

Genetic Variation in Nutrient Uptake and Nutrient Use Efficiency of Oil Palm.

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ABSTRACT

Observations of the vegetative and reproductive biomass produced annually and the mineral element contents have been conducted on diverse oil palm plant materials tested in a genetic test in Indonesia. The results show that the nutrient uptake (for trunk growth, leaf renewal and bunch export) greatly varies (CV = 10% for N uptake and 17% for K uptake) with the origins of the planting materials considered. For equivalent production, the uptake in nutrients of certain plant material may differ very significantly; for the same level of uptake in nutrients, production can vary significantly. This study supports the hypothesis that the optimal nutrient thresholds are intrinsically linked to the plant material. It assumes that some planting materials have different needs and that a fertilizer regime could be adapted to their specific needs without losses in performance. To confirm these assumptions, the need of implementing specific experimental devices with differentiated fertilization regimes is discussed.

Keywords: Oil palm, nutrient uptake, plant genetics

INTRODUCTION

Oil palm cultivation in Southeast Asia has dramatically increased over the last decade, particularly in Indonesia, which is the highest producing country: the estimated harvested area has more than doubled from 2.8 million ha to 6.6 million ha, and the production of crude palm oil has risen from 9.6 million tonnes to 26.9 million tonnes for the period 2002-2012 (FAO Stat 2014). In the same period, the consumption of potash fertilizers in the Indonesian agricultural sector has more than tripled from 260.000 to 950.000 tonnes of potassium oxide (K_2O); nitrogen fertilizers have increased by 50% from 1.97 million tonnes to 2.95 million tonnes nitrogen (N), and the consumption of phosphate fertilizers has risen from 254.000 to 680.000 tonnes of phosphorus pentoxide (P_2O_5) (FAO stat 2014). Oil palm, which is predominantly cultivated in low fertility tropical soils and whose cultivation is characterised by high nutrient removal in its harvest products, contributes significantly to the increase in fertilizer consumption at the national level. At the plantation level, the cost of the fertilizer input that is required to sustain high yields over several crop cycles (Dubos and Flori, 2014) ranges from 46% of the total cultivation costs in Thailand (Silalertruksa et al., 2012) to 70% in Malaysia (Goh et al., 2003).

To reduce the application of mineral fertilizers, the recycling of palm oil mill effluent, empty fruit bunches or compost is widely used, but this is often impracticable for an entire plantation due to the limited supply and high cost of transporting organic fertilizers away from the mill. In large plantations, foliar diagnosis is the main way to assess nutrient status and fertilizer requirements (Foster 2003). This diagnosis is supported by multi-factorial fertilizer trials that provide data to calculate the response curves and surfaces and the optimum content to achieve the best economic

yield. Fertilizer recommendations are adjusted on that basis by comparing the leaf content with the optimum levels (Webb 2009).

However, differences in the foliar levels among various genetic origins are reported, thus complicating the interpretation of the results and their extrapolation to plantings of diverse origins (Tan and Rajaratnam 1978; Jacquemard et al., 2009; Ollivier et al., 2013; Lee et al., 2014). In Malaysia, breeders recommend revising the current generalized critical levels of leaf nutrients based on inland and coastal areas, and they support a site- and planting material-specific approach. (Lee et al., 2011)

In addition to leaf mineral content, it is well known that the genetic characteristics of oil palm contribute to producing genetic variability in morphological traits such as height, canopy size, bunch size, the amount of mesocarp, kernel content and vigorous levels (Soh et al., 2003). Meanwhile, a high level of variability in yield has been observed in oil palm progenies (Norziha et al., 2008).

It is likely that the genetic variability in organ size and organs' mineral content is linked to differences in nutrient uptake and the efficiency between oil palm origins, but despite all of the efforts made in this area of research, this genetic variability is still relatively unknown. Recent findings have shown significant differences in nitrogen uptake among 9 different oil palm genotypes (Law et al., 2012), as demonstrated using the ^{15}N labelling method. However, that study was performed in a greenhouse on 6- and 9-month-old plants, which can be analysed by using destructive methods to measure their nutrient uptake with a limited budget. Such a method would be unaffordable on adult palms in a commercial plantation, and no direct measurement of N uptake has been reported on adult palms. In our present study, the amount of nutrients immobilized in plant

biomass and used for the crop was calculated by assessing the above-ground biomass of the various compartments of the palm (trunk, leaves, and bunches) and their respective nutrient concentrations with non-lethal tree-sampling methods.

Fageria et al., (2008) and other authors used non-fertilized/fertilized comparisons to discuss the efficiency of fertilization, but they focused on the agronomical or physiological efficiency of fertilization, which can be defined as the proportion of fertilizer that is actually used by the crop, regardless of its production (Corley and Tinker 2003). For oil palm, no study that differentiates genotypes by their ability or effective use of the resources given to their production has been found. This paper uses observations made in a genetic trial in Indonesia to discuss the nutrient effectiveness of oil palm origins, defined as the ability to produce a higher economic yield with a given quantity of applied or absorbed nutrient compared with other plants under similar growing conditions.

MATERIALS AND METHODS

Description of Study Site

The study was conducted at the Aek Loba estate, which is located on the littoral plain of North Sumatra, Indonesia, along the Malacca strait (2° 38'56" N latitude and 99°40'52" E longitude). The average elevation is 35 m above sea level. The climate of the experimental site is humid tropical and highly favourable to oil palm. The mean annual rainfall is 2255 mm and well distributed over the year, with 134 rainy days. The annual rainfall during 2003-2013 varied from 1488 mm in 2010 to 2962 mm in 2003. The mean temperature ranges from 22°C (minimum) to 32°C (maximum). The average relative humidity varies from 62% to 69% (Climate, Average Weather of Indonesia. 2015). The soils of Aek Loba are rhyolitic soils of volcanic origin derived from erupted material from Lake

Toba. The soil of the experimental site is sandy loam, comprising 78% sand, 8% silt and 14% clay at 0-60 cm soil depth. The Exchangeable Cation Capacity (CEC) of the soil is low at 9.3 cmol kg^{-1} . The soil is moderately acidic, with a pH of 5.7, 1.7% organic carbon, 0.06% N and 32 mg kg^{-1} P Bray.

The experiment was established in 2003 and followed a first generation of oil palm planted in the 1970s. The oil palms are planted at a spacing of $9.0 \times 9.0 \text{ m}$ triangle (143 palms/ha).

Planting Material

The experiment is a variety trial planted with 25 oil palm crosses, composing a nearly complete factorial mating design between 5 Deli Dura derived from sources selected since the end of the 1950s by various institutions and 6 Tenera from various origins (table 1). These parents have been chosen in very different origins to represent a wide genetic diversity that might actually be used in an oil palm breeding scheme.

Each Dura was crossed with at least 3 Tenera, and each Tenera was crossed with at least 3 Dura.

The experimental design is a 5×5 balanced lattice with 6 replicates; each elementary plot contained 16 palms (4 rows x 4 palms).

Fertilization

The sources of fertilizers applied in the experiment at the adult stage were urea, rock phosphate, muriate of potash and dolomite (table 2). All nutrients are applied at the same rates for all trees, regardless of their genetic origin. The rates are sufficiently high to ensure that yield is not limited by an insufficient supply of the added nutrients.

Over the 10-year period, the 23 kg of urea, 12.15 kg of phosphates, 24 kg of muriate of potash and 11 kg of magnesium fertilizers applied per palm represented a quantity in elements of 10895 g of N, 4083 g of P_2O_5 , 14745 g of K_2O and 2449 g of magnesium oxide (MgO).

Pruned leaves were fully recycled and disposed in windrows for one of every two interlines.

Observations and Measurements:

Crop Yield

Individual yield data (number and weight of fresh fruit bunches) were recorded every month for all trees from entry into production from Y3 (2006) until Y10 (2013). The average Fresh Fruit Bunch (FFB) produced per year by mature palms was computed for each tree using Y6 to Y10 data.

Bunch Components and Oil Extraction Rate

The analyses of the bunch components, which returned the biomasses of stalks and spikelets, fibres, shells and kernels per kg of fresh bunch, were performed twice on 40 palms per cross according to the IRHO/IGK9 standard (IRHO, 1996). The dry matter (DM) content of the stalks and spikelets was assessed to be 45% of the fresh weight, according to bunch dissections performed in the Ivory Coast (IRHO, 1992).

The determination of the oil content of the mesocarp was performed using the Soxhlet method.

Vegetative Measurements and Estimation of Biomass Production

A non-destructive approach was used to estimate the aboveground biomass production in trunks, leaves and bunches. The frond base biomass, which was estimated to be 20% of the total frond biomass (Henson et al., 2012), and the root biomass, which was estimated to represent 14% (Corley, 2003) or 17% (Jourdan, pers.comm) of the total biomass, were not considered in this study.

Ten years after planting, 2 trees per cross and per replicate (12 trees per progeny) were chosen, and a series of samples was taken on all aboveground plant tissues.

1) Fronds

The frond of rank 17 was cut down as close to the stalk as possible and used to represent all the mature fronds (Aholouké et al., 2013) for the biomass of frond parts. The fresh weight of petioles, rachis and all leaflets was recorded, and subsamples were taken to evaluate the dry matter content and perform a chemical analysis of each part.

For leaflets, a subsample was taken from a 10-cm-long section for one of every 10 leaflets. For the rachis, two 5-cm-long sections were cut at $1/3$ and $2/3$ of its length, and for the petiole, a 5-cm section was cut. All of the subsamples were dried in an oven at 65°C until the mass was stable and then weighed.

In addition, the number of frond bases was observed on one spire of the stem.

The average number of fronds produced per year was estimated for each sampled tree by the number of frond bases divided by 7, assuming that frond bases produced before the age of three cannot be observed.

The biomass produced per year in each frond part was estimated for each sampled tree using the product of the number of fronds per year multiplied by the biomass of that part in frond 17.

To obtain a rough estimate of the total frond biomass and the total aboveground vegetative biomass of a palm at the age of 10, we used 33 functional fronds (which is the typical number borne by a correctly managed oil palm) multiplied by the total biomass of parts from frond 17.

2) Trunks

Trunk diameter was measured at a height of 1.5 m using a calliper whose tips were placed between leaf scales.

Two samples were taken perpendicularly at a height of 1.5 m using a 60-cm-long Pressler auger with a 5.5 mm diameter. For each sample, the gimlet was pushed into the stem between leaf scales to a depth of half the diameter. The volumes and both the fresh and dry weights of the cylinders removed from the stem were measured.

The trunk biomass per unit length was estimated for every sampled tree using the product of the volume of a one-meter-long cylindrical stem multiplied by the wood density.

Height measurements from the ground to the base of the 33rd leaf were performed on every palm in the trial at the ages of 6 and 9 years. The annual growth rate was computed for every tree in the trial.

Determination of Tissue Concentration

To limit the number of analyses, the subsamples per organ were grouped by progeny.

In a K nutrition experiment in Indonesia, where K analyses were performed on all ranks, Lamade et al., (2014) considered the leaf of rank 17 to be a good middle estimator of potassium (K) status in the crown.

Representative subsamples of each organ were oven-dried at 65°C for 72 h until reaching a constant weight to determine the dry biomass, ground and then sieved through a 0.5 mm mesh sieve. The samples were then analysed to determine their nutrient concentration at the CIRAD laboratory (CIRAD, US 49, Montpellier, France). The concentration of N was determined using the Dumas method (NF ISO 13878) with an elemental analyser (Leco Trumac N). The concentrations of

phosphorus (P), K, calcium (Ca), and magnesium (Mg) were determined using inductive coupled plasma -- optical emission spectrometry (ICP-OES Agilent 720-ES) after double calcination extraction (Pinta, 1973). The mineral nutrient contents are expressed as a percentage of dry matter, i.e., percentage of biomass.

For bunches, the mineral nutrient contents of each bunch part (stalks and spikelets, fibres, kernels, and shells) were not observed, and a common value found by Zeller and cited in IPNI (1957) was assumed for all crosses (table 3).

Statistical Analyses and Estimation of Mean Nutrient Uptake

In addition to the growth and renewal of the roots, the nutrient uptake corresponds to the growth of the stem, which remains stored for the duration of the crop cycle; the renewal of the leaves, which have a shorter life cycle and are eventually exported; and the production of reproductive organs (Corley and Tinker 2003).

The annual increase in biomass of the stem was estimated as the product of the average trunk biomass per unit length (kg/m) multiplied by the growth of the palm in m/year. Because the sampled trees were not the same for measuring these two singular traits (growth was available for every tree, though trunk biomass per unit length was available only for the sampled trees), the increase in biomass was not available for every tree, and the mean value of this composite trait was not estimable directly using all of the data. A bivariate mixed model with an unstructured covariance structure between traits was therefore used to estimate the cross means for both singular traits and the covariance between them. The mean annual increase in biomass was estimated for each cross as the product of the cross means for the two singular traits plus the covariance between

the traits. The standard error of the means was computed assuming that the estimation of the cross means for singular traits is approximately independent. A t-test was used to perform mean comparisons at the 0.05 level for the composite trait.

In the same way, the biomass exported annually in the various bunch parts was estimated by the product of annual FFB multiplied by the proportion of each bunch part in the bunch. Because the FFB was known for every tree but not bunch component analysis, the cross means for these two singular traits and the covariance between them were estimated using a bivariate mixed model, and the mean annual biomass produced in each bunch part for every cross was computed as the product of the means for singular traits plus the covariance.

The biomass produced every year in frond parts (i.e., petiole, rachises and leaflets) are also composite traits, but in this case, the singular traits (number of fronds emitted per year and the weight of a given part in the 17th frond) were observed on the same sampled trees. Thus, the cross means could be estimated directly from the products computed for every tree.

The nutrient uptake of each compartment was computed for every cross as the product of the annual biomass produced in the compartment multiplied by the nutrient content of the compartment as it was measured for that cross.

General Combining Ability of the Parents

The cross means for every traits and their standard-errors were used to estimate the General Combining Ability (GCA) of the Dura and Tenera parents with an analysis of variance (ANOVA) that included additive parent effects and the cross effect (interaction between the parents) to test the appropriateness of an additive model. GCAs were computed as Least-Squares means (SAS, 2011) for each level of the Dura and Tenera factors. LSmeans are the means adjusted to correct for the

effect of the partners in each cross and are used to estimate the observation as though all Dura parents had crossed with all Tenera parents in a balanced mating design. Means comparisons were performed with Tukey's test at the 0.05 level.

The MIXED procedure of the SAS software (SAS Inc., Cary, NC, USA) was used to perform the calculations.

The parental effectiveness in nutrient use was compared graphically.

RESULTS

Genetic Variation in Vegetative Growth, Biomass Partitioning and Yields

The GCA of Dura and Tenera parents (mean value of their offspring) for the vegetative measurements and the biomass of trunk and leaves observed at the age of 10, as well as the mean annual fresh fruit bunch production and crude palm oil production observed from 6 to 9 years after planting, are presented in Table 4.

For almost all of the observed growth characteristic variables, i.e., aboveground biomass and yield, significant differences are observed between the Dura parents and the Tenera parents. In all cases, the interaction Dura parent * Tenera parent reveals F values that are considerably lower than the F values of the main effects and are often not significant. Therefore, the effect of a parent (Dura or Tenera) seems to be affected little by its partner in a cross, and a parent can be characterised by its additive value alone.

Because the greatest diversity in genetic origins occurs between Tenera parents, the F values for all of the vegetative traits and biomass are also higher between these parents.

At 10 years, the trunk represents slightly less than two thirds of the aboveground biomass (excluding the reproductive organs), varying from 61% to 66% for the Dura parent and from 60% to 69% for the Tenera parent. The frond biomass, which represents up to one third of the aboveground biomass, comprises the rachis, leaflets and petiole, which represent 39.4%, 37.4% and 23.2% of frond biomass on average, respectively.

The Tenera TNi, TYa and TLmYa, which exhibit a strong vegetative development, are in opposition to TDeAn, TCo and TLm, which exhibit a less powerful vegetative growth. The TLm shows the lowest growth in height, which is characteristic of the La Mé origin and a very low trunk biomass. The total aerial biomass of palms contrasts greatly according to the Tenera parent, varying from 245 kg on average for offspring of TCo to 339 kg for offspring of TNi (standard error of the means approximately 10 kg).

The variables corresponding to the vegetative development of the Duras show that DDe-B and DDe-AB parents transmit a stronger vegetative development than do DDe-A2c, DDe-A4c and DDe-C. The total aerial biomass among Dura origins varies from 264 kg for DDe-C to 313 kg for DDe-B.

The differences among Dura origins are, however, much less marked than those among Tenera origins.

In term of yields, amongst Dura parents, DDe-C, whose offspring are less bulky, is the one of the highest yielders, and DDe-B, which demonstrates stronger vegetative development with a high biomass, shows the lowest yield.

Among Tenera parents, TLm appears to be the highest yielder, approaching nearly 9T of crude palm oil (CPO) per hectare per year (8.8T/ha/yr -- se = 0.14T), followed by TNi; the lowest yield is found with TDeAn.

Genetic Variation in Organ Nutrient Contents

The average nutrient contents (N, P, K and Mg) for 4 palm organs (leaflet, rachis, petiole, trunk) corresponding to the 5 Dura parents and 6 Tenera parents are given in table 5.

As observed, there are gradients of levels for all elements observed, depending on the organs. The nitrogen, phosphorus and magnesium concentrations are highest in photosynthetic organs. It is the reverse for potassium, which has its highest contents in heterotrophic organs (rachis, petiole, trunk), and for chlorine, which is not presented here. The potassium and chlorine contents decrease along the following gradient: trunk>petiole>rachis>leaflet.

Significant differences in the mean content are observed among Dura parents for N in the trunk, for P in the rachis, petiole and trunk, for K in all organs except in the trunk, and for Mg in the rachis only.

Significant differences in content are found among Tenera parents for all of the elements in the trunk and leaflets (except for P in this last organ). In the rachis and petiole, significant differences among Tenera parents are found for P, K, and Mg.

Nitrogen content does not fluctuate greatly among Dura or Tenera parents in the rachis and petiole organs, with mean levels of 0.34% and 0.43% of DM, respectively. The nitrogen level in the leaflet is also quite stable among Dura parents, with an average level of 2.46% of DM. However, significant differences in N content are observed in leaflets among Tenera parents and range from

2.31% to 2.62% of DM for TDeAn and TLmYa, respectively. Significant differences in nitrogen levels are also observed in the trunk within both Dura and Tenera parents in a range of 0.56% to 0.8% of DM found for TLm and TDeAn, respectively.

No significant difference was noticeable among Dura or Tenera parents in the leaflet phosphorus concentrations. The average content is 0.16% of DM. However, in the other organs, the P content occurs at lower concentrations, and significant differences are found. The P levels range from 0.082% to 0.133% of DM in the rachis for TDeAn and TLmYa, respectively from 0.048% to 0.074% of DM in the petiole for TDeAn and TLmYa, respectively, and from 0.050% to 0.068% of DM in the trunk for DDe-A2c and DDe-B, respectively.

For potassium, the situation is more contrasted, and significant differences are observed among Tenera parents in all organs and among Dura parents in all organs except in the trunk. In the leaflets, the K content fluctuates between 0.86% and 1.02% of DM for DDe-A4c and DDe-C, respectively. It is even more accentuated in Tenera parents, where the K values range from 0.76% to 1.10% of DM for TDeAn and TNi, respectively. The mean K content in the rachis is higher, fluctuating from 1.32% to 1.84% of DM for DDe-B and DDe-C, respectively and from 1.26% to 1.79% of DM for TDeAn and TLm, respectively. In the petiole, the mean K content is even higher, occurring in a range between 1.42% and 2.10% of DM for DDe-B and DDe-C, respectively and from 1.41% and 1.91% for TDeAn and TLmYa, respectively. The highest concentrations of K are observed in the trunk and range from 2.16% to 2.73% for the Dura parents and from 1.92% to 3.59% of DM for TCo and TLm, respectively.

The mean magnesium content does not fluctuate greatly among Dura parents in the leaflets (0.184% -- 0.224% of the DM), petioles (0.094% -- 0.129% of the DM) and trunk (0.121% -- 0.148% of the

DM), as significant thresholds were not reached to differentiate them. For the rachis, DDe-B appears to be significantly lower than DDe-AB. A more contrasted situation is observed among Tenera parents, with significant differences observed among them for all organs. In the leaflets, the Mg content fluctuates from 0.171% to 0.228% for TNi and TYa, respectively. In the rachis, the mean Mg varies from 0.056% to 0.091% for TLm and TYa, respectively. In the petiole, the TLm mean content of 0.068% of the DM is also found to be significantly lower than TLmYa or TDeAn, with 0.128% of the DM.

Genetic Variation in Nutrient Uptake per Palm and per Year

The mean uptake of nutrients for vegetative maintenance (growth of the trunk and leaf renewal) and reproductive organs (excluding male inflorescences) calculated per year and per palm for the 5 Dura parents and 6 Tenera parents is presented in table 6. In the two left columns, two scenarios are presented: the first with the restitution of leaves representing the common situation in plantations and the second with the restitution of the leaves and Empty Fruit Bunch (EFB).

The total nitrogen uptake corresponds to an average of 1710 g N per palm and per year for all confounded parents. Nitrogen uptake for leaf renewal represents 65% of the total aerial vegetative and reproductive N uptake. N leaf uptake by DDe-A2c appears to be significantly lower compared with other Dura parents, relative to the lower number of fronds emitted per year and a weaker rachis and petiole section. Leaf N uptake by TYa appears to be significantly higher compared with other Tenera parents due to a larger number of leaflets per frond, a high dry leaf weight and a greater petiole width.

The mean N uptake for annual trunk growth represents 11% of the total yearly N uptake by all parents confounded. However, the N trunk yearly uptake varies quite widely, particularly within Tenera parents, and ranges from 119 g to 280 g per palm for TLm and TNi, respectively.

When the leaves with or without EFB are recycled, there are no significant differences observed in N uptake among Dura parents. However, significant differences are still observed among Tenera parents, and the nitrogen uptake of TNi is found to be significantly higher than that of TDeAn or TCo.

Potassium is the major nutrient in quantity for oil palm, with a mean of total uptake by all confounded Dura and Tenera parents of 2830 g of K₂O per palm per year. Of this amount, 56% is dedicated to leaf renewal, 17% is exported with the crop, and the trunk is confirmed as a major stock organ for K for the remaining 27%.

The amount of K oxides mobilized for trunk growth per year among the different origins and parents contrasts greatly. As observed, it varies from 634 to 896 g of K₂O per palm per year, respectively, for DDe-C and DDe-B amongst the Dura parents, and it fluctuates from 570 to 959 g of K₂O per palm per year for TCo and TLmYa, respectively, among the Tenera parents.

The annual K leaf uptake by DDe-C appears to be significantly higher than that of other Dura parents due to the higher number of fronds emitted per year and the high K concentration found in the rachis and petiole; in contrast, the K leaf uptake by DDe-A2c is significantly lower. Among Tenera parents, TDeAn with 1211 g/palm of annual K₂O uptake dedicated to the leaves was the lowest quantity observed, compared with the highest observed: TYa, with 1773 g/palm of K₂O uptake.

K₂O uptake for the bunches is obviously related to the yield. DDe-C, TLm and TNi, which are the most productive parents, have significantly higher uptake compared with other parents.

When the leaves and EFB are recycled, the K₂O uptake by the DDe-AB and DDe-B parents is significantly higher than that of other Duras. In the same recycling scenario, the K₂O uptake by TDeAn or TCo parents is lower than those of other Tenera.

The average annual phosphorus uptake for all genetic material represents 465 g/palm of P₂O₅: 53% was used for leaf renewal, 39% was used for production through the bunches and only 6% was used for the trunk. The total annual uptake in P₂O₅ for DDe-A2c and DDe-A4c parents is significantly lower than those of the other three Dura Deli parents. Among Teneras, the total annual uptake in P₂O₅ for TYa was significantly higher than those of all other Tenera parents, particularly TDeAn and TCo, whose P uptakes were the lowest observed.

The average annual uptake of magnesium for the confounded parents represents 358 g/palm of MgO: 58% was used for leaf renewal, 24% was used for the exported crop and 17% was used for the trunk growth.

Among Dura parents, the mean MgO uptake for the annual trunk growth is significantly higher for DDe-B than for DDe-A2c and DDe-A4c parents, and among the Tenera parents, the annual uptake of TNi for trunk growth is more than 2.4 times higher than that of TLm, TCo or TDeAn. For leaf renewal, the annual uptake by DDe-A4c and DDe-AB is significantly higher than that by DDe-C and DDe-A2c. Among Tenera parents, the uptake by TYa for leaf renewal is significantly higher than those of all other Tenera parents, with TDeAn and TLmYa being intermediate.

The total MgO uptake by DDe-A2c is significantly lower than other Dura, but when leaves are recycled, DDe-A4c is the lowest. When both leaves and EFB are recycled, MgO uptake by DDe-A2c and DDe-A4c parents are the only ones significantly lower than DDe-B.

MgO uptake by TNi with or without restitution is always significantly higher than the uptake by other Tenera parents, particularly towards TDeAn and TCo parents, which is most likely due to the very high Mg concentration in the trunk.

Parent Effectiveness in Nutrient Use

The effectiveness in N and K₂O use by the parents is presented in Graph 1.

Among the parents with yields close to or greater than 7.5t CPO/ha/year, the total N uptake without leaf recycling for TYa is 22% higher than that of DDe-A2c. For the parents with CPO yields lower than 7.5t/ha, the total N uptake without leaf recycling for DDe-B is 16% higher than that of TDeAn. However, when the leaves are recycled, N uptake by the high-yielding parents is 19% higher for TNi compared with DDe-A2c. For the lower yield parents, N uptake by TLMYa is 12% higher than that by TCo or TDeAn.

Among the parents with yields close to or greater than 7.5t CPO/ha/year, the total K₂O uptake by TLM is 20% higher than that by DDe-A2c without recycling. However, with recycling, K₂O uptake by TNi is the highest, 22% higher than the uptake by DDe-C. For the lower CPO-yielding parents, K₂O uptake by TLMYa is 43% higher than by TCo or TDeAn when leaves are recycled.

When we observe the amount of elements used per tree per year to produce one tonne of oil, the variability is consistent. This amount varies from 198 g of nitrogen for TLM to 277 g of nitrogen for

DDe-B when there is no recycling of leaves or from 69 g of nitrogen for TLm to 89 or 90 g of nitrogen for DDe-B, TLmYa and TNi when the leaves are recycled.

The same calculation made for K shows a total uptake that varies from 339 g of K_2O for DDe-A2c to 444 g of K_2O for TLmYa for producing one tonne of CPO with no recycling of leaves, and this uptake is reduced from 142 g of K_2O for DDe-C to 205 g of K_2O for TLmYa when the leaves are recycled.

For P, when the leaves are recycled, the amount of P_2O_5 used per tree per year to produce one tonne of oil varies from 27 g for TLm to 34 g for TLmYa. Similarly, the MgO needs vary from 17 g to 27 g for TLm and TNi, respectively.

When comparing the total uptake without leaf recycling with the quantities of fertilizers applied annually and representing 1208 g N, 397 g P_2O_5 , 1675 g K_2O and 242 g MgO per palm (calculated over the period of the adult phase), we note that these fertilizer supplies do not cover the uptake. However, when we consider the return of nutrients by the leaves, the fertilizer applications are largely in surplus and most likely occur in a sufficient quantity to cover root growth, which is not accounted for in this study.

DISCUSSION

The Concern Raised by the Wide Variability of Nutrient Concentration in Organs

These results highlight contrasted leaflet concentrations for most observed elements (N, P, K, Mg) between the different genetic origins of Dura and Tenera, thus confirming the previously published results (Ollivier et al, 2013) and showing the additive nature of transmission of this character by a group of the same origin.

Thus, the high variability of content values found for almost all of the elements in the leaflet confirms the hypothesis of specific optimum levels per type of planting material.

With the classic fertilizer recommendation methodology based on critical levels of foliar content, such differences in leaf content would most likely result in significant differences in terms of the rates of fertilizer recommended among the different origins planted on commercial blocks.

For example, among the other nutrients, potassium is the most abundant inorganic cation in plant cells and is vital for plant growth, and its availability strongly determines the crop yield. In our case, TDeAn or DDa3c parents then receive a higher K fertilizer regime compared with TNi or DDe-C parents. However, the findings of the study indicate that such a strategy is most likely counter to productivity because the TDeAn or DDa3c K uptake is among the lowest observed values, and it is doubtful that adding more K would increase its efficiency.

In the same way, TNi or DDe-C would receive less K fertilizer, which appears irrelevant because the K uptakes by these parents are among the highest observed values.

This study also confirms that the uptake of nutrients by the palm cannot be reliably deduced from the leaf analysis results alone, as the reserve levels of nutrients in the rachis and trunk are high (Foster and Prabowo Noto, 2003). The study further shows that it is difficult to draw general rules and that it is not easy to find a tissue that would be appropriate for diagnosing all elements and all crosses.

The trunk appears to be a strategic compartment because it stocks a large quantity of nutrients, particularly K. In our study, the K mobilized in the trunk represents 67% to 76% of the total vegetative aboveground K (excluding reproductive organs), which is close to the value of 72% observed for 11-year-old palms (Dubos et al., 2011).

The K concentrations in the trunks in our study are particularly high and variable in a range of 1.9% to 3.6% of DM, and above of those reported by Ng et al. (2003), with concentrations of 1.60% to 2.15% K in the DM of 6- to 15-year-old fertilized palms, or by Dufrêne (1989) in Ivory Coast on 15-year-old palms with K content between 1.0 and 1.2% of the DM.

The highest F value ($F = 110$) among Teneras is found for the aboveground magnesium vegetative mass due to enormous differences in the Mg mass in the trunk ($F = 130$). This is mainly due to the high content in Mg in the trunk for TNi individuals. This particularity is very strange compared with the Mg leaflet content for this origin, which appears to be the lowest, or with that of the rachis or petiole, which appear among the lowest.

The importance of the trunk in the results presented here requires a more effective sampling method for measuring the biomass of the stipe in similar future studies.

Unlike the leaflet or the stem, other organs such as the petiole or the rachis show less variation in nutrient content between materials. Foster and Prabowo Noto (1996) and Teoh and Chew (1987) considered the yield to be seriously limited when the K content of the rachis did not reach 1% of DM; this threshold was not reached in any of the parents tested in our study because K in the rachis varies from 1.26 to 1.79%, most likely confirming that the K supply is sufficient. However, the genetic background of the material used in these cited authors is most likely different than the one used in this study.

It is interesting to observe that the K concentration in the rachis in the Felda study comparing various clone origins and DxP hybrids (Lee et al., 2014) was found to occur in a similar range (1.18% to 1.68% of DM) compared with our study, though the Felda study used a K fertilizer regime that was 1.8 times higher.

Unlike an agronomic test, where differences in levels can be interpreted agronomically according to the applied nutrition, the differences observed between genotypes must be considered without being able to elucidate the mechanism that leads to these differences, and these differences are most likely intrinsically linked to genotypes.

The statistical analysis of the various measurements highlighted the great variability in nutrient uptake within the different Duras or Teneras parents. However, with the same hearty fertilization regime, the contrasting variations in nutrient uptake observed between plant materials of different origins draw our attention to the agronomic or economic and environmental consequences that could result.

Nutrient Uptake Differs Greatly between Materials; What are the Real Needs?

When comparing nutrient uptake with nutrient input, we note that the surplus is particularly important for nitrogen. For all of the parents that were confounded when the leaves are recycled, the N uptake used for trunk growth and bunch export represents only 50% of the N fertilizer regime and only 40% of it when the leaves and EFB are recycled. TDeAn and TCo are among the parents that consume the least nitrogen, and TNi consumes the most nitrogen. We also observe that for the same N uptake, some parents perform better than others. In this way, a difference in yield of 1.23tCPO/ha/an is observed between DDe-A2c and DDe-B, with a similar N uptake (with leaf recycling) of 617 and 622 gr N per year per palm, respectively. In the same manner, a difference in yield of 1.8tCPO/ha/an is observed between TLm and TLmYa for a similar uptake of 602 and 590 gr of N per palm per year, respectively.

Similarly, when the leaves are recycled, the total uptake in K_2O represents nearly 75% of what is applied through potassium chloride (KCl) fertilisation but only 53% of the KCl supply when both leaves and EFB are recycled. In the same manner as observed for nitrogen, TDeAn and TCo consume 30% less K_2O than do TLMYa or TNi. As observed for N, large variations in yield are observed between parents that have similar K_2O uptake; the yield gap between TLM and TLMYa is more than 1.8t CPO/ha/year for a very similar uptake of 1421 and 1428 gr of K_2O per palm per year, respectively.

The total yearly uptake of P_2O_5 and MgO with leaf recycling represents 55% and 61% of the P205 and MgO fertilizer regime, respectively, when all parents are confounded. This uptake is reduced to 45% and 41% of the P_2O_5 and MgO fertilizer regimes, respectively, when both leaves and EFB are recycled. Similar to what is observed for N and K, disparities are observed between parents for their effectiveness in using P and Mg.

The study raised questions regarding the veracity of maintaining the same fertilizer regime with certain genotypes that appear to consume less fertilizer than others for the same level of yield. However, we do not know how the balance was established for each cross between the vegetative developments of the organs; the mineral element contents and the production following the fertilizer regime used in this study may vary if we modify this fertilizer regime. To answer these questions, appropriate mineral nutrition x genotype experiments are therefore of paramount importance in regards to their environmental and economic incidences.

In a number of annual crop species, a considerable variation in the efficiency of nutrient uptake and utilization has been identified among the existing genotypes for a variety, as the amount of biomass or economic yield per unit of nutrient taken up (Rengel and Damon, 2008). This is not yet

the case for oil palm; the existence of specific nutritional requirements and nutrient efficiency according to oil palm genotypes is still relatively unknown, and this factor is therefore not considered a selection criterion for the planting material. However, this factor justifies the detailed measurement of the levels and performance under varying nutrition conditions to obtain more information. The sensitivity of different plant tissues in reflecting changes in nutrient uptake and responding to nutrient additions should be investigated in controlled field experiments. It is obvious that there is a need for specific studies to determine whether fertilizer regimes require adjustment depending on the nutrient status and uptake.

Nonetheless, it seems impossible to establish a field fertilizer trial for each progeny used at a commercial level. A strategy based on the determination of a nutrient index to characterise each progeny could then be proposed. This nutrient index could be tentatively determined at the nursery stage, thus allowing for an exhaustive screening of the planting material. Progenies presenting similar behaviour can then be grouped together. Then, specific field fertilizer trials with representative progenies from each group could be established. These studies need to be accompanied by physiological observations such as related differences in functional traits (leaf area, height, and diameter) and metabolism (e.g., photosynthesis, soluble sugars, starch accumulation).

In the meantime, it may be recommended to create plantations with as many homogeneous sectors as possible to optimize fertilization when the means to do it are available.

Limited and costly resources are now forcing us to investigate how the demands of the plants can be satisfied with adequate fertilizer applications. To maintain high oil palm yields, it is essential to

screen oil palm for genotypes that have superior nutrient uptake abilities, thus permitting the limitation of nutrient losses from soil through processes such as leaching and gaseous emissions.

It is therefore a great challenge for breeders to develop a strategy towards better-performing genotypes that are more efficient in their nutrient use and can distribute more resources to reproductive organs to form economic output. A stronger prioritization of these areas of research is needed to meet the demands for low-input agriculture or to counter declines in soil fertility, thereby minimizing fertilizer costs and achieving both economic and environmental sustainability.

CONCLUSION

Practitioners often use the same reference levels to establish fertilizing tables in the same agro-ecological environment. Rules for fertilizing decisions are often used that do not account for the planting materials applied.

Our study clearly demonstrates that the nutrient levels are tightly linked to the origin of the oil palm planting material. Under the same growing conditions and with a similar fertilizer regime, all of the planting materials were significantly different in most of the nutrient concentrations of the observed organs.

Not accounting for origin can lead to inappropriate recommendations. Practitioners may either apply insufficient fertilizer to enable the expression of the genetic potential of oil palm varieties, or they may apply too much fertilizer, which has a negative economic impact because fertilizer is the major operating cost and has a detrimental effect on the environment.

Thus far, there has been no functional hypothesis to explain the differences in the plant organ nutrient contents observed between planting materials. The first observations on the morphology and reproductive pattern suggest differences in the biomass between different materials.

The present study permits the exhibition of the distribution and allocation of nutrients in the aerial part of both vegetative and reproductive organs for a range of various oil palm planting materials.

It shows that high yields are not always correlated with high uptake of nutrients in palm organs. Furthermore, for the same level of production, the nutrient uptake may vary up to 30-40% of a type of plant material to another.

The fertilizer regime used in this study appears to be moderate compared with the fertilizer practices that are often used in Malaysia. Nevertheless, the total aerial uptake for both vegetative and reproductive organs are very often very well covered by the fertilizer regime that is applied when the pruned leaves are recycled.

The study questions whether significant savings could be made if fertilizer regimes can be adapted to the type of planting material. It appears to be of paramount importance to study whether the measured uptake and production would be drastically modified with a change in fertilizer regimes.

Therefore, aside from selecting higher productivity palms for efficient oil production, evaluating their costs in nutrient uptake should also be a priority.

Thus, there is most likely a great deal of effort to be made in the future to fine-tune the critical levels in contrasted oil palm varieties to specifically adapt fertilization to oil palm and improve our knowledge of the efficiency of fertilization recovery. This may open a gate to identifying genetic material that uses less input or is more adapted to inherent soil fertility.

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Table 1: Origin of the parents and Mating Design

		Tenera						
		IDENT	TLmYa	TNi	TCo	TYa	TLm	TDeAn
		Origin	La Mé x Yangambi	Nigeria	Congo	Yangambi	La Mé	Deli x Angola
Dura Deli	IDENT	Cycle	3	2	2	2	2	4
	DDe-A2c	2	X	X	X		X	X
	DDe-A4c	4	X	X	X	X	X	X
	DDe-AB	3	X	X	X	X		X
	DDe-B	2			X	X		X
	DDe-C	2	X	X	X		X	

Table 2: Quantity of fertilizers applied since planting in gr per plant and equivalents in N or oxydes

Year	Mineral fertilizers in g per palm							Equivalent in gr per palm			
	Urea	RP	TS P	KCl	Dolomi te	Kieseri te	NP K 15- 15- 15	N	P20 5	K20	Mg 0
2003		500					110 0	165	305	165	
2004	700						100 0	472	150	150	
2005	1550		900	1800		700		713	405	1080	189
2006	2500		125 0	3000		1000		1150	563	1800	270
2007	2500	1000		2500		2000		1150	280	1500	540
2008	2750	1250		2750	1250			1265	350	1650	250
2009	2750	500		2000	1000			1265	140	1200	200
2010	2750	1500		3000	1250			1265	420	1800	250
2011 2013	2500	1750		3000	1250			1150	490	1800	250
total10yr	2300 0	1000 0	215 0	2405 0	7250	3700		1089 5	408 3	1474 5	244 9

Table 3: Mineral content of N and oxides of the different components of the bunch by Zeller cited in IPNI 1957.

	% in DM		% in ashes		
	N	Ashes	P2O5	K2O	MgO
Stalk and spikelets	0.420	4.20	3,13	28,47	3,89
Fibers	0.924	3.55	11,49	12,00	4,81
Shells	0.364	1.56	7,36	6,87	4,05
Kernels	1.148	1.80	43,40	26,00	1,14

Table 4: ANOVA results of the effect of genotype (Dura and Tenera parents) on vegetative measurements, biomass of trunk and leaves observed at 10 years of age, fresh fruit bunch (FFB) production and crude palm oil (CPO) production observed from 6 to 9 years after planting. Different letters indicate that the means are significantly different (Tukey test, $p < 5\%$).

	Length of rachis for leaf of rank 17	Height of palm below leaf of rank 33	Biomass of trunk	Biomass of total leaves	FFB 6-9 years	CPO 6-9 years
Dura parents	m	m	kg DM	kg DM	Kg/yr/palm	T CPO/ha/yr
DDe-B	5,86 a	4,72 a	190,95 ab	112,7 a	182,07 c	6.50 d
DDe-A4c	5,49 c	4,35 bc	193,12 a	99,9 b	193,38 c	7.09 c
DDe-A2c	5,55 bc	4,29 c	179,53 ab	100,9 b	217,11 b	7.73 b
DDe-AB	5,77 ab	4,70 a	195,41 a	105,0 ab	211,20 b	7.45 b
DDe-C	5,30 c	4,63 ab	160,58 b	103,1 ab	233,15 a	8.27 a
Tenera parents						
TNi	5,45 bc	5,48 a	236,57 a	102,73 ab	225,73 b	7.94 b
TYa	5,60 abc	4,55 b	196,66 b	110,10 a	202,03 c	7.49 c
TDeAn	5,62 abc	4,31 bc	166,86 cd	104,17 a	185,57 d	6.62 e
TLm	5,76 a	4,10 c	160,03 d	106,42 a	246,79 a	8.78 a
TLmYa	5,71 ab	4,39 bc	191,25 bc	109,27 a	196,77 cd	6.96 d
TCo	5,42 c	4,40 bc	152,15 d	93,38 b	187,40 cd	6.66 d e
	F (p value)	F (p value)	F (p value)	F (p value)	F (p value)	F (p value)
Dura main effect	9.6 (0.000)	5.7 (0.000)	4.9 (0.001)	3.7 (0.006)	31.4 (0.000)	22.0 (0.000)
Tenera main effect	5.0 (0.000)	32.1 (0.000)	21.8 (0.000)	8.8 (0.000)	40.9 (0.000)	45.1 (0.000)
Dura *Tenera interaction	1.8 (0.048)	1.5 (0.138)	1.1 (0.342)	2.9 (0.001)	1.6 (0.105)	1.3 (0.191)

Table 5: Mean nutrient content (N,P,K, Mg) in each organ of Dura and Tenera parents. Different letters indicate that means are significantly different (Tukey test, $p < 5\%$).

		Elements															
		N				P				K				Mg			
organ	Parents	Ident	% D M	Ident	% D M	Ident	% D M	Ident	% D M	Ident	% D M	Ident	% D M	Ident	% D M	Ident	% D M
Leaflet	Dura	De-A2c	2.428a	DDe-B	2.478a	De-A2c	0.157a	DDe-B	0.163a	De-A2c	0.945a	DDe-B	0.923ab	De-A2c	0.200a	DDe-B	0.208a
		De-A4c	2.425a	DDe-AB	2.412a	De-A4c	0.157a	DDe-AB	0.161a	De-A4c	0.858b	DDe-AB	0.945a	De-A4c	0.224a	DDe-AB	0.211a
		De-C	2.554a			De-C	0.159a			De-C	1.020a			De-C	0.184a		
	Tenera	TeAn	2.306c	TNi	2.435abc	TeAn	0.155a	TNi	0.158a	TeAn	0.765c	TNi	1.104a	TeAn	0.220a	TNi	0.171c
		Tlm	2.561ab	TCO	2.378bc	Tlm	0.158a	TCO	0.156a	Tlm	0.891b	TCO	0.972b	Tlm	0.209ab	TCO	0.184bc
		TlmYa	2.617a	TYa	2.461abc	TlmYa	0.165a	TYa	0.166a	TlmYa	0.933b	TYa	0.965b	TlmYa	0.222a	TYa	0.228a
Rachis	Dura	De-A28	0.348	DDe-	0.329	De-A23	0.093	DDe-	0.094	De-A25	1.605	DDe-	1.320	De-A28	0.068	DDe-	0.061

		c	a	B	a	c	b	B	b	c	ab	B	b	c	ab	B	b
		DD e- A4 c	0. 35 1 a	D D e- A B	0. 36 0 a	DD e- A4 c	0. 09 4 b	D D e- A B	0. 11 2 a	DD e- A4 c	1. 55 5 ab	D D e- A B	1. 65 7 ab	DD e- A4 c	0. 08 6 ab	D D e- A B	0. 08 8 a
		DD e- C	0. 34 3 a			DD e- C	0. 09 6 ab			DD e- C	1. 84 1 a			DD e- C	0. 07 4 ab		
	Tenera	TD eA n	0. 32 8 a	T Ni	0. 34 8 a	TD eA n	0. 08 2 b	T Ni	0. 10 3 b	TD eA n	1. 26 1 b	T Ni	1. 49 6 ab	TD eA n	0. 08 6 a	T Ni	0. 07 1 ab
		TL m	0. 34 3 a	T C o	0. 36 1 a	TL m	0. 09 4 b	T C o	0. 09 1 b	TL m	1. 79 2 a	T C o	1. 76 8 a	TL m	0. 05 6 b	T C o	0. 07 0 ab
		TL mY a	0. 34 7 a	T Y a	0. 35 0 a	TL mY a	0. 08 4 b	T Y a	0. 13 3 a	TL mY a	1. 62 8 ab	T Y a	1. 62 8 ab	TL mY a	0. 07 7 ab	T Y a	0. 09 1 a
Petiole	Dura	DD e- A2 c	0. 40 6 a	D D e- B	0. 42 3 a	DD e- A2 c	0. 05 0 b	D D e- B	0. 06 1 ab	DD e- A2 c	1. 57 4 b	D D e- B	1. 41 8 b	DD e- A2 c	0. 09 4 a	D D e- B	0. 10 3 a
		DD e- A4 c	0. 45 3 a	D D e- A B	0. 45 8 a	DD e- A4 c	0. 06 1 ab	D D e- A B	0. 05 1 b	DD e- A4 c	1. 70 5 b	D D e- A B	1. 72 0 b	DD e- A4 c	0. 12 9 a	D D e- A B	0. 11 4 a
		DD e- C	0. 42 4 a			DD e- C	0. 06 6 a			DD e- C	2. 09 7 a			DD e- C	0. 09 8 a		
		TD eA n	0. 45 9 a	T Ni	0. 42 3 a	TD eA n	0. 04 8 c	T Ni	0. 05 7 ab c	TD eA n	1. 41 3 b	T Ni	1. 67 6 ab	TD eA n	0. 12 8 a	T Ni	0. 09 9 ab
		TL m	0. 41 0	T C o	0. 45 1	TL m	0. 05 4	T C o	0. 06 2	TL m	1. 84 5	T C o	1. 67 6	TL m	0. 06 8	T C o	0. 11 4

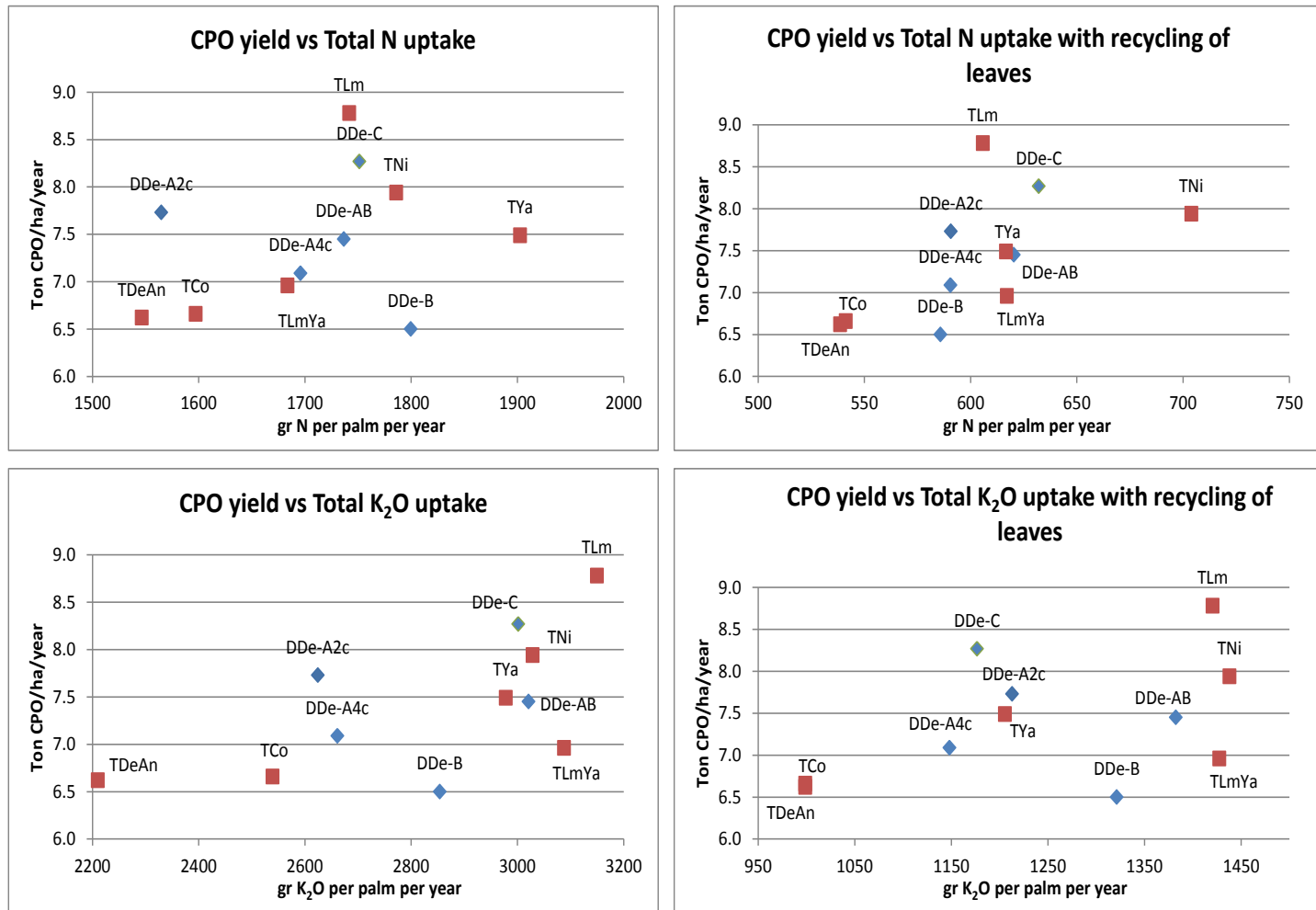
		a		a		bc		ab		a		ab		b		a	
		TL mY a	0. 40 3 a	T Y a	0. 45 0 a	TL mY a	0. 05 1 bc	T Y a	0. 07 4 a	TL mY a	1. 91 2 a	T Y a	1. 69 5 ab	TL mY a	0. 12 8 a	T Y a	0. 10 8 ab
Trunk	Dura	DD e- A2 c	0. 63 2 bc	D D e- B	0. 72 4 ab	DD e- A2 c	0. 05 0 b	D D e- B	0. 06 8 a	DD e- A2 c	2. 50 0 a	D D e- B	2. 49 8 a	DD e- A2 c	0. 12 1 a	D D e- B	0. 14 8 a
		DD e- A4 c	0. 75 9 a	D D e- B	0. 68 2 ab c	DD e- A4 c	0. 05 2 b	D D e- B	0. 05 9 ab	DD e- A4 c	2. 23 1 a	D D e- B	2. 72 6 a	DD e- A4 c	0. 12 3 a	D D e- B	0. 13 0 a
		DD e- C	0. 57 6 c			DD e- C	0. 05 7 ab			DD e- C	2. 16 2 a			DD e- C	0. 14 0 a		
	Tenera	TD eA n	0. 71 2 ab	T Ni	0. 80 0 a	TD eA n	0. 05 0 b	T Ni	0. 05 9 ab	TD eA n	2. 06 0 c	T Ni	2. 09 9 c	TD eA n	0. 11 9 b	T Ni	0. 19 5 a
		TL m	0. 56 1 c	T C o	0. 66 8 bc	TL m	0. 06 1 ab	T C o	0. 05 0 b	TL m	3. 59 5 a	T C o	1. 92 2 c	TL m	0. 12 2 b	T C o	0. 11 3 b
		TL mY a	0. 65 4 bc	T Y a	0. 65 2 bc	TL mY a	0. 06 3 a	T Y a	0. 05 9 ab	TL mY a	2. 80 1 b	T Y a	2. 06 5 c	TL mY a	0. 12 7 b	T Y a	0. 11 9 b

Table 6: Mean nutrient uptake and standard error of the means in N, P2O5, K2O and MgO in gr per palm and per year for the different Dura and Tenera parents for both vegetative and reproductive components with restitution of leaves and EFB or not. Different letters indicate that the means are significantly different (Student's t test, $p < 5\%$).

Nutrient	Group	Parent	Trunk	Leaves	Bunches	Total uptake	Total uptake with leaves restitution	Total uptake with leaves and EFB restitution
			in gram of nutrient per palm per year					
N	Standard Error		17	44	7	48	18	18
	Dura	DDe-A2c	157 bc	974 b	433 b	1565 b	591 a	459 a
		DDe-A4c	206 a	1105 a	385 c	1696 a	590 a	470 a
		DDe-C	147 c	1119 a	485 a	1751 a	632 a	491 a
		DDe-AB	194 ab	1116 a	426 b	1737 a	620 a	490 a
		DDe-B	231 a	1214 a	355 d	1800 a	586 a	471 a
	Tenera	TDeAn	167 bc	1008 b	372 c	1547 d	539 c	429 c
		TLm	119 c	1136 b	486 a	1742 b	606 b	458 bc
		TLmYa	193 b	1067 b	424 b	1684 bc	617 b	496 b
		TNi	280 a	1082 b	424 b	1786 ab	704 a	551 a
		TCo	165 bc	1056 b	377 c	1597 cd	541 c	429 c
		TYa	198 b	1286 a	419 b	1903 a	617 b	496 b
P2O5	Standard Error		3	8	3	9	4	4
	Dura	DDe-A2c	28 c	212 d	190 b	430 b	218 b	177 bc
		DDe-A4c	31 bc	240 c	170 c	442 b	202 c	164 d

		DDe-C	33 bc	243 bc	214 a	490 a	247 a	203 a
		DDe-AB	38 b	260 ab	187 b	485 a	225 b	184 b
		DDe-B	49 a	272 a	154 d	474 a	202 c	167 cd
	Tenera	TDeAn	27 b	212 c	165 d	403 c	192 c	158 c
		TLm	29 b	239 b	210 a	477 b	239 a	192 a
		TLmYa	42 a	223 bc	194 b	459 b	235 ab	197 a
		TNi	48 a	244 b	176 c	468 b	224 b	176 b
TCo	28 b	229 bc	165 d	422 c	193 c	158 c		
TYa	42 a	326 a	189 b	557 a	231 ab	193 a		
K₂O	Standard Error		48	60	10	77	50	49
	Dura	DDe-A2c	714 b	1411 c	499 b	2624 c	1213 bc	839 b
		DDe-A4c	696 b	1513 bc	452 c	2661 bc	1148 c	806 b
		DDe-C	634 b	1825 a	543 a	3001 a	1177 bc	774 b
		DDe-AB	890 a	1639 b	493 b	3021 a	1382 a	1012 a
		DDe-B	896 a	1533 bc	426 c	2854 ab	1321 ab	995 a
	Tenera	TDeAn	578 c	1211 d	421 c	2210 c	999 c	688 c
		TLm	860 ab	1729 ab	561 a	3150 a	1421 a	999 ab
		TLmYa	959 a	1660 abc	469 b	3088 a	1428 a	1083 a
		TNi	890 a	1591 bc	548 a	3029 a	1438 a	1004 ab
		TCo	570 c	1540 c	429 c	2539 b	999 c	679 c
		TYa	739 b	1773 a	467 b	2978 a	1206 b	861 b
	MgO	Standard Error		6	9	1	11	6
Dura		DDe-A2c	51 b	179 c	91 b	320 b	142 bc	91 b
		DDe-A4c	55 b	233 a	80 c	368 a	136 c	89 b
		DDe-C	61 ab	191 bc	98 a	350 a	159 a	104 ab
		DDe-AB	62 ab	224 a	89 b	375 a	151 ab	101 ab
		DDe-B	78 a	219 ab	77 c	374 a	155 ab	110 a
Tenera		TDeAn	46 bc	220 b	77 d	343 b	123 c	81 c

	TLm	42 c	185 c	103 a	330 bc	145 b	88 bc
	TLmYa	62 b	215 b	82 bc	359 b	144 b	97 b
	TNi	112 a	181 c	99 a	392 a	211 a	152 a
	TCo	46 c	185 c	79 cd	309 c	124 c	81 c
	TYa	60 bc	268 a	83 b	412 a	143 b	96 bc



Graph 1: CPO produced per ha and per year* vs nutrient uptake in N and K₂O in gr per palm per year for the different Dura and Tenera parents with or without recycling of leaves. * mean yield observed between 6 to 9 years after planting. Tenera in red square and Dura in blue diamond.