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Oil palm (*Elaeis guineensis* Jacq.) genetic differences in mineral nutrition: potassium and magnesium effects on morphological characteristics of four oil palm progenies in Nigeria (West Africa)☆

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Abstract – We compared four oil palm (*Elaeis guineensis* Jacq.) progenies' morphological growth characteristics to reveal genotypic differences in plant growth and assess their adaptability in Nigeria's environment in response to different levels of potassium chloride (KCl) and kieserite fertilizer applications. The studied progenies (C1, C2 and C3 of *Deli* × *La Mé* origin and C4 of *Deli* × *Yangambi* origin) represent a wide genetic diversity of oil palm and have shown among a population of 116 different progenies, a contrasting K and Mg leaflet concentrations that covered the extreme ranges of leaflet concentrations in these minerals. The trial consisted of a completely randomized split-plot factorial design with six replicates, where progenies, considered as sub-factor were treated with combinations of 3 levels of potassium chloride (0, 1.5, 3.0 kg of KCl palm^{-1} year^{-1}) and kieserite (0, 0.75, 1.5 kg of $MgSO_4$ palm^{-1} year^{-1}) fertilizers (main factor), respectively. Growth characteristics differed significantly among progenies, but not in all studied years. In all progenies, KCl treatments significantly increased the average annual collar girth increment and projected canopy area. Adding 3.0 kg palm^{-1} year^{-1} of KCl significantly increased the total leaf area of progeny C4. Kieserite applications did not have an effect on progenies' growth characteristics whereas potassium showed to be the main mineral needed for oil palm growth. It was shown that with equal amounts of fertilizers applied, progeny C3 had better morphological traits than the other progenies, suggesting that the effective nutrient requirements should be assessed for each individual progeny and that fertilization should be adapted accordingly.

Keywords: : oil palm / genetic origin / genetic background / morphological characteristics / growth / leaflet mineral concentrations

Résumé – Différences génétiques en nutrition minérale chez le palmier à huile (*Elaeis guineensis* Jacq.) : effet du potassium et du magnésium sur les caractéristiques morphologiques de quatre descendances de palmier à huile au Nigéria (Afrique de l'Ouest). Nous avons comparé les paramètres morphologiques de croissance de quatre descendances de palmier à huile (*Elaeis guineensis* Jacq.) aux fins de révéler les différences génétiques dans la croissance des plants et d'étudier leurs adaptabilités à

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l'environnement du Nigéria en réponse à différents apports de chlorure de potassium (KCl) et de Kieserite ($MgSO_4$). Les descendances étudiées (C1, C2 et C3 d'origine *Deli* × *La Mé* et C4 d'origine *Deli* × *Yangambi*) représentent une large diversité de palmier à l'huile et ont montré au sein d'une population de 116 descendances génétiquement différent, des teneurs foliaires contrastées en K et Mg qui ont couvert les extrêmes de concentrations foliaires pour ces minéraux. Le dispositif expérimental a consisté en un essai factoriel split-plot complètement randomisé avec six répétitions, et où les descendances, considérées comme facteur secondaire, ont été testées avec les combinaisons possibles de 3 niveaux de chlorure de potassium (0 ; 1,5 ; 3,0 kg de KCl palmier^{-1} an^{-1}) et magnésium (0 ; 0,75 ; 1,5 kg de $MgSO_4$ palmier^{-1} an^{-1}), respectivement (facteur principal). Les caractéristiques morphologiques de croissance ont significativement différé entre les descendances, mais pas pour toutes les années d'observation. Chez toutes les descendances, les traitements de KCl ont significativement augmenté l'accroissement annuel moyen de la circonférence au collet et de la projection de la canopée des plants. L'application de 3,0 kg de KCl palmier^{-1} an^{-1} a significativement augmenté la surface foliaire totale de la descendance C4. L'application de la kiésérite n'a eu aucun effet sur les paramètres de croissance des descendances étudiés alors que le potassium s'est révélé être le principal minéral nécessaire à la bonne croissance des plants de palmier à huile dans l'environnement du Nigéria. Il a été démontré qu'avec une application similaire de fertilisant, la descendance C3 a eu de meilleurs traits de croissance morphologique que les autres descendances, suggérant ainsi que les besoins nutritionnels effectifs soient calculés pour chacunes des descendances et que la fertilisation y soit rigoureusement adaptée.

Mots clés : palmiers à huile / origines génétiques / patrimoine génétique / caractéristiques morphologiques / croissance / concentrations minérales foliaires

Highlight

- Oil palm progenies' growth characteristics are determined by their genetic backgrounds.
- K is the main mineral involved in oil palm morphological growth in the Nigerian environment.
- Mg does not have an effect on the tested progenies' growth characteristics.

1 Introduction

Oil palm (*Elaeis guineensis* Jacq.) is the main supplier of vegetal oil in the world (USDA, 2020). Oil palm produces an average yield about 3.8 t ha^{-1} y^{-1} of oil, which is six to nine times higher than the yield of other oilseed crops (Skurtis *et al.*, 2010). Oil palm productivity has been continuously improved (Durand-Gasselin *et al.*, 2000; Rival and Levang, 2010) by crossing different oil palm genotypes with useful traits such as fresh fruit bunch (FFB) yield, mesocarp thickness and consequently shell thinness (Cochard *et al.*, 2001; Durand-Gasselin *et al.*, 2006; Durand-Gasselin *et al.*, 2011; Junaidah *et al.*, 2011; Corley and Tinker, 2016). Oil productivity over the lifespan of the oil palm is determined using several different factors, among which researchers have focused particularly on slow trunk growth rates to extend the economic life of the palm (Baudouin *et al.*, 1997; Tailliez and Koffi, 1992; Durand-Gasselin *et al.*, 2009; Verheye, 2010; Bonneau *et al.*, 2014; Bonneau *et al.*, 2017; Konan *et al.*, 2014; Fan *et al.*, 2015; Corley and Tinker, 2016). The trunk growth rate varies between 25 and 65 cm per year (Cochard *et al.*, 2001; Konan *et al.*, 2014), depending on environmental and genetic factors (Cochard *et al.*, 2005; Verheye, 2010). It has been shown that growth characteristics vary according to oil palm genetic origins (Nouy *et al.*, 1999; Konan *et al.*, 2014; Corley and Tinker, 2016). We consequently assumed that this would also be the case for four selected progenies with different genetic backgrounds (Tab. 1). However, growth characteristics are also essential parameters to assess palm trees' mineral uptake and use (Goh *et al.*, 1999; Marschner *et al.*, 2007; Prabowo *et al.*, 2012). In an earlier study conducted in Indonesia on the same progenies, it has been shown that their leaflet K and Mg concentrations vary significantly from one to another, after having received equal amounts of fertilizers (Ollivier *et al.*, 2017). These minerals (K and Mg) play diverse roles in palm growth and development and have a number of physiological and enzymatic functions: K is a crucial element that directly affects photosynthesis and gas exchange (Legros *et al.*, 2009; Lamade *et al.*, 2014), and cell turgor pressure. Mg is necessary for photosynthesis reactions as it is the central molecule of chlorophyll, and improves oil quality traits (Gerendás and Führs, 2013). K and Mg are also involved in enzyme mechanisms (Taiz and Zeiger, 2006). Substantial amounts of K are needed to ensure palm growth. Moreover, mineral (K and Mg) requirements are calculated on the basis of leaflet mineral concentrations to assess maximum growth and yield in oil palm industrial plantations (Dubos *et al.*, 2019).

The main purpose of this study is to assess the growth and morphological characteristics of the selected oil palm progenies studied in order to reveal genotypic differences in plant growth under different fertilization regimes. In this study, we also evaluated the effect of fertilizers (KCl and kieserite) treatments on the progenies palms' growth in Nigeria (West African) environment.

2 Materials and methods

2.1 Study site

The study was carried out in Nigeria, in one of the oil palm plantations belonging to Presco Plc company in Ologbo town

Table 1. Genetic characteristics, varieties, and genetic origins of the parents of the different oil palm progenies (PIC, 2011).

Progenies	*Dura* (male parent)	*Dura* origins	*Pisifera* (female parent)	*Pisifera* origins	Genetic origins
C1	PO 2630 D	DA 10 D × DA 3 D	PO 2766 P	LM 10 T AF	D × L
C2	PO 3174 D	DA 115 D AF	PO 2973 P	LM 5 T × LM 10 T	D × L
C3	PO 3174 D	DA 115 D AF	PO 4747 P	LM 5 T AF	D × L
C4	PO 4953 D	Unknown	PO 4260 P	LM 238 T × LM 511 P	D × Y

D × L: *Deli* × *La Mé*; D × Y: *Deli* × *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 × LM 10 T).

near Benin-City (Supplementary Fig. S1), Edo State district (N6.03652° E 5.55609° at an elevation of 20 m a.s.l). Between 1996 and 2018, average annual rainfall in the study area in Nigeria was 2,066 mm (Bonneau *et al.*, 2014). In the same period between 1996 and 2018, average annual temperatures ranged from 25.0 °C to 27.8 °C, and average annual radiation was 13.78 MJ m^{-2} d^{-1}. Prior to the beginning of the experiment, the study site was a humid and largely degraded sub-tropical forest where cassava (*Manihot esculenta*) and plantain (*Musa* spp.) were cultivated after deforestation. The experimental land consisted of a vast sedimentary formation with a flat landscape containing ferralsols (FOA nomenclature) (Bonneau *et al.*, 2017). Soils are deep, very sandy on the surface, with a gradual increase in clay content with depth and include no coarse elements. Soil fertility was low at the onset of the trial (Tab. 2).

2.2 Planting material

Four different oil palm (*Elaeis guineensis* Jacq.) progenies (progenies C1, C2 and C3 from *Deli* × *La Mé* origin, and progeny C4 from *Deli* × *Yangambi* origin; Tab. 1) were selected for this study among 116 high-yielding progenies that were previously studied in a varietal trial that aimed the comparison of their yield performances in Aek Loba Timur (Sumatera Utara province, Indonesia) (Ollivier *et al.*, 2017). Between 4 to 7 years after planting (YAP) in Nigeria, average leaflet K concentrations were 0.857, 0.792, 0.725 and 0.981% of dry matter (DM) and average leaflet Mg concentrations were 0.260, 0.249, 0.301 and 0.269% of DM, for progenies C1, C2, C3 and C4, respectively (Dassou *et al.*, 2018). All progenies used were *Tenera* crosses from two different genetic origins and were initially selected based on similar good fresh fruit bunch (FFB) and crude palm oil (CPO) production in Indonesia and subsequently on their contrasting leaflet K and Mg concentrations under equal fertilizer applications (PIC, 2011). The progenies are the result of collaborative breeding for oil palm yield improvement by the National Agricultural Research Institute of Benin (INRAB), the International Center of Agronomic Research for Development (CIRAD, France) and its subsidiary company PalmElit.

2.3 Seedling and palm fertilization management

Germinated seeds were treated in the pre-nursery and main nursery as recommended by CIRAD (2008). At the age of eight months in the nursery, only oil palm seedlings that met growth planting criteria were selected for the experiment: 0.6 to 1 m in height, 18 to 22 cm of collar girth, 6 to 8 functional fronds, and absence of disease or nutrient deficiency symptoms (CIRAD, 2008).

In the plantation, basal and uniform dressing fertilization was carried out in the first year after planting (YAP) so as to start the trial conditions as homogeneously as possible. In the second year, a basic application of urea (1,000 g $palm^{-1}$) and triple superphosphate (500 g $palm^{-1}$) was applied. Also, from the second year onwards, a gradient of K and Mg fertilizer amounts was applied during the first seven years in the main fertilizer plots. The fertilizer application schemes with three levels of fertilizer (K0–K1–K2 and Mg0–Mg1–Mg2, respectively) are presented in Table 3.

2.4 Experimental design

The experimental design (Supplementary Fig. S2) consisted of a factorial split-plot trial with two factors: mineral nutrition (MN) × genetic material (GM), set up in Nigeria on about 33 ha with oil palms spaced 9 meters apart in a staggered, equilateral triangle design, resulting in a planting density of 143 plants ha^{-1} in 2011 (PIC, 2012). Measurements were taken for five years, from Y3 (2013) to Y7 (2017). All combinations of three levels of potassium chloride (KCl: 60% K_2O) and three levels of kieserite ($MgSO_4$: 27% MgO) were tested resulting in a total of nine fertilizer treatments considered as random effects in main plots, applied to the four oil palm progenies that were considered as subplots, resulting in a total of 36 subplots per replicate. The experiment consisted of six replicates, and therefore 216 subplots. Each subplot area was about 631 m^2. In each subplot, data were collected from three rows of three studied (useful) palms, *i.e.* data were collected from a total of 1,944 useful palms in the trial. Within each, the useful palms were surrounded by border palms in all directions (45 border palms per fertilizer plot, or a total of 2,430 border palms for all 54 fertilized plots). About 350 additional border palms were planted along the sides of the road to protect the studied palms and their main border palms from attacks by rodents that may emerge from the adjacent forest.

3 Parameters measured

3.1 Growth factors

The averages of a number of oil palm growth parameters resulting from all the fertilizer treatments on the progenies

Table 2. 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	pH co	Organic matter (%)	Organic carbon (%)	Total N (‰)	C/N	Total P (mg/kg)	Available P (mg/kg)	Ca^{2+} (me/100 g)	Mg^{2+} (me/100 g)	K^+ (me/100 g)	Na^+ (me/100 g)	Al^{3+} (me/100 g)	S (Ca. Mg. K. Na) (me/100 g)	CEC (me/100 g)	TS (%)
			Fine	Coarse																		
Nigerian	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).

were used to compare growth characteristics between the oil palm progenies in Nigeria. CIRAD–IGK protocols were used to measure growth:

- oil palm height (Ph) was assessed from the fourth year on by measuring the length from petiole base (stump) of the leaf rank 33 to the soil surface. This measurement cannot be done before 3–4 YAP because until then, oil palm trees are stemless;
- oil palm collar girth (CG) was determined by measuring the circumference of the stem at the soil surface;
- oil palm frond length of rank 17 is the length of the petiole from the point closest to where the petiole is attached to the stem to the end of the rachis;
- oil palm leaf area of rank 17 was assessed following Tailliez and Koffi (1992) by measuring the total length of the rachis and petiole of the frond rank 17, while the rachis length is divided into 10 sections, one normal (*i.e.* undamaged) leaflet is selected in the middle of each section and removed from the same side of the leaf in each section. The 10 leaflets are arranged on a pallet ranked according to their apparent size (Supplementary Fig. S3). Leaflet widths (in cm) are measured at 10 cm intervals along the leaflet. Each 10 cm section of the leaflet is then considered as a trapezium where the two widths measured at the top and bottom form the bases of the trapezium with a height of 10 cm. The remaining part of the leaflet (*i.e.*, above the last section with a length of 10 cm) is considered to be an isosceles triangle. Leaflet area was then computed by adding all surface areas of each 10 cm trapezium-shaped leaflet section together with the area represented by the edge of the leaflet isosceles triangle.

The surface area of leaf 17 ($l_{17}a$ expressed in m^2) was estimated as follow:

$$L_{17a} = 2 \times [(n1 \times lft1) + (n2 \times lft2) + \dots + (n10 \times lft10)]/10\,000, \qquad (1)$$

(Eq. (1), Tailliez and Koffi, 1992), where:

- n1 to n10 = number of leaflets per rachis section;
- lft1 to lft10 = surface area of each selected leaflet from each section of the rachis.

Total leaf surface area of each progeny was obtained by multiplying the surface area of leaf 17 by the average number of new fronds emitted over the last four years.

The number of emitted fronds was counted following their rank appearance in the oil palm phyllotaxy described by IRHO (1960) and Fan *et al.*, (2015);

- oil palm projected canopy area on the ground was measured as a circle of which the palm trunk base was in the center;
- oil palm stem volume (V_{stem}) was estimated as:

$$V_{stem} = \frac{Ph \times CG^2}{4\pi}. \qquad (2)$$

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 × 15)	Borax	Kieserite	Urea	TSP	K (KCl)			Mg (kieserite)			NaCl	N (34%)	P_2O_5 (50%)	K_2O (60%)	MgO (27%)	B_2O_3 (11%)	K_2O (60%)			MgO (27%)		
							K 0	K 1	K 2	Mg 0	Mg 1	Mg 2	K0						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	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

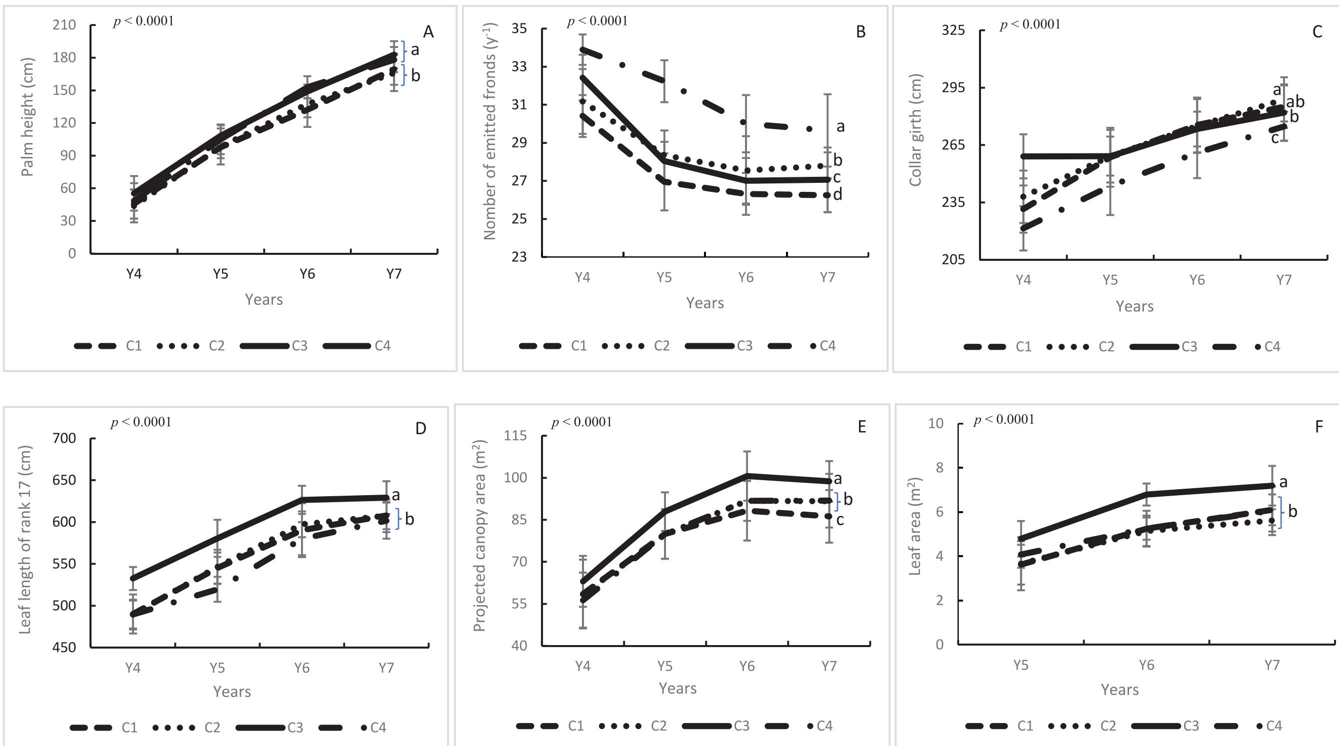

Fig. 1. Variation in the morphological parameters of oil palm progenies observed from 4 until 7 YAP. Different letters (a, b, c and d) indicate significant differences in the different parameters between oil palm progenies. YAP: year after planting. Capital letters (A, B, C, D, E and F) indicate the growth parameters measured.

Oil palm height, collar girth and frond length are expressed in centimeters (cm), while leaf area and projected canopy area are expressed in cm^2 and oil palm stem volume in cm^3. Results of the trunk volumes are not presented in Figures 1 and 2.

3.2 Increase in growth factors

Yearly increases in oil palm stem height, number of emitted fronds and length of the rank 17 leaf were assessed from 4 to 7 years after planting (YAP). Additionally, yearly increases in oil palm collar girth and projected canopy area were assessed from 1 to 7 YAP, thus including the period from 1 to 3 YAP, during which oil palm stem diameters show the largest increases (Corley and Tinker, 2016). Annual increases in oil palm leaf area were recorded from 5 to 7 YAP. In each subplot, unproductive palms were withdrawn from the analysis.

3.3 Statistical analysis

A mixed model was used for the analysis of variance (ANOVA) of changes in growth factors. In this study, growth parameters were averaged across all fertilizer treatments. To account for the split-plot nature of the design, a mixed-effects model was used, with the sub-block effects (*i.e.*, fertilizer × block interaction) as a random factor. The model was used to compare growth characteristics according to the progenies. Tukey's multiple comparison test was applied to verify the significance of parameter means between progenies.

Statistical analyses were conducted in XLSTAT (Version 2018–7, www.xlstat.com) and R version R-3.6.0 of Windows.

4 Results

4.1 Growth characteristics of oil palm progenies

Highly significant differences ($P < 0.0001$) were found between progenies for a number of vegetative growth parameters (Fig. 1). Differences in progenies' genetic background (Tab. 1) show that only the number of emitted fronds (NEF) differed significantly in all four progenies in each studied year. In all progenies, the number of emitted fronds decreased each year until the plants reached 6 YAP, whereas all other parameters increased over the observation period. All growth parameters except palm tree height stabilized around 6–7 YAP. Height increased at an annual average rate of 41, 39, 42 and 43 cm in progenies C1, C2, C3 and C4, respectively, with no significant differences between the annual growth rates in progenies C3 and C4 (Fig. 1A).

The average number of emitted fronds per year was 27.5, 28.9, 28.6 and 31.5 for progenies C1, C2, C3 and C4, respectively. No significant difference in NEF was found between progenies C2 and C3 (Fig. 1B).

In all years, progeny C4 had the smallest average collar girth, whereas progenies C1 and C2 had the largest collar girth. Progeny C3 reached its maximum girth at 4 YAP (Fig. 1C). Considering the stem as a cylinder, progeny C3 compensated for its smaller diameter by its taller stature. Its trunk volume at

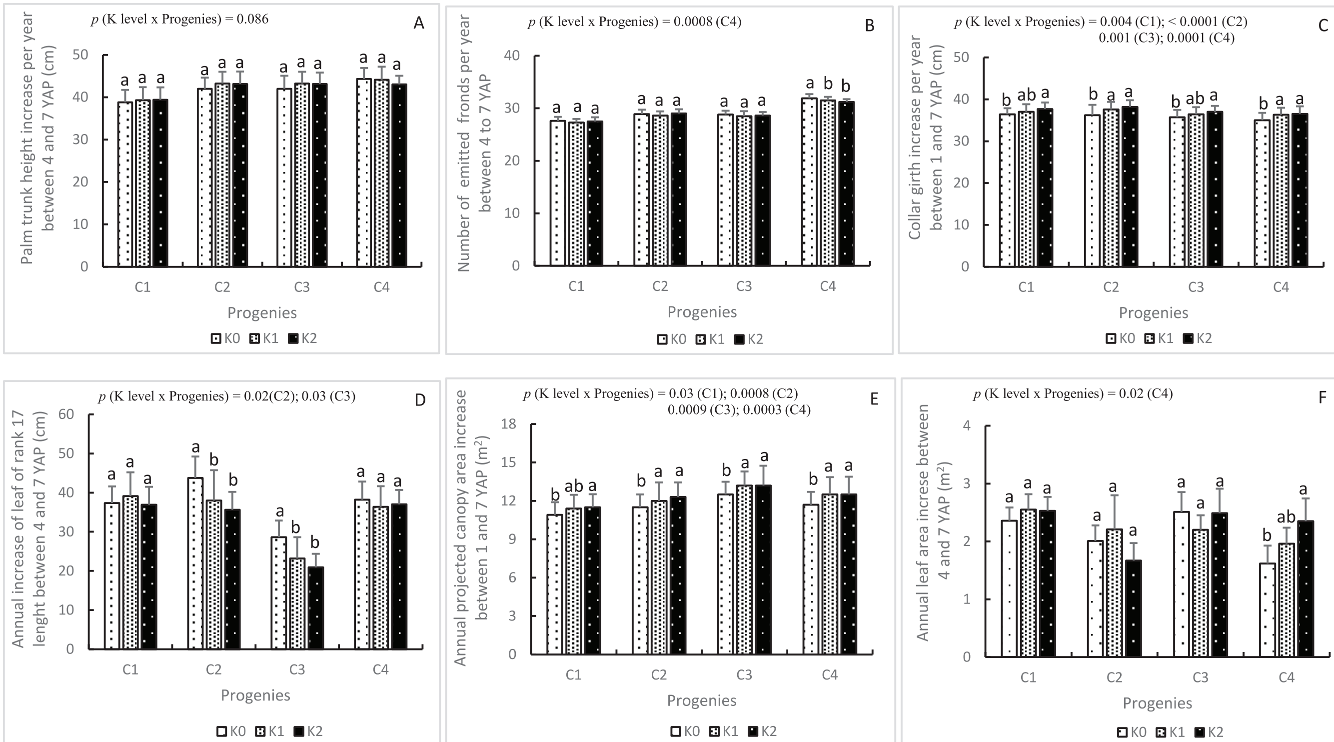

Fig. 2. Stem height increase (A), number of emitted fronds per year (B), collar girth increase (C), annual length increase for leaf rank 17 (D), annual projected canopy increase (E) and annual leaf area increase (F) for oil palm progenies subjected to different KCl levels in Nigeria. The letters (a, b and c) explain the significant ($P \leq 0.05$) differences between progenies observed at 7 years old, revealed by a Tukey test. YAP: year after planting.

7 YAP (1.13 m^3) was 3.9%, 17.6% and 6.8% higher than that of progenies C1 (1.09 m^3), C2 (0.93 m^3) and C4 (1.06 m^3), respectively. Average annual girth increments in progenies C1, C2, C3 and C4, were respectively, 15.7, 18.2, 13.7 and 17.6 cm.

Progenies C1, C2 and C4 had similar frond lengths in all years, except in 5 YAP when progeny C4 had significantly shorter fronds. Progeny C3 had 20 to 30 cm higher frond length than progenies C1, C2 and C4. The average annual increase in frond length in C1, C2 and C4 was 37.7, 39.1, and 37.2 cm, respectively. The annual increase in frond length in progeny C3 (32 cm) was significantly lower than that in the other three progenies (Fig. 1D).

Progeny C3 had a larger projected canopy area than that of all the other progenies, in all measurement years. At 7 YAP, progenies C1, C2, C3 and C4 showed a mean annual increase in canopy projected area of 10.2; 11.4; 11.9 and 11.1 m^2, respectively (Fig. 1E).

Progeny C3 had a significantly larger leaf area than the other progenies in all years (Fig. 1F). At 7 YAP, progeny C3 had 18% more leaf area than progenies C1 and C4, and 29% more than progeny C2 and its annual average total leaf area increase was 9%, 0.6% and 17% higher than that of progenies C4, C1 and C2, respectively.

Progeny C3 showed a better vegetative development (leaf length, leaf area and projected canopy area) than the other progenies in all measurement years.

4.2 KCl and kieserite effects on oil palm progeny growth

We found a significantly positive KCl effect in all progenies for the annual increase in collar girth, projected canopy area and area of leaf rank 17, whereas there was no effect for $MgSO_4$ applications ($P = 0.485$). However, effects differed between progenies (Fig. 2A–F). We could not find significant differences between the four progenies for oil palm stem height increases between 4 and 7 YAP (Fig. 2A). Only in progeny C4 did increasing potassium applications (from K0 to K2) significantly ($P = 0.0008$) decrease the total number of fronds emitted annually between 4 and 7 YAP (Fig. 2B). In the latter progeny (C4), the annual number of emitted fronds decreased from 31.9 to 31.5 and 31.2 for K0 to K1 and K2 treatments, respectively (Fig. 2B).

In all progenies, a significant KCl effect was found for the average annual collar girth increment between 1 and 7 YAP. In progeny C1, the annual collar girth increment increased by 0.6 cm and 0.7 cm between K0–K1 and K1–K2 treatments, respectively, whereas in progeny C3, these increases were respectively 0.7 cm and 0.6 cm. Collar girth increments were only significant between K0–K1 for progenies C2 (1.4 cm) and C4 (1.3 cm) (Fig. 2C).

KCl significantly reduced the frond length increment from 43.7 cm (K0) to 38.0 cm (K1) and further (but not significantly) to 35.6 cm (K2) in progeny C2, and from 28.6 cm (K0) to

23.2 cm (K1) and further (but not significantly) to 20.9 cm (K2) in progeny C3 (Fig. 2D).

In all progenies, when compared to K0, K1 increased the projected canopy area, with 0.5, 0.7 and 0.8 m^2 on average per year, for progenies C2, C3 and C4, respectively, whereas no significant differences were found in the projected canopy area for any of the progenies between K1 and K2. In progeny C1, only the projected canopy area increment of oil palms with treatment K2 was significantly different from that of the palms with treatment K0 (Fig. 2E). The area increment of leaf 17 only significantly increased in progeny C4 (from 1.62 m^2 for K0 to 2.35 m^2 for K2) (Fig. 2F).

Significant interaction ($P < 0.001$) between the effects of K and Mg applications was observed in all progenies for some studied years for several growth parameters (Supplementary Tab. S1). Moreover, K and Mg interactions was significant ($P = 0.04$) on average increase per year of projected canopy area, with treatments K2Mg0, K1Mg1 and K1Mg2 exhibiting higher and statistically similar average annual increases of projected canopy area, whereas K0Mg0 showed the lowest value and the other five K × Mg exhibited intermediate values.

K × progeny interaction was significant ($P = 0.011$) only for average leaf area increase with K2 × C3 exhibiting the highest average leaf area, whereas K2 × C2 and K0 × C4 showed the lowest average leaf area increase. For none of the growth parameters, there was a significant interaction between Mg and any of the progenies.

5 Discussion

5.1 Growth characteristics of the four oil palm progenies

In a density trial in Obaretin (the second PRESCO oil palm plantation located in Benin-City (Edo state) in the same district as the current experiment), Bonneau *et al.*, (2017) observed that average oil palm trunk length increased regularly and steadily with an annual growth rate of 35 cm, whereas the collar girth stabilized at around 265 cm at 9 YAP. The latter annual growth rate is lower than that of the progenies tested in the present study, in which annual growth rates ranged from 39 to 43 cm a year. This can be explained by the genetic differences between the progenies used in our study and those used by Bonneau *et al.* (2017) as well as the length of the observation period, which was 4 to 7 YAP in our study, compared 7 to 12 YAP in the study by Bonneau *et al.* (2017). According to Jacquemard and Baudouin (1987), oil palm trunks have a sigmoidal growth rate until 8–9 YAP, and a sigmoid decreasing growth rate from 10 YAP onwards. The differences between the growth rate in our study and that of Bonneau *et al.* (2017) might also be explained by local environmental conditions. In our trial, the soil was more fertile and rainfall/soil humidity was higher than in the study of Bonneau *et al.* (2017). Our experiment (Ologbo plantation) took place in a degraded forest zone whereas the Obaretin site (Bonneau *et al.*, 2017) is located in an oil palm replantation area with lower soil organic matter content.

On average, growth parameters such as collar girth, tree height and the length of the rank 17 frond of the progenies tested in our study, were lower than those assessed by Bonneau *et al.* (2017) at the same age. The oil palm progenies tested in our study originate from breeding programs aiming at developing more compact planting material (*i.e.* with shorter internodes; Durand-Gasselin *et al.*, 2000; Cochard *et al.*, 2005; Konan *et al.*, 2014). Above 13 m in height, oil palms are no longer economically viable because of increased cost of harvest (fruit bunches in tall palms are more difficult to harvest; Cochard *et al.*, 2001; Konan *et al.*, 2014). Estimating the age at which our progenies will reach a height of 13 m, taking into account their yearly increase in height, the expected life cycle of progenies C1, C2, C3 and C4, would be 32, 33, 31 and 30 years, respectively.

The progenies tested in this study have an average frond length of 6 m, which is the middle of the wide range of oil palm frond lengths (4 m to 8 m), as reported by Jourdan (1995).

In Benin, Nodichao *et al.* (2008) tested four oil palm progenies on trees aged 4 to 5 YAP and reported 26 to 30 fronds emitted per year. These numbers are in line with our results and confirm that the number of emitted fronds varies with oil palm progenies. Hartley (1988), Corley and Tinker (2016) reported that the frond emission rate decreases with age, which was also confirmed in our study. Corley and Tinker (2016) reported that the number of leaves produced each year by a plantation palm ranged between 30 and 40 at 2–4 YAP and gradually declined to 20–25 per year from 8 YAP onwards.

Rees and Tinker (1963) estimated leaf area values of 5.2, 6.7, 7.0, 9.9, 9.7 and 11.2 m^2 for oil palms aged 7, 10, 14, 17, 20 and 22 YAP, respectively, near Benin-City in Nigeria, (WAIFOR: West African Institute for Oil palm Research, that subsequently became NIFOR: Nigerian Institute For Oil palm Research). At 7 YAP, palms of progeny C2 and C3 had the smallest and largest leaf area, respectively, which were respectively 1.08 and 1.4 times larger than that of the oil palms studied by Rees and Tinker (1963) at the same age. These differences are probably the result of progress made in oil palm breeding since the 1960s (Durand-Gasselin *et al.*, 2000, Cochard *et al.*, 2005).

In all progenies, leaf-related morphological parameters, *i.e.*, frond length, projected canopy area and leaf area, reached maximum at 6 YAP, indicating that the physiological maturity of the leaves of the different progenies was reached at that age. The significant differences in growth variables observed among the progenies tested in our study are probably determined genetically (Nouy *et al.*, 1999; Konan *et al.*, 2014; Corley and Tinker, 2016), *i.e.* linked with the specific physiological traits of the different genetic origins of the oil palms (Jacquemard *et al.*, 2002). This difference in growth morphology between progenies may also be related to differences in leaflet mineral concentrations which were found to be specific to each progeny (Dassou *et al.*, 2022b).

5.2 Effect of K and Mg fertilizer applications on oil palm progeny growth

K fertilization has frequently been reported to have a positive effect on oil palm growth (Kusnu *et al.*, 1996; Dubos *et al.*, 1999; 2010; Bonneau *et al.*, 2018). This was confirmed by our results for collar girth and projected canopy area in all progenies, as well as for the leaf area increase for progeny C4, which increased significantly with increasing KCl levels.

The negative effect of KCl on rank 17 frond length for progenies C2 and C3 might possibly be explained by the high yield (with increasing KCl levels) recorded between 5 to 8 YAP (Dassou *et al.*, 2022a). Fruit bunches are mineral sinks that store K, to the detriment of K potentially accumulating in fronds (Dubos *et al.*, 2010; Legros *et al.*, 2006). The negative effect of K on frond length was more pronounced for progeny C3, which also had a higher bunch weight in comparison with progeny C2 (Dassou *et al.*, 2022a). Moreover, only progenies C2 and C3 exhibited K- category among all progenies tested in this study, indicating that they have a low K status compared to progenies C1 and C4 which exhibited K+ status (Dassou *et al.*, 2022b). However, the average projected canopy area of the palms of progenies C2 and C3 between 5 to 8 YAP increased with KCl levels when compared to the palms of the other progenies. This can be explained by their genetic background. Progenies C2 and C3 share the same female parent genotype, but have different male parent genes (Tab. 1).

The contrast between the positive effect of KCl on the average projected canopy area of the palms of progenies C2 and C3, and the negative effect on the increase in average rank 17 leaf length for the same progenies, might be explained by the fact that frond length was measured on the rank 17 fronds only, whereas the projected canopy area is determined by the most overarching oil palm leaves.

Our findings suggest that throughout the experimental period, the K2 treatment resulted in the highest and lowest average annual leaf area increase in progenies C3 and C2, respectively, in Nigerian ecological conditions. The fact that the same K rate (K2) induced contrasting growth development behaviors in two genetically different planting materials (progenies C2 and C3), underscores the need to assess mineral requirements (at least for K and Mg) of oil palm progenies in their specific ecological cultivation conditions.

Deli × *Yangambi* material (progeny C4) has a high, genetically determined frond emission potential compared to that of *Deli* × *La M*é material (progenies C1, C2 and C3) (Corley and Tinker, 2016). The reduction in the number of emitted fronds with increasing KCl rates observed for the palms of progeny C4 was therefore probably linked to the yield increase observed for palms with treatments K1 and K2 compared to treatment K0, which may have depressed its vegetative growth (Dassou *et al.*, 2022a).

The high frond emission in progeny C4 explained its high bunch number, as each frond is predestined to produce one inflorescence that can become male or female (Corley and Tinker, 2016). However, progeny C4 produced more male (69%) than female (31%) inflorescences (Dassou *et al.*, 2022a). It is known that *Deli* × *Yangambi* material, such as C4 palms, produces relatively more male inflorescences in less favorable ecologies (Nouy *et al.*, 1999), such as the one in our experiment (Nigeria) with lower rainfall conditions compared to Southeast Asia (Bonneau *et al.*, 2014; Ollivier *et al.*, 2017). This finding is important in solving low pollination problems (lack of pollen or very low male inflorescences production in the plantation) occurring in some oil palm plantations and suggests adding *Deli* × *Yangambi* material in, or around plantations composed of *Deli* × *La M*é oil palm material which are known to be female material, having very high female inflorescences production (Dassou *et al.*, 2022a).

The high development of aerial organs (length and area of leaf rank 17, projected canopy area) in C3 palms irrespective of fertilizer treatments, compared to those of the other progenies, might be explained by their genetic background. Many studies (Trehan, 2005; Marschner *et al.*, 2007; Yanbo *et al.*, 2008; Hassan *et al.*, 2011) have demonstrated that efficient potassium use positively affects plant growth. However, further studies are needed to verify whether the palms of progeny C3 indeed have a relatively higher potassium use efficiency than the other progenies.

Growth parameters were unaffected by our Mg treatments, which was also found by Kusnu *et al.* (1996) and Bonneau *et al.* (2018). This lack of $MgSO_4$ effect on growth parameters might be explained by the fertility of the soil in our trial, which had high levels (as generally found in ferralsols in tropical zones) of exchangeable Mg (Tab. 2). As a result, Mg was abundantly available to our oil palms and supplying more Mg had no effect on growth parameters (Kusnu *et al.*, 1996).

6 Conclusion

All progenies were shown to have different morphological growth traits with progeny C3 producing the most biomass in Nigeria's environment. Our results suggest that differences in progenies' growth are the result of their genetic background. Potassium is the main mineral involved in oil palm morphological growth and development in Nigeria's environment, compare to magnesium. However, with 3 kg KCl palm^{-1} (K2), progeny C3 developed the highest annual leaf area growth whereas progeny C2 exhibited the lowest value, suggesting the need of assessing the mineral requirements (at least for K and Mg) of different planting materials in their specific ecological cultivation conditions found in Nigeria according to their specific needs.

Conflict of interests

Olivier DASSOU, Hervé Aholoukpè and Apollinaire Mensah are employed by INRAB. Stephen Peprah is employed by Presco. Jean Ollivier, Xavier Bonneau and Albert Flori are employed by CIRAD of which PalmElit is subsidiary company and of which Tristan Durand-Gasselin is the CEO. All these companies have a collaborative partnership.

The authors declare they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

Supplementary material

Fig. S1. Map of Africa showing the location of Nigeria in Africa (left) and Benin-City and Ologbo oil palm estate in Nigeria (right).
Fig. S2. Experimental layout.
Fig. S3. Graduated pallet with leaflets ranked according to their apparent leaflet area. Source: Tailliez and Koffi (1992).
Table S1. K × Mg interactions on oil palm growth parameters.

The Supplementary Material is available at http://www.ocl-journal.org//10.1051/ocl/2022024/olm.

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