Physiological and agronomic behavior of commercial cultivars of oil palm (*Elaeis guineensis*) and OxG hybrids (*Elaeis oleifera* x *Elaeis guineensis*) at rainy and dry seasons

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Abstract

Oil palm is the most productive and efficient oilseed crop in the world. Oil palm is planted in various geographical areas, where the frequency of extreme weather events is expected to increase because of climate change. The characterization of the response of oil palm cultivars to climatic conditions will allow identifying sources of tolerance to different types of stress caused by climate change, leading to the determination of the best genotype x environment relationships. The physiological responses, oil quality and yield of 11, six-year-old commercial oil palm cultivars with different origins were evaluated in two periods of contrasting climate conditions (rainy and dry seasons between the years 2008 and 2010). We found that the first impact of a period with water deficit was the reduction on gas exchange of all cultivars. Photosynthesis fell between 25% to 40% and transpiration decreased between 10% and 50%. During the dry season, leaf sugar concentration increased respect to the rainy season between 14% to 114%, and certain cultivars showed up to 27% higher photosynthetic water use efficiency. This variation could be due to the genetics of different cultivars. No significant differences were observed between the seasons in terms of oil quality. In general, changes in oil palm physiology observed in response to water deficit were related to the ability of the palm to adapt and survive periods of drought stress. The cultivars evaluated showed a good response to dry periods, with the IRHO being the most outstanding at each evaluated season .

Keywords: photosynthesis, transpiration, water deficit, water use efficiency.
Abbreviations: A_{sat}_Photosynthesis with saturate light; Ψ_{leaf}_Leaf water potential; WUE_p_photosynthetic water use efficiency; Fv/Fm_The maximum quantum yield of PSII.

Introduction

Approximately 17 million hectares worldwide are planted with oil palm, which produce more than 33% of the world's supply of oils and fats (Fedepalma, 2016). The phenomena associated with climate change have strongly affected oil palm-growing areas, to the extent that in many cases it has not been possible to obtain the expected yields, leading to a loss of profitability for agribusiness and adverse impacts on the supply of oil to the world market (Barcelos, 2015; Pirker et al., 2016; Rival, 2017) . The most important factors likely to be affected by climate change are water and temperature. They are determining factors for oil palm yield in the tropics and subtropics (Romero et al., 2007; Corley and Tinker, 2008), due to their impact on fruit set, influence on inflorescence abortion and sexual differentiation, among others (Henson et al., 2005). Water is the main factor in photosynthetic biochemical processes, in addition it is the most important means of absorption and transport of soil nutrients (Cao et al., 2011). During the dry season, photosynthesis can be inhibited due to an increased vapor pressure deficit that causes stomata to close (Smith, 1989; Dufrene and Saugier, 1993). Dry seasons are associated with high temperatures, which induce a reduction in

photochemical efficiency (Corley et al., 1973) negatively affecting photosynthesis and, thus, productivity. The relationship between the intensity and duration of dry and rainy seasons throughout the year is reflected in how most of the harvest is concentrated in short periods of time (Henson and Chai, 1998). The increased incidence of water deficit and thermal stress in many oil palm-growing regions as a result of climate change increases the urgency of understanding how crops respond and adapt to these stresses (Berger et al., 2016). Some studies have shown that modern cultivars are not well-adapted to recent climate changes (Martre et al., 2017). That finding is why oil palm breeding programs should be a multidisciplinary team effort that involves molecular tools (Rival, 2017), understanding the response of oil palm cultivars to limiting conditions due to abiotic (Rivera et al., 2012; Suresh et al., 2012; Jazayeri, 2015) and biotic factors (Moreno-Chacn and Camperos-Reyes, 2013; Avila et al., 2014; Navia et al., 2014) and conducting socioeconomic and crop feasibility studies either by defined agro-climatic regions (Pirker et al., 2016) or site-specific cases where oil palm plantations can be established (Rhebergen et al., 2016), estimating limitations in available

land (Meijide et al., 2017). In Colombia, there is a wide variety of oil palm genetic materials from different origins that can be used to start the search for sources of tolerance to different stresses. For example, *E. guineensis* cultivars are grown from breeding programs in Malaysia, Zaire, Nigeria, Ivory Coast, Indonesia and Papua New Guinea and have been developed for the environmental conditions of those areas (Rey et al., 2004). Additionally, OxG interspecific hybrids (*E. guineensis x E. oleifera*) are also grown in response to plant health problems that *E. guineensis* suffered in South America (Zambrano and Amblard, 2007). These interspecific hybrids have several advantages in terms of slow growth, high production of fresh fruit bunches and oil quality, which make them very promising materials for commercial cultivation worldwide. Despite the high yield potential of the OxG interspecific hybrids and high production of *E. guineensis* cultivars, there are differences in growth and productivity caused by the genotype-environment interactions (Rafii et al., 2012). Thus, it is necessary to better study the cultivars behaviour under different environments to place them under the conditions where they can achieved the best possible performance, according to the soil/climate conditions of each area and their eco-physiological response (Romero et al., 2007).

The purpose of this research was to characterize the physiological and agronomic behavior of different commercial oil palm cultivars under contrasting climate conditions as a first step to identify sources of tolerance to the stress imposed by extreme conditions resulting from climate change. This information could be used to determine the best planting location for each cultivar according to the response to changing and limiting conditions, particularly in terms of water supply (Kallarackal et al., 2004).

Results

Physiological parameters

Leaf water potential (Ψ_{leaf}; Fig 1.) showed significant differences between cultivars and between seasons. During the rainy season, less negative values (maximum Ψ_{leaf}: -0.99 MPa and minimum Ψ_{leaf}: -0.66 MPa) were recorded for all cultivars compared to the dry season (maximum Ψ_{leaf}: -1.50 MPa and minimum Ψ_{leaf}: -1.06 MPa). The IRHO 1001 cultivar had the lowest Ψ_{leaf} difference between the evaluated periods, with 27% higher water tension in the rainy compared to the dry season, whereas the OxG 2783 hybrid showed the greatest Ψ_{leaf} difference: 116% more negative in the dry season than the rainy. Additionally, the gas exchange response (Fig 2), as evidenced by the maximum values of photosynthesis (A_{sat}=15.47 $\mu molCO_2m^{-2}s^{-1}$) and transpiration (E=4.18 $mmolH_2Om^{-2}s^{-1}$), was recorded for the IRHO 1001 cultivar; whereas ASD DXG had the lowest A_{sat} (11.89 $\mu molCO_2m^{-2}s^{-1}$) and ASD DXN the lowest E (3.70 $mmolH_2Om^{-2}s^{-1}$). During the dry season, IRHO 1001 had the highest A_{sat} (10.59 $\mu molCO_2m^{-2}s^{-1}$) and E (3.7 $mmolH_2Om^{-2}s^{-1}$). ASD DXN had the lowest values for photosynthesis and transpiration (8.11 $\mu molCO_2m^{-2}s^{-1}$ and 1.87 $mmolH_2Om^{-2}s^{-1}$, respectively). These values indicate that for the dry season the cultivars had, in general, a 25% to 40% lower A_{sat}, and lower values for E by 9% to 50% compared to the rainy season values.

As for the photosynthetic water use efficiency (WUE_p), the response was quite heterogeneous, and although differences were found between cultivars and seasons, there was no consistent pattern: some cultivars (i.e., Corpoica, IRHO 1001, IRHO 1401, OxG 2783) showed a reduction of up to 37% in WUE_p in the transition from the rainy to dry season, wherease other cultivars (ASD DxN, DAMI 114,112, IRHO2528) had an improvement of up to 23% in WUE_p. The maximum quantum yield of PSII (Fv/Fm) remained similar between seasons and cultivars, although with significant differences (p <0.5). It was found that for all evaluations the Fv/Fm was above the benchmark value (>0.80) for healthy plants.

Biochemical parameters

The biochemical variables evaluated (proline and reducing sugars) showed statistically significant differences between seasons and between cultivars. All cultivars showed a decrease in proline concentration during the transition from rainy to dry season, with reductions between 11.41% in the IRHO 2528 cultivar and 39.63% in the Corpoica cultivar. In contrast, during the same transition, the concentration of reducing sugars was 14.91% higher in the Unilever cultivar and up to 114% higher in the IRHO 1001 cultivar, compared to the rainy season (Fig. 3)

Oil production and quality parameters

The cultivars showed a trend in yield increase over time. In 2008, the palms were 5 years old (3 years of production) which explains, to a large extent, a normal increase of this variable due to their growth stage. However, significant differences were found between cultivars over time, with ABW ranging between 6.7kg - 10.6kg for the first year, 10.2kg - 13.1kg for the second and 10.5 kg - 14 kg in the last year evaluated. The averages for each year were 8.68 kg for year 1, 11.69 kg for year 2 and 12.05 kg for year 3. Figure 4 presents the variation in ABW for each cultivar over the evaluation period, which was correlated with the rainfall during the 6 months before harvest.

We attempted to determine whether the harvesting time of the year influenced oil quality. Therefore, bunches harvested in dry and rainy seasons were evaluated (Figure 5). No differences were found in the percentage of fatty acids due to the harvesting time of the year. However, as expected, there were statistically significant differences regarding the concentration of oleic, palmitic, stearic acids, and iodine index in OxG hybrid cultivars compared to *E. guineensis*. Additionally, a tendency toward higher concentrations of stearic acid was observed in *E. guineensis* during the dry-season harvest.

Discussion

The evaluation of the commercial oil palm cultivars in Palmar de la Vizcaína uncovered a differential response to environmental conditions. Oil palm water status during the rainy season showed adequate hydration, with leaf water potential (Ψ_{leaf}) greater than -1 MPa, similar to that seen in well-hydrated oil palm seedlings under semi-controlled conditions (Suresh et al., 2012) and below that reported for 4-year-old irrigated palms at three sites in India (Kallarackal

et al., 2004) However, during the dry season, the water potentials were more negative due to lower soil water availability. Ψ_{leaf} values (-1.5 MPa) during the dry season indicate a medium level of stress; therefore, the response of cultivars such as IRHO 1001, with lower leaf water potential during the dry season with respect to the rainy season, may be an indicator of a mechanism associated with water deficit response (Azzeme et al., 2016).

During the rainy season, the cultivars reached the maximum photosynthetic values due, in part, to the effect of low Ψ_{leaf} which inhibits stomatal closure, allowing the palms to maintain high transpiration rates. This behavior was also observed in oil palms under field conditions in eastern Colombia (Bayona and Romero 2016) and in oil palm seedlings under mesh-house conditions (Silva et al. 2017). When environmental conditions changed during the transition to the dry season, all cultivars showed a significant reduction in CO_2 assimilation and transpiration rate, a generalized response in many species subjected to water stress (Cruz et al., 2016; Gleason et al., 2016; Li et al., 2017; Urban et al., 2017). The cultivars evaluated showed gas exchange adjustments in response to changes in environmental factors in the short term. This underpins the importance of understanding the physiological plasticity that results from the genotype-environment interaction (Gratani, 2014).

The maximum efficiency of photosystem II (Fv/Fm) was stable regardless of the season, and despite having significant differences among cultivars. Values were between 0.80 and 0.85, which is considered to be in the range for healthy plants and similar to that found in cotton (Yi et al., 2016), suggesting that there was no damage to PSII. This might be associated with some protective factor such as the accumulation of pigments (chlorophyll a, b and carotenes), such as occurs in *Moringa oleifera* when it is exposed to water deficit (Araújo et al., 2016). Additionally, a significant reduction in the Fv/Fm index in *Elaeis guineensis* seedlings was observed after 14 days without irrigation (Suresh et al. 2010), suggesting that adult plants may be more tolerant to drought, as there is a great difference in pigment contents between seedlings, juvenile palms and adult palms (Apichatmeta et al., 2017) as well as a better formed root structure in adult plants.

Although the photosystem II efficiency did not reflect a stressful event, an overall reduction in gas exchange was observed in the dry season, because drought is one of the most important factors that inhibit photosynthesis (Sami et al., 2016). Therefore, the accumulation of compounds associated with tolerance to water deficit was quantified. These compounds include sugars that accumulate in response to stress, can function as osmolytes to maintain cell turgor, and have the ability to protect membranes and proteins from stress damage (Krasensky and Jonak, 2012). Oil palm cultivars respond biochemically, triggering the accumulation of sugars during the dry season. For example, IRHO 1001 increased sugar levels by 114% and improved WUE$_p$ by 27%. Similar results have been observed in different species under stress conditions (Wu et al., 2014; Pandey and Shukla, 2015; Harsh et al., 2016) and in oil palm seedlings under water stress conditions (Rivera et al., 2012) . Proline content, which acts as an osmotic adjustment mediator and a source of carbon and nitrogen, was also quantified (dos Santos and Verissimo, 2013). Although an increase in the concentration of proline has been reported in seedlings subjected to water deficit (Mohd Hannif, 1997; Yamada et al., 2011), this response in adult palms under field conditions was not found in this research. In fact, the proline concentration decreased in all cultivars during the dry season. The Ψ_{leaf} values found in the dry season are not lower than -1.5 MPa, which suggests that the palms were subjected to moderate to low stress, unlike the -2.16 MPa reported by Mohd Hannif (1997). On the other hand, it has been established that more metabolic energy may be required for the biosynthesis of nitrogen-rich compounds such as proline compared to carbon-rich compounds, such as carbohydrates (Kim et al., 2016). In this way, less metabolic energy can be used for osmotic adjustment in plants with some degree of tolerance; therefore, a relatively lower level of proline and a relatively higher level of carbohydrates are maintained, as was observed in this study (Harsh et al., 2016).

Regarding production, it was found that cultivars such as IHRO 1401, OxG 2783 and ASD DXN had high positive correlations (R = 0.98, 0.82 and 0.72, respectively) between average bunch weight (ABW) and the amount of rainfall 6 months before harvest. Cultivars with low to negative correlations were also found, such as IRHO 2528, OxG 2803 and ASD DXG, which is evidence that some cultivars are more sensitive to rainfall, resulting in differences in ABW. Additionally, despite the short dry periods, the yields of the cultivars evaluated were relatively uniform, similar to those reported for Malaysia (Corley and Tinker 2008), with no more than 40% production concentration in peak months, as it is the case in areas with marked dry seasons (Carr, 2011).

The response of the cultivars regarding fatty acid profile in contrasting seasons did not show significant differences. This response is similar to that reported for olive and almond trees subjected to water-deficit stress (Zhu et al., 2015), where the oil quality showed very small variations that may not reflect the response to water deficit, unlike other annual oilseeds such as soybean, sunflower and canola that significantly change the concentrations of fatty acids in response to drought stress (Ali et al., 2009; Zarei et al., 2010; Candogan et al., 2013).

For the evaluation of genotypes, it is very important to know their response in different environments (Feller, 2016). To this end, hierarchical clustering was performed using the Wards method based on the physiological and biochemical responses of the 11 cultivars to dry and rainy seasons (Fig 6). This analysis generated two large clades, clearly differentiated by sampling season. In the rainy season, there are two groups: Group A, with two subgroups: ASD cultivars that share Deli Dura as the female parent and, although one has Calabar (ASD DXG) and the other Nigeria (ASD DXN) as male parents, both are from the NIFOR (Nigerian Institute for Oil Palm Research) breeding program. There are also Dami cultivars that may have the same genetic base as the Deli Dura as female parents but with Avros as male parent. The second subgroup consists of Corpoica, Unilever cultivars and the OXG hybrid. The first two of this subgroup share a male parent from Congo (Yangambi) and are probably linked to the hybrid by the La Mé parent. Group B consists of Deli x La Mé, i.e., IRHO cultivars. Cultivars of Group A, compared to Group B, had, on average, 10% less CO_2 fixation, 30% higher proline concentration and 16% higher sugar concentration.
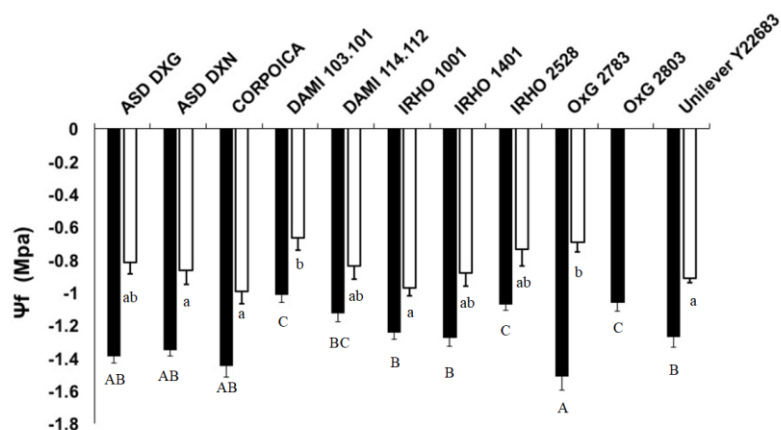
Fig 1. Leaf water potential (Ψ_{leaf}) in 11 oil palm cultivars, under field conditions in the dry season (black boxes) and rainy season (white boxes). Means with different letters are significantly different above the SE-bar (n=9) indicate significant differences according to Tukey's test (p < 0.05).

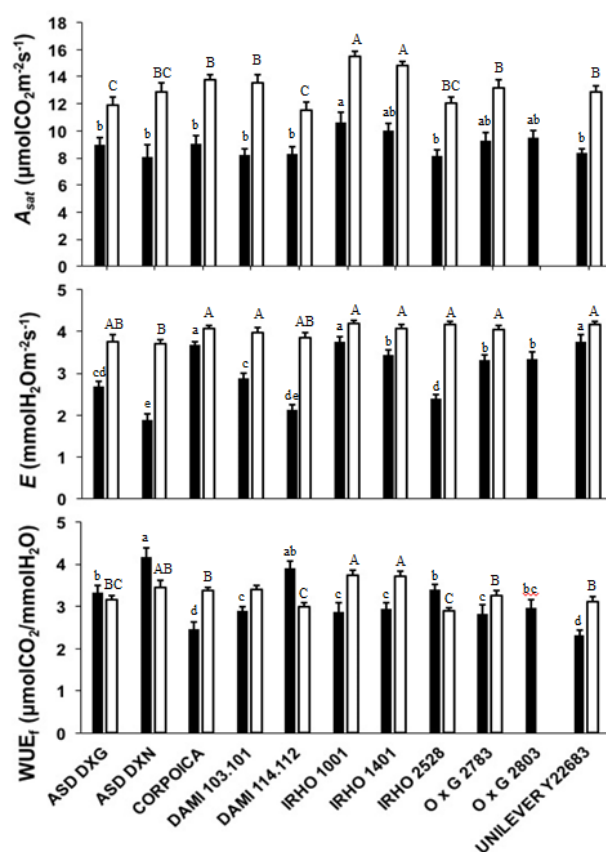**Fig 2.** Photosynthetic rate (Asat), transpiration rate (E), photosynthetic water use efficiency (WUE$_A$) in 11 oil palm cultivars under field conditions in the dry season (black boxes) and rainy season (white boxes). Means with different letters are significantly different above the SE-bar (n=9) indicate significant differences according to Tukey's test (p < 0.05).

This part of the dendrogram showed a clustering similar to that reported from SRR-type molecular markers (Arias et al., 2012), suggesting that during the rainy season these cultivars express general traits associated with the molecular markers used (Martre et al., 2017).

However, when the environmental conditions changed to dry season, the phenotypic response was different. The second part of the clade, as during the rainy season, shows the formation of 2 groups, but the association of the cultivars was different. A group C was formed by ASD DxG, IRHO 2528, Dami 114.112 and ASD DxN cultivars, which have Deli as the female parent but different male parents (Calabar, La Mé, Avros and Nigeria, respectively). Group D had greater heterogeneity, with Deli x Avros (Dami 103.101), Deli x La Mé (IRHO 1001, IRHO 1401), Deli x Yangambi (Corpoica), Ekona x Yangambi (Unilever) and Coarí x La Mé (OxG 2783 and OxG 2803). The response of the cultivars of Group C, compared to those of Group D, showed lower rates
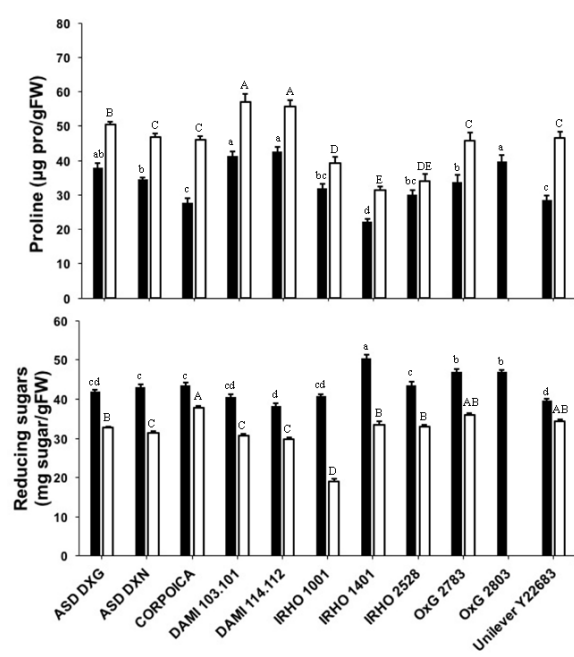
Fig 3. Leaf concentration of proline and reducing sugars in 11 oil palm cultivars, in the dry season (black boxes) and rainy season (white boxes). Means with different letters are significantly different above the SE-bar (n=9) indicate significant differences according to Tukey's test (p < 0.05).
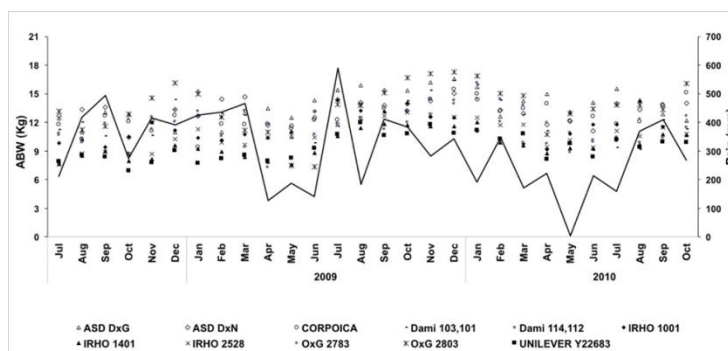

Fig 4. Rainfall behavior (line) and average bunch weight (ABW) of 11 commercial cultivars over the 3-year evaluation period.
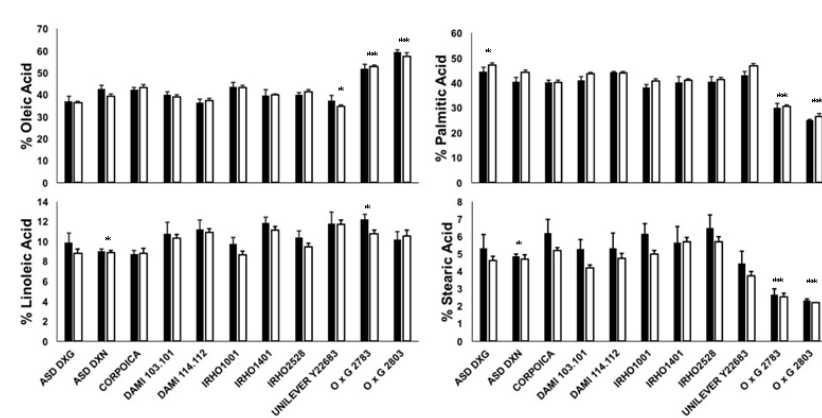

Fig 5. Fatty acid composition in fruits of 11 oil palm commercial cultivars harvested in the dry season (black boxes) and rainy season (white boxes). Vertical bars represent SE for n = 4, Values marked with * are significantly different at p <0.05
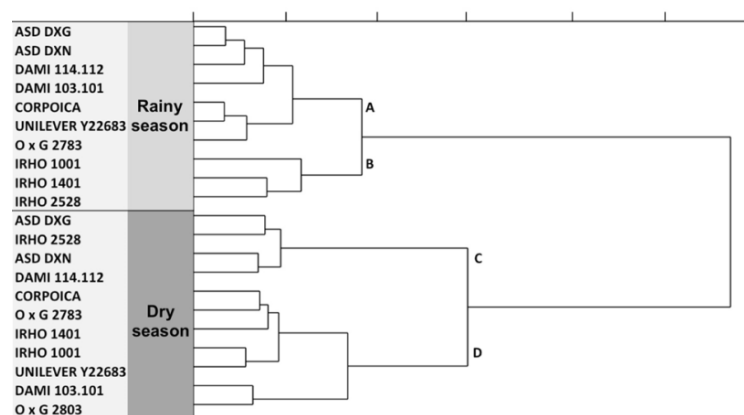
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Fig 6. Ward's method dendrogram (minimum variance – Multi-base) of 11 oil palm cultivars, based on physiological (Asat, E, PWUE, and Ψ_{leaf}) and biochemical data (concentration of proline and reducing sugars) obtained during dry and rainy seasons.

of photosynthesis and transpiration, an improvement in photosynthetic water-use efficiency and lower sugar levels. These characteristics show the susceptibility of the cultivars of group C to lack of water during the dry season.

Materials and methods

Location

This work was carried out between 2008-2010 in the Experimental Field Palmar de la Vizcaína, Department of Santander - Colombia (6° 58 N, 73°42 O). The site is located 140 m above sea level, with a relative humidity of 75%, average temperature of 29°C, and bimodal average annual rainfall of 3200 mm. The eco-physiological variables (Supplementary Table 1) were recorded in two consecutive years during the dry season (precipitation less than 30mm per month January 2008 - 2010) and the rainy season (precipitation more than 300mm per month September 2008 -2010).

Plant materials

Eleven commercial cultivars were selected as being the most used in the different regions of Colombia: 9 cultivars of the *Elaeis guineensis* species and 2 of the OxG interspecific hybrid (*E. oleifera x E. guineensis*) (Supplementary Table 2). The palms were planted in an Agronomic Management Unit (UMA) in La Vizcaína combined association (LV – Fluvaquentic Eutrudept), which is characterized by homogeneous climate and soil conditions. The palms were planted from commercial seed and after a year of nursery in 2004 on a 10-ha parcel of land in a triangular pattern with a planting distance of 9x9 m and 10x10 m for *Elaeis guineensis* and the OxG hybrid, respectively. The experiment was planted under a randomized block design, with three replicates, and 16 palms per plot. Measurements of physiological variables were taken from the middle third of leaf 17. Data were captured between 9:00 a.m. and 11:00 a.m., when photosynthesis is at its peak (Bayona-Rodríguez et al. 2016).

Physiological parameters

To quantify gas exchange (photosynthesis, transpiration and stomatal conductance) a portable photosynthesis meter

(LI6400XT, LiCor, Inc. USA) was used. The CO_2 parameters were set at 400 ppm, PAR radiation 1000 $\mu molm^{-2}s^{-1}$, block temperature at 30°C and flow at 170 $mmols^{-1}$. Measurements were taken on 3 leaflets per palm. Chlorophyll fluorescence was determined by a fluorescence chamber (LI6400-40) coupled to the LI6400XT portable photosynthesis system. A total of 3 leaflets were taken per palm, adapted to darkness for 2 hours, and the maximum quantum yield of PSII (Fv/Fm) was measured. Leaf water potential was measured with a pressure chamber (Schölander Pump, Soil Moisture, USA), using 3 leaflets per palm.

Biochemical parameters

Tissue from the leaflets that were used to measure gas exchange was collected and preserved in liquid nitrogen. Next, the tissue was macerated in liquid nitrogen. Reducing sugars were quantified using the Somogyi method (Somogyi 1945). For each sample, 0.2 g of macerated tissue was extracted with sodium acetate buffer (50 mM pH 5.0) and centrifuged at 4° C. A 10 µl aliquot was taken from the recovered supernatant and Somogyi I (200µl) and Somogyi II (50µl) reagents were added, samples were boiled for 20 minutes. Then Nelson reagent (250µl) and distilled water (750µl) were added, and the absorbance at 660 nm was determined. Proline was quantified using ninhydrin in acid solution (Bates et al. 1973): 0.25 g of macerated tissue was extracted with sulfosalicylic acid (3%) and centrifuged at 6000 rpm. For the assay, 1 ml of ninhydrin (prepared in situ) and 1 ml of glacial acetic acid were added to 1 ml of supernatant. Samples were then incubated for 1 h at 98° C, cooled in ice-water and then 3 ml of toluene was added. After 3 minutes, the organic phase was collected and the absorbance was determined at 520 nm.

Oil production and quality parameters

To determine the production of each cultivar, production records were kept, consisting of in situ weighing of each bunch harvested per palm, throughout the research study period. For each contrasting season, a sample of four bunches of each material was taken, and measurements were performed according to the bunch analysis protocol described by (Rincón et al. 2013), and an extraction and

quantification of fatty acids was performed according to the protocol described by (Cadena et al. 2013).

Statistical analysis

The information was obtained by sampling in a completely randomized design and analyzed by SAS software. Analysis of variance was performed and comparisons were made using the Tukey test. An analysis was carried out for the main components of the physiological and biochemical variables.

Conclusion

According to the evaluation, oil palm cultivars under contrasting climate conditions showed the highest rates of photosynthesis and transpiration during the rainy season, and the gas exchange in all cultivars was affected to varying degrees by the dry season. It was found that cultivars have a differential response to contrasting climate conditions in terms of osmolyte concentration. The harvesting time of the year did not affect the acid profile of any of the cultivars studied. Cultivars such as IRHO 1001, IRHO 1401, CORPOICA, Unilever and the hybrid OxG 2783 have a high potential to withstand dry periods, therefore they can be recommended for regions with prolonged dry periods or in places where the application of irrigation is difficult. The cultivars Dami 114.112, ASD and IRHO 2528 were more susceptible to drought and should be planted with caution in regions with limited water supply.

Acknowledgements

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