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Oil palm (*Elaeis guineensis* Jacq.) genetic differences in mineral nutrition: environmental effects on leaflet mineral concentrations of four oil palm progenies[☆]

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Abstract – Oil palm fertilizer requirements are based on leaflet mineral concentrations. Four oil palm progenies representing a wide genetic diversity of *Elaeis guineensis* species and with contrasting K and Mg leaflet concentrations were tested in Indonesia and Nigeria, environments which differ predominantly in climate. During 5 years, we compared oil palm progenies' leaflet mineral concentrations between both countries under abundant fertilizer applications to investigate the extent to which they depend on the environment. In the two studied environments, leaflet concentrations significantly differed between progenies for K, Mg and Ca, but the country effect was not found significant ($p = 0.352$) for any leaflet mineral's concentration. In both countries, progenies ranked similarly in their mineral categories (lowest and highest cation concentrations within the 4 progenies population), indicating that leaflet mineral concentrations in the tested oil palm progenies are mainly determined by their genetic background. For each progeny, with abundant fertilization, K, Mg and Ca proportions to total leaf cation charge (TLCC) were similar, irrespective of the environments in which the palms were cultivated. We have strong indications that foliar concentrations of K, Mg and Ca are determined by genetic factors which dominate the environmental effect. However, it remains uncertain whether differences in oil palm foliar concentrations between different oil palm progenies imply that they require specific fertilizer amounts to attain an optimal production.

Keywords: oil palm genetic origins / genetic determination / leaf analysis / leaflet mineral concentrations

Résumé – Différences génétiques en nutrition minérale chez le palmier à huile (*Elaeis guineensis* Jacq.) : effet de l'environnement sur les concentrations minérales foliaires de quatre descendance de palmier à huile. Les besoins en engrais du palmier à huile sont calculés sur la base des concentrations minérales foliaires. Quatre descendance (*progenies*) de palmier à huile représentant une large diversité génétique de l'espèce *Elaeis guineensis* Jacq. et ayant des concentrations foliaires contrastées en K et Mg ont été testées en Indonésie et au Nigéria, des environnements qui diffèrent principalement par le climat. Pendant 5 années, nous avons comparé les concentrations minérales foliaires de ces 4 descendance entre les deux pays sous un apport abondant d'engrais pour étudier dans quelle mesure elles dépendent de

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l'environnement pour l'assimilation de nutriments. Dans les deux environnements étudiés, les concentrations foliaires ont différé significativement entre les descendances pour K, Mg et Ca, mais l'effet pays n'a pas été significatif ($p = 0.352$) pour aucune des concentrations minérales foliaires. Dans les deux pays, les descendances se sont classées similairement dans leurs catégories minérales (concentrations de cations les plus faibles et les plus élevées au sein de la population des 4 descendances), ce qui indique que les concentrations minérales foliaires des descendances de palmier à huile étudiées sont principalement déterminées par leur patrimoine génétique. Pour chaque descendance, et avec une fertilisation abondante, les proportions de K, Mg et Ca par rapport à la charge cationique totale des feuilles (TLCC) ont été similaires indépendamment des environnements dans lesquels les palmiers ont été cultivés. Nous avons de fortes indications que les concentrations foliaires de K, Mg et Ca sont déterminées par des facteurs génétiques qui dominent l'effet environnemental. Cependant, il reste incertain si les différences des concentrations foliaires de palmier à huile entre les différentes descendances impliquent qu'elles nécessitent des quantités d'engrais spécifiques pour atteindre une production optimale.

Mots clés : origines génétiques des palmiers à huile / détermination génétique / analyse foliaire / concentrations minérales foliaires

1 Introduction

Oil palm (*Elaeis guineensis* Jacq.) is a perennial crop of which an edible vegetable oil (palm oil) is extracted from the mesocarp (reddish pulp) of its fruit (Corley and Tinker, 2016). Palm oil is the most widely-used oil in the world (Omont, 2010), with around 72 million tons of global production in 2018 (FAOSTAT, 2020). Indonesia is the world's largest palm oil producer and consumer, providing about half of the global palm oil supply (41 million tons, either 57%). In 2016, Indonesia produced over 34.6 million tons of palm oil and exported nearly 73% of it. In 2020, Indonesian oil palm plantations stretched across 13 million ha. The average Indonesian palm oil yield (4.5 t ha^{-1}) is higher than the world's average palm oil yield (3.8 t ha^{-1} of oil) (FAOSTAT, 2020). However, Nigeria is the fifth producer of palm oil in the world (WorldAtlas, 2020). Since 1965, it has been the leading producer in Africa (Bassey, 2016) with up to three million ha of harvested oil palm area and total palm oil production reaching one million tons in 2019 (USDA, 2020). Despite the importance of palm oil for the Nigerian economy (Gharleghi and Chan, 2013; Bassey, 2016), the genetic origins, nutrient uptake, nutrient use efficiency, plant growth, and plant production performance of Nigerian oil palms are poorly documented. Although Nigeria is Africa's top palm oil producer, it is still importing palm oil to satisfy the demand of its ever-growing population. The average Nigerian palm oil yield (0.48 t ha^{-1} of oil) is less than one fifth of the world's average (FAOSTAT, 2020), mainly due to producers' limited access to inputs and the weak performance of the genetic planting material used. This low oil yield leads to expansion of the oil palm cultivation area with extensive replanting campaigns in areas deliberately deforested for oil palm planting. One of the factors that most frequently hampers palm production, development and growth in Africa (Nigeria) is inadequate nutrient uptake (Goh *et al.*, 1999) due to the low fertility of the ferralsols on which oil palm is generally produced in tropical areas. To optimize oil palm growth, development and production, mineral fertilizers are used, particularly in industrial plantations, usually with a fertilizer management plan designed to avoid excessive fertilizer applications (Sundram, 2010; Bonneau *et al.*, 2018). Excessive fertilizer applications unnecessarily increase production costs,

damage the environment and contribute to climate change and soil acidification (Bessou and Pardon, 2017; Pardon *et al.*, 2020). To determine the appropriate fertilizer amounts to be applied, leaf analysis is commonly used. It helps to tailor leaflet mineral concentrations to plant requirements (Dubos *et al.*, 2019). It is known that environmental conditions (Ciríaco da Silva *et al.*, 2011) and genetic characteristics of progenies may affect the mineral concentrations in oil palm leaflets (Nouy *et al.*, 1999; Corley and Tinker, 2016). However, the extent to which these two factors affect the progenies' mineral concentrations has still not been documented. To study this, we chose 4 oil palm progenies which exhibited contrasting mineral concentrations in an experiment in Indonesia and compared them in an experiment in Nigeria. The growing environments differ mostly in precipitation patterns. In Nigeria, the average total rainfall (2.066 mm in the period 1996 to 2018, Bonneau *et al.*, 2014) is lower than in Indonesia (2.233 mm in the period 1995 to 2014, Ollivier *et al.*, 2017; Nouy *et al.*, 1999). Moreover, Nigeria's ecology is characterized by an average annual water deficit (lack of water that occurs when water demand exceeds supply) of 240 mm between 1996 and 2018, compared to in Indonesia where no water deficit has been registered for the same period (Bonneau *et al.*, 2014; Ollivier *et al.*, 2017). It is not clear whether in dryer areas such as in West Africa (particularly in Nigeria), progenies can exhibit the same foliar mineral concentrations as in Indonesia. We hypothesize that the genotype is the most important factor that determines leaf mineral concentrations. We therefore further assume that the four progenies are at least classified into the same leaflet mineral categories (lowest and highest cation concentrations, *i.e.*, category (+): leaflet mineral concentration (l_{mc}) $>$ al_{mc} and category (-): $l_{mc} <$ al_{mc} ; where al_{mc} is the average leaflet mineral concentration of the four progenies) in both environments. We limited our examination of mineral categories to potassium (K), magnesium (Mg) and calcium (Ca) because it has been reported that quantities of minerals contained in the whole mature oil palm organs rank as follows $K > Mg = Ca > P > N$ (Khalid *et al.*, 2000). This also implies that oil palms mainly absorb K, Mg and Ca, from the soil.

The set of four oil palm progenies that was tested in Nigeria was chosen amongst a wide genetic diversity composed of 116 *Elaeis guineensis* progenies. Their leaflet K and Mg

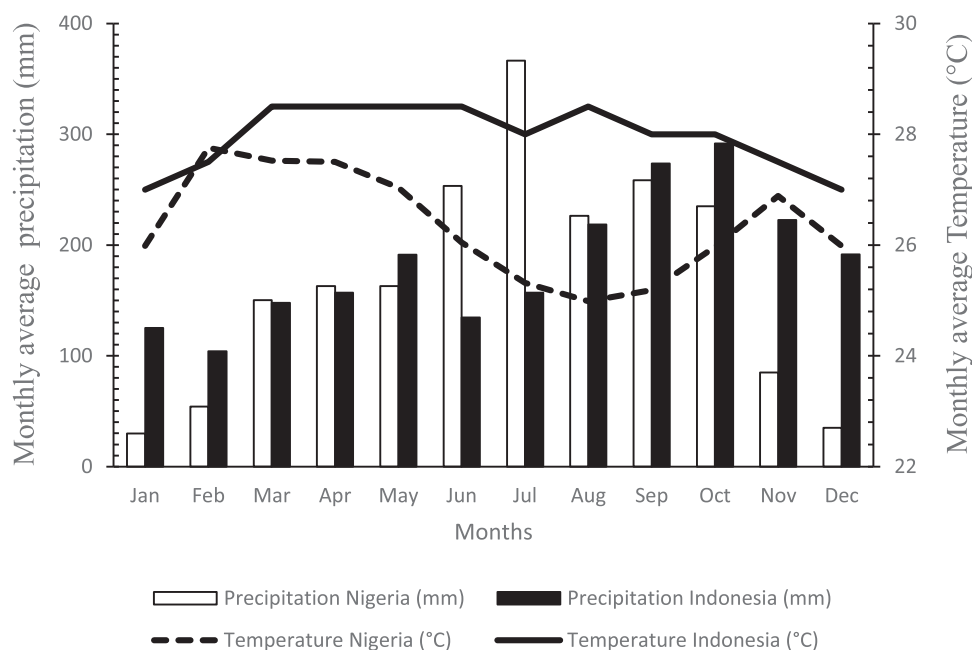


Fig. 1. Ombrothermic diagram from Nigeria (average from 1996 to 2018) and Indonesia (average from 1995 to 2014).

concentrations covered the extreme ranges of leaflet concentrations in those minerals (Supplementary Fig. SF 1). In the Indonesian experiment, they have shown a good bunch/oil production ratio ($> 8 \text{ t ha}^{-1}$ of crude palm oil: CPO) (Ollivier *et al.*, 2017).

The aim of this study was to examine to what extent environmental conditions can affect mineral concentrations in leaflets of different oil palm progenies. We further use the concept of ranking progenies in mineral categories to discuss whether it is useful in determining fertilizer requirements in a specific environment.

2 Materials and methods

2.1 Study site

The study was carried out in both Nigeria (2011–2018) and Indonesia (2003–2013). The Nigeria trial was installed in an oil palm plantation belonging to Presco Plc company in Ologbo village near Benin City, Edo State district (N 6.03652° E 5.55609° at an elevation of 20 m a.s.l.). Between 1996 and 2018, average annual rainfall in Nigeria's study area was 2.066 mm (Bonneau *et al.*, 2014). Rainfall distribution is monomodal, with a dry season from November to March, and a rainy season from April to October (Fig. 1). According to Bonneau *et al.* (2014), rainfall is fairly regular, and it is highly unlikely that oil palms suffer from drought in this area unless an exceptionally dry period occurs. Nevertheless, an El Niño phenomenon occurred and resulted in more than five months of unusual drought with just 338.7 mm total precipitation between November 2015 and March 2016. In the study area, between 1996 and 2018, average annual temperatures ranged 25.0 °C to 27.8 °C, and average annual radiation was $13.78 \text{ MJ m}^{-2} \text{ d}^{-1}$.

The experimental site in Indonesia (Aek Loba Timur estate) is located on the littoral plain of North Sumatra, along the Malacca strait (2°38' 56" N latitude and 99°40' 52" E longitude at an elevation of 35 m.a.s.l.). Between 1995 and 2014, the average annual rainfall in the Indonesian study area was 2.255 mm (Ollivier *et al.*, 2017), well distributed over the year (Fig. 1). Average annual temperature ranged 27.0 °C to 28.5 °C. Annual average radiation was lower than in Nigeria according to Quencez, (1996).

Before the Nigerian 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. Indonesia's experimental site was an oil palm replanting area. In both Nigeria and Indonesia, the experimental land consisted of a vast sedimentary formation with a flat landscape and ferralsol soil type (FOA nomenclature) (Bonneau *et al.*, 2017; Ollivier *et al.*, 2017). The soils are deep, very sandy on the surface, with a gradual increase in clay content with depth, and do not include coarse elements. Soil fertility was lower in Nigeria than in Indonesia, especially in organic matter. Table (ST) 1, summarizes the soil characteristics at the onset of the trials in both Indonesia and Nigeria.

2.2 Planting material

Four different oil palm (*Elaeis guineensis* Jacq.) progenies were selected for this study. Their selection was based on similar highest fresh fruit bunch (FFB) and crude palm oil (CPO) production in Indonesia and further on observed contrasting leaflet K and Mg concentrations after equal fertilizer applications (PIC, 2011). All progenies used were *Tenera* crosses from two different genetic origins. Progenies C1, C2 and C3 are from *Deli* × *La Mè* origin and progeny C4

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

Progenies	<i>Dura</i> (Male parent)	<i>Dura</i> origins	<i>Pisifera</i> (Female parent)	<i>Pisifera</i> origins	Genetic origins
C1	PO 2630 D	DA 10D × 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).

from *Deli* × *Yangambi* origin (Tab. 1). These 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

Progenies' palm seedlings were produced following the same methodology (CIRAD, 2008) for both Indonesia and Nigeria plantations. Palm seeds were maintained in a germination room for three to four months. Germinated seeds were sown in a pre-nursery and the seedlings were grown for three months in the shade, after which they were transferred to an unshaded nursery and kept there for eight more months before being transplanted to the field. In the pre-nursery and nursery stages, irrigation and fertilization were performed regularly to improve all progenies seedlings' growth, uniformly. Abnormal seedlings were discarded each month. At the end of the nursery period, only palm seedlings that met growth planting criteria were selected for plantation. At the age of eight months in the nursery, only oil palm seedlings with 0.6 to 1 m in height, 18 to 22 cm of collar girth, 6 to 8 functional fronds, and showing no disease and nutrient deficiency symptoms (CIRAD, 2008), were selected for the experiment.

In the Nigerian 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 applications schemes with three levels of fertilizer (K0-K1-K2 and Mg0-Mg1-Mg2, respectively) are presented in Table (ST) 2-A.

In Indonesia, over the 8-years period (2003–2011) urea and phosphorus (15.5 kg palm⁻¹ and 4.8 kg palm⁻¹, respectively), representing 7.5 kg palm⁻¹ of N and 2.6 kg palm⁻¹ of P₂O₅,

were applied much more abundantly than in Nigeria (in comparison with the K₂Mg₂ treatment; *i.e.*, the highest fertilization level for the Nigerian experiment), where all palms received similar N and P fertilization. However, the applied quantities of muriate of potash and magnesium fertilizers (15.05 kg palm⁻¹ and 7.2 kg palm⁻¹, respectively), representing 11.2 kg palm⁻¹ of K₂O and 1.7 kg palm⁻¹ of MgO in Indonesia were similar to the quantities applied in the K₂Mg₂ treatment in Nigeria (10.8 kg palm⁻¹ of K₂O and 2.0 kg palm⁻¹ of MgO) which we use here to compare with the Indonesian experiment. The fertilizer application schemes of the variety trial in Indonesia are presented in Table (ST) 2-B.

2.4 Experimental design

In Nigeria, a factorial split-plot design trial with two factors (mineral nutrition (MN) × genetic material: GM) was set up on 33 ha with oil palms spaced 9 m apart in a staggered, equilateral triangle design, resulting in a planting density of 143 plants ha⁻¹ in 2011 (PIC, 2012). All combinations of three levels of potassium chloride (KCl: 60% K₂O) and three levels of kieserite (MgSO₄: 27% MgO) were tested, giving a total of nine fertilizer treatments considered as random effects, applied to the four oil palm progenies considered as subplot, making a total of 36 subplots per replicate. The experimental design contained six replicates, giving a total of 216 subplots. However, in the present paper, we only report results on fertilizer treatment K₂Mg₂. Each subplot area measured ≈ 631 m². In each subplot, data were collected from three rows of three useful palms. Within each fertilized plot, the palms in each subplot were surrounded by border palms in all directions (45 border palms per fertilizer plot). About 350 additional border palms were 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. Measurements were taken for five years, from Y3 (2013) to Y7 (2017).

The experiment in Indonesia is a variety trial planted in 2004 with 25 oil palm progenies, composing a nearly complete

factorial design (5×5 balanced lattice) with 6 replicates; each subplot contained 16 palms (4 rows \times 4 palms). Palms were spaced 9 m apart in a staggered, equilateral triangle design, resulting in a planting density of 143 plants ha^{-1} . Measurements were taken for eight years from YAP 3 (2006) until YAP 8 (2011) (Ollivier *et al.*, 2017).

2.5 Parameters measured

2.5.1 Leaflet nutrient concentrations: leaf analysis

At both experimental sites (Nigeria and Indonesia), leaflet nutrient concentrations were analyzed each year in December. Three leaflets were sampled on each side (left and right) at the middle of leaf rachis of rank 17 (Ollivier *et al.*, 2017) from each of the nine central useful palms in each subplot in Nigeria and from each of the sixteen central useful palm in each subplot in Indonesia. Leaflet samples were dried in an oven at 80 °C for at least 48 h (CIGE, 2013). K, Mg and Ca concentrations were analyzed using the standard CIRAD laboratory protocol for plant tissue analysis (CIRAD, US 49, France), which uses inductive coupled plasma-optical emission spectrometry (Model: ICP-OES Agilent 720-ES) after double calcination extraction following Pinta (1973), Doğan and Akinci (2011) and Ciriaco da Silva *et al.* (2011).

In addition to K, Mg and Ca, analyses were also carried out on nitrogen (N), phosphorus (P) and chlorine (Cl) leaf mineral concentrations, in order to assess the interaction effects of their leaflet concentrations on the main minerals tested in this experiment. Mineral concentrations are expressed as a percentage (%) of leaflet dry matter (DM).

Total leaf cation charges (TLCC) and mineral proportions

Total leaf cation charges (TLCC) were calculated following Fairhurst and Mutert (1999); Foster (1999) and Corley and Tinker (2016):

$$\text{TLCC} = \left((\text{Leaflet K}/\text{MM}_K) + (\text{Leaflet Ca}/\text{MM}_{Ca}) + (\text{Leaflet Mg}/\text{MM}_{Mg} \times 1000) \right). \quad (1)$$

TLCC is expressed in centimol per kg (cmol kg^{-1}) of leaflet dry matter (DM).
and

$$[\text{m}\%] = \left(\frac{(\text{Leaflet m}/\text{MM}_m \times 1000)}{\text{TLCC}} \right), \quad (2)$$

where [m %] is the leaflet mineral proportion, followed by the standard of deviation (sd),
with

$$\text{MM}_m = \text{MA}_m / V, \quad (3)$$

where:

- Leaflet m: leaflet mineral concentration;
- MM: molecular mass;
- MA: atomic mass ($\text{MA}_K = 39.1 \text{ g/mole}$; $\text{MA}_{Ca} = 40.078 \text{ g/mole}$ and $\text{MA}_{Mg} = 24.305 \text{ g/mole}$);
- V: Valence;
- m: mineral (K, Mg and Ca).

2.5.2 Assessment of the oil palm progenies' mineral category

Since oil palm grew faster in Indonesia than in Nigeria, average leaflet K, Mg and Ca concentrations were calculated from the 3rd to the 6th YAP in Indonesia and from the 4th to the 7th year after planting (YAP) in Nigeria to enable adequate comparison of the progenies' mineral (K, Mg and Ca) categories between both countries, in Nigeria and Indonesia (PIC, 2011).

To compare leaflet mineral concentrations of oil palm progenies between the Indonesia and Nigerian ecologies, the progenies' mineral categories were determined. This parameter was assessed based on the concentrations of K, Mg and Ca relative to TLCC (Eq. 2).

For each progeny, a Tukey test was performed on each K, Mg and Ca concentration. The four progenies were then classified in mineral categories. We used $^+/-$ signs to distinguish the progeny categories: (category +): leaflet mineral concentration ($\text{lmc} > \text{almc}$) and category (-): $\text{lmc} < \text{almc}$; where almc is the average leaflet mineral concentration of the four progenies (Jacquemard *et al.*, 2009).

2.6 Statistical analysis

A mixed model was used for the analysis of variance (ANOVA) of progenies' leaflet mineral concentrations and the country effect. In this study, parameters (leaflet mineral concentration and mineral proportion) were averaged across all 9 useful palms of each subplot of the K_2Mg_2 fertilizer treatments in Nigeria and all 16 useful palms of each subplot in Indonesia. To account for the split-plot nature of the Nigerian design, a mixed-effects model was used, with the sub-block effects (*i.e.*, fertilizer \times block interaction) as a random factor. The model was used to compare the average leaflet mineral concentrations and minerals proportions (between 3 to 6 YAP in Indonesia and 4 to 7 YAP in Nigeria), according to the progenies in both countries. Tukey's multiple comparison test was applied to compare which means of the different parameters significantly differed between progenies and countries.

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

3 Results

3.1 Differences in leaflet K, Mg and Ca concentrations between progenies grown in Indonesia and Nigeria

In both Indonesia and Nigeria, differences in leaflet potassium (K), magnesium (Mg) and Calcium (Ca) concentrations averages were highly significant ($p < 0.0001$) between progenies (Tabs. 2 and 3).

In Indonesia, progeny C4 had the highest average leaflet K concentration, whereas progeny C2 and C3 had the lowest values, which were not significantly different from each other. Progeny C1 had intermediate leaflet concentrations (Tab. 2). Progenies were ranked according to their average leaflet K concentrations (3–6 YAP) as $C4 > C1 > C3 \geq C2$ (Tab. 2).

Leaflet Mg concentrations were significantly different across all four progenies with progeny C3 having the highest

Table 2. Average K, Mg, and Ca concentrations (% of leaflet dry matter), total leaf cation charge (TLCC), and mineral proportions (% relative to TLCC), observed in the leaflet of rank 17 fronds of four oil palm progenies evaluated from 3 to 6 YAP in Indonesia (PIC, 2011).

Progenies	K concentration (%)	Mg concentration (%)	Ca concentration (%)	TLCC (cmol kg ⁻¹ DM)	[K] (%)	[Mg] (%)	[Ca] (%)	Mineral categories
C1	1.11 b	0.201 d	0.84 c	83.1 c	34 b	20 c	46 c	K{+} Mg{-} Ca{-}
C2	0.82 c	0.224 c	1.15 a	91.6 a	23 c	20 c	57 a	K{-} Mg{-} Ca{+}
C3	0.86 c	0.303 a	0.98 b	91.4 a	24 c	27 a	49 b	K{-} Mg{+} Ca{+}
C4	1.27 a	0.250 b	0.83 c	89.9 b	36 a	23 b	42 d	K{+} Mg{+} Ca{-}
p	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	

YAP: Year after planting, p: Probability.

Different letters (a, b, c, and d) indicate significant differences in parameters among oil palm progenies according to a Tukey's test. Progenies were classified in 2 categories: category (+): leaflet mineral concentration (lmc) > almc and category (-): lmc < almc; where almc is the average leaflet mineral concentration of all progenies (Jacquemard *et al.*, 2009).

[K], [Mg], [Ca]: Mineral proportions (% relative to TLCC).

Table 3. Average K, Mg and Ca concentrations (% of leaflet dry matter), total leaf cation charges (TLCC) and mineral proportions (% relative to TLCC) of the K₂Mg₂ fertilizer treatment, observed in leaflets of rank 17 fronds of the oil palm progenies, evaluated from 4 to 7 YAP in Nigeria.

Progenies	K concentration (%)	Mg concentration (%)	Ca concentration (%)	TLCC (cmol kg ⁻¹ DM)	[K] (%)	[Mg] (%)	[Ca] (%)	Mineral categories
C1	1.09 b	0.260 b	0.91 a	95.0 c	30 b	23 c	48 c	K{+} Mg{-} Ca{-}
C2	0.98 c	0.261 b	1.03 a	97.9 b	26 c	22 d	52 a	K{-} Mg{-} Ca{+}
C3	0.90 c	0.308 a	1.01 a	98.7 a	23 d	26 a	51 b	K{-} Mg{+} Ca{+}
C4	1.26 a	0.261 b	0.76 b	91.6 d	35 a	24 b	41 d	K{+} Mg{+} Ca{-}
p	< 0.0001	0.03	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	

DM = Dry matter; YAP: Year after planting, p: Probability.

Different letters (a, b, c and d) indicate significant differences in the different parameters among oil palm progenies according to a Tukey's test. Progenies were classified in 2 categories: category (+): leaflet mineral concentration (lmc) > almc and category (-): lmc < almc; where almc is the average leaflet mineral concentration of all progenies (Jacquemard *et al.*, 2009).

[K], [Mg], [Ca]: Mineral proportions (% relative to TLCC).

leaflet Mg concentration and progeny C1, the lowest. Progenies were ranked according to their average leaflet Mg concentrations (3–6 YAP) as followed C3 > C4 > C2 > C1.

Progeny C2 had the highest leaflet Ca concentration whereas progenies C1 and C4 had the lowest and significantly similar values and progeny C3 had an intermediate leaflet Ca concentration. Progenies were ranked according to their average leaflet Ca concentrations (3–6 YAP) as C2 > C3 > C1 ≥ C4 (Tab. 2).

In Nigeria, progeny C4 also had the highest average leaflet K concentration and progeny C3 had the lowest (Tab. 3). Progenies were ranked according to their average leaflet K concentrations (4–7 YAP) as C4 > C1 > C2 > C3 (Tab. 3).

Progeny C3 exhibited a significantly higher average leaflet Mg concentration compared to the other three tested progenies (Tab. 3). Progenies were ranked according to their average leaflet Mg concentrations (4–7 YAP) as C3 > C4 ≥ C2 ≥ C1 (Tab. 3).

Progeny C2 had the highest leaflet Ca concentrations and progeny C4 had the lowest (Tab. 3). Progenies were ranked

according to their average leaflet Ca concentrations (4–7 YAP) as C2 ≥ C3 ≥ C1 > C4 (Tab. 3).

However, the country effect was not significant (p = 0.352) for any leaflet cation's concentrations. The latter showed that the environment did not affect leaflet mineral concentration in the tested oil palm progenies.

3.2 Oil palm progenies' mineral proportion and mineral category

In Indonesia, average leaflet [K] was 29.3 ± 6.7%, average leaflet [Mg] was 22.5 ± 3.3% and average leaflet [Ca] was 48.5 ± 6.4% (Tab. 2) whereas in Nigeria, average leaflet [K] was 28.4 ± 4.5%, average leaflet [Mg] was 23.4 ± 1.4% and average leaflet [Ca] was 48.2 ± 4.3% (Tab. 3).

In Indonesia, progenies C2 and C3 had statistically equal leaflet [K], whereas in Nigeria, leaflet [K] differed across all progenies. In the two studied environments (Nigeria and Indonesia), progeny C3 ranked last and progeny C4 ranked first for leaflet [K] among all tested progenies. All progenies

Table 4. Average N, P and Cl concentrations (% of leaflet dry matter), evaluated from 4 to 7 YAP in Nigeria and 3 to 6 YAP in Indonesia

Countries	Progenies	Leaflet mineral concentration (% of DM)		
		N	P	Cl
Nigeria	C1	2.85 a	0.169 a	0.58 a
	C2	2.79 b	0.166 b	0.58 a
	C3	2.75 b	0.162 b	0.55 b
	C4	2.67 c	0.160 c	0.59 a
Indonesia	C1	2.85 a	0.168 b	0.79 a
	C2	2.81 a	0.166 b	0.77 b
	C3	2.83 a	0.166 b	0.75 b
	C4	2.75 b	0.173 a	0.79 a

DM = Dry matter.

Different letters (a, b, c and d) indicate significant differences in the different parameters between oil palm progenies according to a Tukey's

were classified in the same K category in the two environments (Nigeria and Indonesia). K category of progenies C1 and C4 was (+) whereas that of progenies C2 and C3 was (−) (Tabs. 2 and 3).

Progeny C2 ranked last for leaflet [Mg] among all the progenies tested in Nigeria, whereas in Indonesia progenies C1 and C2 had similar leaflet [Mg]. Progeny C3 ranked first for leaflet [Mg] among all the progenies in both environments. Progenies were in the same Mg category in the two environments (Nigeria and Indonesia). Mg category of progenies C1 and C2 was (−) whereas that of progenies C3 and C4 was (+) (Tabs. 2 and 3).

In both Nigeria and Indonesia, leaflet [Ca] differed significantly between all progenies. Progenies in both countries were ranked similarly based on leaflet [Ca]. Therefore, progenies were classified in the same Ca categories in the two countries. Ca category of progenies C1 and C4 was (−) whereas that of progenies C2 and C3 was (+) (Tabs. 2 and 3).

In both environments, each progeny in the (+) category for K, was classified in the (−) category for Ca and vice versa. However, this was not the case for progenies' K and Mg categories (Tabs. 2 and 3).

3.3 Other minerals

In both environments, average nitrogen (N), phosphorus (P) and chlorine (Cl) concentrations significantly differed between progenies ($p < 0.0001$).

In Nigeria, progenies' C1, C2, C3 and C4 average leaflet N concentrations were 2.85%, 2.79%, 2.75% and 2.67% of DM, respectively, whereas average leaflet P concentrations were 0.169%, 0.166%, 0.162% and 0.160% of DM, respectively. Progeny C1 had the highest leaflet N and P concentrations, whereas progeny C4 had the lowest concentrations of these minerals. Progeny C3 had the lowest leaflet Cl concentration (0.55%) which was significantly lower than that of progenies C1 (0.58%), C2 (0.58%) and C4 (0.59%), among which no significant differences were found (Tab. 4).

In Indonesia, average leaflet N concentrations were 2.85%, 2.83%, 2.81% and 2.75% whereas average leaflet P concentrations were 0.168%, 0.166%, 0.166% and 0.173% of DM for

progenies C1, C2, C3 and C4, respectively. Progeny C1, C2 and C3 had statistically similar values for leaflet N concentrations, but significantly higher than that of progeny C4, whereas the latter had significantly higher leaflet P concentration than that of progenies C1, C2 and C3 which were similar. Average leaflet Cl concentrations were 0.79%, 0.77%, 0.75% and 0.79% of DM for progenies C1, C2, C3 and C4, respectively. Progenies C1 and C4 had similar and statistically higher leaflet Cl concentrations compared to progenies C2 and C3 of which leaflet Cl concentrations were also similar (Tab. 4).

4 Discussion

4.1 Change in leaflet K, Mg and Ca concentrations with oil palm age and according to genetic origins

Leaflet Mg concentrations in some of the progenies tested in this study were within the normal range of leaflet magnesium concentrations, which is 0.3–0.45% of DM for oil palm trees younger than 6 YAP, and between 0.25% and 0.4% of DM for trees older than 6 YAP (Fairhurst, 1996; 1998; Fairhurst *et al.*, 2005; Rankine and Fairhurst, 1999).

A number of experiments conducted in Africa (Cameroon: 22–24 YAP), Latin America (Peru: 11–13 YAP, Colombia: 14–16 YAP, Ecuador: 16–18 YAP) and Southeast Asia (two different trials in Indonesia: 9–11 and 14–16 YAP) on the yield response to magnesium fertilizer treatments (Dubos *et al.*, 1999), revealed that leaflet Mg concentration of oil palms of *Deli × La Mé* origin was the lowest among oil palm origins including *La Mé* and *Yangambi* oil palms, as well as *Deli × La Mé* and *Deli × Yangambi* progenies. This was not the case in our study as in both Nigeria and Indonesia, leaflet Mg concentrations of progeny C3 (*Deli × La Mé* progeny) were always higher than those of progeny C4 (*Deli × Yangambi* progeny) (Tabs. 2 and 3). A progeny's leaflet Mg concentration is therefore probably related to its genetic background and can therefore probably be useful to determine the progeny's Mg requirements.

In our experiment, the differences in leaflet Mg concentrations observed between the progenies could be explained by their different Mg absorption capacities which is linked to their Mg requirements (Ollivier *et al.* 2017), but also by different

Mg partitioning within the palm trees (Dubos *et al.* 2010; Corley and Tinker, 2016) or by different Mg losses (efflux) (Dubos *et al.* 1999, 2019; Corley and Tinker, 2016).

According to Fairhurst *et al.* (2005), Rankine and Fairhurst (1999) and Bonneau *et al.* (2017), leaflet K concentrations remain more or less constant throughout the oil palm life cycle, *i.e.*, between 1% and 1.3% in oil palm trees younger than 6 YAP and between 0.9 and 1.2% in older oil palm trees. Leaflet K concentration recommended by the latter authors is in the range of the leaflet K concentration of some progenies tested in the present study. The high leaflet K concentrations observed in progeny C4 in both environments is probably linked to its high K absorption capacity in environments where K is abundantly available (Naquiddin *et al.*, 2020). In our study, the tested progenies received abundant K and Mg fertilization in both countries (Nigeria and Indonesia) as 1.2 kg K₂O palm⁻¹ and 0.15 kg MgO palm⁻¹ and are sufficient to not induce K or Mg deficiencies which can limit the productivity (PalmElit, 2019; Fairhurst and Caliman, 2001; Fairhurst *et al.*, 2005). The first Mg deficiency symptoms usually appear when leaflet Mg concentrations are between 0.20% and 0.24% (Dubos *et al.*, 1999). However, Fairhurst and Caliman (2001) reported the appearance of the first Mg deficiency symptoms below a threshold of 0.25% of leaflet Mg concentration in sensitive progenies whereas other progenies can tolerate leaflet Mg levels as low as 0.15%. Even in palms with the lowest leaflet K concentrations, no K deficiency symptoms were observed in any of the progenies tested in this study, probably because visual K deficiency symptoms appear very late, and only when leaflet K concentration < 0.5% of DM (Fairhurst *et al.* 2005).

The high leaflet K concentrations observed in progeny C4 in both environments, may also be explained by a better-developed root system. Nodichao (2008, 2011) demonstrated genotypic variability in the development and distribution of the oil palm root system under different potassium fertilization and irrigation regimes. The high leaflet K concentration in progeny C4 may also be explained by its genetic origin (*Deli* × *Yangambi*) which is known to be less productive (Nouy *et al.*, 1999; Cros *et al.*, 2013) than that of oil palms of *Deli* × *La Mé* genetic origin, such as the C1, C2 and C3 progenies tested in the present study. The weight of harvested bunches of oil palms of *Deli* × *La Mé* origin can reach 1.8 times that of oil palms of *Deli* × *Yangambi* origin (Cros *et al.*, 2013). Progeny C4 (*Deli* × *Yangambi*) was subjected to lower K exports through the harvested bunches (as it had a lower yield), which may result in higher K concentrations in its leaves. Conversely, the lowest leaflet K concentration observed in progeny C3 could be explained by its genetic origin (*Deli* × *La Mé*) as oil palms of that origin are the highest bunch producing palms, compared to *Deli* × *Yangambi* oil palm materials (Nouy *et al.*, 1999; Cros *et al.*, 2013).

If progeny C3 showed the largest vegetative development and growth compared to the other progenies, we can assume that the lowest leaflet K concentrations observed in this progeny may also be explained by K dilution in its oil palm tissue. This hypothesis needs further research to be confirmed.

Calcium (Ca) is a mineral that is sufficiently present in most tropical soils and is therefore abundantly available to the palms. Ca is therefore normally not applied as a fertilizer, except for palms in acidic soils which should be treated with

Ca for liming (Terra, 2014; IPNI, N°18-11041). The amount of Ca in oil palm tissue influences oil palm's K and Mg absorption and use (Ciriaco da Silva *et al.*, 2011). Also, Teoh and Chew (1988b) concluded that relationships between minerals can influence the leaflet mineral concentrations of an oil palm progeny. The latter can explain the fact that in the studied progenies when leaflet K concentration is high, its leaflet Mg or Ca concentrations are lower and vice versa. This could also explain differences in leaflet N, P and Cl concentrations observed between progenies.

4.2 Progenies' mineral concentrations, proportions and categories: environmental effects and interaction between K and Mg

In our experiments with abundant K and Mg fertilization, the environment had no influence on oil palm leaflet mineral concentrations of none of the oil palm progenies considered in this study. As a consequence, the mineral (K, Mg and Ca) proportions of each progeny were also similar between the two environments. The absence of difference in leaflet mineral concentrations between Nigeria and Indonesia, despite the differences in rainfall (Fig. 1), and consequently in soil humidity, as well as solar radiation (Quencez, 1996) between both environments, may be related to the specific and unchanged capacity in mineral uptake of each progeny. This hypothesis needs further studies to be confirmed.

According to Knecht *et al.* (1977), palm tree age can also influence leaflet mineral concentrations. However, the one-year difference in palm age between the Nigerian and Indonesian experiments is sufficiently small to assume that it did not influence differences in leaflet mineral concentrations between the two environments.

The absence of differences in progenies' mineral categories between the two ecologies shows that the mineral category of the four oil palm progenies is mainly geared by their genetic background (Ollivier *et al.*, 2015), suggesting that progeny is the most important factor determining leaflet mineral concentrations.

Oil palm mineral requirements depend on physiological parameters such as the historical mineral status of the whole plant and the sink strength of the aerial system (number of functional leaves, presence of male and female inflorescences), which may vary over the seasons (Lynch, 1995; Legros *et al.*, 2006).

Prabowo *et al.* (2012) have demonstrated that palms of a given progeny have different nutrient requirements depending on the ecology in which they are grown. The fact that in our study, leaflet mineral concentration categories do not depend on the cultivation environment (at least not in Nigeria and Indonesia) does not necessarily mean that oil palm progenies have the same mineral requirements in different environments, but rather means that each progeny has a specific mineral status. The observed differences in leaflet mineral concentrations between progenies under the same conditions (Tabs. 2 and 3) underpin the latter conclusion. *E.g.*, progeny C3 was the vegetal material with the highest leaflet Mg concentrations and the lowest leaflet K concentrations, whereas progeny C4 exhibited the highest leaflet K concentrations, irrespective of the environment (Nigeria and Indonesia).

Moreover, the abundant K and Mg fertilizers applied to the progenies in our study have most probably offset possible negative environmental effects on nutrient absorption and repartition, so that these minerals have reached their saturation levels in the leaflet tissues of the tested progenies.

Observing similar leaflet mineral concentrations in contrasting environments such as those of Nigeria and Indonesia does not mean that these progenies will necessarily achieve similar yields in both environments as the yield is largely influenced by climate conditions. The higher solar radiation (Quencez, 1996) and the lack of well-distributed rainfall over the year observed in Nigeria's environment, are the main factors that limit oil palm production in West Africa, as was shown in Benin (Nouy *et al.*, 1999). Sufficient water is needed for photosynthesis and metabolite synthesis. Water limitation induces stomatal closure which limits CO₂ absorption during photosynthesis (Legros *et al.*, 2006; Lamade *et al.*, 2014; Fabre *et al.*, 2020) and consequently decreases yield (Legros *et al.*, 2006; Lamade *et al.*, 2014; Fabre *et al.*, 2020).

The fact that the selected progenies' mineral (Mg and K) categories were the same in Nigeria as in Indonesia, implies that in our experiment, the environment had no effect on leaflet mineral concentrations. This suggests that with sufficient fertilization, the mineral uptake capacity of each progeny does not depend on the environment (precipitation patterns).

5 Conclusion

We found that in both Nigeria and Indonesia, progeny C3, which is of *Deli* × *La Mé* origin, had the highest leaflet Mg and the lowest leaflet K concentrations, whereas progeny C4, which is of *Deli* × *Yangambi* origin, had the highest leaflet K concentration. Our results show that under a non-limiting supply of K and Mg fertilizers, the considered oil palm progenies' leaflet mineral concentrations and consequently, their mineral requirements as well as their mineral proportions, do not depend on the cultivation environment and therefore that the genotype is the most important factor determining leaflet nutrient concentrations. Our four oil palm progenies' leaflet mineral concentrations were ranked in the same order in Nigeria as in Indonesia. Our results further suggest that the tested progenies' mineral categories are geared by their genetic backgrounds. This raises two new research questions:

–Are differences in leaflet mineral concentrations between oil palm progenies linked to differences in growth and/or morphological characteristics?;

–Are differences in leaflet mineral concentrations of different oil palm progenies linked to different oil and bunch (weight/number) yields between progenies in specific environments?

To answer these questions, future research should further explore differences in performance and mineral categories among progenies tested in this study. This will be instrumental in selecting oil palm progenies that require less fertilizer to obtain a given yield, or that are more compatible with marginal zones such as West African areas that are characterized by

infertile soils resulting from intensive farming without restitution of mineral and organic matter and by relatively low precipitation which limits mineralization. The answers to these research questions will also guide industrial plantation managers, who can improve oil palm profitability by supplying adequate fertilizer applications. Moreover, developing oil palm material that makes more efficient use of fertilizers will favor smallholder oil palm plantations for whom fertilizers are often the most expensive production factors.

Supplementary Material

Supplementary Fig. (SF) 1. Leaflet K and Mg contents of 116 high yielding oil palm progenies tested on Aek Loba Timur genetic block in Indonesia showing the four best contrasting progenies that survived the trial based on their mineral contents used to set up the mineral nutrition (MN) × genetic material (GM) trial in Nigeria.

“*Av*” is the average of leaflet mineral (K or Mg) concentration of an oil palm population and “*sd*” is its standard deviation.

Supplementary Table (ST) 1. Physico-chemical soil characteristics at the onset of the Nigerian and Indonesian trials.

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).

Supplementary Table (ST) 2. Fertilizer application scheme (in g of fertilizer per palm) in Nigeria (A) and Indonesia (B).

The Supplementary Material is available at <http://www.ocl.fr/10.1051/oc/2022016/olm>.

Declaration of competing interests

Olivier Dassou and Hervé Aholoukpè are employed by INRAB of which Adolphe Adjanohoun is the General Director. Reinout Impens 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-Gasselín 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.

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