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Fitting of photosynthetic response curves to photosynthetically active radiation in oil palm

Ajuste de las curvas de respuesta fotosintética a la radiación fotosintéticamente activa en palma de aceite

Yurany Dayanna Rivera-Méndez¹ and Hernán Mauricio Romero^{1,2*}

ABSTRACT

Light saturation curves represent the response of the net photosynthetic rate to the photosynthetically active radiation. These curves were obtained from individual leaves of oil palm genotypes (*Elaeis guineensis*, *E. oleifera* and the O×G interspecific hybrid) without any type of biotic or abiotic stress, fitting three nonlinear models: the rectangular hyperbolic model (Michaelis-Menten), the non-rectangular hyperbolic model (Prioul and Chartier) and the exponential model (Mitscherlich). The research was conducted at Barrancabermeja (Santander, Colombia) with the aim to compare the adaptations of these models and to identify the most suitable model for the crop. The rectangular hyperbolic model was qualitatively and quantitatively the most appropriate to describe the oil palm response under different conditions, in terms of the coefficient of determination (R^2), the mean squared error (MSE) and the standard error (SE); therefore, using this model, the photosynthetic parameters showed higher and more realistic correlation (r) with the measured values. The non-rectangular hyperbolic model was the least appropriate model to estimate the maximum photosynthesis, dark respiration, saturation points, light compensation and photosynthetic efficiency. Thus, the rectangular hyperbolic model is the fastest, simplest and most appropriate option to access the light curve information in oil palms and can be incorporated into the gas exchange and growth models into the whole palm production system.

Key words: Colombia, dark respiration, light compensation point, light saturation point, maximum photosynthesis, photosynthetic efficiency.

RESUMEN

Las curvas de saturación de luz representan la respuesta de la tasa de fotosíntesis neta a la radiación fotosintéticamente activa. Éstas se obtuvieron a partir de hojas individuales de genotipos de palma de aceite (*Elaeis guineensis*, *E. oleifera* y el híbrido interespecífico O×G) sin ningún tipo de estrés biótico o abiótico, y fueron utilizadas para ajustar tres modelos no lineales: el hiperbólico rectangular (Michaelis-Menten), el hiperbólico no rectangular (Prioul y Chartier), y el exponencial (Mitscherlich). La investigación se llevó a cabo en Barrancabermeja (Santander, Colombia), y buscó comparar las adecuaciones de cada modelo e identificar el más preciso para el cultivo. La hipérbola rectangular fue cualitativa y cuantitativamente el modelo más adecuado para describir tal respuesta en todas las condiciones de estudio, en términos de coeficiente de determinación ajustado (R^2), cuadrado medio del error (CME) y error estándar (EE); y por ello sus parámetros fotosintéticos mostraron una correlación (r) más alta y realista con los valores medidos. El modelo hiperbólico no rectangular fue el menos adecuado para estimar la fotosíntesis máxima, la respiración oscura, los puntos de saturación y compensación de luz, y la eficiencia fotosintética. Así, el modelo hiperbólico rectangular es la opción más rápida, sencilla y robusta para acceder a la información de las curvas de luz en palma de aceite, que puede ser incorporada en modelos de crecimiento a nivel de planta y sistema productivo.

Palabras clave: Colombia, eficiencia fotosintética, fotosíntesis máxima, punto de compensación lumínico, punto de saturación lumínico, respiración en oscuridad.

Introduction

Photosynthesis is the process used by plants to transform less than 5% of the incident solar radiation into the energy needed to drive carbon dioxide fixation to form the organic matter of plant tissues, and to promote plant growth (Solarte *et al.*, 2010). The radiation used in photosynthesis range between 400 to 700 nm of the solar

radiation spectrum and is known as photosynthetically active radiation (PAR) (Azcón-Bieto *et al.*, 2008). The PAR intercepted and absorbed by the leaves, and the efficiency of the conversion of carbohydrates into chemical energy are key factors to understanding plant growth (Woittiez *et al.*, 2017). One way to study these factors is with light saturation curves, which represent the response of the net photosynthetic rate to the PAR (Fig. 1). These curves

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show that there is no photosynthetic assimilation in the dark, and the CO_2 emitted is a result of mitochondrial respiration (dark respiration); as the photon flux increases, the CO_2 uptake increases until it equals the CO_2 release to respiration (Taiz and Zeiger, 2010). At this PAR value, which is called the light compensation point, the net CO_2 exchange of the leaf is zero, and an increase above it results in a proportional increase in the rate of photosynthesis (Azcón-Bieto *et al.*, 2008). The initial part is essentially linear, and its slope corresponds to the light-use efficiency by chloroplasts or photosynthetic efficiency (Φ). At a high PAR, the photosynthetic response begins to stabilize and reaches its maximum capacity (maximum photosynthesis), and beyond this point, an increase in PAR does not affect the rate of photosynthesis (light saturation point) (Lobo *et al.*, 2013).

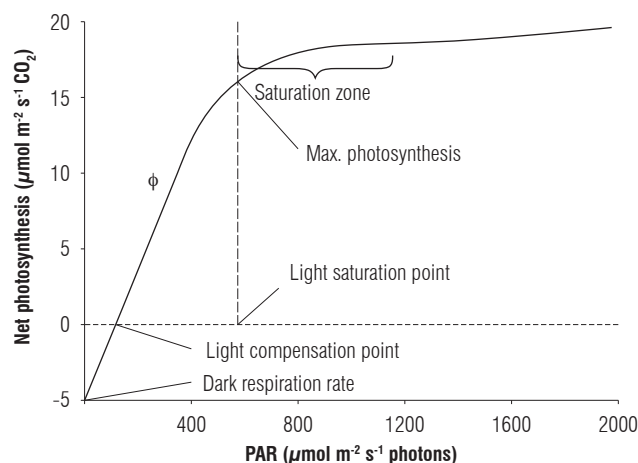


FIGURE 1. Ideal light saturation curve which represents the photosynthetic rate response to the PAR.

To access the information derived from these curves, it is necessary to fit it with nonlinear regression models (Marino *et al.*, 2010), because they have simple formulas that can be easily parameterized and interpreted. The effectiveness of the used model depends on the information that is expected to be known and the suitability of the model for the ecophysiology of the species (Gomes *et al.*, 2006).

Oil palm is an important crop worldwide due to its oil production for human consumption and industrial uses, especially for the biodiesel industry. So, it is now the most used vegetable oil worldwide, reaching about 32% of the global oils and fats production (Woittiez *et al.*, 2017). Oil palm is a perennial crop with a very long growth period and high biomass production which economic cycle may last up to 30 years. In Colombia the crop has an average participation of 9.5% in the production of permanent

crops and 5.7 % in national agricultural production, it is the second largest oil palm producer outside Southeast Asia, and the largest producer in South and Central America (Fedepalma, 2016).

Oil palm productive cycle must adjust its photosynthetic and metabolic dynamic based on the soil and climate characteristics of the area where it is grown, aiming to produce the photoassimilates needed to grow and develop reserve structures and fruit bunches (Corley and Tinker, 2015). Thus, the study of the physiological processes that regulate and intervene directly on oil palm production, primarily the increase in photosynthetic capacity (Peláez *et al.*, 2010), is a potential tool for the selection of highly productive cultivars (Rivera *et al.*, 2013a). Several studies have been conducted on the physiological and morphological characterization of oil palms, particularly in terms of photosynthesis, transpiration and the environmental factors that affect their morpho-physiological processes (Ayala and Gómez, 2000; Corley and Tinker, 2015; Jazayeri *et al.*, 2015; Peláez *et al.*, 2010; Rivera *et al.*, 2012; Rivera *et al.*, 2013a; Rivera *et al.*, 2013b; Rivera *et al.*, 2016; Romero *et al.*, 2007; Ruiz and Henson, 2002); however these studies have not parameterized the information provided by the light saturation curves in a simple but robust model for breeding purposes. Thus, the aim of this research study was to identify the most appropriate nonlinear model to fit light saturation curves in oil palm, based on the suitability of the model (goodness of fit criteria), and to provide practical and efficient selection and breeding criteria for the crop.

Materials and methods

Location

The study was carried out at the Experimental field “Palmar de La Vizcaína” (6°59’3.22”N and 73°42’20.93”W), owned by the Oil Palm Research Center (Cenipalma) and located in Barrancabermeja (Santander, Colombia), at an altitude of 125 m a.s.l., with the following climatic conditions:

	Min	Max	Average
Temperature (°C)	16.4	44.3	28.6
Relative humidity (%)	33.0	100.0	81.2
Precipitation (mm year ⁻¹)	2,843	4,463	3,579

Plant material

A total of 35 plants ($n = 35$) of three oil palm genotypes, without any type of biotic or abiotic stress, were evaluated: six plants of *Elaeis oleifera* ($n = 6$), nine plants of *Elaeis guineensis* ($n = 9$), and twenty plants of interspecific hybrid

(*E. oleifera* \times *E. guineensis*) (n = 20) in both the nursery stage and the adult stage (≥ 6 years after planting).

Plants at the nursery stage received 1 mm d⁻¹ of water through a drip irrigation system, while the adult palms (at the definitive site) were not irrigated, because precipitation satisfied their evapotranspiration rate (5 mm d⁻¹). In terms of fertilization, chemical sources were used, in the quantities necessary to reach the levels established as adequate by Rincon *et al.* (2012), and Arias and Beltrán (2010) for nursery and adult palms, respectively.

Experimental conditions

The light saturation curves were obtained using the infra-red gas analyzer IRGA - LI-6400 (LI-COR Inc., Lincoln, NE, USA), evaluating the middle section of leaf No. 3 of palms in the nursery stage and the central leaflets of leaf No. 17 in the adult palms under full sunlight conditions (8:30 to 11:30 h). The following conditions were set in the IRGA chamber: 30°C temperature, 400 $\mu\text{mol CO}_2$ concentration, 2.5 kPa saturation vapor pressure, and 3% of maximum coefficient of variation. Initial experimental condition was a saturating PAR level of 2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photons, and then it was reduced every 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photons to a value of 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photons (2,000 - 1,800 - 1,600 - 1,400 - 1,200 - 1,000 - 800 - 600 - 400 - 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photons). At this rate, the spacing between values was reduced to determine the light compensation point (200 - 150 - 50 - 20 - 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photons).

Statistical analysis

The photosynthesis data based on PAR were fitted to three nonlinear models (Tab. 1), the rectangular hyperbolic model (Michaelis-Menten), the exponential model (Mitscherlich), and the non-rectangular hyperbolic model (Prioul and Chartier), using the statistical package Statistix 9.0®

(Analytical Software, USA) and following the methodology proposed by Solarte *et al.* (2010) for the first two models and the Photosyn Assistant® (Dundee Scientific, UK) software for the remaining model. Finally, the photosynthesis data sampled and fitted to the three models were compared using univariate linear regressions with the statistical package of Microsoft Excel 2013. Using the goodness-of-fit criteria, the most appropriate model was selected to predict the photosynthetic parameters: photosynthesis rate as a function of PAR, maximum photosynthesis (A_{max}), light saturation point ($\text{PAR}_{\text{saturating}}$), dark respiration (D_R), photosynthetic efficiency (Φ) and light compensation point (LCP) in oil palms.

The criteria used were: the adjusted coefficient of determination (R_a^2) which measures the proportion of the total variability explained by the model and further corrected by the sample size (n); the standard error (SE), which explains the variability produced by unknown distorting factors; the mean squared error (MSE), which measures the variance of the prediction error or the difference between the estimated and the actual data; and the correlation (r) or degree of association between the actual data and the data estimated by the model (Montgomery, 1992). Additionally, a significance test (F-test, $P \leq 0.05$) was performed to estimate the overall adequacy of the model.

Results

The sampled values of the photosynthetic response of oil palms to the PAR overlapped, mainly, with the values obtained by fitting the rectangular hyperbolic model (Michaelis-Menten) and the exponential model (Mitscherlich); in contrast, the non-rectangular hyperbolic model (Prioul and Chartier), overestimated the values in all three cases

TABLE 1. Models evaluated to fit the light saturation curves in oil palm. Adapted from: Gomes *et al.* (2006) and Marino *et al.* (2010).

Model	Information provided					
	A_{max}	Saturating PAR	D_R	Φ	LCP	θ
Rectangular hyperbolic: Michaelis-Menten $A = \frac{A_{\text{max}} * \text{PAR}}{(K + \text{PAR})} - R_d$	X	X	X	+	+	
Exponential: Mitscherlich $A = A_{\text{max}} * (1 - \text{Exp}(-\Phi * (\text{PAR} - P_c)))$	X		+	X	X	x
Non-rectangular hyperbolic: Prioul and Chartier $A = \left\{ \frac{A_{\text{max}} + (\Phi * \text{PAR}) - [(A_{\text{max}} + (\Phi * \text{PAR}))^2 - (4 * \Phi * \theta * A_{\text{max}} * \text{PAR})^{0.5}]}{(2 * \theta)} \right\} - R_d$	X	+	X	X	+	X

A: photosynthesis based on PAR; A_{max} : maximum photosynthesis; K: light saturation constant = $\frac{1}{2} \text{PAR}_{\text{saturating}}$; $\text{PAR}_{\text{saturating}}$: light saturation point; D_R : dark respiration; Φ : photosynthetic efficiency; LCP: light compensation point; θ : dimensionless term of convexity. X: information provided directly by the equation; +: estimated information.

of CO₂ assimilation (Fig. 2). Specifically, the rectangular hyperbolic model (which has the shape of a rectangular hyperbola) was quantitatively more accurate to describe the oil palm photosynthetic rate in function of the PAR under the study conditions, and therefore, its predicted photosynthetic parameters showed a higher, significant ($P \leq 0.05$) and more realistic association (correlation) with the measured values (Fig. 3). Hence, this model, displayed four optimal criteria of goodness-of-fit: maximum r , maximum adjusted R^2_a , minimum MSE and minimum SE (Tab. 2).

TABLE 2. Goodness-of-fit criteria of the non-linear models to describe the photosynthesis response of oil palms to the PAR. The optimal values of each criterion are highlighted.

Criteria	Model		
	Rectangular hyperbolic: Michaelis-Menten	Exponential: Mitscherlich	Non-rectangular hyperbolic: Prioul and Chartier
r	0.997**	0.994**	0.905**
R^2_a	0.995	0.988	0.819
MSE	44.69	102.15	1721.24
SE	0.321	0.485	1.989

** Significance F-Test for the model ($P \leq 0.05$). r : coefficient of correlation between the actual and the estimated photosynthesis for the model; R^2_a : coefficient of determination fitted to the model; MSE: mean squared error of the model; SE: standard error of the model.

The rectangular hyperbolic model ($A_{\max} * PAR_i / (K + PAR_i) - D_R$), which assumes a reversible photosynthetic response, is simple in its calculation and in the present study allowed to obtain the maximum photosynthesis, saturating PAR and dark respiration directly, and led to the estimation of photosynthetic efficiency and light compensation point. Photosynthetic efficiency was estimated by a linear regression between photosynthesis (A) and 0-300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photons of PAR (ensuring this was significant and with an R^2 greater than 0.90). The light compensation point (LCP), was also estimated using the same linear regression but leveling photosynthesis to zero

$$(A = 0): \text{LCP} = - \frac{(\frac{\text{Saturating}_{\text{PAR}}}{2} * D_R)}{(D_R + A_{\max})}$$

Thus, the photosynthetic rates of *E. guineensis*, *E. oleifera* and the O×G hybrid were positive from approximately 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photons, with lower values at lower PAR intensities. As the PAR increased the photosynthetic rates increased initially linearly (up to 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photons) and then diverged from the linear response in a small transition stage to a saturation PAR value of approximately 545 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photons. Finally the photosynthesis reached a maximum value in a very stable section in which a

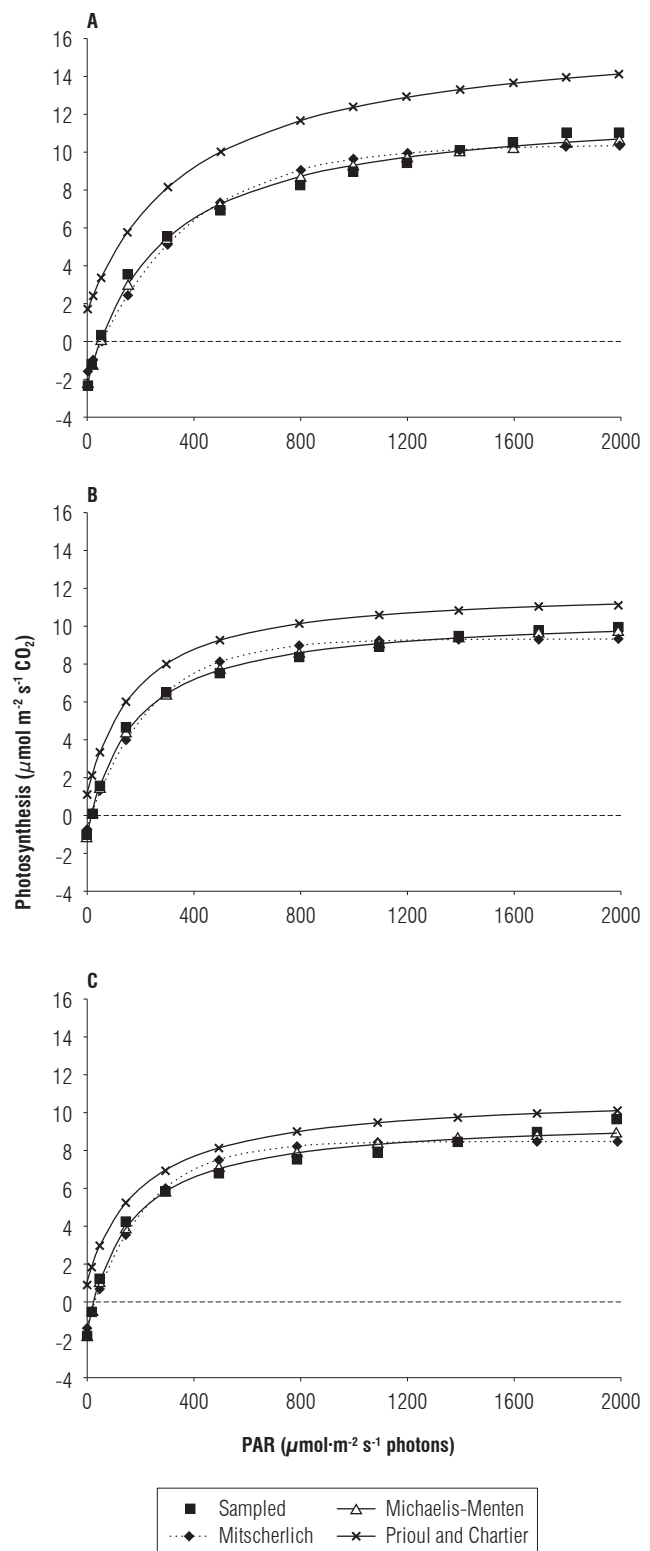


FIGURE 2. An example of light saturation curves fitting in oil palm genotypes with the non-linear models: the rectangular hyperbolic (Michaelis-Menten), the exponential (Mitscherlich) and the non-rectangular hyperbolic (Prioul and Chartier) models: (A) *E. guineensis*, (B) *E. oleifera* and (C) the O×G hybrid.

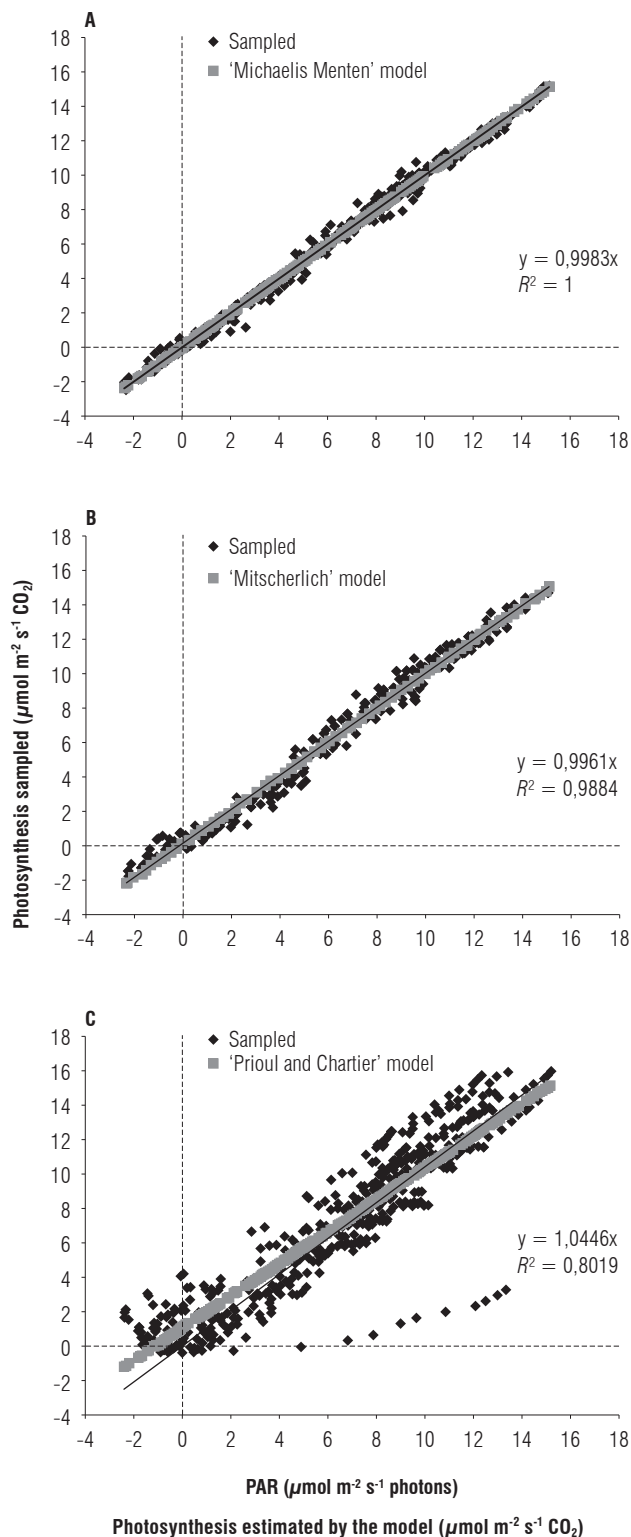


FIGURE 3. Adjusted regression between the actual and the estimated photosynthesis for the non-linear models in oil palms: (A) The rectangular hyperbolic model: Michaelis-Menten; (B) The exponential model: Mitscherlich; (C) The non-rectangular hyperbolic model: Prioul and Chartier.

progressive increase in PAR had no effect on the assimilation rate. Therefore, at approximately $20 \mu\text{mol m}^{-2} \text{s}^{-1}$ photons the net CO_2 exchange of the oil palm leaf was zero and the photosynthetic rate equaled the production of CO_2 by respiratory processes ($1.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ of CO_2). Moreover, the fraction of photons that reached the leaf tissue and was used to generate the transport of electrons (Φ) was 0.022 mole of CO_2 /mole of photons (equivalent to 1 mole of CO_2 for each 45 photons absorbed), and finally, the maximum photosynthesis was $13 \mu\text{mol m}^{-2} \text{s}^{-1} \text{CO}_2$ which became saturated at a PAR of $545 \mu\text{mol m}^{-2} \text{s}^{-1}$ photons (Tab. 3).

Discussion

The non-linear rectangular hyperbolic model (Michaelis-Menten) was selected as a general model to fit the oil palm photosynthetic response curves to PAR, not only because it met the goodness-of-fit criteria commonly used in model fitting, but also because it can be easily stipulated with a common statistical software such as Microsoft Excel® (Lobo *et al.*, 2013). This model, which estimates the maximum photosynthesis, the dark respiration, the photosynthetic efficiency and the light compensation and saturation points, can be used in oil palm breeding programs and in eco-physiological performance comparisons of oil palm cultivars. The differences in photosynthetic performance are practical and efficient criteria to predict the yield performance of oil palm cultivars (Peláez *et al.*, 2010; Rivera *et al.*, 2013a), because the photoassimilates are responsible not only for the dry matter productions required for vegetative growth and plant maintenance but also for the bunch-filling.

Genetic, edaphic, climatic or agricultural management factors can affect through photosynthesis, the production of fresh fruit bunches and plant growth and maintenance (Woittiez *et al.*, 2017), and several research studies have shown that there is a relationship between photosynthesis and the production of oil palm; therefore, increased rates of photosynthesis lead to higher productivity. Consequently, conditions that limit the photosynthesis components (water, sunlight, CO_2 , nutrients, chlorophyll and leaf area), adversely affect this process, resulting in lower production of bunches, decreased growth and lower resistance to pests and diseases (Cayón, 1999; Romero *et al.*, 2007).

Accordingly, it is pertinent to understand the values obtained: the mean photosynthetic parameters estimated using the rectangular hyperbolic model (Michaelis-Menten) correspond to the values reported for C3 plants such as oil palms. The maximum rate of assimilation (12 to 15

TABLE 3. Mean (χ) \pm standard error (SE) of the photosynthetic parameters obtained from the light saturation curves fitted to the rectangular hyperbolic model (Michaelis-Menten) in oil palms.

Genotype	A_{\max} ($\mu\text{mol m}^{-2} \text{s}^{-1} \text{CO}_2$)			Φ (mole of CO_2 /mole of photons)			PAR_{sat} ($\mu\text{mol m}^{-2} \text{s}^{-1}$ photons)			D_n ($\mu\text{mol m}^{-2} \text{s}^{-1} \text{CO}_2$)			LCP ($\mu\text{mol m}^{-2} \text{s}^{-1}$ photons)		
	χ	\pm	EE	χ	\pm	EE	χ	\pm	EE	χ	\pm	EE	χ	\pm	EE
<i>E. guineensis</i>	14.9	\pm	0.7	0.025	\pm	0.001	579	\pm	51	-1.8	\pm	0.2	37	\pm	5
<i>E. oleifera</i>	12.0	\pm	0.9	0.023	\pm	0.002	393	\pm	40	-1.3	\pm	0.1	22	\pm	3
OxG Hybrid	12.3	\pm	0.9	0.020	\pm	0.002	575	\pm	48	-0.7	\pm	0.1	16	\pm	2
General	12.9	\pm	0.6	0.022	\pm	0.001	545	\pm	33	-1.1	\pm	0.1	22	\pm	2

A_{\max} : maximum photosynthesis; Φ : photosynthetic efficiency; PAR_{sat} : light saturation point; D_n : dark respiration; LCP: light compensation point

$\mu\text{mol m}^{-2} \text{s}^{-1} \text{CO}_2$) was found within the intervals reported by Corley and Tinker (2015), Ruiz and Henson (2002), Larcher (2003), Romero *et al.* (2007) and Jazayeri *et al.* (2015) for *E. guineensis* (12-16 $\mu\text{mol m}^{-2} \text{s}^{-1} \text{CO}_2$), by Peláez *et al.* (2010) and Rivera *et al.* (2013a) for *E. oleifera* (9-17 $\mu\text{mol m}^{-2} \text{s}^{-1} \text{CO}_2$), and by Rivera *et al.* (2012) and Rivera *et al.* (2013b) for the OxG hybrids without any type of biotic or abiotic stress (9-18 $\mu\text{mol m}^{-2} \text{s}^{-1} \text{CO}_2$). The light compensation (14-40 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photons) and saturation (400-600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photons) points were similar to the values obtained in sun plant leaves (LCP: 20-30 and PAR_{sat} : 400-600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photons) and higher than those recorded in shade plant leaves (1-10 and 60-200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photons, respectively), suggesting these parameters vary with the species, the development stage and the orientation of the leaf, as well as with different growth factors, particularly temperature and light (Ögren and Evans, 1993). The photosynthetic efficiency (0.020-0.025 mole of CO_2 /mole of photon) was one-half the value reported for C3 plants (0.05 mole of CO_2 /mole of photon = 1 mole CO_2 fixed by 20 absorbed photons) under natural conditions, due mainly to a higher photorespiratory rate, but not to a photoinhibition process as the other photosynthetic parameters suggest (Azcón-Bieto *et al.*, 2008). Finally, the mitochondrial respiration under dark conditions (1 $\mu\text{mol m}^{-2} \text{s}^{-1} \text{CO}_2$) was two-fold higher than the values reported for C3 plants at 25°C (Byrd *et al.*, 1992). This difference can be attributed to a higher temperature (30°C), and to adequate leaf protein content (leaves did not show chlorosis), since this proportion of the carbon lost by the plant depends on the temperature and the leaf nitrogen content (Machado and Reich, 2006).

Conclusion

The photosynthetic rate of the individual oil palm (*E. guineensis*, *E. oleifera* and the OxG interspecific hybrid) leaves, showed a curvilinear relationship with the PAR intensity, which increased gradually with the increase of

available PAR until a maximum value and then became stable because of inhibition of the photosynthetic apparatus due to a raised leaf temperature and CO_2 limitations. This behavior could be easily accessed and analyzed with the rectangular hyperbolic model (Michaelis-Menten), and could be incorporated into gas exchange or growth models at the plant and ecosystem levels, every time that photosynthesis is not limited by the availability of water, nutrients, light or CO_2 . However, it does not imply that the rectangular hyperbolic model is suitable for every plant species, although it is the best model for *Vochysia divergens* (Lobo *et al.*, 2013), *Oryza sativa* (Ye, 2007) and several herbaceous species (Marino *et al.*, 2010), because the photosynthetic capacity and the efficiency are represented with dynamic models, whose coefficients must be carefully checked and adjusted to the type of metabolism of the plant (C3, C4 or CAM), the environmental factors (incident radiation, temperature, water, nutrients) and even to the leaf ontogeny (Solarte *et al.*, 2010; Ye, 2007).

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