$ (t ha^{-1}) = RB_{tree} (Kg) x $\frac{143}{1000}$ (Eq. 4; Dassou *et al.* 2021)

Root biomass distributions within the soil were presented in Mg ha^{-1} and in percentage according to the sampling zones, horizons, root types and the oil palm progenies.

Root diameter, volume, surface and length

Apart from the root biomass, four other root parameters (diameter, volume, surface and length) were assessed from the fresh root scan images. Fast image processing and reliable measurements of the fresh roots were obtained after washing with distilled water. Each root sub-sample (aliquot) was scanned at 600 dpi on the grayscale double scan EPSON 10000XL A3 format scanner (Seiko Epson Corporation, Singapore). From these pictures (scanned root images) the above mentioned four oil palm root development parameters were assessed using "ImageJ software 1.49, (http://imagej.nih.gov/ij/plugins/nifti.html)" and the plugin IJ_RHIZO_V0beta, assuming cylindrical root shapes.

Specific Root Length (SRL)

Specific root length is a ratio between the root length of a sample and its biomass. This root development parameter was assessed only for the fine root that are more involved in water and nutrient uptake. Specific root length (SRL), expressed in m g^{-1}, was assessed using equation 5:

$SRL_{RF} = [\frac{Length\ RF}{\text{Biomass RF}}]$ (Eq. 5), with RF: fine roots

Statistical tests

A mixed model was used for the analysis of variance (ANOVA), in which the fertilizer treatment was considered as a random effect. This allows to compare root biomass, surface, volume, length, diameter and SRL according to sampling zones, horizons, root types, progenies and fertilizer treatments.

Tukey's multiple comparison test was run to compare which means of the different parameters are significantly different between progenies and also to observe the fertilization effect on the progenies root system.

The coefficient of determination (R squared or R^2) was used to identify the most relevant parameter to discriminate oil palm progenies (more the R^2 is, more selective the progenies are). This parameter can then be used in the selection of the more efficient planting material for mineral uptake.

Software packages used for statistical analysis were XLSAT, (Addinsoft, 2019, Version 2018-7, www.xlstat.com) and R, version R-3.6.0 of windows, 32/64 bit.

Results

Oil palm progenies total root biomass (TRB)

There was no difference between progenies in the TRB production ($p = 0.621$). TRB of 8-year-old oil palm trees in Nigeria growing environment, sampled between topsoil and 1 m deep amounted to 5.23 ± 0.37 Mg ha^{-1} for all progenies on average, with 4.93 ± 0.20, 5.15 ± 1.16, 5.07 ± 0.66 and 5.78 ± 0.94 Mg ha^{-1}, for progenies C1, C2, C3 and C4, respectively (Fig. 2).

Primary (R1), secondary (R2) and fine (RF) root biomass values were also similar between all tested progenies (p = 0.476, 0.06 and 0.472 for R1, R2 and RF, respectively) and primary root never exceeds 80% of the total root biomass (TBR) for any of the tested oil palm progeny.

297 Primary roots (R1) were estimated at 3.81 ± 0.27 Mg ha^{-1} on average with 3.72 ± 0.05, 3.47 ±
298 0.08, 4.03 ± 0.09 and 4.02 ± 0.1 Mg ha^{-1} for progenies C1, C2, C3 and C4, respectively.
299 Secondary roots (R2) biomass was 3.6 times less than primary root biomass with 1.06 ± 0.26
300 Mg ha^{-1} on average and 0.94 ± 0.11, 1.2 ± 0.02, 0.75 ± 0.01 and 1.3 ± 0.7 Mg ha^{-1} for progenies
301 C1, C2, C3 and C4, respectively. The most important root type for water and mineral uptake
302 (fine roots: RF) represented the lowest palm root biomass with only 0.37 ± 0.10 Mg ha^{-1} on
303 average and 0.27 ± 0.10, 0.48 ± 0.1, 0.29 ± 0.03 and 0.43 ± 0.6 Mg ha^{-1} for progenies C1, C2,
304 C3 and C4, respectively (Fig. 2).

305

306 **Root biomass distribution according to the different sampling zones**

307 Significant differences ($p < 0.0001$) of the TRB were observed between sampling zones
308 for all progenies (all horizons combined, Fig. 3). Results showed that Z0 zone was concerned
309 by the significantly lower percentage of root biomass, whatever the progeny. For all progenies,
310 root biomass increased progressively from Z0 zone (0.77 ± 0.17 Mg ha^{-1} in average) until Z3
311 zone (2.3 ± 0.36 Mg ha^{-1} in average) where the highest percentage of root biomass was found
312 with more or less similar amount in Z1 and Z2 zones (1.11 ± 0.18 and 1.05 ± 0.08 Mg ha^{-1} in
313 average for Z1 and Z2, respectively). However, no difference was observed between progenies
314 for TRB in any of the sampling zone, excepted Z0 zone (under the palm trunk; $p = 0.027$). Oil
315 palm root biomass available in Z0 zone at 8-year old amounted to 0.77 ± 0.17 Mg ha^{-1} in
316 average. Progeny C4 had the highest amount estimated to 0.90 ± 0.15 Mg ha^{-1} (16 %), whereas
317 progeny C2 had the lowest amount 0.52 ± 0.09 Mg ha^{-1} (10 %) and progeny C1 and C3 had an
318 intermediate and similar amount (0.82 ± 0.07 and 0.85 ± 0.17 Mg ha^{-1} which represented in
319 both progenies C1 and C3, 17 % of the TRB) (Fig. 3).

Significant differences ($p < 0.0001$) of root type biomass was also observed between sampling zones for all progenies (all horizons combined). Primary roots were the most produced type of roots, irrespective of the sampling zones and the progenies. Its biomass followed almost the same trend as the TRB distribution regarding the different sampling zones. Only Z0 ($p = 0.024$) and Z2 ($p = 0.025$) showed significant difference between tested oil palm progenies for their primary and secondary root biomass, respectively. In Z0, progenies C3 and C4 had the highest and similar amounts of primary root (0.83 ± 0.09 Mg ha^{-1} and 0.87 ± 0.16 Mg ha^{-1}: 98 and 97 % of Z0 total root biomass, respectively), whereas progeny C2 had the lowest amount estimated to 0.50 ± 0.10 Mg ha^{-1} (96 % of Z0 total root biomass) and progeny C1 had an intermediate amount of primary root biomass, estimated at 0.79 ± 0.14 Mg ha^{-1} (97 % of Z0 total root biomass) (Fig. 3). R1 percentage displayed by the different tested progenies showed that the sampling zone Z0 is essentially occupied by primary roots. In Z2, progeny C4 had the highest amount of secondary root biomass estimated to 0.32 ± 0.05 Mg ha^{-1} (28 % of Z2 total root biomass), whereas progeny C3 had the lowest amount of secondary root biomass estimated at 0.19 ± 0.03 Mg ha^{-1} (19 % of Z2 total root biomass) and progenies C1 and C2 had an intermediate and similar secondary root biomass amounts (0.21 ± 0.02 Mg ha^{-1} and 0.27 ± 0.03 Mg ha^{-1}: 21 and 26 % of Z2 total root biomass, respectively) (Fig. 3).

In all sampling zones, fine roots remained similar between the tested progenies.

Root biomass distribution according to the different sampling horizons

TRB were significantly different between soil layers (all sampling zones combined), irrespective of the progenies ($p < 0.0001$) indicating a depth effect in root distribution. The deepest layer was concerned by a significantly lower percentage of root biomass among all sampling layers, whatever the tested progenies ($p = 0.037$). Results showed that for each oil

palm progeny, TRB were similar between layers H1 (2.04 ± 0.24 Mg ha^{-1} in average either 39 % of TRB) and H2 (2.24 ± 0.13 Mg ha^{-1} in average, either 43 % of TRB) (Fig. 4).

However, no difference was observed between progenies' TRB for the sampling horizons, excepted in H3 soil layer ($p = 0.046$). Oil palm root biomass available in H3 at 8-year- old amounted to 0.95 ± 0.20 Mg ha^{-1} in average, either 18 % of TRB. Progeny C4 had the highest amount of TRB in H3, estimated to 1.22 ± 0.13 Mg ha^{-1} (21 %), whereas progeny C2 had the lowest amount 0.76 ± 0.16 Mg ha^{-1} (15 %) and progeny C1 and C3 had an intermediate and similar amount (0.89 ± 0.11 and 0.94 ± 0.11 Mg ha^{-1} which represented in both progenies C1 and C3, 18 % of the TRB) (Fig. 4).

Results also showed that for each oil palm progeny, primary (R1), secondary (R2) and fine root (RF) biomass were significantly different ($p < 0.0001$) according to soil layers (Fig. 4). Progenies C2 and C4 produced the highest and similar amounts of R1 in the first two soil layers (H1 and H2) before to decrease onward. By contrast, the highest amounts of R1 for progenies C1 and C3 were observed in the layer H2, of which biomass was significantly higher than those of the top layer (H1). The latter in turn was significantly higher than the amounts of R1 in the deepest layer (H3) (Fig. 4).

Progeny C4 produced similar amount of secondary root biomass in the first two soil layers (H1 and H2) before to decrease onward, pointing out its high level of R2 ramification from R1, whereas progeny C1, C2 and C3 showed their highest amount of R2 biomass in second soil layer (H2) only, with significantly lowest amount of R2 in the top soil layer (H1) for progeny C1 and in the deepest soil layer for progeny C2 and C3. For progeny C1, H3 was concerned by an intermediate amount of R2 which was observed in the top soil layer for progenies C2 and C3.

The distribution of progenies' RF biomass between the three soil layers was similar with highest amount in the topsoil, which decreased downward and remained similar in the two subsequent soil layers (H2 and H3). However, no difference was observed between progenies for RF biomass according to each soil sampling horizon.

Plasticity of oil palm root system and potassium and magnesium effects on oil palm progenies' fine root biomass

Even if there was no effect of potassium (K) and magnesium (Mg) on the oil palm progenies' TRB ($p = 0.456$), their effects were highly significant ($p < 0.0001$) on the fine root (RF) biomass (Fig. 5_a,b). Considering the RF biomass, none of the sampling zones Z0 and even Z1 (where fertilizers were applied) did not exhibited any effect of K and Mg fertilization in any of the three soil layers (H1: 0-20cm, H2: 20-50cm and H3: 50-100cm) (Fig. 5_a,b). Significant effect of K was observed on fine root biomass already from Z2 for progeny C3 and C4 before all the progenies became significant in Z3 zone (Fig. 5 a,b). Indeed, results showed that the effects of fertilizer applied in Z1 zone (which is approximatively located at 1 m from the oil palm trunk, radially distributed) were observed specifically for all progenies in zone Z3 (located at 2-3.5m from the fertilizer application zone) and in the first (H1) soil layer (Fig. 5_a). In that location (Z3H1), progenies C1 and C4 reacted only at K2 whereas progenies C2 and C3 already responded at K1. Progeny C2 increased significantly its fine root biomass between K0 and K1 from 0.16 ± 0.1 Mg ha^{-1} to 0.22 ± 0.1 Mg ha^{-1}. At K2 (0.23 ± 0.04 Mg ha^{-1}), the fine root biomass did not differ from that of K1.

K2 increased significantly progeny C3 RF biomass (0.12 ± 0.1 Mg ha^{-1}) compared to K0 (0.04 ± 0.1 Mg ha^{-1}), whereas K1 dose was intermediate (0.07 ± 0.04 Mg ha^{-1}) between K0 and K2 (Fig. 5_a).

391 Compared to K0, K2 significantly increased progeny C1 RF biomass from 0.04 ± 0.1 Mg ha^{-1}
392 to 0.12 ± 0.1 Mg ha^{-1}, whereas no difference was observed between RF biomass observed at
393 K0 and K1 (0.05 ± 0.04 Mg ha^{-1}).

394 In the other side, K2 significantly increased progeny C4 RF biomass from 0.10 ± 0.04 Mg ha^{-1}
395 to 0.26 ± 0.1 Mg ha^{-1} compared to K0, whereas no difference was observed between RF biomass
396 observed between K0 and K1 (0.12 ± 0.1 Mg ha^{-1}) (Fig. 5_a).

397 Magnesium effect was significantly perceptible only in the first horizon layer of Z3 zone and
398 especially on progeny C2. The effect was observed between K1 and K2 from 0.1 ± 0.04 Mg ha^{-1}
399 to 0.42 ± 0.1 Mg ha^{-1}. However, there is no significant difference between K0 and K1 (Fig.
400 5_b).

401

402 **Adaptation of the root development parameters in the selection of more efficient oil**
403 **palm progeny for mineral uptake**

404 Root diameter (D) and specific root length (SRL) are two other root traits that
405 discriminated, to some extents, the progenies and that can explain the different capacities to
406 mobilize mineral from the soil, especially the sampling location Z3H1 where fertilization
407 effects were significant on the root system.

408 Progeny C4 (*Deli* x *Yangambi* origin) had the widest diameter for the fine roots ($P = 1.1\ 10^{-5}$;
409 Table 4) and consequently the lowest SRL (P = 0.002; Table 4). Progeny C4 fine root diameter
410 was significantly higher than those of the three other progenies (C1, C2 and C3: *Deli* x *LaMe*
411 origin) which was similar. At the opposite, the latter progenies had similar and significantly
412 higher SRL than progeny C4 with a lowest root diameter, consequently (Table 4).

RF biomass, RF surface area, RF length and RF volume were significantly similar across all progenies even with values of progenies C2 and C4 which are the double of that of progenies C1 and C3.

Discussion

Total root biomass and root type production according to oil palm progenies

Significant differences were observed between 4-year-old oil palm progenies' TRB by Nodichao *et al.* (2011) in Benin. Their estimations ranged from 2.41 ± 0.3 to 3.22 ± 0.25 Mg ha^{-1}, where the root biomass of commercial *Tenera* material (C1001F: DA115 D self x LM 2T self, and having the same Dura origin as progenies C2 and C3 tested in our study) was estimated at 2.87 ± 0.17 Mg ha^{-1}. Their estimations are about two times lower than ours, probably due to the difference in age of the two studied plantations. This difference can also be explained by difference in genetic origins of the tested material in both studies and difference in the environmental conditions in Benin and Nigeria.

In a recent study, aiming at the establishment of a root sampling protocol (in Benin environmental conditions) for the assessment of oil palm root biomass (RB), Dassou *et al.* (2021) estimated RB at 0.84 ± 0.03 Mg ha^{-1} for 2-year-old oil palms and 22.23 ± 0.81 Mg ha^{-1} for 16-year-old oil palms. The latter value was about four times higher than our observations, indicating the constant increase in RB with the palm ages (Fig. 6) and their continual establishment from juvenile to adult plants (Jourdan 1995; Jourdan and Rey 1997). Thus, this increase could be related to the exponential increase in root production with age by young oil palms where only 6 root types were observed in young oil palm root system, whereas the adult oil palm has 8 root types with the same number (4) of topological root order (Jourdan and Rey 1997). Indeed, 2 years after planting, the R2 biomass increased suddenly and reached 0.57 Mg ha^{-1} at 3-year-old, while the fine root biomass amounted to 0.215 Mg ha^{-1} at the same stage

438 (Jourdan 1995). However, 8th month after germination, numerous primary roots emerged from
439 the root plate and at the end of the young stage, R1 biomass represents more than 40% of TRB
440 and this amount increases thereafter to stabilize at around 80% in adult stage (Jourdan 1995;
441 Dassou *et al.* 2021), as observed in our study.

442

443 **Root biomass distribution according to the sampling zones and horizons**

444 In our study, RB for 8-year-old palm tree sampled in Z0 zone until 1m deep, ranged
445 between 10 and 17 %, depending on the progenies. The significant difference observed between
446 progenies for the amount of RB in that zone could be explained genetically. However, progenies
447 with a higher amount of RB in Z0 zone did not exhibit the highest mineral uptake efficiency
448 (MUE).

449 In a drier environment as in Benin, Dassou *et al*. (2021) observed for 1m deep sampling
450 profile, 11% of root biomass in Z0 zone for 2-year-old palm trees, whereas it was estimated at
451 16% for 16-year-old palm trees. These results showed that RB amount found in Z0 zone varied
452 according to palm age, given the continuous emission over time of vertical primary root
453 biomass (R1VB) beneath the palm tree through reiteration (Jourdan *et al.* 2000). Moreover,
454 according to preliminary observations in Benin, the primary root biomass in Z0 amounted to
455 20% of total root biomass (TRB) in 4-year-old oil palms (Nodichao 2008) and reached 17% in
456 11-year-old oil palms in Sumatra, Indonesia (Jourdan, unpublished data). Comparing the latter
457 observations with those of Nodichao (2008); Dassou *et al.* (2021) and the ones of our study,
458 variations of RB amount in Z0 zone could also be explained by environmental conditions as
459 rainfall (availability of water in the soil) or soil physical and chemical properties. The roots
460 located in this zone Z0 are predominantly vertical primary roots (97 % of RB in Z0 Zone, in
461 average) that have a positive perception of the gravitropism (Jourdan *et al.* 2000) with a strict

462 vertical direction of growth oriented to deep soil layers (Jourdan and Rey 1997) giving access
463 to deep water and nutrients. High amount of RB in that same zone (Z0) could result from drier
464 and more nutrient-depleted soil conditions that constrained the oil palm to develop more vertical
465 roots to reach deeper soil layers for more favorable water and nutrient content. However, this
466 pattern may also be linked to the continuous emission of new Vertical primary roots (R1V)
467 beneath the palm tree through reiteration, rather than their direct formation from the root plate
468 zone.

469 The fact that secondary root (R2) biomass significantly differed between progenies in zone Z2
470 showed that each progeny adopts specific strategy to efficiently access to the nutrients and water
471 from the soil. This latter point indicates that both root architecture and structural traits are major
472 determinants of mineral uptake efficiency (MUE). Secondary root biomass of all progenies in
473 Z2 zone ranged similarly to the leaflet K concentration (progenies' leaflet K concentrations
474 between 4 to 7 YAP ranged as follow C4 > C1 > C2 > C3; Dassou *et al. 2022a,b*), whereas Z2
475 zone R2 biomass ranged as follow C4 > C1 > C2 > C3). The fact that the observed rank
476 concerning the mineral uptake efficiency (Dassou *et al.* 2025) was not translated through the
477 root biomass distribution can be explained by the whole physiological process of mineral
478 relocation, mineral efflux through harvest, fronds pruning and mineral mobility (Dubos *et al.*
479 2010; Dassou *et al.* 2022a).

480 In Columbia, Rüegg (2017) shows a lack of effects in oil-palm TRB between zones in the
481 shallow rooting profile (0-30 cm). But, when the weeding circle (fertilizer application zone)
482 was included in the analysis, the effect of the distance from the tree was only significant in the
483 RF biomass in the topsoil (0-10 cm) (Rüegg *et al.* 2019), whereas TRB was evenly distributed
484 in the three sampled layers (0-10 cm, 10-20 cm and 20-30 cm) (Rüegg 2017). However, in our
485 study, significant differences were observed between sampling zones for all progenies' TRB as

well as with their root types. These observations can be explained by physiological strategies adopted by each progeny to efficiently absorbed maximum amount of water and minerals.

Previous studies have shown that primary roots accounted for 80% of TRB (Jourdan 1995; Nodichao *et al.* 2011; Dassou *et al.* 2021) and were mainly located in the top 100 cm soil layer radially distributed around the palm trees (Jourdan and Rey 1997). A part of them (20-40% depending of the oil palm age), located under the palm tree, could reach the depth of 6 m in favourable soil conditions (Jourdan and Rey 1997). Even though fine roots accounted for less than 20% of the TRB, they preferentially colonized the topsoil (0-20 cm) layer where nutrient content is richer. Our results are in agreement with these previous observations.

Secondary roots were mostly evenly distributed throughout the whole root profile despite the different ecotypes (Dassou *et al.* 2021, Nodichao *et al.* 2011, Nelson *et al.* 2006; Syahrinudin 2005; Khalid *et al.* 1999; Henson and Chai 1997). This was not the case in our study and the observed differences can be explained by heterogeneity in soil nutrient content caused by fertilizer applications with different ranges of leaching and by differences in soil textures and structures with an increase in silt and clay content (where nutrients are adsorbed) with soil depth.

Potassium and magnesium effect on the root system

The lack of any effect of KCl and kieserite (Mg) applications on the TRB could be explained by the large part of primary roots in TRB (80%) and by the fact that they are not so responsive to nutrient content in the soil as stimuli (Aholoukpè *et al.* 2016) and probably because their main role is to anchor the palm into the ground (Atger 1992; Ennos 2000). By contrast, fine roots represent a small part of TRB (<20%) but are strongly sensitive to soil nutrient content as they are considered as the most important root type for water and nutrient uptake (Marschner *et al.* 1991; Nelson *et al.* 2006; Tinker and Nye 2000) and as they proliferate

511 in presence of organic matter or humidity (Aholoukpè *et al.* 2016; Jourdan 1995; Nodichao
512 2008; Dassou *et al.* 2021). This is why fine roots were more accumulated in the topsoil layer,
513 generally rich in organic matter through aerial litter accumulation (Aholoukpè *et al.* 2016). It
514 was also the reason why only fine roots were considered in order to assess minerals effect on
515 oil palm root system plasticity and the assessment of root development parameters in the
516 selection of more efficient oil palm progeny in minerals uptake. Fertilizer applications also
517 stimulate root growth as reported by Lopèz-Bucio *et al.* (2002). Indeed, potassium effect on
518 fine root was observed far from the fertilizer application zone in the weeding cercle. This result
519 is original as it shows that to assess fertilization effects on mature oil palm trees, sampling only
520 the location Z3H1 is enough instead of to excavate the whole simplified Voronoi, which
521 purpose is to assess the TRB produced by the palm tree or to sample the fertilizer application
522 zones as thought (Aholoukpè 2013).

523

524 **Root development parameters, root traits and strategy of root system in soil resources**
525 **acquisition**

526 According to Seethepalli *et al.* (2021), root characteristics including length, diameter,
527 volume, and SRL are critical to understand plant and soil functions. In our study, the latter root
528 parameters were estimated on the basis of the root biomass in order to identify the suitable root
529 parameter to discriminate the more efficient oil palm progeny in mineral uptake. We found that
530 specific root length (SRL) and root diameter (D) were the primary root development parameters
531 structuring the progenies in genetic origins (*Deli* x *LaMé* and *Deli* x *Yangambi*). Indeed,
532 progeny with high SRL have low D and vice versa. Putri (2015) estimated for 12-years-old
533 palms, between 0-15cm soil depth, fine roots' SRL at 9.3 and 10.9 mg^{-1} in the weeding cercle
534 and under the frond stack, respectively, whereas between 15-30 cm, they were respectively
535 estimated at 9.6 and 11.6 mg^{-1}. These estimations are higher than the values obtained in our

study and can be explained by difference in age between the two tested plantations. Ostonen *et al.* (2007) observed in their study on natural forest trees that SRL decreased significantly under fertilization, showing that with availability of nutrient in the soil, palms produce more biomass per cm unit of root length as a response to chemical fertilizer applications that can increase root weight in a quadratic way especially when the roots were previously in a nutrient-deficit soil (Fageria 2013). Thus, like other root parameters, SRL is influenced by environmental factors such as water and nutrient availability, soil depth and physical conditions, as well as by crop variety, age, and genotype (Oliveira *et al.* 2000; Fageria 2013). The latter case was confirmed in our study, where SRL differed across oil palm genetic origins and was suggested by Atkinson and Dawson (2000) to be an indicator on how plants respond to environmental changes including responses to resource availability in the soil and competitive ability with other roots. Indeed, the low SRL observed in progeny C4 (*Deli* x *Yangambi* origin) fine roots could be explained by their greater diameter and higher lifespan (Salahuddin *et al.* 2018; Maurice *et al.* 2010) than those of progenies C1, C2 and C3 (all *Deli* x *LaMe* origin) which had higher SRL, low root diameters and low lifespan, consequently. The latter observation shows the close relation between these three root parameters such as root diameter, the SRL and the lifespan of the root (Salahuddin *et al.* 2018). The higher nutrient uptake efficiency of the latter progenies (mostly progenies C3 and C2 which are highest bunch / oil producer; Dassou *et al.* 2022a) could be explained by their higher SRL. According to Salahuddin *et al.* (2018) and Maurice *et al.* (2010), higher SRL plants may have higher mineral uptake capacity. A high SRL indicates that the progenies have invested in the root production process, less carbon to produce the same root length, which suggests its ability to proliferate more easily within soil and shows a high capacity for water and nutrient intake compare with progenies of which roots have a low SRL value (Fageria 2013; Eissenstat *et al.* 2000; Eissenstat 1991). On *Citrus* root studies, Eissenstat (1992) implied that roots with a high SRL had a high rate of root proliferation and a high rate of water

561 extraction. Despite, progeny C1 had higher SRL compared to progeny C4 and that progeny C4
562 had higher K and Mg uptake capacity than the latter progeny C1 (Dassou *et al.* 2025) could be
563 explained by the fact that, progenies developed many other physiological mechanisms in
564 mineral use after minerals have been up took as mineral exportation from the field (efflux),
565 photosynthesis, oleo synthesis, relocation etc. which can be in different range according to
566 progenies. The latter's can explain higher amount of minerals in progenies with lower SRL
567 compare to higher SRL progenies having lower amount of minerals in their tissues.

568 Progenies' annual bunch production per palm was ranked as C3 > C2 > C1 > C4, with
569 respectively 15.8, 14.2, 13.1 and 12.2 FFB Mg ha^{-1} $year^{-1}$ (Dassou *et al.* 2022a). Among all
570 progenies, C3 had the highest K and Mg contents in the whole tree (Dassou *et al.* 2025). With
571 similar TRB between progenies and knowing that C3 progeny had the highest total standing
572 palm biomass and FFB/CPO production (Dassou *et al.* 2022a) with the highest mineral uptake
573 capacity for both K and Mg (Dassou *et al.* 2025), let us assume that the C3 progeny root system
574 would be the more efficient to capture soil mineral resources. Hence, progeny C3 root system
575 would be that with the best strategy to fit with the mineral sink of the aerial part of the tree
576 (Legros *et al.* 2006) and be able to satisfy the amount of mineral and water needed for its growth
577 and production.

578 Therefore, root diameter (R^2 = 0.337) and specific root length (R^2 = 0.237) are specific root
579 traits that can be put forward and suggested to breeders to finetune in the selection of the more
580 efficient oil palm progenies concerning the mineral uptake as also proposed by Ostonen *et al.*
581 (2007) who considered the SRL as an indicator of nutrient availability**.** Establishing of causal
582 hierarchical links among root traits will provide a hypothesis-based framework to identify the
583 most parsimonious sets of traits with the strongest links on functions, and to link efficient
584 mineral uptake to planting material.

Conclusion

Total root biomass was similar between all tested progenies whereas there were differences between them for primary root in Z0 zone, secondary root in Z2 zone and for total root biomass in the deeper soil layer (H3). Total root biomass (TRB) and biomass for each root type (primary: R1, secondary: R2 and fine root: RF) were differently distributed according to sampling zones and soil horizons. This study on the root system of oil palm progenies allows to assume that difference in mineral uptake between oil palm progenies could be related to rooting strategy of each of them. To assess fertilization effect on the root system architecture and development, our results suggested to focus root observations only at 3 to 4.5m from the tree (Z3 zone) and in topsoil (H1 soil layer: 0-20 cm). Progeny C3 was pointed as the progeny with the most efficient root system for water and soil mineral resources acquisition. We advocate that root diameter (D) and specific root length (SRL) should be deeply evaluated in the way of screening the most efficient planting materials that are capable to absorb more mineral with the lowest amount of root which could be less expensive for the palm tree in terms of carbon requirements. This study can be used as base line study of oil palm root growth at different management practices. However, it remains uncertain whether progeny C3 is the highest mineral use genotype for CPO and vegetative or reproductive biomass production.

Declaration of competing interest

Ethics Approval and Consent to Participate

The paper content has not been previously published nor is under consideration for publication elsewhere. The authors have contributed to the paper and have agreed to be listed as co-authors.

Consent for Publication

The authors have read and commented on this manuscript and have agreed to submit this manuscript to the journal.

Conflict of interest

We declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Credit authorship contribution statement

Olivier S. DASSOU: Project conception, Data collection & curation, Data analysis, Writing original draft, Writing – review & editing. **Hervé AHOLOUKPE**: Writing – review & editing. **Albert FLORI**: Conceptualization, Data curation, Formal analysis. **Reinout IMPENS**: Writing – review & editing. **Wouter VANHOVE**: Supervision, Writing – original draft, Writing – review & editing. **Emile DE MEYER**: Writing – review & editing. **Jean OLLIVIER**: Project conception, Supervision, Investigation, Methodology, Writing – review. **Léifi NODICHAO, Christophe JOURDAN, Eduardo DE LA PEÑA**: Project conception, Supervision, Project administration, Writing – review & editing.

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TABLE CAPTIONS:

Table 1:

Physico-chemical soil characteristics at the onset of the Nigerian trials.

N: Nitrogen, C: Carbon, MOS: Soil Organic matter, P: Phosphorus, Al: Aluminium, Na: Sodium, Ca: Calcium, Mg: Magnesium, S: Base ion (cation) sum, CEC: Cation exchange capacity, TS: Saturation rate, pHco: pH cobalt (Soil acidity assessed using the cobaltihexamine method)

Table 2:

Genetic characteristics, varieties, genetic origins of the parents of the different oil palm progenies, and leaflet nutrient concentrations with yield characteristics of the tested progenies (PIC, 2011)

D x L: *Deli* x *La Mé*;

D x Y: *Deli* x *Yangambi*

The last letter after the PO number (e.g., PO 2630 D or PO 2766 P or LM 10 T) indicates the main varietal group: P = *Pisifera*, D = *Dura*, and T = *Tenera*

Progenies C1, C2, C3 and C4 are all *Tenera* crosses (They all come from crosses between a *Dura* and a *Pisifera* variety)

Data in the *Dura* and *Pisifera* columns show the genetic material from which female inflorescences and male inflorescences (pollen) were used to obtain the progenies.

AF refers to self-pollinated trees (e.g. LM 10 T AF = LM 10 T x LM 10 T).

FFB: Fresh Fruit Bunch

CPO_{mill} : crude palm oil in the mill

Bunch number, FFB and CPO Yields figures are average data from 5 to 8 years after planting (YAP).

a, b, c and d indicate the differences in parameters between progenies revealed by the Tukey test.

Table 3:

Fertilizer application scheme (g of fertilizer per palm) in Nigeria

Table 4:

Oil palm progenies discrimination against fine root traits that could explain mineral uptake efficiency in the sampling position Z3H1

SRL: Specific Root Length, RRR: Root Ramification Rate, $RRR_{RF/R2(S)}$: number of fine roots per surface unit of secondary root, $RRL_{R2/R1(S)}$: number of secondary roots per surface unit of primary root, P: probability, R^2: coefficient of determination, R^2 adjusted: coefficient of determination adjusted, The letters (a, b, c) show significant differences between progenies according to the different root development parameters. Differences between progenies were at 5% level ($p < 0.05$, Tukey test, $n = 60$).

856 **FIGURE CAPTIONS**

857 Figure 1:

858 Voronoi space (hexagonal zone) of a sampled oil-palm tree within commercial planting design
859 made up of 12 rectangular triangles (called Voronoi triangle) with equal areas (a). The Voronoi
860 edges are at half distance between the observed palm and its six immediate neighbours (b). One
861 of the 12 Voronoi triangles, inside the equilateral triangle formed by three neighbour palms,
862 located in the footpath zone where soil fertility is considered to be homogeneous (Aholoukpè
863 *et al*., 2016) (c). Each triangle was divided into 6 different sampling zones according to distance
864 to the centre of the tree: under the tree trunk (Z0), from 0 - 1m (Z1), from 1 m to 2.5 m (Z2c
865 +Z2s) and from 2.5 to 4.5m (Z3c+Z3s) from the centre of the tree trunk. Together with zones
866 Z0 and Z1, the 70 cm strip from the base of Z1 up to Z3, form the simplified Voronoi (SV, d)
867 inside which roots were sampled and later extrapolated to the volume of the complete Voronoi
868 (CV, d) triangle. *a = 30° arc portion; c=collar girth of the trunk; r = radius; Z0: 30° section*
869 *of the trunk; Z1: zone where fertilizers were applied; Z2 (Z2= Z2s + Z2c): transition zone*
870 *between Z3 zone (Z3 = Z3s + Z3c) and the fertilization area.* Windrow are the zones where
871 fronds are piled (b) and footpath zones are the passages between planting lines where harvest
872 operations are performed. Each footpath and windrow are located after every two planting lines
873 (b).

874 Source: Adaptation to Dassou *et al.* (2021)

875

876 Figure 2:

877 Root biomass (Mg ha^{-1}) produced per progeny (C1, C2, C3 and C4), irrespective of the fertilizer
878 treatment applications. TRB (white bars): R1+R2+RF, R1 (grey bars): primary or coarse roots,
879 R2 (horizontal hatch bars): secondary or medium roots; RF (cross hatch bars): fine or tertiary

and quaternary roots. The same letter above bars indicate similarity in root biomass between progenies ($p = 0.621$, Tukey test, $n = 60$). The percentages (%) displayed account for the part of the total root biomass (TRB) per root types regarding to the different oil palm progenies (C1, C2, C3 and C4).

Figure 3:

Root biomass (Mg ha^{-1}) produced per progeny (C1, C2, C3 and C4) according to the sampling zones (Z0, Z1, Z2 and Z3), irrespective of the fertilizer treatment applications. TRB (white bars): R1+R2+RF, R1 (grey bars): primary or coarse roots, R2 (horizontal hatch bars): secondary or medium roots; RF (cross hatch bars): fine or tertiary and quaternary roots. The different letters above bars indicate significant differences of root biomass for each root type according to distance to tree (Z0: under the palm, Z1: up to 1m, Z2: from 1 m to 2.5 m and Z3: up to 4.5 m from the centre of the sampled tree) ; ($p < 0.05$, Tukey test, $n = 60$). The percentages (%) displayed account for the part of all root types per sampling zone regarding to distance to palm tree (Z0, Z1, Z2 and Z3).

Figure 4:

Root biomass (Mg ha^{-1}) produced per progeny (C1, C2, C3 and C4) according to the soil sampling layers/horizons (H1, H2 and H3), irrespective of the fertilizer treatment applications. TRB (white bars): R1+R2+RF, R1 (grey bars): primary or coarse roots, R2 (horizontal hatch bars): secondary or medium roots; RF (cross hatch bars): fine or tertiary and quaternary roots. The different letters above bars indicate significant differences of root biomass for each root type according to soil layers (H1: 0-20cm, H2: 20-50cm and H3: 50-100cm) ; ($p < 0.05$, Tukey

903 test, n = 60). The percentages (%) displayed account for the part of all root types per sampling
904 horizon regarding to soil depths (H1, H2 and H3).

905

906 Figure 5:

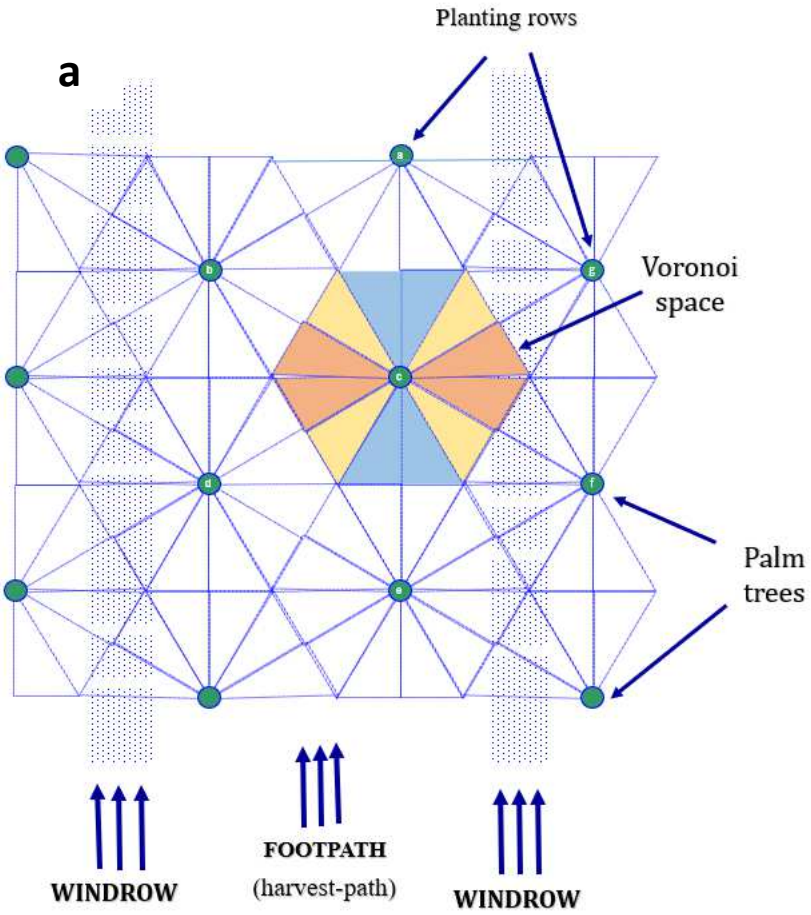
907 KCl (a) and kieserite (b) effects on oil palm progenies' (C1, C2, C3 and C4) fine (tertiary and
908 quaternary) root biomass (Mg ha^{-1}) according to the sampling soil layers (H1: 0-20cm, H2: 20-
909 50cm and H3: 50-100cm), sampling zones (Z0, Z1, Z2 and Z3) regarding to the different levels
910 of potassium chloride (KCl: K0, K1 and K2) and kieserite ($MgSO_4$: Mg0, Mg1 and Mg2)
911 fertilizations. Differences between K and Mg levels were at 5% level ($p < 0.05$, Tukey test, n =
912 60).

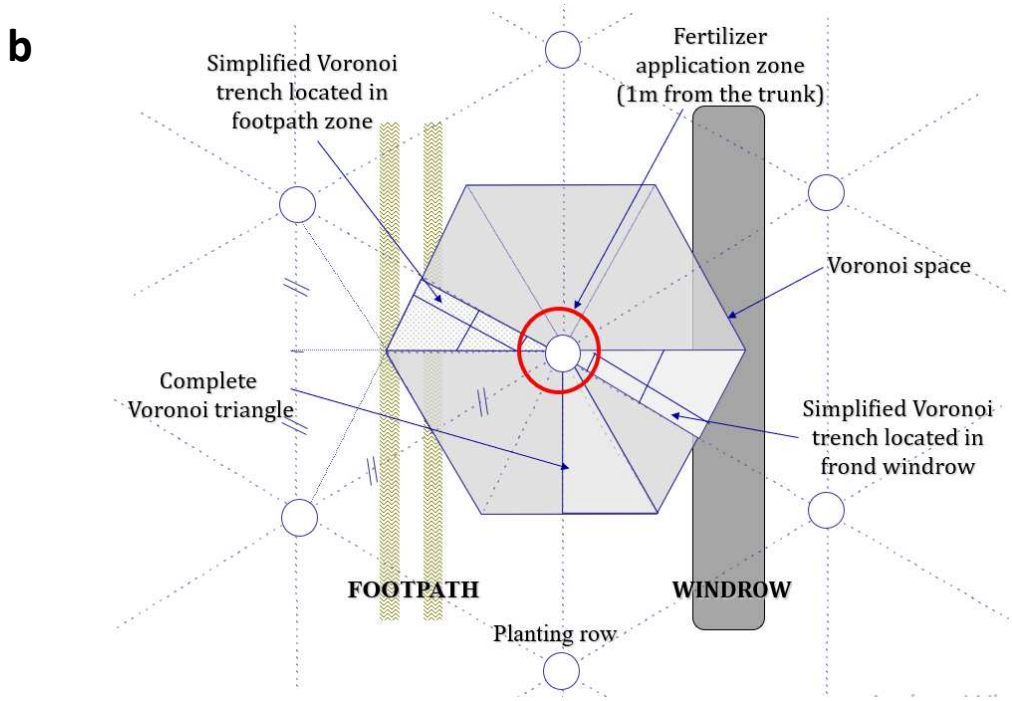
913

914 Figure 6:
915 Oil palm root biomass according to the age (Year after planting: YAP) in Mg ha^{-1}.
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917

Figures et Tableaux





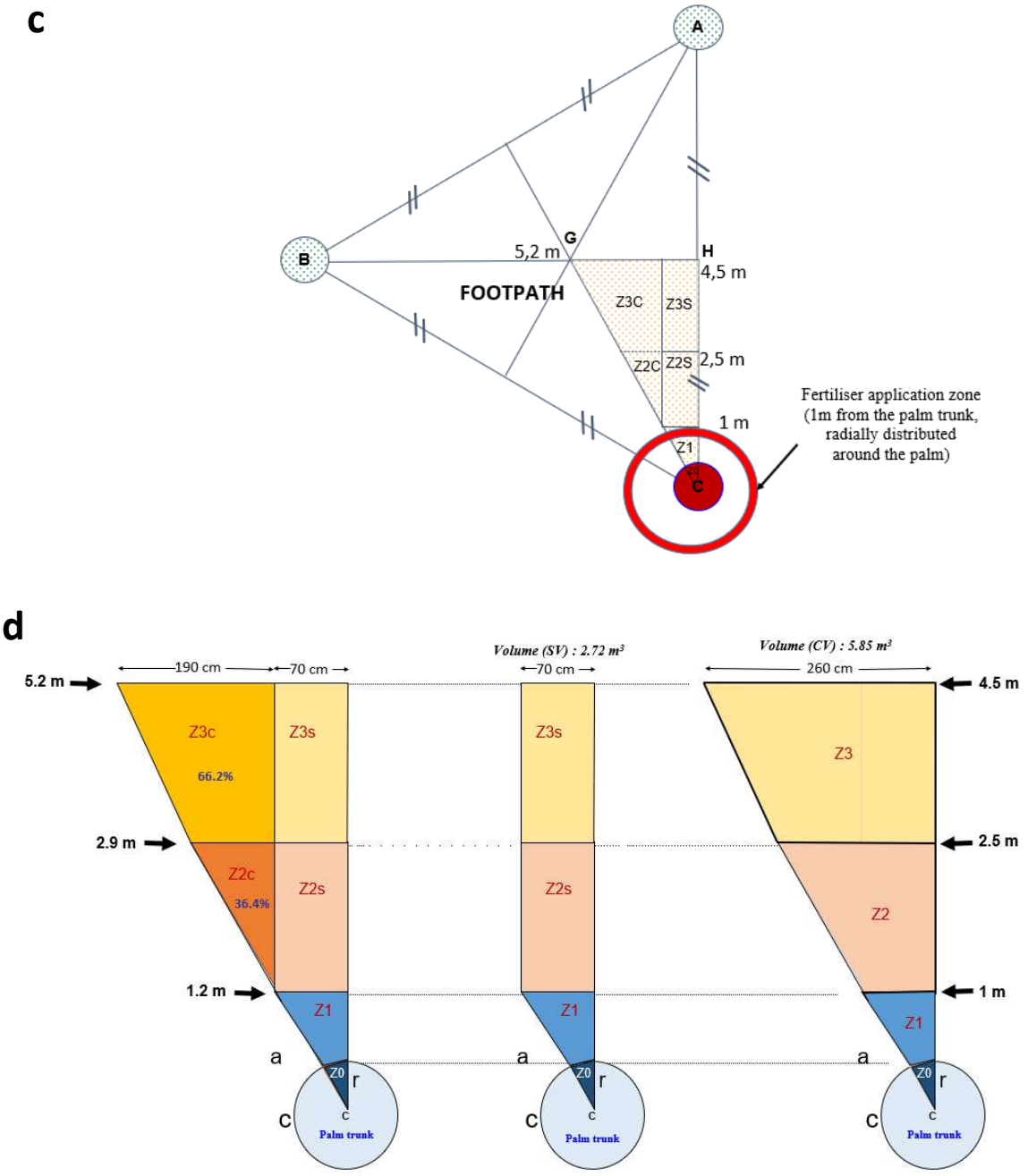


Figure 1: Voronoi space (hexagonal zone) of a sampled oil-palm tree within commercial planting design made up of 12 rectangular triangles (called Voronoi triangle) with equal areas (a). The Voronoi edges are at half distance between the observed palm and its six immediate neighbours (b). One of the 12 Voronoi triangles, inside the equilateral triangle formed by three neighbour palms, located in the footpath zone where soil fertility is considered to be homogeneous (Aholoukpè *et al.*, 2016) (c). Each triangle was divided into 6 different sampling zones according to distance to the centre of the tree: under the tree trunk (Z0), from 0 - 1m (Z1), from 1 m to 2.5 m (Z2c + Z2s) and from 2.5 to 4.5m (Z3c + Z3s) from the centre of the tree trunk. Together with zones Z0 and Z1, the 70 cm strip from the base of Z1 up to Z3, form the simplified Voronoi (SV, d) inside which roots were sampled and later extrapolated to the volume of the complete Voronoi (CV, d) triangle. *a = 30° arc portion; c=collar girth of the trunk; r = radius; Z0: 30° section of the trunk; Z1: zone where fertilizers were applied; Z2 (Z2= Z2s + Z2c): transition zone between Z3 zone (Z3 = Z3s + Z3c) and the fertilization area.* Windrow are the zones where fronds are piled (b) and footpath zones are the passages between planting lines where harvest operations are performed. Each footpath and windrow are located after every two planting lines (b).
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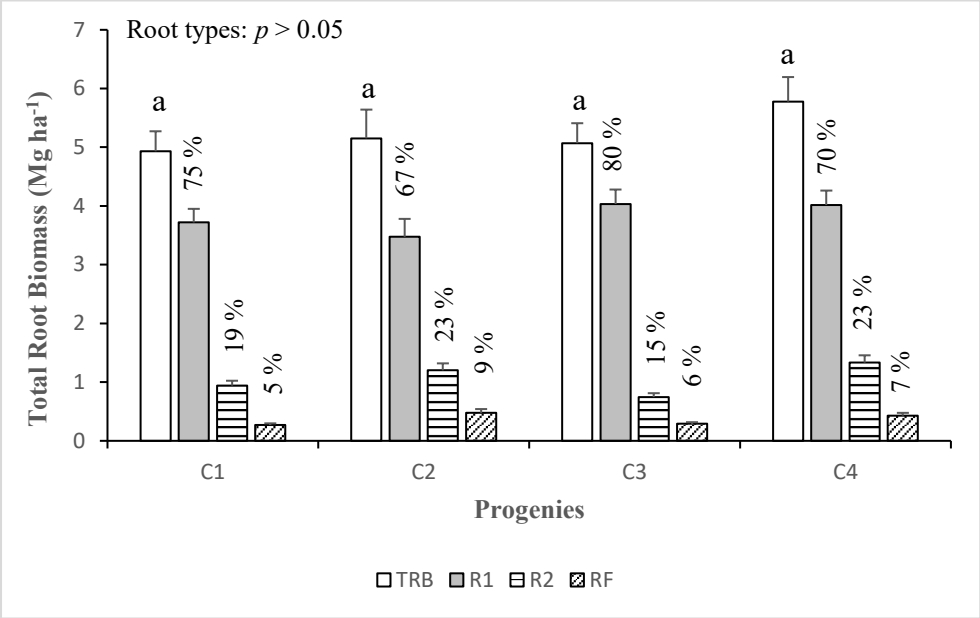


Figure 2: Root biomass (Mg ha^{-1}) produced per progeny (C1, C2, C3 and C4), irrespective of the fertilizer treatment applications. TRB (white bars): R1+R2+RF, R1 (grey bars): primary or coarse roots, R2 (horizontal hatch bars): secondary or medium roots; RF (cross hatch bars): fine or tertiary and quaternary roots. The same letter above bars indicate similarity in root biomass between progenies (p = 0.621, Tukey test, n = 60). The percentages (%) displayed account for the part of the total root biomass (TRB) per root types regarding to the different oil palm progenies (C1, C2, C3 and C4).

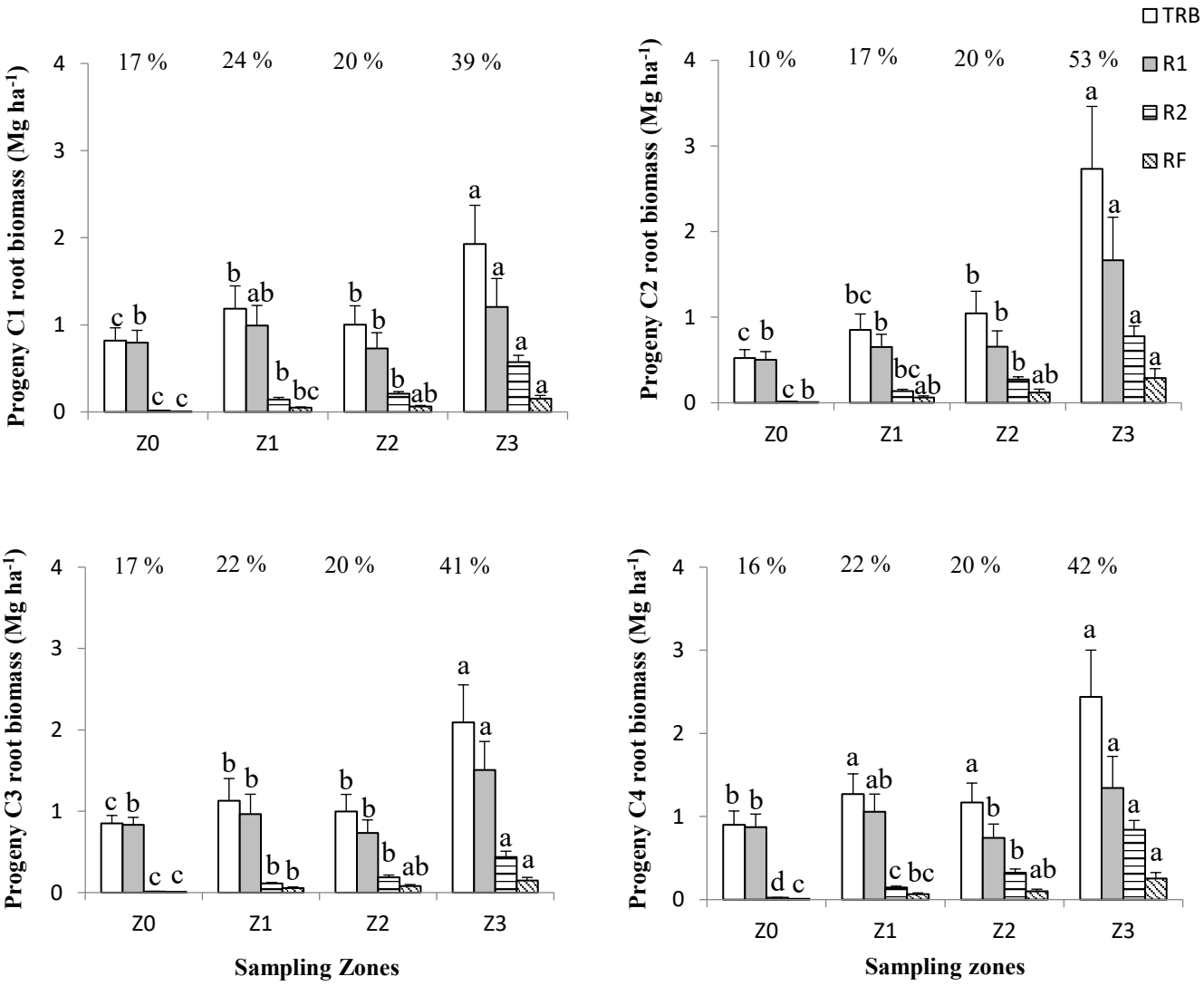


Figure 3: Root biomass (Mg ha^{-1}) produced per progeny (C1, C2, C3 and C4) according to the sampling zones (Z0, Z1, Z2 and Z3), irrespective of the fertilizer treatment applications. TRB (white bars): R1+R2+RF, R1 (grey bars): primary or coarse roots, R2 (horizontal hatch bars): secondary or medium roots; RF (cross hatch bars): fine or tertiary and quaternary roots. The different letters above bars indicate significant differences of root biomass for each root type according to distance to tree (Z0: under the palm, Z1: up to 1m, Z2: from 1 m to 2.5 m and Z3: up to 4.5 m from the centre of the sampled tree) ; ($p < 0.05$, Tukey test, $n = 60$). The percentages (%) displayed account for the part of all root types per sampling zone regarding to distance to palm tree (Z0, Z1, Z2 and Z3).

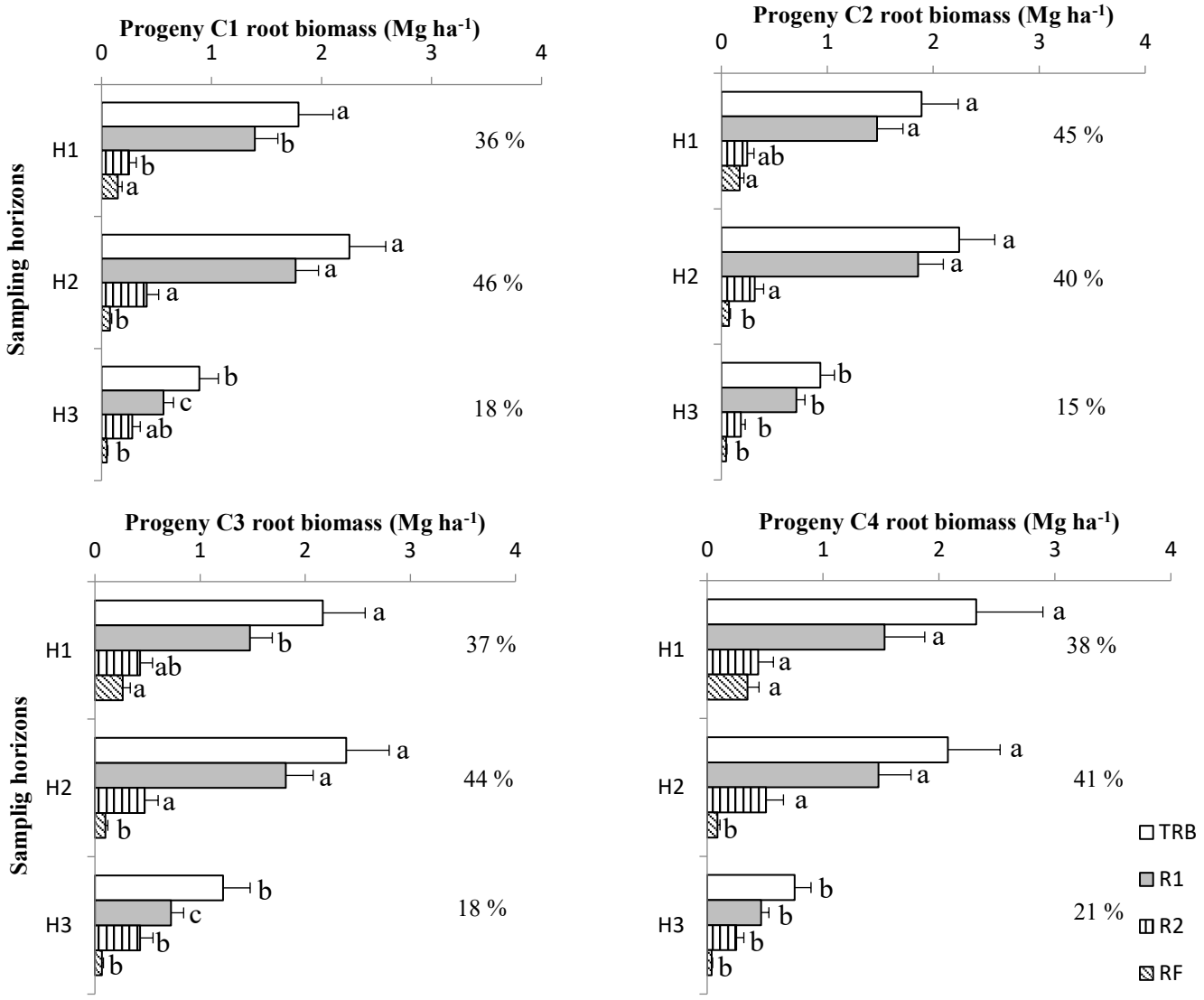
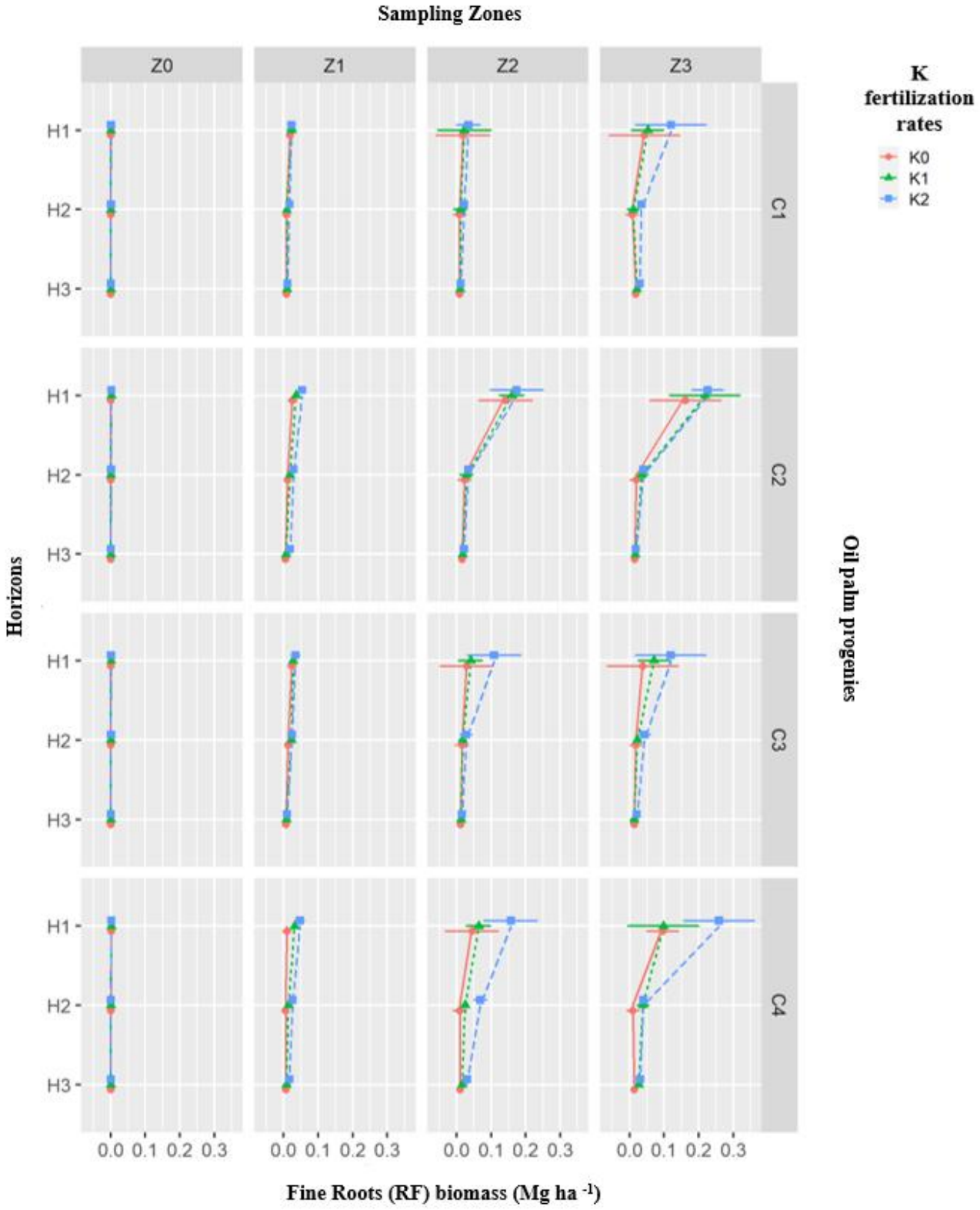


Figure 4:
Root biomass (Mg ha^{-1}) produced per progeny (C1, C2, C3 and C4) according to the soil sampling layers/horizons (H1, H2 and H3), irrespective of the fertilizer treatment applications. TRB (white bars): R1+R2+RF, R1 (grey bars): primary or coarse roots, R2 (horizontal hatch bars): secondary or medium roots; RF (cross hatch bars): fine or tertiary and quaternary roots. The different letters above bars indicate significant differences of root biomass for each root type according to soil layers (H1: 0-20cm, H2: 20-50cm and H3: 50-100cm) ; ($p < 0.05$, Tukey test, $n = 60$). The percentages (%) displayed account for the part of all root types per sampling horizon regarding to soil depths (H1, H2 and H3).

a-


Sampling Zones
Z0
Z1
Z2
Z3
K fertilization rates
K0
K1
K2
H1
H2
H3
C1
C2
C3
C4
Horizons
Oil palm progenies
0.0 0.1 0.2 0.3
Fine Roots (RF) biomass (Mg ha -1)

b-

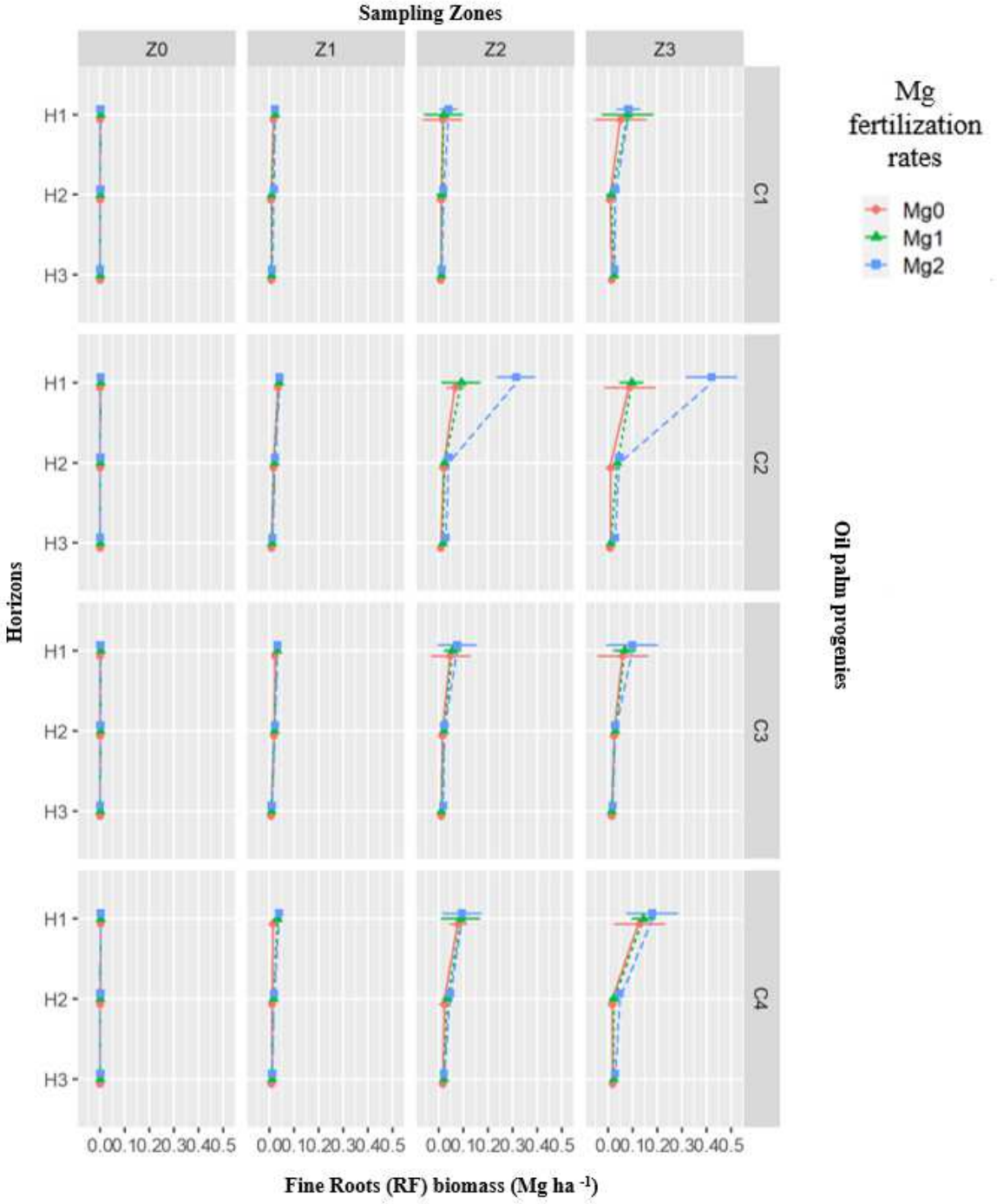


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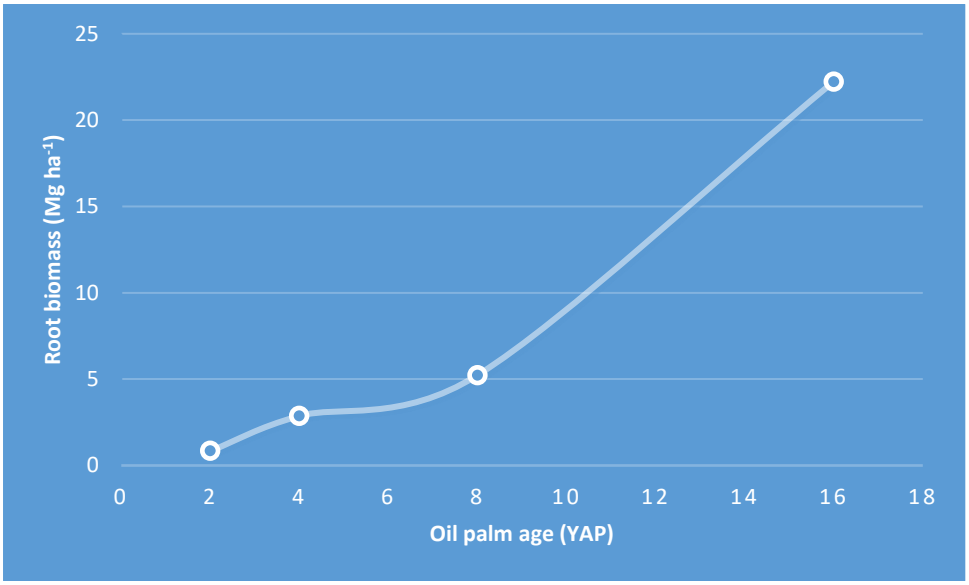


Figure 6: Oil palm root biomass according to the age (Year after planting: YAP) in Mg ha^{-1}.

Tables

Table 1. Physico-chemical soil characteristics at the onset of the Nigerian trials

Site	Horizon (cm)	Granulometry					Acidity		Organic Matter				P content		(Cations) Exchange Complex contents							
		Clay (%)	Slit (%)		Fine sand (%)	Coarse sand (%)	pH water	pHco	Organic matter (%)	Organic Carbon (%)	Total N (‰)	C/N	Total P (mg/kg)	Available P (mg/kg)	Ca^{2+} (me/100g)	Mg^{2+} (me/100g)	K^{+} (me/100g)	Na^{+} (me/100g)	Al^{3+} (me/100g)	S (Ca. Mg. K. Na) (me/100g)	CEC (me/100g)	TS (%)
			Fine	Coarse																		
NIGERIA	**0 - 20**	12.33	1.69	1.11	13.79	71.1	5.47	4.31	1.57	0.91	0.65	13.93	125	2.9	1.54	0.37	0.09	0.03	0.04	2.04	2.34	86.88
	20 - 70	14.3	1.89	1.17	13.46	69.19	4.95	4.12	0.74	0.43	0.29	14.84	122.5	1.7	0.5	0.16	0.05	0.04	0.41	0.74	1.53	49.11
	70 - 95	21.98	1.67	0.72	11.27	64.37	4.78	4.08	0.52	0.3	0.23	13.24	145	1.2	0.27	0.08	0.04	0.04	0.67	0.43	1.5	27.39
	95-150	25.32	1.59	1.12	12.71	59.28	4.65	4.01	0.39	0.23	0.2	11.51	147.5	1.1	0.19	0.06	0.04	0.03	0.88	0.32	1.59	19.5

N: Nitrogen, C: Carbon, P: Phosphorus, Al: Aluminium, Na: Sodium, Ca: Calcium, Mg: Magnesium, S: Base ion (cation) sum, CEC: Cation exchange capacity, TS: Saturation rate, pHco: pH cobalt (Soil acidity assessed using the cobaltihexamine method)

Table 2. Genetic characteristics, varieties, origins of the parents of oil palm progenies, leaflet nutrient concentrations and yield characteristics of the tested progenies (PIC, 2011)

Progenies	C1	C2	C3	C4
Dura (Female parent)	PO 2630 D	PO 3174 D	PO 3174 D	PO 4953 D
Dura origins	DA 10D x DA 3 D	DA 115 D AF	DA 115 D AF	Unknown
Pisifera (Male parent)	PO 2766 P	PO 2973 P	PO 4747 P	PO 4260 P
Pisifera origins	LM 10 T AF	LM 5 T x LM 10 T	LM 5 T AF	LM 238 T x LM 511 P
Genetic origins	D x L	D x L	D x L	D x Y
K uptake efficiency (kg of K palm^{-1})	3.35	3.81	3.86	3.31
Mg uptake efficiency (kg of Mg palm^{-1})	0.42	0.46	0.54	0.45
Average bunch numbers produced per palm	14.4 a	14.3 a	13.6 b	11.4 c
FFB Yield (Mg ha^{-1} y^{-1})	13.10 c	14.20 b	15.80 a	12.20 d
CPO_{mill} yield (Mg ha^{-1} y^{-1})	3.60 c	3.95 b	4.41 a	3.23 d

D x L: *Deli* x *La Mé*; D x Y: *Deli* x *Yangambi*. The last letter after the PO number (e.g., PO 2630 D or PO 2766 P or LM 10 T) indicates the main varietal group: P = *Pisifera*, D = *Dura*, and T = *Tenera*; Progenies C1, C2, C3 and C4 are all *Tenera* crosses (between a *Dura* and a *Pisifera* variety); Data in the *Dura* and *Pisifera* columns show the genetic material from which female inflorescences and male inflorescences (pollen) were used to obtain the progenies. AF refers to self-pollinated trees (e.g., LM 10 T AF = LM 10 T x LM 10 T); FFB: Fresh Fruit Bunch; CPO_{mill} : crude palm oil in the mill; Bunch number, FFB and CPO yields are average data from 5 to 8 years after planting (YAP).

a, b, c and d indicate the differences in parameters among progenies revealed by the Tukey test

Table 3. Fertilizer application scheme in Nigeria (in g of fertilizer per palm)

Years after planting	Months	Quantities of applied fertilizers												Equivalent in g per palm of nutrients									
		Basal dressing fertilizer					Treatment fertilization							Basal dressing fertilization					Experimental treatment fertilization					
		NPK (3 x 15)	borax	Kieserite	Urea	TSP	K (KCl)			Mg (kieserite)			NaCl						K_2O (60%)			MgO (27%)		
							K 0	K 1	K 2	Mg 0	Mg 1	Mg 2	K0	N (34%)	P_2O_5 (50%)	K_2O (60%)	MgO (27%)	B_2O_3 (11%)	K0	K1	K2	Mg0	Mg1	Mg2
	June	500	0	0	0	0	0	0	0	0	0	0	0	75	75	75	0	0	0	0	0	0	0
1	July	0	10	150	0	0	0	0	0	0	0	0	0	0	0	0	40.5	1.1	0	0	0	0	0	0
	October	750	0	0	0	0	0	0	0	0	0	0	0	112.5	112.5	112.5	0	0	0	0	0	0	0	0
	April	0	20	0	500	0	0	0	0	0	0	0	0	170	0	0	0	2.2	0	0	0	0	0	0
2	May	0	0	0	0	500	0	200	400	0	150	300	0	0	250	0	0	0	0	120	240	0	40.5	81
	October	0	0	0	500	0	0	300	600	0	0	0	0	170	0	0	0	0	0	180	360	0	0	0
3	May	0	20	0	0	0	0	400	800	0	300	600	0	0	0	0	0	2.2	0	240	480	0	81	162
	October	0	0	0	0	0	0	600	1200	0	0	0	0	0	0	0	0	0	0	360	720	0	0	0
4	May	0	50	0	0	0	0	1500	3000	0	500	1000	500	0	0	0	0	5.5	0	900	1800	0	135	270
	March	0	0	0	0	0	0	1500	3000	0	0	0	0	0	0	0	0	0	0	900	1800	0	0	0
5	April	0	0	0	0	0	0	0	0	0	500	1000	0	0	0	0	0	0	0	0	0	0	135	270
	October	0	0	0	0	0	0	0	0	0	0	0	1000	0	0	0	0	0	0	0	0	0	0	0
	March	0	0	0	0	0	0	1500	3000	0	0	0	0	0	0	0	0	0	0	900	1800	0	0	0
6	May	0	0	0	0	0	0	0	0	0	500	1000	500	0	0	0	0	0	0	0	0	0	135	270
	October	0	0	0	0	0	0	0	0	0	250	500	500	0	0	0	0	0	0	0	0	0	67.5	135
7	May	0	0	0	0	0	0	1500	3000	0	0	0	0	0	0	0	0	0	0	900	1800	0	0	0
	October	0	0	0	0	0	0	0	0	0	750	1500	0	0	0	0	0	0	0	0	0	0	202.5	405
8	March	0	0	0	0	0	0	1500	3000	0	0	0	0	0	0	0	0	0	0	900	1800	0	0	0
	October	0	0	0	0	0	0	0	0	0	750	1500	0	0	0	0	0	0	0	0	0	0	202.5	405
TOTAL		1250	100	150	1000	500	0	9000	18000	0	3700	7400	2500	527.5	437.5	187.5	40.5	11	0	5400	10800	0	999	1998

Table 4. Oil palm progenies discrimination against root traits that could explain mineral uptake efficiency in the sampling position Z3H1

Progenies	RF Diam (mm)	RF Biom (Mg ha^{-1})	RF Surf (m^2 ha^{-1})	RF Leng (km ha^{-1})	RF Vol (dm^3 ha^{-1})	RF SRL (mg^{-1})
C1	0.69^b	0.089^a	1431.82^a	839.77^a	238.64^a	8.48^a
C2	0.70^b	0.221^a	3548.39^a	2096.07^a	586.34^a	8.66^a
C3	0.71^b	0.092^a	1440.60^a	832.78^a	244.38^a	8.46^a
C4	0.79^a	0.164^a	2330.85^a	1155.49^a	458.27^a	6.86^b
R^2	***0.347***	***0.076***	***0.070***	***0.068***	***0.074***	***0.237***
R^2 adjusted	***0.312***	***0.027***	***0.020***	***0.018***	***0.025***	***0.196***
P	***<0.001***	***0.215***	***0.254***	***0.266***	***0.225***	***0.002***

RF= fine roots, Diam = Diameter, Biom = Biomass, Surf = Surface, Leng= Length, Vol = Volume, SRL: specific root length, P: probability, R^2: coefficient of determination, R^2 adjusted: adjusted coefficient of determination. The letters show significant differences between progenies according to the different root traits.
Differences between progenies were at 5% level ($p < 0.05$, Tukey test, $n = 60$).