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Genotypic variability of oil palm root system distribution in the field. Consequences for water uptake

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Abstract Previous studies relating root systems and drought tolerance in oil palm focused mainly on biomass. Yet, total root length (TRL), total root surface area (TRS), and root distribution in the soil better determine water uptake. These morphological traits were studied on 3 oil palm genotypes displaying a contrasting drought tolerance. A new concept of potential root water extraction ratio (PRER) was developed using measured half-distances between roots and some assumptions about the distance of water migration from soil to root. PRER was determined in conjunction with soil moisture extraction efficiency (SMEE). The presumed tolerant genotype (T) had higher TRL, TRS and PRER than the susceptible genotype (S), whilst the performance of the control genotype (I) was intermediate. Surprisingly, during a period of moderate water deficit, T had a lower SMEE than S, which was interpreted successfully with PRER, as the result of a better access to a large volume of soil and of a slower drying out of the soil around the roots. PRER appears as a helpful indicator for comparing or ranking genotypes, and for addressing better the complexity of the genetic variability of drought tolerance.

Keywords Benin · Drought tolerance · *Elaeis guineensis* · Root biomass · Root length density · Soil moisture extraction efficiency

Abbreviations

df	degrees of freedom
Et_i	root water extraction per soil layer i between two dates ($cm^3\ d^{-1}$)

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AET	actual evapotranspiration (mm d^{-1})
PET	potential evapotranspiration (mm d^{-1})
FTSW	fraction of transpirable soil water (no dimension)
I	control oil palm genotype with intermediate drought tolerance
PAW	potential available water in soil (mm)
PRER	potential root extraction ratio for water (no dimension)
r	maximum distance of water migration to root surface area (cm)
R1	primary root or coarse root
R2	secondary root or medium root
R3	tertiary root
R4	quaternary root
(R3+R4)	fine roots
RD	average distance between roots (m)
RER	root elongation rate (cm d^{-1})
RLD	root length density (m m^{-3})
RS$_i$	total root surface area in the soil layer i
S	oil palm genotype susceptible to drought
SMEE	actual soil moisture extraction efficiency
θ_{z_i}	volumetric water content at soil layer z_i (cm^3 cm^{-3})
θ_{fcz}	volumetric water content at field capacity at soil layer z (cm^3 cm^{-3})
T	drought tolerant oil palm genotype
TRDM	total root dry matter (kg m^{-2})
TRL	total root length (km m^{-2})
TRS	total root surface area (m^2 m^{-2})
VPD	vapor pressure deficit (kPa)
V$_t$	total soil volume (m^3)
V$_u$	maximum soil volume available to root for water uptake (m^3)
ΔS$_i$	variation of water stock per soil layer i between two dates
Δz	thickness of a soil layer between z_n and z_{n-1} depth (cm)

Introduction

Oil palm yields more oil per hectare than any other oil crops (Corley and Tinker 2003). It is grown in several tropical countries under a wide range of rainfall conditions. The optimum annual rainfall for oil palm to achieve its maximum production capacity is 1,800 mm, well distributed throughout the year (Corley and Tinker 2003). Oil palm is susceptible to water deficits and in years with very severe deficits, vegetative damage can even result in palm death (Nouy et al. 1999). The ability of the oil palm to extract and use water has become a very important issue in zones with marginal rainfall (Cornaire et al. 1994). Various studies have been conducted on oil palm root systems in relation to water stress, but they primarily focused on root biomass (Cornaire et al. 1994). However, total root length (TRL) and root length density (RLD) are relevant traits for models showing access to water and minerals in soil (Chopart 1996; Tinker and Nye 2000).

Jourdan and Rey (1997a, b) used a root architecture model to estimate total root surface area and total root length for oil palms in Ivory Coast. Corley and Tinker (2003) obtained some first estimations of total root length in oil palms depending on age, in Malaysia. However, to our knowledge, no work has yet truly quantified total root length or surface area in situ for all types of oil palm roots, along with their spatial distribution in soil and comparing genotypes.

Root growth rate is often seen as another characteristic of adaptation to drought (Annerose and Cornaire 1994). Jourdan and Rey (1997a) carried out the first detailed study on oil palm root growth dynamics and architecture, but only on one genotype, but little is known about the genotypic variability of root growth rate in oil palms, along with its seasonal variations.

In earlier studies on the role played by the root system in oil palm drought tolerance, the physiological aspect of roots was barely taken into account, if at all (Cornaire et al. 1994; Nouy et al. 1999). However, various studies (Huang and Fry 1998; Jackson et al. 2000; Steudle 2000) have shed light on how root physiology affects water uptake in the dry season.

In Benin (West Africa), different oil palm genotypes are known to have highly contrasting yields and mortality rates under water stress (Maillard et al. 1974). Initial attempts to explain that situation focused on aerial organs: photosynthesis, transpiration, stomatal regulation or the carbohydrate reserve metabolism and protoplasmic resistance (Adjahossou and Vierra Da Silva1978). There has only been a few studies on rooting depth (Nelson et al. 2006; Nodichao 2008), but without completely explaining

the overall performance of oil palms under water stress.

To gain a clearer understanding of the different performances exhibited by different oil palm genotypes under water stress, we conducted a study on the morphological and physiological traits of the roots of 3 contrasting oil palm genotypes in the field. In addition to conventional root parameters (length, surface area, biomass), we also used two functional parameters: potential root extraction rate for water (Chopart 1999) and the soil moisture extraction efficiency of roots (Proffit et al. 1985; Wiersum 1987; Salih et al. 1999). The purpose of the study was to gain a clearer understanding of the role played by roots in the genotypic variability of oil palm drought tolerance. In particular, these results should add to the success of varietal selection work in improving oil palm drought tolerance.

Material and methods

Plant material and environmental characteristics

This work was undertaken in a varietal performance trial at the CRAPP Research centre (Centre de Recherche en Agriculture sur les Plantes Pérennes) in Benin (West Africa) at the Obèkè site (2°35' longitude East, 6°55' latitude North), where the climate is of the subequatorial type with a short dry season (August-September) and a long and pronounced dry season (November–March). The average rainfall is 1,200 mm year^{-1}, but there is considerable interannual variation. The zone is considered marginal for oil palm growing and the water deficit can sometimes reach 750 mm year^{-1} (Nouy et al. 1999). Potential evapotranspiration is 3.5 mm d^{-1} on average. The annual mean minimum and maximum temperatures are 22°C and 30°C, respectively. The soil is of the 'ferralsol' type (FAO-UNESCO, 1989). In the top 0.15 m, the soil is generally sandy (loamy sand in general). The clay content is 10% in this horizon and gradually increases with depth, reaching 55% on average between 1.2 and 1.7 m, whilst the silt content is less than 7% throughout the profile (Nodichao 2008). The average volumetric soil moisture at field capacity varied according to depth (down to 1.7 m) between 0.16 and 0.35 cm^3 cm^{-3}, while the permanent wilting point (-1,500 kPa) varied between 0.08 and 0.24 cm^3 cm^{-3}. The infiltrability has been estimated at

64.3 cm h^{-1} by the internal drainage method (Vachaud et al. 1978). The dry bulk density ranged between 1,400 kg m^{-3} and 1,600 kg m^{-3} in the top 0.5 m. It increased slightly with depth, without exceeding 1,700 kg m^{-3} at 2.5 m. The potential available water in soil (PAW) was 195 mm on average over a depth of 2.5 m (Nodichao 2008). Observations were carried out on 4-year-old palms in the field planted in equilateral triangular spacing. Three oil palm genotypes (C2001, C1001F and C6446), divided into Fisher blocks with three replicates, were studied for their degree of drought tolerance. Genotype C2001, derived from cross (LM4004 × DA10D) × LM2T is presumed to be susceptible to drought (S), genotype C6446 derived from cross DA8D × (LM13T × LM9T) is presumed to be drought tolerant (T). The intermediate genotype (I) was C1001F derived from cross DA115D × LM2T. The presumed drought tolerance of the genotypes is based on the performance of their parents in relation to drought in the field. According to Nodichao (2008), under conditions in Benin, the tolerant genotype C6446 exhibits a higher frond production rate and fresh fruit bunch production than the susceptible C2001: 30 as opposed to 26 fronds year^{-1} and 39 as opposed to 29 kg palm^{-1} year^{-1}, respectively. According to the same author, the intermediate genotype C1001F has a growth rate (27 fronds year^{-1}), closer to that of the susceptible cross, but has a higher fresh fruit bunch yield (46 kg palm^{-1} year^{-1}).

Soil moisture characteristics in the field

The volumetric water contents of the soil were measured with a neutron moisture meter (503 DR Hydroprobe®, CPN International, Inc, USA) each week during the dry season and fortnightly once the rains had resumed. Four neutron probe access tubes were installed around each observed palm. One tube was installed at point G, the centre point between 3 neighbouring palms (Fig. 1a) and the other 3 were installed 0.75 m, 2.25 m and 3.75 m from the observed palm, at the centre of zones 1 (0–1.5 m), 2 (1.5–3 m) and 3 (3–4.5 m from the palm) (Fig. 1b). There were three replicates per genotype. The probe was calibrated against gravimetric measurements. Soil moisture around the access tubes was measured between November 21st 2001 and May 15th 2002 every 0.1 m down the soil profile to a depth of 2.5 m (beyond the maximum root depth for 4-year old palm trees), enabling us to calculate the total stock
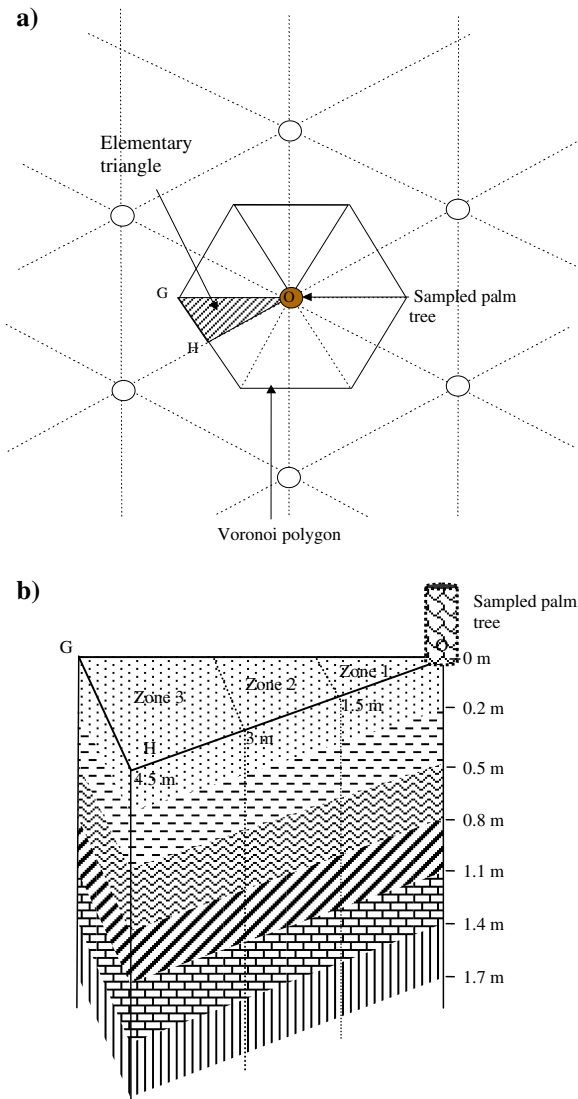
Fig. 1 Voronoi polygon **a** defined as the half-distance between the sampled palm tree and neighbouring palms (hexagonal in standard oil palm planting design). Root sampling areas **b** inside the elementary triangle according to palm distance and rooting depth

of water in the soil S between a depth of 0 and 2.5 m on each date.

$$S = \Delta z \sum_{i=1}^{n} \theta_z \qquad (1)$$

where $\Delta z = z_i - z_{i-1} = 10 \, cm$ in our case;

n number of soil layers of Δz thickness to reach the z_n depth

θ_{z_i} volumetric water content (cm cm^{-3}) at depth z_i.

The average stock of water of each palm tree was calculated from the 4 neutron probe access tubes with the assumption that each tube was representative of the entire zone. This water stock S was then used to calculate the actual evapotranspiration (AET). Without rain, AET was calculated by difference in S between two dates assuming no drainage during dry season (November 2001 to March 2002). The daily potential evapotranspiration (PET) was calculated during the same period using Eq. 2:

$$PET = a*E_{pi} + b*S \qquad (2)$$

where E_{pi} is the Piche atmometer (Piche, 1872) which was shown by Thom et al. (1981) to be closely proportional to the complete convective second term of the Penman's equation (1948). S is the atmospheric shortwave radiation of the first component of the Penman's equation. Values of the parameters a and b (0.208 and 0.202, respectively) were those used by Dufrêne et al. (1992) for oil palm tree experiments conducted in Ivory Coast, in similar climatic conditions as those encountered in the study. Daily values of E_{pi} and S were measured at the meteorological station located a few km away from our experimental field.

The soil water content at field capacity (θ_{fcz}) at each soil depth z was determined in situ by following soil water content for 21 days after a big rain using the internal drainage method (Vachaud et al. 1978). We assumed a linear relationship between $\ln(\theta_{z_i})$ and time (t_i) for soil drying during these 21 days (Eq. 3).

$$\ln(\theta_{z_i}) = a*t_i + b \qquad (3)$$

where θ_{z_i} =volumetric water content at soil layer z_i at the period t_i of soil drying (cm^3 cm^{-3}); a and b were constants, with

$$b = \ln(\theta_{fcz}) \qquad (4)$$

And finally,

$$\theta_{fcz} = e^b (cm^3 \, cm^{-3}) \qquad (5)$$

Using this total stock of water, wilting point (measured using a pressure plate) and field capacity (measured by Eq. 5 in field conditions) values, we calculated the fraction of transpirable soil water (FTSW) (Sinclair and Ludlow 1986), defined as 100% at field capacity. PAW down to one metre (in mm of water) was also estimated from volumetric

water content at field capacity and at the lower limit of extractable soil.

Root distribution and water uptake

Root samples were taken by excavation in an elementary triangle representing the minimum space enabling data extrapolation within Voronoi polygon (Honda 1978; Snowdon et al. 2002). Under our planting conditions, the elementary triangle amounted to 1/12 of the hexagonal space occupied by the sampled palm (Fig. 1a). We sampled a single triangle per palm, per genotype and per replicate. All triangles were located on the planting row where no frond piles were placed. Root samples were taken inside 3 zones based on the distance from the palm with 6 soil layers per zone down to a depth of 1.7 m (Fig. 1b). That depth corresponded to the root front of a 4-year-old oil palm observed in a preliminary study in Benin (Nodichao unpublished data). There were three replicates per genotype. The root samples from each soil layer were separated according to their diameter and their topological order (see Jourdan and Rey 1997a) into primary roots (coarse roots or R1, with diameter >10 mm), secondary roots (medium roots or R2, with $2 < diameter \leq 10$ cm), and tertiary then quaternary roots (fine roots or R3+R4, with root diameter ≤ 2 mm). The different categories of roots were washed and scanned to estimate the surface area and length of the roots by image analysis using WinRHIZO software (Regent Instruments Inc. 2001). The analysed roots were dried at 80°C for 48 h and weighed to determine the biomass. This provided us with access to representative values for total root dry matter (TRDM), total root length (TRL) and total root surface area (TRS) per m² of soil.

Rhizotrons (Jourdan and Rey 1997a) were installed 0.2 m from the foot of the observed palms. Each rhizotron consisted of an 0.8×0.8 m sheet of Plexiglas. Six rhizotrons (3 trees with 2 rhizotrons) were installed per genotype in sub-horizontal (sloping 20° from the horizontal) and sub-vertical (sloping 20° from the vertical) position. A total of 18 rhizotrons were installed. Roots were observed every 7 days and traced onto a sheet of transparent polyethylene fitted to the rhizotrons. Different coloured indelible marker pens were used to differentiate between successive measurements. The drawings traced were entered on a digitizing

table and analysed by RhizoDigit software (CIRAD© 2003), enabling us to quantify root growth.

By determining the root length density (RLD, m m⁻³) we were able to estimate the average distance (RD) between roots (Gardner, 1960) for each soil compartment studied.

$$RD = \alpha * (RLD)^{-0.5} \qquad (6)$$

where $\alpha = (4/\pi)^{0.5}$

This RD is a simplification of reality, as it is based on the assumption that roots are parallel and equal distances apart in the small volume considered. From this RD, it was possible to estimate the fraction of soil available for water uptake. To do so, we consider a root characterized by a very small length and diameter. We can define then a cylinder volume (V_t) around this root, with same length and a radius equal to half distance between this root and neighbours (RD/2). This cylinder with a very small length can be considered as a disk. At the root contact ($r = 0$), we considered that PAW could be totally used and conversely, at a distance r from root, no water could be taken up, even in severe drought conditions.

That concept, applied here to soil water depletion, sets out to estimate the maximum fraction of soil that can be used by the plant, via its roots, to feed the crop, taking into account: (a) the average distances (RD) between those captor organs, per small volume of soil, (b) the maximum distance (r) to water movement to the root captor in the soil, (c) a linear water depletion between the root and the distance, r. In this concept, it is considered that the water supply to the plant in the soil primarily occurs through the displacement of water by diffusion from retention sites in the soil towards the root. A depletion zone for the fraction of available water therefore tends to become established around the root. After a certain period of extraction without replenishment, the profile becomes stable, as the root has depleted all the useful water.

Consequently, the ratio between the volume of soil potentially accessible to the root for water uptake (V_u) and the total volume of soil assigned to that root (V_t) can be defined as the potential root extraction ratio (PRER):

$$PRER = V_u / V_t \qquad (7)$$

We estimated PRER from the RLD of all the roots. Several mathematical functions can be used to determine the decline in accessibility depending on the distance from roots, from the simplest (constant) to the most complex (non-linear exponential decrease, or similar formulas for water table drawdown around a well, for example). In our study, we adopted simple assumptions, to remain coherent with the objective and with the available field data. Thus, all the roots of the young palms were considered to take up water equally along their whole length in a period of water deficit, even if some anatomical studies on oil palm roots have concluded differently (Ruer, 1967). In addition, we used a linear function to estimate the decrease in water accessibility depending on the distance from roots, following earlier tests. Given the above assumptions, PRER can be considered as an indicator of the degree of potential soil water extraction by roots, useful to compare and rank genotypes.

In the simplification adopted here and in cylindrical geometry (Fig. 2), V_t was a cylinder around each root with a radius equal to the half-distance between the roots, and the potentially useful volume of soil V_u was a cone, with a base radius of r. The available fraction of soil water (between 1 at the root surface and 0 at r distance from root) decreases linearly from root to r (Fig. 2). Then, for a single root the volume of soil potentially accessible to the root for water uptake (V_u) is considered as a cone which the height dimension is the maximum available fraction of soil water at the root surface (1). The surface area of the

cone base is then $\pi * r^2$. Without competition between roots (Fig. 2a), i.e. if the half-distance between roots exceeds r (RD/2≥r), then Eq. 7 is expressed by Eq. 8, where r and RD should be expressed with the same unit:

$$PRER = 4/3 * (r/RD)^2 \tag{8}$$

If RD/2≤r, there is competition between 2 roots to capture water (Fig. 2b) and Eq. 8 no longer applies. Available water located in the competition zone can be allocated half to one root and half to the other. V_u has then two components V_{u1} (cylinder) and V_{u2} (cone). In Fig. 2b, the y value, ranging from 0 to 1, defined the limit of competition zone for soil water depletion and also defined the limit between V_{u1} and V_{u2}. V_{u1} and V_{u2} can then be calculated by:

$$V_{u1} = \pi * (RD/2)^2 * (1 - y) \tag{9}$$

$$V_{u2} = \pi * (RD/2)^2 * (y/3) \tag{10}$$

Then, substituting $V_{u1} + V_{u2}$ for V_u in Eq. 7, PRER can be reduced to (Chopart 1999):

$$PRER = 1 - RD/(3 * r) \tag{11}$$

PRER therefore tends towards 1 when roots are very close to each other or when the migration distance is very great. We assumed that the maximum distance for water migration in the soil to the root (r) was 0.1 m for local soil conditions and according to
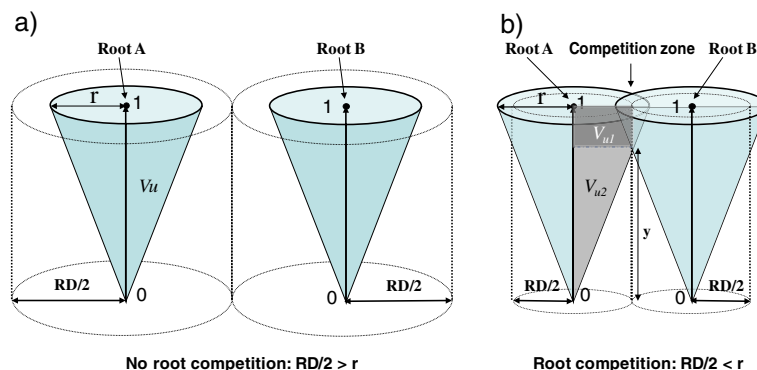

Fig. 2 Diagram of the potential root extraction ratio concept (PRER) for 2 close roots (A and B with length close to 0 and shown here as points). The height dimension of cones is the available fraction of water (between 1 at root surface and 0), depending on distance (r) from the root, with linear weakening of the water uptake capacity shown here by the uptake cone (V_u): without **a** and with **b** competition between roots

previous studies (Chopart 1996; Lang and Gardner 1970; Tardieu 1988).

The soil moisture extraction efficiency (SMEE, cm^3 d^{-1} cm^{-2}), taken from work by Wiersum (1987), was calculated using Eq. 12:

$$SMEE_i = (Et_i/RS_i) \qquad (12)$$

where Et_i = the volume of water extracted per day by the roots (cm^3 d^{-1}) in a volume of soil with a thickness of i (cm^3) depending of the distance to the palm (Fig. 1) and RS_i = is the total root surface area (cm²) in the same volume of soil i of each rooting zone.

SMEE was calculated between November 21st 2001 and January 3rd 2002, at the start of the dry season for each zone of observations. We carried out a simplified calculation of root water extraction (Et_i) per layer of soil i between 2 dates by simple difference in the water stock (ΔS_i) in layer i, using the method proposed by Kalms et al. (1982). This was possible because drainage flow, evaporation and capillary rise were considered negligible, along with an absence of rainfall over this period and with the soil and climate characteristics.

Data analysis

Analyses of variance were performed with GenStat software (version 4.2) using two procedures. We tested the genetic variability of the overall morphological root traits (TRDM, TRS, TRL) and the genetic variability of the development indicators for the different root categories by a one-way analysis of variance. All data conformed to normality's assumption. The General Linear Model procedure was used to test the variability of RLD, RD, PRER, SMEE and AET/PET depending on the location in the soil, FTSW and the genotype. The comparison of means was performed according to the least significant difference (LSD)or t test at the 5% or 1% threshold.

Results

Morphological characteristics of the root system

On average, genotype T produced more fine root dry matter (TRDM) than S (Table 1). Genotype I produced an intermediate quantity of TRDM of fine roots. Total root surface area (TRS) of fine roots and more particularly total root length (TRL) measured on the 3 genotypes followed the same trends as TRDM production (Table 1).

Most of the TRDM consisted of coarse roots (R1) and fine roots (R3+R4) in all the genotypes (Table 1). The dry matter for R1 was between 40 and 45% of TRDM in all the genotypes without any notable

Table 1 Total living root biomass (TDRM), surface area (TRS) and length (TRL) of different root types on three 4-year-old oil palm genotypes planted in the field in Benin

Root variable	Root type	Oil palm genotype		
		T	I	S
TDRM (kg m^{-2})	R1	0.13±0.02a	0.12±0.01a	0.11±0.01a
	R2	0.05±0.01a	0.06±0.01a	0.04±0.01a
	R3+R4	0.14±0.02a	0.11±0.01ab	0.09±0.02b
TRS (m^2 m^{-2})	R1	0.42±0.22a	0.38±0.21a	0.35±0.16a
	R2	0.39±0.02a	0.45±0.12a	0.34±0.10a
	R3+R4	1.86±0.54a	1.49±0.28a	1.13±0.32a
TRL (km m^{-2})	R1	30±4	27±2	25±1
	R2	45±12	53±11	40±2
	R3+R4	410±65a	324±25ab	238±71b

The values shown are means±standard deviation (sd)

Genotypes T, I and S are defined as drought tolerant, drought intermediary and drought susceptible respectively

R1: primary or coarse roots; R2: secondary or medium roots; R3+R4: tertiary and quaternary or fine roots

For the same root variable and root type, values followed by similar letters are not significantly different at $p<0.05$ (LSD test, $n=3$)

difference. The dry matter for fine roots was between 37 and 44% of TRDM. For the total root surface area and length, fine roots accounted for most of the root system. Indeed, the total surface area of fine roots exceeded 60% of the whole root system in the 3 genotypes (Table 1). Total fine root length amounted to 85%, 80% and 79% of total root length in genotypes T, I and S respectively (Table 1). Significant differences between genotypes were revealed by partitioning root parameter variances between the depth, distance from the palm, and their interactions (Table 2). In addition, significant differences in root density were found between genotypes for the sampling depth or the sampling zone (Table 2). However, there were no significant interactions between zones, genotypes and rooting depth (Table 2).

In agreement with the statistical analyses, the highest root length density was found between 0 and 0.5 m in depth for the three genotypes, independently of the sampling zones. RLD fell exponentially with depth (Fig. 3a, b, c).

The distances between roots (RD) were <0.1 m in this soil layer, at all distances from the stem (Fig. 3d, e, f). Below 1 m in depth, the RLD values became low at all distances from the palm and for the three genotypes, whereas the RD values differed from one genotype to the next and depended on the distance from the stem (Fig. 3d, e, f). The RLD of genotype T

was always higher than that of genotype S and genotype I had intermediate results (Fig. 3a, b, c). The differences in RLD and RD were greater deep down and at the greatest distance from the stem at low values, due to the squared relationship between them (Fig. 3c, f). However, the analysis of variance did not reveal any significant "genotype × horizon" or "genotype × horizon × zone" interaction at the 5% level.

Variations in root elongation rate (RER) were greater over the year than between years, in connection with the alternating dry and wet seasons (Fig. 4a, b). RER for R1 roots was less variable than for medium roots (R2) and fine roots (R3+R4). RER virtually came to a halt in the dry season, even for genotype T, presumed to be drought tolerant (Fig. 4a, b), and the number of dead roots rose (Fig. 4c). RER was rapid during the wet season (Fig. 4a, b), but with no marked difference between genotypes (Fig. 4b).

Water uptake during a dry period

As for RLD (Fig. 3a, b, c), the fraction of soil potentially usable by roots for water uptake (PRER) decreased with depth and with distance from the palm (Fig. 5a, b, c). In the areas of soil close to surface (0–0.5 m) and furthest from the palm (between 3 and 4.5 m from the palm, Fig. 5c), the differences in RLD between genotype S and the others were greater than

Table 2 Analyses of variance for total root dry matter density (TRDM), total root length (TRL), total root surface area (TRS)

Source of variation	df	Mean square		
		TRDM	TRL	TRS
Block stratum	2	0.01	50,981	0.87
Block × depth stratum				
Depth	5	3.34***	5,607,613***	160.66***
Residual	10	0.03	63,548	1.74
Block × depth × distance stratum				
Distance	2	5.68***	6,791,692***	254.81***
Depth × distance	10	1.21***	1,120,675***	38.87***
Residual	24	0.05	100,122	2.66
Block × depth × distance × units stratum				
Genotype	2	0.1***	374,850***	8.37***
Depth × genotype	10	0.03***	125,814**	2.47**
Distance × genotype	4	0.06***	96,173	2.61*
Depth × distance × genotype	20	0.02	38,210	0.85
Residual	72	0.01	46,793	0.97

*, **, *** significant at the $p<0.05$, $p<0.01$ and $p<0.001$ levels, respectively ($n=3$ blocks, $n=6$ soil depths, $n=3$ distances to tree, $n=3$ genotypes)
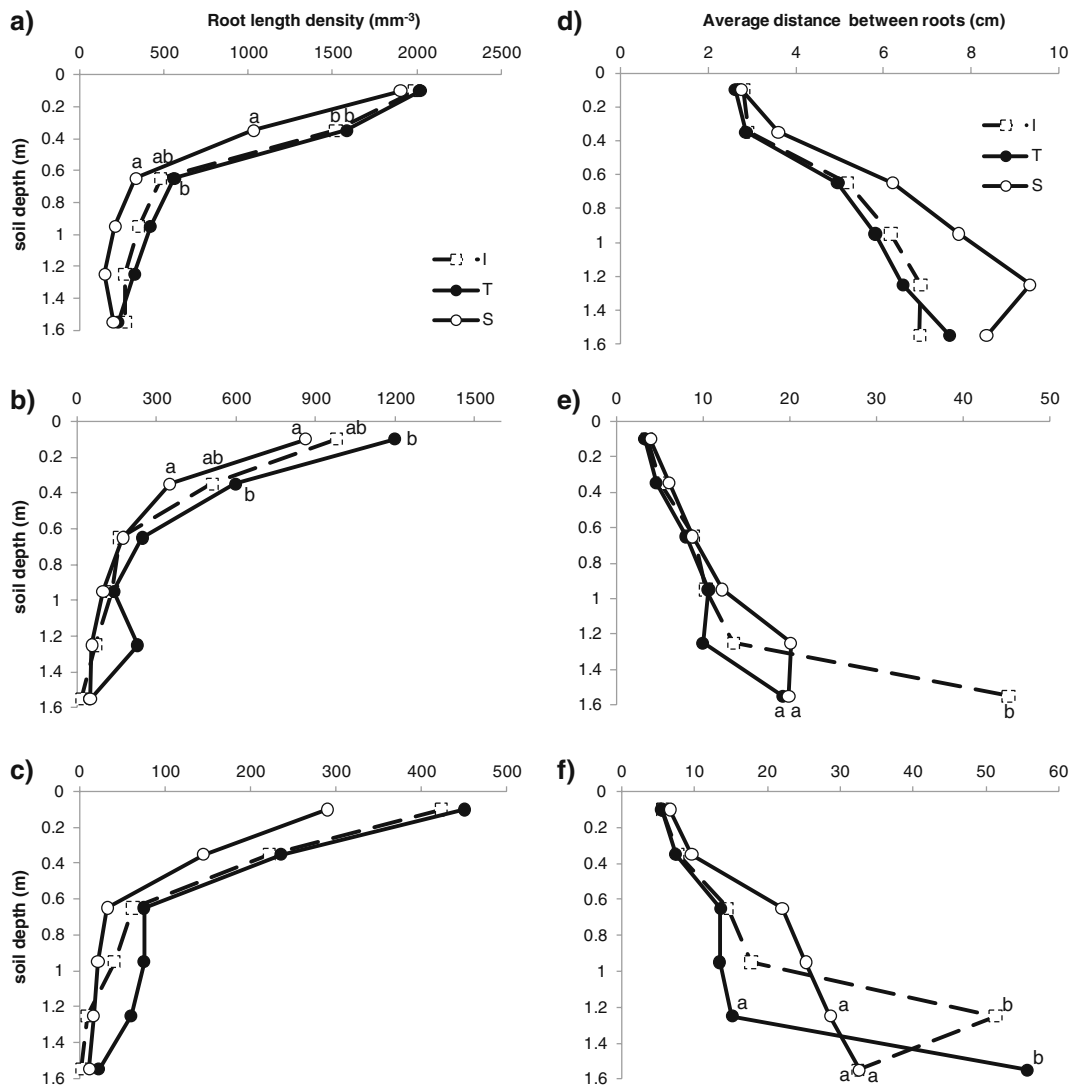
Fig. 3 Root length density (RLD, m m^{-3}, at 0–1.5 m **a**, 1.5–3 m **b** and 3–4.5 m **c** from the palm) and average distance between roots (RD, cm, **d** to **f**) depending on depth and distance from the palm for 3 oil palm genotypes. Genotypes T, I and S are defined as drought tolerant, drought intermediary and drought susceptible, respectively. For each depth, different letters indicate significant differences between genotypes (LSD test, $p<0.05$, $n=3$)

the differences in PRER. However, between 1 m and 1.5 m in depth where RLD was very low, PRER was to some extent linearly related to RLD. At this high distance from the palm, the volume of potentially usable soil explored by the roots of genotype T was more than 50% of the total volume of soil, whereas it was only 20% for genotype S.

The soil moisture extraction efficiency (SMEE) values increased with depth and distance from the palm. They differed from one genotype to the next. It

was genotype T, presumed to be tolerant, with the most developed root system (Tables 1 and 2, Figs. 3, 5a, b, c), that had the lowest SMEE, especially at sites furthest from the palm (Fig. 5f).

The AET/PET ratio decreased with FTSW (Fig. 6a) according to a linear tendency ($R^2>0.73$) for all the genotypes. However, for the same FTSW value, the AET/PET ratio of genotype T was always the lowest during the dry period. On the other hand, even with a FTSW of 65%, all genotypes presented

Fig. 4 Trends over the year for the number (Nb) of growing roots **a**, fine root (R3+R4) growth **b** and mortality **c**. Average monthly rainfall is shown by the bars and the dry seasons (short and long) are shown by the shaded zones. Genotypes T, I and S are defined as drought tolerant, drought intermediary and drought susceptible, respectively
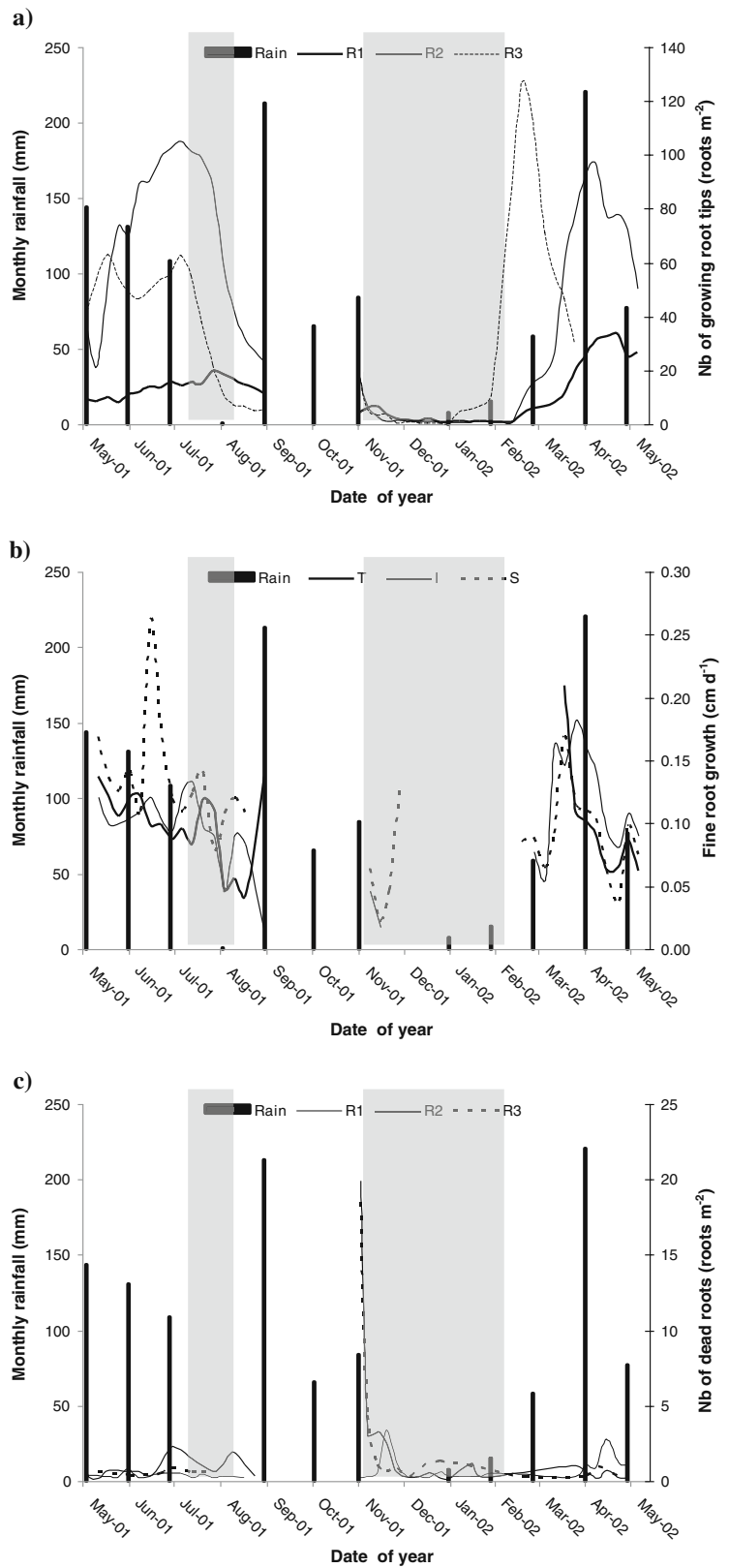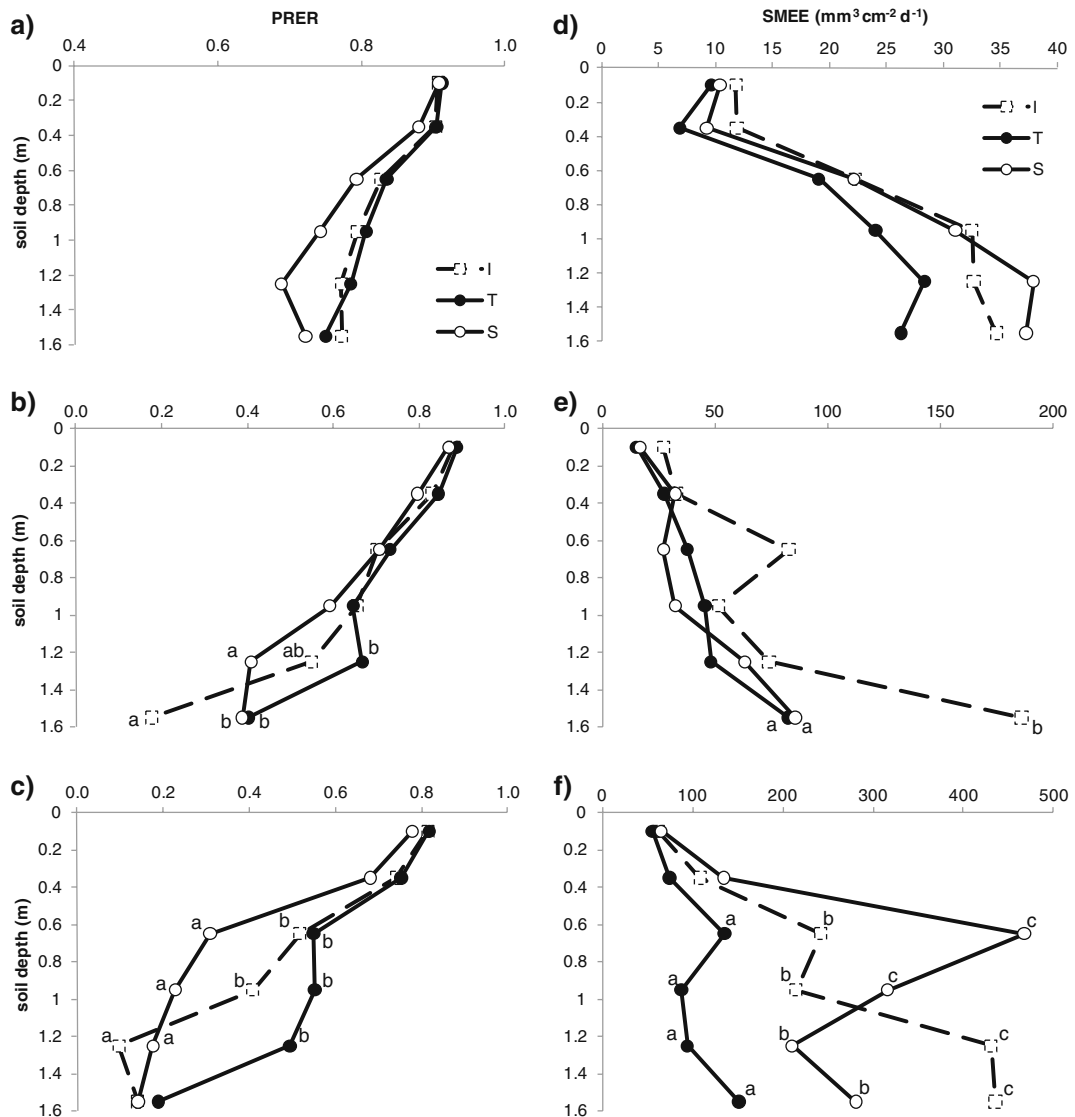
Fig. 5 Soil exploration rate for water uptake (PRER, at 0–1.5 m **a**, 1.5–3 m **b** and 3–4.5 m **c** from the palm) and soil moisture extraction efficiency per unit of root surface area (SMEE, mm³ cm⁻² d⁻¹, **d** to **f**) depending on depth and distance from the palm in 3 oil palm genotypes. Genotypes T, I and S are defined as drought tolerant, drought intermediary and drought susceptible, respectively. For each depth, different letters indicate significant differences between genotypes (LSD test, $p<0.05$, $n=3$)

AET/PET ratio below 1, indicating an inability to satisfy PET demand. The difference between genotype T and the others was increased when FTSW fell to 60%.

The fraction of transpirable soil water (FTSW) was monitored over a longer period of around 150 days down to a depth of 2.5 m (Fig. 6b). FTSW was initially 67% for genotype T and 60% for genotype S. That difference may have been due to

greater water consumption by susceptible genotype S over the previous period. After the start of the FTSW study, for the following 90 days without rainfall, the drop in FTSW for genotype T, from 67 to 51%, was similar to that for genotype S (from 60 to 43%). Genotype I, whose root characteristics were intermediate, caused the soil to dry out more. However, none of the three genotypes showed any marked signs of water stress.
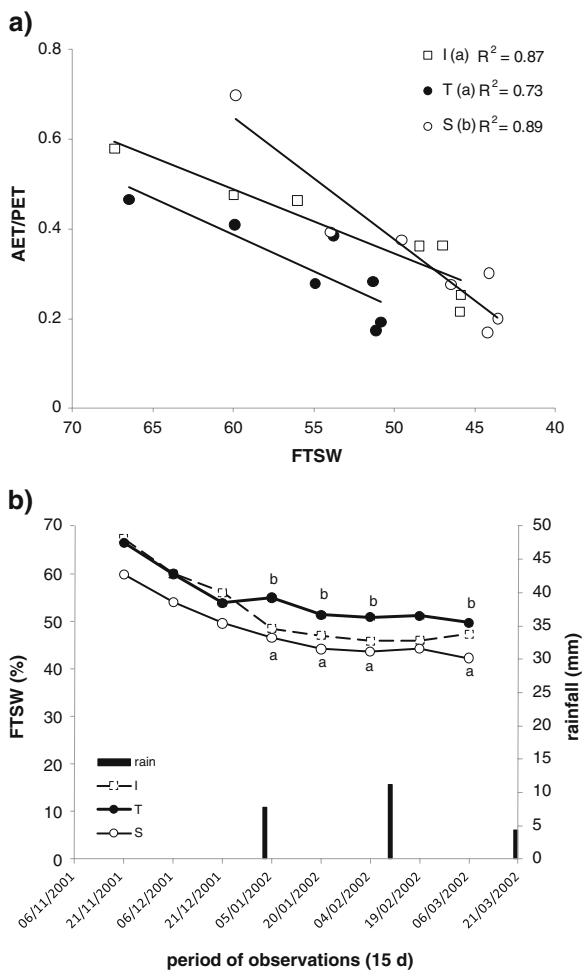
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Fig. 6 Relationship between AET/PET ratio and fraction of transpirable soil water (FTSW, a) and variation of the FTSW during the dry season b, per 15-day period beginning on November 21st of 2001. Rainfall (mm) is cumulated over each 15-day period. Genotypes T, I and S are defined as drought tolerant, drought intermediary and drought susceptible, respectively. For Fig. 6a: Data were modelled by linear equations. For each genotypes, R^2 is given and similar letters following genotype symbols are not significantly different at $p<0.05$ (LSD test). For Fig. 6b: For each date, different letters indicate significant differences between genotypes (LSD test, $p<0.05$, $n=3$)

Discussion

Genotypic variability of the root systems

The root standing biomass (3 t/ha) found for genotypes I and T were comparable to the simulated values obtained by Jourdan and Rey (1997b) for a 4-year-old palm under similar conditions in Ivory Coast. However, that level of total root biomass remained below the 4 t/ha obtained by Henson and Chai (1997) in Malaysia under wetter conditions than those in Benin and Ivory Coast. The halt in root elongation during the dry season must have limited root biomass production in Benin and may explain the differences between the results in Benin and those in Malaysia. However, palm root production was greater than reported by Ouvrier (1995) in Ivory Coast (1.4 t/ha), also on 4-year-old oil palms. That difference may have been due to the root sampling method. The auger used by Ouvrier (1995) in Ivory Coast did not seem suitable for taking samples of coarse oil palm roots which account for more than 40% of total root biomass (Table 1). As well as producing larger root biomass (Table 1), the tolerant genotype (T) also produced more fronds and bunches than the susceptible genotype (S) (Nodichao 2008). It therefore seems possible to improve oil palm drought tolerance by increasing the vigour in general, root system in particular, without penalizing yields. This result confirms that oil palm genotypes exist with high yields and also a well-developed root system, which is an important drought tolerance trait (Cornaire et al. 1994). Likewise, it was shown more recently in wheat that improving root development by chromosomal translocation has a positive effect on grain production and drought resistance (Ehdaie et al. 2003).

The total surface area and total root length of oil palm roots were measured in detail in the field. These measurements are highly laborious, even with root imaging techniques (Costa et al. 2000; Danjon et al. 2000), and have not been taken in earlier work on oil palm root development (Tailliez 1971; Henson and Chai 1997). The total root lengths measured on all the genotypes were close to the estimations of 32–45 km/palm, i.e. 458 and 643 mm^{-2} reported by Tinker (1976) and quoted by Corley and Tinker (2003) for a 4 to 6-year-old oil palm plantation on coastal soil in Malaysia, but the values obtained were well over the estimations made by Jourdan and Rey (1997b). Total root length (TRL) measured for genotype I was three times greater than Jourdan and Rey's simulation (1997b) on a genotype (C1001) of the same genetic family. The total root surface area (TRS) predicted by the same authors was two times smaller than the TRS measured here. This shows the need to carry out even more direct root length and surface area measurements in the field, in different ecosystems, to improve knowledge of the oil palm root system and to model

growth and water uptake for this crop. RLD distribution with depth (Fig. 3) revealed an exponential type decrease and this result tallied with those conventionally obtained in both oil palm (Henson and Chai 1997; Nelson et al. 2006) and other crops (Chopart et al. 2007). In each of the three genotypes, SMEE values increased with depth and distance from the palm. This may have been linked to greater residual moisture during the SMEE study in areas of soil distant from the base of the stem.

The four-year-old palms studied produced as much coarse root biomass (R1) as fine root biomass (R3+ R4), but less medium root biomass (R2). However, the total fine root surface area was three to four times greater than the R1 surface area. The difference in total length between R1 and fine roots was even greater (10 to 14 times greater fine root length). Despite the small quantity of R2 dry matter compared to R1 (less than 50%), the total R2 length was twice as great as for R1. That variability in specific root lengths and specific root surface areas, depending on topological root order, confirmed that simply measuring root biomass is not enough to describe root architecture.

The first statistical analyses (Table 2) did not reveal any significant differences in total dry matter, total root surface area and total root length between the 3 genotypes. Other authors have had the same difficulty with oil palm root data (see Nodichao 2008). However, this difficulty in revealing the genetic diversity of oil palm root systems in the field was overcome during the ANOVA by dividing up total root production data between different sources of variation. That division helped to discriminate genetic variation in rooting depth, lateral extent of roots around the palms, and their interactions.

Genotype T, which was presumed to be drought tolerant, had a greater biomass, root length and root surface area than the other genotypes, notably the presumed susceptible genotype S. This confirms the results obtained by Cornaire et al. (1994), who showed that genotypes with genes from the DA8D parent often had more roots than other oil palm genotypes.

Genotypic variability in water uptake

Genotype T, presumed drought tolerant, also had the best soil exploration ratio for water uptake (PRER).

That better water uptake potential on a whole root system scale for genotype T was due to a higher RLD throughout the examined soil volume, also better distributed throughout the soil (Chopart 1999; Da Matta 2004). The difference in PRER between two genotypes was particularly great in the deep layers, where the RLD of genotype T was significantly higher than in genotype S. Greater and deeper root development is an asset for gaining access to a larger quantity of water (Cintra et al. 1992; Annerose and Cornaire 1994; Da Matta 2004). The root system of genotype T was denser and therefore potentially more efficient than genotype S at obtaining water. Yet water uptake expressed as the volume of water taken up per root surface area per day (SMEE) was lower for genotype T than for genotype S, which had a less well developed and less well distributed root system. That difference in SMEE between genotypes T and S may have had several causes. Genotype T's water needs may have been less. Maybe the transpiration of that genotype was better regulated. Alternatively, since the total root surface area of genotype T was almost 40% greater (Table 1), the same total quantity of water could have been taken up more slowly by the roots. Consequently, the root system of genotype T enabled: (i) potential access to a larger volume of soil, (ii) slightly slower drying out of the soil around the roots (lower SMEE). Thus, genotype T seemed more adapted to withstanding more severe or longer periods of water stress. This may help to explain its drought tolerance found in earlier studies.

The relationship between AET/PET ratio and FTSW (Fig. 6a) shows that transpiration rate of genotype T decreased more rapidly than that of genotype S during the dry period. Genotype T seems to be physiologically more sensitive to vapour pressure deficit and soil drying than the others (Nodichao 2008). This physiological sensitivity could help genotype T to withstand a longer dry period thanks to early regulation of transpiration and better exploration of the soil, leading to overall better water economy (Fig. 6b). Meanwhile, genotype S appeared to have exhausted more soil water at beginning of the dry period, which decreased drastically its available soil water resource over the dry period. It is notable that for all genotypes, even with FTSW values greater than 65% (Fig. 6a), the AET/PET ratio mean values were lower than 1 during the entire dry period. This could be the consequence of the great sensitivity of

oil palm stomata to VPD (Dufrêne and Saugier 1993; Smith 1989).

The water supply to the whole plant was studied through FTSW trends over a dry period with little rainfall (Fig. 6b). The two genotypes T and I had exactly the same FTSW at the beginning of the period and the consumption of genotype I was greater than that of T, suggesting lower water needs for T, which has lower productivity than I (Nodichao 2008). On the other hand, the lower FTSW for genotype S at the beginning of the rain-free period, compared to genotypes T and I, may have been due to greater water consumption by genotype S during the period prior to observations (a week without rainfall). This result explained the lower FTSW for genotype S at the end of the dry period since soil water extraction by the two genotypes S and T was similar during the entire period. After 90 days without significant rainfall (8 and 11 mm rainfalls only), genotype T had dried out the profile less than the others and, moreover, it had a more developed root system, especially deep down, which was more efficient in terms of its ability to extract water. Consequently, genotype T seemed better armed to withstand a long period of drought, even beyond 90 days. In fact, in addition to its lower apparent water requirements than other genotypes, genotype T, with its denser root system well distributed in the soil, was enabled to extract water more slowly per unit of root surface area and thereby to dry out the soil around the root more slowly. These results tallied with the conclusions reached by Cao (2000). Among the favourable traits for adapting plants to drought in heathland forests, that author includes the development of a deep root system and efficient stomatal regulation.

PRER estimation in our study did not set out to simulate the true functioning of water uptake by roots, but is proposed here as a useful indicator for genotype comparison or ranking, for instance. Mechanistic modelling of water uptake (e.g. Deery et al. 2009) calls for the use of parameters that are difficult to measure in situ on a root scale and therefore only rarely used in agricultural studies. The simplified approach proposed here, which merely set out to assess the final stable status in the soil once all the available water has been taken up, was designed to improve measurement of the maximum available water in the soil (PAW). PAW is usually calculated exclusively from measurements in the laboratory

without taking the root profile into account. Yet the latter is essential for defining the fraction of water in the soil that is "available" to the crop.

We adopted three assumptions in our study to calculate the potential root extraction ratio (PRER). The first considered that water uptake took place uniformly along the entire root axis, from tip to base. This assumption was doubtless very simplistic, but very conventional (Atkinson 1986; Habib et al. 1991; Tardieu 1988; Taylor and Klepper 1978). However, it seemed acceptable for this study based on varietal comparison. The second assumption concerned the maximum water migration distance in the soil towards the root, which can vary considerably depending on soil, the initial water status of the soil, the extraction rate, and the time after rainfall, etc. However, once exhaustion of the available resource reaches a stable state, the maximum distance for water migration to the root takes on a value of a few centimetres (Maertens et al. 1974), usually between 5 and 15 cm (Maertens, personal communication). Under our sandy soil conditions, and for this varietal comparison trial, the average value of 10 cm seemed to be a sufficiently representative value for an initial study comparing the hydric functioning of three oil palm varieties. The third assumption put forward in this study was relative to the law of decreasing uptake capacity depending on distance from the root. The model adopted was a linear decrease for its simple and rapid application.

These three assumptions had already been successfully tested on maize subjected to water stress in the field (Chopart 1996). In fact, a very good linear relationship was established between soil desiccation at the end of a dry period and the PRER value. On the other hand, the same conventional relation, attempted with the average RLD per depth level, did not fit satisfactorily (Chopart 1996). Chopart's results show the merits of the PRER concept, whereby (i) competition between roots can be taken into account, and (ii) estimating a useful volume of soil for water supply depending on root system characteristics. Especially, it allows root clumping, which can affect water uptake capacities for the same average RLD per horizon (Tardieu et al. 1992). Although, PRER concept allowed the classification of contrasting oil palm genotypes in this study, it will be useful to calibrate this concept by measuring root sap flow along with soil water content and total root surface

area and length in each soil layer, thus attempting to convert the PRER indicator into a model.

There has been little focus to date on potential (PRER) and actual (SMEE) water uptake by root systems in studies of drought tolerance in palms. Our results revealed classification differences for the three genotypes depending on whether we considered potential or actual water uptake from the soil. In fact, PRER, expressed as a rate or as a percentage of the total soil column throughout the root zone, was an indicator of functioning if the crop was under strong and prolonged stress. SMEE was used to measure the root extraction rate per cm² of roots during a relatively moderate dry period. These two functional root characteristics were therefore complementary. They can help in understanding the genetic variability of drought tolerance, in all its complexity, which appears not to be linked to just one characteristic of the aerial or underground organs. These results should facilitate early identification of genotypes able to withstand drought. Future studies will gain by combining the below-ground characteristics (TRS, PRER, SMEE) with the physiological traits in use in regular transpiration and soil water balance models (leaf area index, stomatal and hydraulic conductances, water potential gradients).

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