

Potassium efficiency in elite oil palm progenies: Growth, anatomical, and biochemical insights

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ABSTRACT

Potassium (K) serves as a vital macronutrient determining oil palm (*Elaeis guineensis* Jacq.) yield. This research aimed to determine K uptake and use efficiency levels across eight oil palm progenies (Yangambi, DP Avros, DP Langkat, PPKS 239, Simalungun, PPKS 718, PPKS 540, and Dumpy) under K fertilized (K1) and K-omission (K0) conditions, while identifying metabolite compounds and root anatomical properties beneficial for exploratory studies of K absorption and utilization efficiency. Conducted over 24 mo in Yogyakarta Province, Indonesia, using a randomized complete block design factorial with five blocks, the study monitored dry weight, K metrics, anatomical traits, and biochemical profiles. Significant progeny variation occurred 48 wk after planting (WAP) for dry weight, K content, K uptake, K uptake efficiency, and K use efficiency. Cluster analysis classified Yangambi and Simalungun as K-efficient progenies, whereas PPKS 239 was less efficient. During the immature crop stage (96 WAP), shoot dry weight and shoot K content differed significantly among progenies, while root morphology, K uptake efficiency, and K use efficiency showed nonsignificant progeny effects. Leaf sucrose concentration was highest in Yangambi under K fertilization (1.70% w/w) and lowest in Simalungun under K fertilization (0.12% w/w), while root xylem vessel diameter was greatest in PPKS 239 under K deficiency (75.04 μ m) and smallest in Simalungun under K deficiency (34.51 μ m). These findings suggest that leaf sucrose concentration and root xylem vessel diameter may be useful traits for exploratory studies of K uptake and K use efficiency in oil palm progenies.

Key words: *Elaeis guineensis*, fertilizer, leaf succinate, leaf sucrose, oil palm progeny, potassium efficiency.

INTRODUCTION

Oil palm (*Elaeis guineensis* Jacq.) is the primary commodity for vegetable oil production in the world. Its products can be utilized for both food and energy purposes (Cui et al., 2020; Nurwahyuni and Putra, 2020). The need for palm oil continues to increase over time. Consequently, the expansion of oil palm plantations accelerates over the years in pursuit of higher production to meet market needs (Gafur and Putra, 2019; Alam et al., 2020; Irawan and Putra, 2020). The increase of oil palm plantations in Indonesia is evident, with the total cultivated area reaching 17.3 million hectares by 2022 (Palm Oil Magazine, 2024).

The expansion in oil palm plantations has led to increased demand for production inputs, particularly fertilizer, which serves as the main input in the oil palm production process. Fertilizer is applied to meet the essential nutrient needs of oil palm (Riyadi et al., 2020; Putra et al., 2021; 2022). One of the essential macronutrients that determines oil palm yield is K. As a fruit-bearing crop subsequently processed into

oil, K is the main nutrient required by the oil palm to promote fruit development. Its K demand is comparable to that of N (Irawan and Putra, 2020).

Potassium is involved in many crop metabolic processes. The benefits of K for oil palms are primarily functional rather than structural; for instance, K acts as an enzyme activator controlling oil palms' metabolic activities (Mirande-Ney et al., 2020; Akhtar et al., 2022; Gomides et al., 2023). In addition, K is also essential for maintaining gas exchange activities in leaf stomata. The supply of CO₂ from the atmosphere into leaf mesophyll is largely determined by K content by inducing leaf stomata opening. Plants with sufficient K content exhibit greater CO₂ assimilation, attributed to higher stomatal conductance. Wider stomatal opening allows gas exchange to occur more smoothly, contributing to an adequate CO₂ supply in leaf mesophyll (Mohapatra et al., 2023). Potassium is also heavily involved in transporting assimilates from leaves to all parts of crops (Azzawi et al., 2021; He et al., 2022; Yin et al., 2023).

Despite being the most demanded fertilizer in crop production systems, K fertilizer is a non-renewable natural resource. Its availability is often limited in agricultural areas (Oliver et al., 2022). While stocks of K fertilizer are available, farmers may not necessarily be able to access them due to the high price (Swoboda et al., 2022; Basak et al., 2023). Considering the limited availability of K fertilizer, it is imperative to evaluate the efficiency of K uptake and use in oil palm progenies. Currently, numerous oil palm progenies are available; however, information focusing on the efficiency of K uptake and use for each progeny remains limited. Moreover, previous studies have mainly focused on fertilizer management, mineral nutrient status, or general metabolic responses under K deficiency.

Limited information is available regarding the comparative physiological responses of elite oil palm progenies differing in K uptake and utilization efficiency, particularly in relation to anatomical and biochemical characteristics associated with K efficiency. Several anatomical characteristics of organs that are thought to be related to the efficient uptake and utilization of K are the length, width, and density of leaf stomata, and the diameter of root xylem and phloem (White et al., 2021). Therefore, this study was designed to address the knowledge gap about oil palm K efficiency especially regarding the integration of K uptake and utilization efficiency evaluation with targeted anatomical and biochemical characterization of contrasting oil palm progenies under K-deficient and K-sufficient conditions. This study specifically explores the association of root xylem anatomical traits and leaf organic compound accumulation with K efficiency in oil palm seedlings, providing preliminary physiological insights into traits associated with efficient K utilization in elite oil palm progenies. This research aims to determine the efficiency levels of K uptake and K use of oil palm progenies, and determine metabolite compounds and anatomical properties of roots that can be beneficial for exploratory study of efficiency in absorbing and utilizing K in oil palm progenies. Understanding variation in K uptake and use efficiency among oil palm progenies is important for improving nutrient-use efficiency through progeny evaluation and breeding. Identifying progenies with contrasting K-efficiency characteristics may provide a basis for further selection of planting materials with improved nutrient-use traits, while characterization of associated physiological, anatomical, and biochemical traits may help elucidate the mechanisms underlying differences in K efficiency. Such information could support breeders and researchers in developing and evaluating oil palm genetic materials with improved K-use characteristics and may contribute to the development of more efficient nutrient management strategies in oil palm production.

MATERIALS AND METHODS

Experimental design

The study employed a randomized complete block design (RCBD) factorial with five replicates. Treatments consisted of K fertilization (K1 = optimal K treatment; K0 = K-omission treatment) and eight oil palm (*Elaeis guineensis* Jacq.) progenies (Yangambi, DP Avros, DP Langkat, PPKS 239, Simalungun, PPKS 718, PPKS 540, Dumpy). Optimal K referred to stage-specific dosages (Table 1), while K0 received no fertilizer. The experiment covered three stages: Pre-nursery (1-15 wk after planting, WAP), main nursery (16-48 WAP), and immature crop simulation (49-96 WAP). At 16 WAP, seedlings were transplanted into 40 × 40 cm polybags filled with red-yellow podzolic soil, arranged at 90 cm spacing, and maintained until 96 WAP. The polybags were filled with disturbed soil collected from the surface horizon of a Podzol soil profile at a depth of 0-20

cm. The collected soil was homogenized before being used to fill the polybags. The initial experimental population comprised 320 seedlings (2 K levels × 8 progenies × 5 blocks × 4 seedlings). At 48 WAP, 80 seedlings were destructively sampled for determination of dry weight and K-efficiency parameters (Figure 1). The remaining seedlings were maintained until 96 WAP. At 96 WAP, surviving seedlings were evaluated for K content in the root, leaf, and stem. After excluding dead or abnormal seedlings, 48 seedlings were used for whole-plant analysis, including determination of dry weight, K content, and root morphological traits. The K-content data from these 48 seedlings were subjected to cluster analysis to classify the materials into three K-efficiency groups (inefficient, moderately efficient, and efficient) (Figure 2). Based on the resulting cluster classification, three progenies representing contrasting K-efficiency groups were selected for subsequent anatomical and biochemical analyses. A separate set of 54 seedlings from these three selected progenies was then sampled for composite analysis. Three seedlings were combined to form one composite sample, resulting in 18 composite samples for root anatomical and leaf biochemical analyses. Maintenance included daily irrigation (0.5 L polybag⁻¹), fertilizer application 5 cm from the stem base (Table 1), weekly manual weeding, and pest and disease control. For disease control, mancozeb 80% WP (Dithane M-45 80 WP; PT Dow AgroSciences Indonesia, Jakarta, Indonesia) was applied at 2 g L⁻¹. For insect pest control, deltamethrin 25 g L⁻¹ EC (Decis 25 EC; PT Bayer Indonesia, Jakarta, Indonesia) was applied at 0.5 mL L⁻¹. Seedlings were sampled at 48 and 96 WAP. At 48 WAP, samples were oven-dried to constant weight for DM measurement.

Table 1. Application schedule and dosage of urea, KCl, SP-36, and kieserite. WAP: Weeks after planting. Urea (46% N), SP-36 (36% P₂O₅), potassium chloride (KCl; 60% K₂O), kieserite (27% MgO and 22% S), and NPK 12:12:17 (12% N, 12% P₂O₅, and 17% K₂O).

Seedling age (WAP)	Urea dosage	SP-36 dosage	KCl dosage	Kieserite	NPK 12:12:17
	g seedling ⁻¹	g seedling ⁻¹	g seedling ⁻¹	g seedling ⁻¹	g seedling ⁻¹
16	2.0	2.0	0.50	0	0
18	2.5	3.0	0.75	0	0
22	3.5	4.0	1.00	0	0
26	3.5	4.0	2.85	0	0
28	3.5	4.0	2.85	5.0	0
30	3.5	4.0	2.85	0	0
32	3.5	4.0	2.85	5.0	0
34	5.0	6.5	4.25	0	0
36	5.0	6.5	4.25	7.5	0
38	5.0	6.5	4.25	0	0
40, 42, 44, 46, 48	5.0	6.5	4.25	7.5	0
52	100	0	0	0	0
60	0	0	0	0	750
68	0	0	0	0	500
80	0	0	0	0	1250
96	0	0	0	0	750

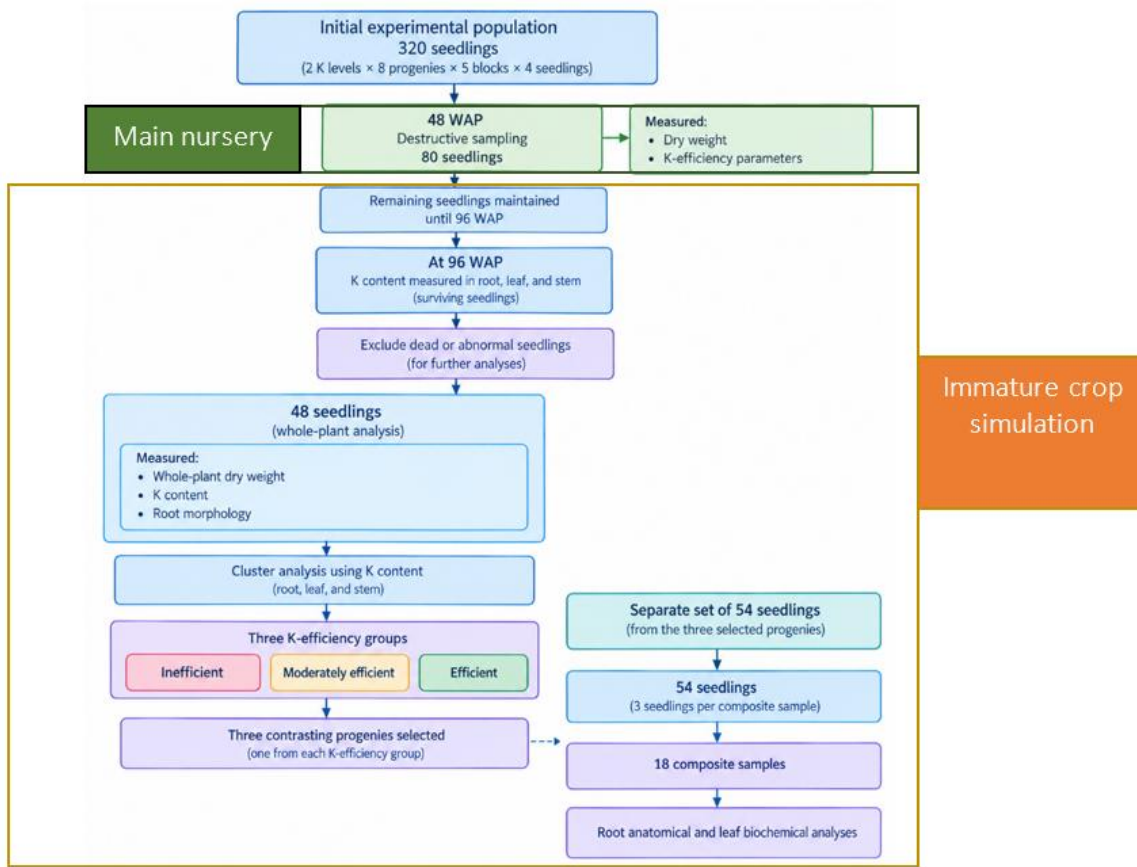


Figure 1. Potassium dynamics study workflow.

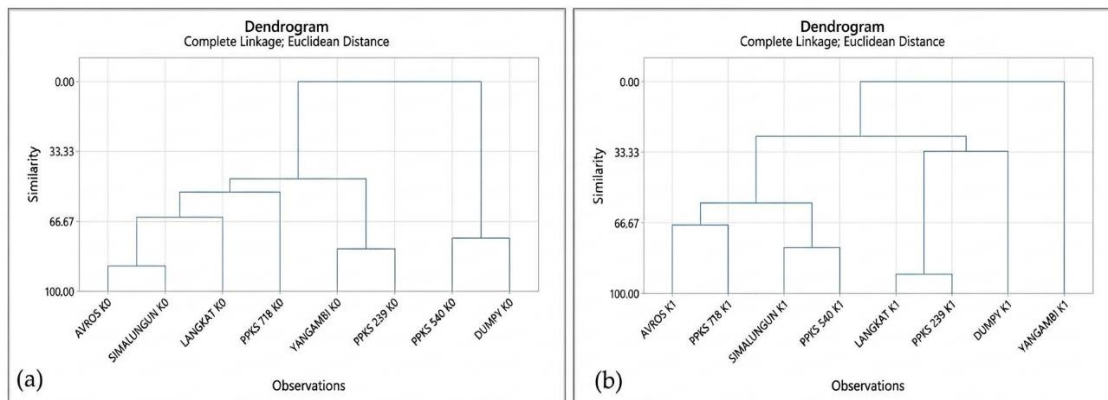


Figure 2. Cluster analysis based on K uptake for each progeny in both treatments (K-omission treatment (a); K1: optimal fertilization treatment (b)).

Root morphology analysis

Root morphological traits were measured at 96 WAP using digital image analysis and gravimetric methods. Fresh root samples were carefully washed under running water to remove adhering soil particles without damaging fine roots. Clean roots were spread uniformly in a transparent tray containing a thin layer of water to minimize overlap and scanned using a digital camera system. Images were analysed using Image Raster 3.0 software (PT Miconos, Yogyakarta, Indonesia) to determine root length (cm) and root surface area (cm²). Root

length was calculated as the total length of all visible root segments in the scanned image, while root surface area was estimated based on pixel-derived measurements calibrated against a known scale. Root volume (cm³) was determined using the gravimetric (water displacement) method (Burdett, 1979). Fresh roots were completely submerged in a graduated cylinder containing a known volume of water. The root system was held fully below the water surface using glass rod without compressing the roots, and the increase in water volume was recorded as root volume.

Potassium content analysis

Potassium content in oil palm seedlings was analysed following the standard procedure described by Eviati et al. (2023). Potassium content analysis was conducted twice, at the main nursery stage (48 WAP) and immature crop stage (96 WAP), each of which used different number of samples. The number of samples used for 48 WAP and 96 WAP stage was 80 and 48 samples, respectively. Plant samples consisting of roots, stems, and leaves were oven-dried until constant weight was achieved and subsequently ground into fine powder. Approximately 0.5 g dried and finely ground sample (< 0.5 mm) was transferred into a digestion tube, followed by the addition of 5 mL HNO₃ (65%, p.a.) and 0.5 mL HClO₄ (60%, p.a.) The mixture was allowed to stand overnight for predigestion. Digestion was then performed using a block digester at 100 °C for 1.5 h, followed by 130 °C for 1 h, 150 °C for 2.5 h, 170 °C for 1 h, and finally 200 °C for 1 h until white fumes appeared and approximately 0.5 mL clear digest remained. The digest was cooled and diluted to 50 mL with deionized water and homogenized. Potassium concentration in the extract was determined by atomic absorption spectrophotometry (AAS; AA-7000, Shimadzu Corporation, Kyoto, Japan) using a K calibration curve, and the results were expressed as percentage (%). The next steps involved the calculation of K uptake (1) and use efficiency (2) of each oil palm progeny using the following formula modified from Dobermann (2007) using the obtained K content from laboratory analysis:

$$KUPTEF = \frac{UOK}{UUK \times AKF} \quad (1)$$

$$KUE = \frac{DWOK \times UUK}{DWUK \times UOK} \quad (2)$$

where, KUPTEF is K uptake efficiency, UOK is K uptake in seedlings fertilized with optimal, UUK is K uptake in seedlings under K-omission treatment, AKF is the amount of K fertilizer applied to each seedling, KUE is K use efficiency, DWOK is dry weight of seedlings fertilized with optimal K, DWUK is dry weight of seedlings under K-omission treatment.

Sucrose and succinate analysis

Biochemical analysis of leaf sucrose and succinate content was conducted at 96 WAP using 18 composite samples from 54 progenies. Sucrose was determined by the Luff-Schoorl method (Dekker, 1950), 500 mg fresh leaf were homogenized, extracted with distilled water, filtered, and adjusted to volume. An aliquot was reacted with Luff-Schoorl reagent, boiled, cooled, then treated with KI and H₂SO₄; liberated iodine was titrated with Na₂S₂O₃ using starch as indicator, and sucrose concentration was expressed as % w/w. Succinate was analysed at LPPT-UGM (Integrated Research and Testing Laboratory at Universitas Gadjah Mada) using HPLC (KNAUER Wissenschaftliche Geräte GmbH, Berlin, Germany) (Magalhães et al., 2024). A total of 500 mg leaf was extracted with LC-grade distilled water through sonication (30 min), vortexing (30 s), and centrifugation (5 min), repeated three times, combined to 10 mL, and filtered (0.45 µm). The extract was injected (50 µL) into a HiPlex Hplus column with variable wavelength detector (VWD)/UV detection at 210 nm, mobile phase 0.005 N H₂SO₄, retention time 20 min. Succinate standards (10-200 mg L⁻¹) were prepared from a 10 000 µg mL⁻¹ stock and injected at 20 µL. Results were expressed as mg kg⁻¹ sample.

Anatomical analysis

At 96 WAP, 18 composite samples from 54 progenies were analysed for leaf stomatal traits (length, width, density) and root xylem and phloem diameter. Stomatal characterization followed Indradewa et al. (2002). Fully expanded leaves were cleaned, coated with transparent nail polish on the abaxial surface, dried, and imprinted using adhesive tape. The replicas were mounted on glass slides and examined under a light microscope at 40X total magnification to measure stomatal dimensions, meanwhile the stomatal density was calculated as stomata per unit area. Root anatomy was prepared according to Ruzin (1999). Fresh roots were washed, sectioned, and fixed in formalin-acetic acid-alcohol (FAA) solution, then dehydrated through graded ethanol,

embedded in paraffin, and sectioned with a microtome. Sections were stained with safranin, mounted on slides, and observed under a light microscope at 40X total magnification. Images were captured using a digital microscope camera with OptiLab Viewer Advance 2 software (PT Miconos, Yogyakarta, Indonesia), and xylem and phloem diameters were measured using Image Raster 3 software (PT Miconos, Yogyakarta, Indonesia).

Data analysis

All data were analysed using two-way ANOVA at the 5% confidence level, except K use efficiency and K uptake efficiency, which were assessed with one-way ANOVA. Further significance testing was conducted using the least significant differences (LSD) method at the 5% level, provided that a significant effect among treatments was obtained. Cluster analysis to determine oil palm progenies for anatomical and biochemical identification was conducted using Minitab version 21.4 (Minitab, State College, Pennsylvania, USA). Meanwhile, the relationship between plant dry weight, K uptake, K uptake efficiency, and K use efficiency was analysed using Pearson correlation. ANOVA and Pearson correlation analyses were performed using the *agricolae* and *corrplot* package in Rstudio version 2025.05.1.

RESULTS AND DISCUSSION

Dry weight and K efficiency of oil palm progenies in main nursery stage

Oil palm progenies differed significantly in seedling dry weight, total K content, K uptake, K uptake efficiency, and K use efficiency (Figure 3). Across both K fertilization treatments, 'Simalungun' and 'Yangambi' consistently exhibited greater dry weight, higher total K content, and higher K uptake than the other progenies. These results indicate that 'Simalungun' and 'Yangambi' possessed a superior capacity to acquire and utilize K during the main nursery stage. Potassium is an essential macronutrient involved in numerous physiological and metabolic processes, including enzyme activation, assimilate transport, osmoregulation, and stomatal regulation (Akhtar et al., 2022; Mohapatra et al., 2023). Consequently, progenies with a greater capacity to acquire K are expected to maintain better growth and biomass accumulation than progenies with lower K acquisition capacity. The higher seedling dry weight observed in 'Simalungun' and 'Yangambi' was accompanied by greater total K content and K uptake, indicating a stronger ability to obtain K from the growing medium. Similar variation in K status among oil palm progenies has previously been reported, suggesting that nutrient acquisition and utilization characteristics differ among genetic backgrounds (Dassou et al., 2022; Mohapatra et al., 2023). Differences in K uptake among progenies were also reflected in K uptake efficiency and K use efficiency. 'Simalungun' and 'Yangambi' exhibited higher efficiencies than the other progenies, suggesting a greater ability to utilize available K for biomass production. Potassium-use efficiency has been widely recognized as an important determinant of plant growth because K is involved in C assimilation, assimilate translocation, and water-use regulation, all of which contribute to biomass accumulation (Ramírez-Builes and Küsters, 2021; Akhtar et al., 2022). Similar relationships between K availability, K-use efficiency, and plant growth have been reported in several crop species. In barley (*Hordeum vulgare* L.), Azzawi et al. (2021) found that K availability strongly affected yield components, including spike number, grain number, and grain weight, among different barley genotypes. In a long-term maize (*Zea mays* L.)-wheat (*Triticum aestivum* L.) rotation, He et al. (2022) reported that appropriate K fertilization increased maize and wheat yields and influenced K-use and K-recovery efficiencies. Likewise, Yin et al. (2023) demonstrated that K application improved K utilization efficiency and yield in foxtail millet (*Setaria italica* L.). These findings across barley, maize, wheat, and foxtail millet support the importance of K acquisition and utilization in maintaining biomass production and yield, while the present study extends this relationship to variation in K efficiency among oil palm progenies. The consistently superior performance of 'Simalungun' and 'Yangambi' across dry weight, total K content, K uptake, K uptake efficiency, and K use efficiency indicates that these progenies possessed greater K efficiency than the other tested progenies under the conditions of this study (Figure 3). In contrast, 'PPKS 239' generally exhibited lower values for these parameters, suggesting lower efficiency in acquiring and utilizing K. These findings demonstrate substantial variation in K efficiency among oil palm progenies and highlight the potential for selecting progenies with improved nutrient-use efficiency for sustainable oil palm cultivation (Woittiez et al., 2019).

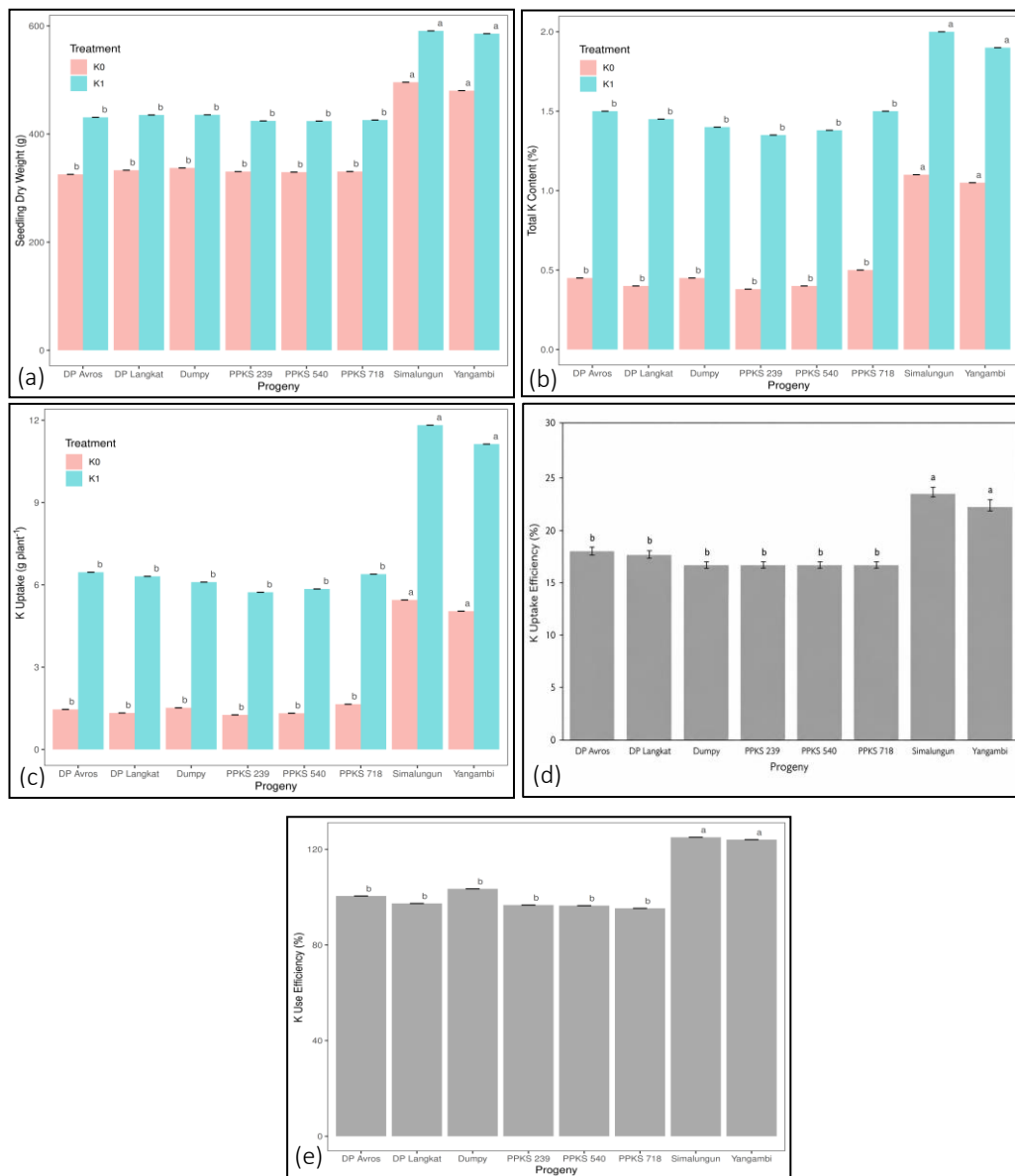


Figure 3. Seedling dry weight (a), total K content (b), K uptake (c), K uptake efficiency (d), and K use efficiency (e) of several oil palm progenies at 48 wk after planting when fertilized with optimal K (K1) and K-omission treatment (K0). Means in K0 or K1 followed by the same letters were not significantly different based on the LSD test ($P < 0.05$). Each bar represents the average values $\pm$ SE.

Dry weight and K efficiency of oil palm progenies in immature crop stage

Dry weight accumulation during the immature crop stage varied among oil palm progenies. Shoot dry weight was significantly affected by progeny, whereas root dry weight was not influenced by progeny, K fertilization, or their interaction (Table 2). Several progenies, particularly ‘Dumpy’, ‘PPKS 540’, ‘DP Avros’, and ‘Simalungun’, produced greater shoot biomass than ‘Yangambi’, ‘DP Langkat’, and ‘PPKS 239’. These findings indicate the existence of genetic variation in growth performance among oil palm progenies during the main nursery stage. Similar differences among oil palm genetic materials have previously been reported and are attributed to inherent variation in growth potential and nutrient utilization characteristics among progenies (Dassou et al.,

2022). Biomass accumulation is an important indicator of seedling vigour because it reflects the overall capacity of plants to convert available resources into vegetative growth. Potassium is involved in numerous physiological and metabolic processes associated with plant growth, including enzyme activation, assimilate translocation, osmotic regulation, and stomatal regulation (Akhtar et al., 2022; Mohapatra et al., 2023). However, K fertilization did not significantly affect root or shoot dry weight during the immature crop stage. This result indicates that differences in biomass accumulation among progenies were more pronounced than differences resulting from K fertilization under the conditions of the present study.

Table 2. Dry weight, K content, and K uptake of oil palm in immature crop stage (96 wk after planting). K0: K-omission treatment; K1: optimal fertilization treatment. Different letters in the column indicate significant differences according to least significant difference test ($P \leq 0.05$); CV: Coefficient of variation; ^{ns}nonsignificant; * $P \leq 0.05$; ** $P \leq 0.01$.

Progeny	K fertilization	Root dry weight	Shoot dry weight	Root K content	Shoot K content	Root K uptake	Shoot K uptake
		g	g	%	%	g plant ⁻¹	g plant ⁻¹
DP Avros	K0	11.13	49.56	1.86	2.88	20.76	142.49
	K1	9.72	51.04	1.58	3.07	15.61	157.68
Dumpy	K0	11.68	64.54	1.95	2.71	22.60	177.80
	K1	12.69	51.15	1.86	3.34	23.20	163.74
Yangambi	K0	8.89	33.57	1.66	3.20	15.71	102.66
	K1	6.89	27.48	1.86	4.01	12.91	99.93
Simalungun	K0	10.83	46.34	1.88	2.64	20.61	125.34
	K1	9.567	53.38	1.56	2.87	14.67	145.05
DP Langkat	K0	10.14	31.39	2.08	3.25	20.78	100.90
	K1	10.51	37.86	2.32	3.50	23.41	120.37
PPKS 239	K0	8.40	28.23	1.62	3.56	14.33	87.43
	K1	10.13	30.05	2.08	3.98	22.24	119.73
PPKS 718	K0	9.64	45.24	1.71	3.39	16.74	153.89
	K1	10.71	41.90	1.8	3.42	19.95	140.88
PPKS 540	K0	12.70	55.15	2.04	3.40	26.41	187.98
	K1	8.77	43.57	1.84	3.59	16.34	161.35
Block		0.0011**	0.0137*	0.8575 ^{ns}	0.0423*	0.0286 ^{ns}	0.0302*
Progeny		0.1441 ^{ns}	0.0181*	0.4730 ^{ns}	0.0324*	0.2443 ^{ns}	0.0618 ^{ns}
K fertilization		0.7026 ^{ns}	0.8708 ^{ns}	0.9658 ^{ns}	0.0358*	0.7613 ^{ns}	0.4799 ^{ns}
Progeny × K fertilization		0.7667 ^{ns}	0.9576 ^{ns}	0.5293 ^{ns}	0.9505 ^{ns}	0.5448 ^{ns}	0.9437 ^{ns}
CV, %		14.18	11.87	33.56	13.45	15.07	8.01

In contrast to biomass accumulation, K uptake efficiency and K use efficiency did not differ significantly among progenies (Table 3). K use efficiency in this study reflected the relative K utilization index expressed in percentage and not as fertilizer recovery. Therefore, the values ranged from below 100% to above 100% indicating that the biomass production per unit absorbed K was higher in the optimal-K treatment than in the omission treatment (White et al., 2021). Root K uptake efficiency, shoot K uptake efficiency, root K use efficiency, and shoot K use efficiency all showed nonsignificant progeny effects. Although numerical variation was observed among progenies, the differences were insufficient to distinguish progenies statistically. These findings suggest that the tested progenies exhibited relatively similar capacities to absorb and utilize K during the immature crop stage. Similar observations have been reported in other crops, where variation in plant growth was not always accompanied by significant differences in nutrient-use efficiency (Azzawi et al., 2021; He et al., 2022; Yin et al., 2023). Collectively, the results indicate that variation among progenies was more clearly expressed in shoot biomass accumulation than in K efficiency traits. While progenies differed in their capacity to accumulate DM, K uptake efficiency and K use efficiency remained relatively stable among the tested genetic materials. Therefore, shoot dry weight was a more sensitive parameter for distinguishing progeny performance than K efficiency traits during the immature crop stage.

Table 3. Potassium uptake efficiency and K use efficiency of oil palm progenies in immature crop stage (96 wk after planting). K-omission treatment; K1: optimal fertilization treatment. Different letters in the column indicate significant differences according to least significant difference test ($P \leq 0.05$); CV: Coefficient of variation; ^{ns}Nonsignificant.

Progeny	Root K uptake efficiency	Shoot K uptake efficiency	Root K use efficiency	Shoot K use efficiency
	%	%	%	%
DP Avros	17.47	26.46	118.72	93.85
Dumpy	28.15	24.25	104.39	82.49
Yangambi	23.73	28.26	92.33	81.95
Simalungun	18.38	30.89	123.61	95.79
DP Langkat	27.03	27.94	93.31	97.05
PPKS 239	41.04	34.13	78.76	91.90
PPKS 718	27.07	26.91	94.11	102.46
PPKS 540	17.19	19.74	119.96	94.57
Block	0.9793 ^{ns}	0.2385 ^{ns}	0.79 ^{ns}	0.35 ^{ns}
Progeny	0.2226 ^{ns}	0.7838 ^{ns}	0.35 ^{ns}	0.94 ^{ns}
CV, %	14.46	12.71	24.51	24.56

Root morphological analysis of oil palm progenies in immature crop stage

Root length, root surface area, and root volume were not significantly affected by progeny, K fertilization, or their interaction (Table 4). These results indicate that the contrasting levels of K uptake and utilization efficiency observed among oil palm progenies were not accompanied by detectable differences in overall root morphological development. Similarly, K deficiency did not induce significant modifications in root length, root surface area, or root volume across the tested progenies.

Table 4. Root morphology of oil palm progenies in immature crop stage (96 wk after planting). K-omission treatment; K1: optimal fertilization treatment. Different letters in the column indicate significant differences according to least significant difference test ($P \leq 0.05$); CV: Coefficient of variation; ^{ns}nonsignificant; * $P \leq 0.05$.

Progeny	K fertilization	Root length	Root surface area	Root volume
		cm	cm ²	cm ³
DP Avros	K0	485.13	215.64	36.67
	K1	243.25	211.02	36.67
Dumpy	K0	463.09	192.17	40.00
	K1	587.70	207.73	53.33
Yangambi	K0	329.66	179.36	30.00
	K1	334.18	158.55	30.00
Simalungun	K0	436.60	236.56	43.33
	K1	434.03	183.48	36.67
DP Langkat	K0	479.41	220.74	36.67
	K1	499.47	243.19	40.00
PPKS 239	K0	381.04	114.28	33.33
	K1	488.90	169.29	40.00
PPKS 718	K0	418.72	236.34	36.67
	K1	463.95	243.95	40.00
PPKS 540	K0	577.98	260.46	43.33
	K1	407.12	190.83	33.33
Block		0.0329*	0.0987 ^{ns}	0.0771 ^{ns}
Progeny		0.1413 ^{ns}	0.1000 ^{ns}	0.4385 ^{ns}
K fertilization		0.9944 ^{ns}	0.7420 ^{ns}	0.5009 ^{ns}
Progeny × K fertilization		0.1588 ^{ns}	0.7126 ^{ns}	0.8496 ^{ns}
CV, %		5.83	7.33	10.61

Root morphological traits are generally considered important for nutrient acquisition because they influence the volume of soil explored by the root system (White, 2019). However, nutrient acquisition efficiency is a complex trait that is not always associated with variation in root size or morphology alone. In the present study, the absence of significant differences in root morphological traits among progenies suggests that root length, root surface area, and root volume were not the primary characteristics distinguishing K-efficient and K-inefficient progenies.

The lack of a significant response to K fertilization further indicates that these root morphological traits remained relatively stable under the experimental conditions (Table 4). Therefore, root length, root surface area, and root volume cannot be considered reliable indicators of K uptake and utilization efficiency in the tested oil palm progenies. Additional studies involving other root characteristics and nutrient acquisition traits are required to better understand the factors associated with K efficiency in oil palm.

Anatomical and biochemical analysis of oil palm progenies in immature crop stage

Anatomical and biochemical analyses were conducted on 'Yangambi', 'Simalungun', and 'PPKS 239', chosen as representative progenies from contrasting K-efficiency groups identified at the seedling stage. 'Yangambi' and 'Simalungun' represented K-efficient progenies, while 'PPKS 239' was K-inefficient (Figure 2). The aim was not to reassess K-efficiency at the immature crop stage, but to identify anatomical and biochemical traits associated with these groups (Tables 5 and 6). During the immature stage, root traits, including morphology, K uptake, uptake efficiency, and use efficiency, showed nonsignificant differences among progenies. Similarly, root K content was unaffected. In contrast, shoot dry weight and shoot K content varied significantly, suggesting stronger progeny effects in aboveground growth and K accumulation (Islam et al., 2025). However, these variables did not consistently separate efficient from inefficient groups, indicating that K-related trait expression may shift with developmental stage and growth conditions (Akhtar et al., 2022; Mohapatra et al., 2023).

Table 5. Leaf sucrose and succinate content of selected oil palm progenies in immature crop stage (96 wk after planting). K-omission treatment; K1: optimal fertilization treatment. Different letters in the column indicate significant differences according to least significant difference test ($P \leq 0.05$); CV: Coefficient of variation; ^{ns}nonsignificant; ** $P \leq 0.01$; *** $P \leq 0.001$.

Progeny	K fertilization	Leaf sucrose	Leaf succinate
		% w/w	mg kg ⁻¹
Yangambi	K0	0.78 ^c	710.48
	K1	1.70 ^a	1001.96
Simalungun	K0	0.80 ^c	1006.457
	K1	0.12 ^e	658.95
PPKS 239	K0	1.07 ^b	1944.153
	K1	0.48 ^d	791.99
Block		0.467 ^{ns}	0.1903 ^{ns}
Progeny		2.21×10^{-8} ^{***}	0.3843 ^{ns}
K fertilization		0.0079 ^{**}	0.3964 ^{ns}
Progeny × K fertilization		5.73×10^{-9} ^{***}	0.2701 ^{ns}
CV, %		9.06	7.71

Table 6. Anatomical characteristics of selected oil palm in immature crop stage (96 wk after planting). K-omission treatment; K1: optimal fertilization treatment. Different letters in the column indicate significant differences according to least significant difference test ($P \leq 0.05$); CV: Coefficient of Variation; ^{ns}nonsignificant; * $P \leq 0.05$.

Progeny	K fertilization	Stomatal density	Stomatal aperture	Stomatal length	Xylem vessel diameter	Phloem vessel diameter
		mm ²	μm	μm	μm	μm
Yangambi	K0	101.00	2.87	9.14	52.03 ^{ab}	10.72
	K1	121.33	2.10	9.43	35.20 ^b	11.53
Simalungun	K0	110.33	3.12	9.42	34.51 ^b	13.52
	K1	126.67	2.60	11.08	65.41 ^{ab}	16.07
PPKS 239	K0	120.33	3.65	11.37	75.04 ^a	15.81
	K1	125.00	2.52	9.27	56.59 ^{ab}	13.84
Block		0.241 ^{ns}	0.4138 ^{ns}	0.1597 ^{ns}	0.4155 ^{ns}	0.0496 [*]
Progeny		0.804 ^{ns}	0.3966 ^{ns}	0.3207 ^{ns}	0.0324 [*]	0.1448 ^{ns}
K fertilization		0.463 ^{ns}	0.0439 [*]	0.9374 ^{ns}	0.8109 ^{ns}	0.7759 ^{ns}
Progeny × K fertilization		0.795 ^{ns}	0.7719 ^{ns}	0.0738 ^{ns}	0.0106 [*]	0.5291 ^{ns}
CV, %		5.66	26.36	12.64	23.74	24.99

Biochemically, leaf sucrose concentration was significantly influenced by progeny, K fertilization, and their interaction. Under K deficiency, ‘Yangambi’ and ‘Simalungun’ accumulated lower sucrose (0.78%-0.80% w/w) than ‘PPKS 239’ (1.07% w/w) (Table 5). Leaf succinate concentration; however, was unaffected. This variation in sucrose suggests differences in carbohydrate partitioning among progenies, consistent with potassium’s role in phloem loading and assimilate transport (Azzawi et al., 2021; He et al., 2022; Yin et al., 2023). Nevertheless, sucrose accumulation appears more associated with progeny classification than a direct mechanism of K efficiency.

Most anatomical traits (stomatal density, length, phloem vessel diameter) did not differ among progenies (Table 6). Stomatal aperture was affected by K fertilization but not progeny. Root xylem vessel diameter; however, varied significantly with progeny and its interaction with K fertilization: Under deficiency, ‘PPKS 239’ had the largest diameter (75.04 μm), while ‘Yangambi’ (52.03 μm) and ‘Simalungun’ (34.51 μm) were smaller. This distinction aligned with their contrasting K-efficiency groups. Although xylem anatomy is linked to resource transport (Ragel et al., 2019; Ramírez-Builes and Küsters, 2021), the lack of significant differences in root K uptake and efficiency suggests these anatomical traits are associated characteristics rather than direct determinants. Correlation analysis revealed positive relationships among anatomical traits: Stomatal aperture with stomatal length ($r = 0.49$; $P \leq 0.05$) and xylem diameter ($r = 0.52$; $P \leq 0.05$), and phloem diameter with xylem diameter ($r = 0.58$; $P \leq 0.05$) (Figure 4). Although K taken up by roots is transported to the shoot through the vascular system, the present correlation analysis did not show a significant association between K uptake and the measured xylem or phloem vessel diameters. Root K uptake was strongly correlated with shoot K uptake ($r = 0.78$, $P < 0.001$), whereas correlations between root or shoot K uptake and xylem vessel diameter were weak ($r = 0.19$ and 0.07 , respectively). Correlations with phloem vessel diameter were also nonsignificant ($r = 0.22$ and 0.43 , respectively). Potassium acquisition and translocation involve multiple processes, including root absorptive capacity, membrane transport, transpiration-driven transport, vascular conductivity, and source-sink regulation (Britto et al., 2021). Recent experimental work also demonstrated that K uptake can vary according to environmental conditions and developmental timing (Ghani et al., 2026). Thus, the weak relationships between vessel diameter and K uptake in the present study may reflect the contribution of multiple physiological and anatomical processes that were not captured by vessel diameter alone. Leaf succinate concentration also lacked associations. Thus, while sucrose concentration and xylem diameter differentiated progenies, no single trait explained variation in K accumulation.

Overall, leaf sucrose concentration ($P \leq 0.001$) and root xylem vessel diameter ($P \leq 0.05$) most clearly distinguished ‘Yangambi’ and ‘Simalungun’ from ‘PPKS 239’. Yet, since these traits were not correlated with K uptake, they should be considered associated characteristics of contrasting K-efficiency groups rather than definitive indicators. Broader evaluation across more oil palm progenies is needed to confirm these relationships.

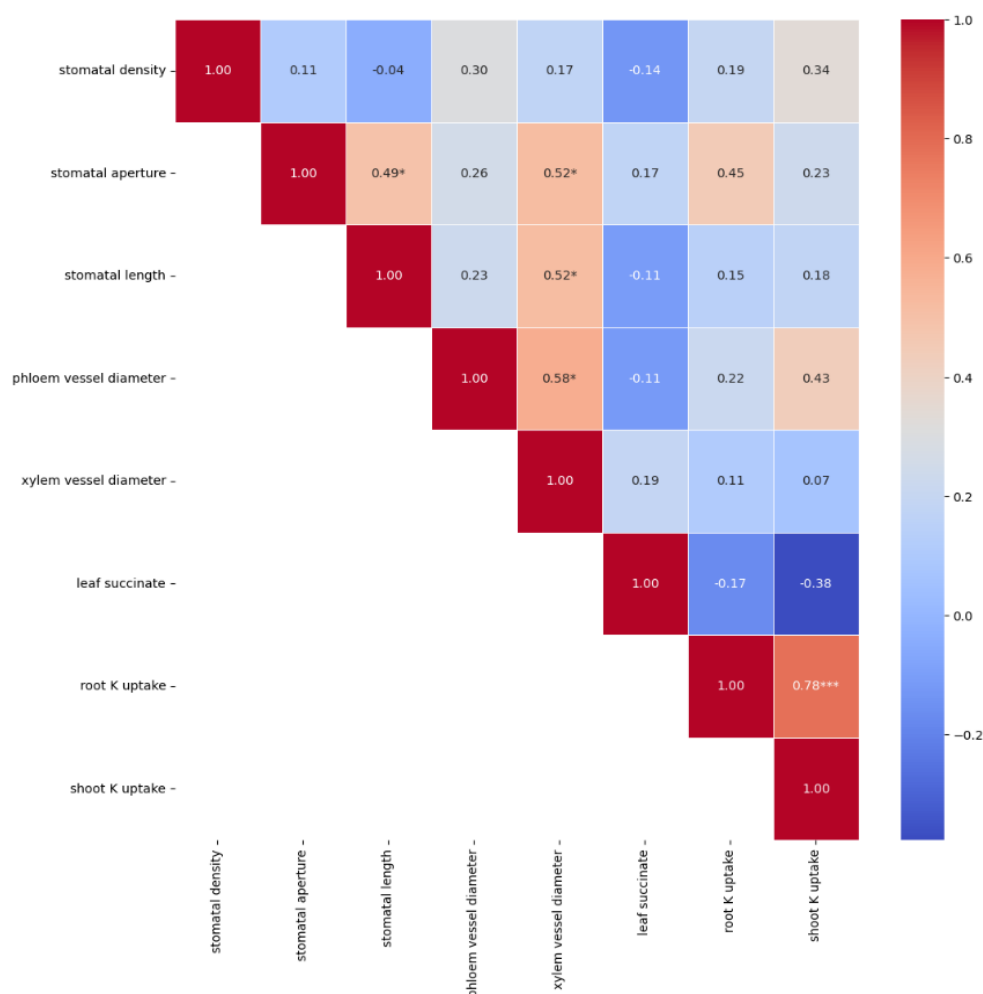


Figure 4. Relationship between anatomical, biochemical, and physiological characteristics of selected oil palm progenies. Positively related parameters are highlighted in red, while negatively related ones are highlighted in blue; * $P \leq 0.05$, *** $P \leq 0.001$.

CONCLUSIONS

Oil palm progenies exhibited variation in K uptake and K use efficiency. Based on dry weight, K content, K uptake, K uptake efficiency, and K use efficiency at the seedling stage, ‘Yangambi’ and ‘Simalungun’ were classified as K-efficient progenies. Among the biochemical and anatomical traits evaluated, leaf sucrose concentration and root xylem vessel diameter showed consistent differences between the efficient and less efficient progenies, while leaf succinate concentration, stomatal traits, phloem vessel diameter, and root morphology showed limited differentiation. These findings suggest that leaf sucrose concentration and root xylem vessel diameter may be useful traits for exploratory studies of K uptake and K use efficiency in oil palm progenies. However, further validation involving a larger number of progenies is required to confirm their applicability.

Author contribution

Conceptualization: E.T.S.P. Methodology: E.T.S.P. Validation: C.W. Formal analysis: B.S. Investigation: S.T.L. Writing-original draft: E.T.S.P. Writing-review and editing: B.S. Visualization: B.S. Supervision: D.I. All co-authors reviewed the final version and approved the manuscript before submission.

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