

Application of Photosynthesis Models to Determine Light Requirements in Three Cacao Clones

Aplicación de los modelos de Fotosíntesis para determinar el requerimiento de luz en tres clones de cacao

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ABSTRACT

Numerous articles show that light, water, CO₂, and chlorophyll participate in the wonderful process of photosynthesis, and however, it is necessary to determine the conditions with which the assimilation of CO₂ are optimized in the cocoa crop, a subject with conceptual divergences due to the understory origin of the plant. Photosynthesis in cocoa clones (e.g., CCN51, FSV41, and LK40) to establish their light requirements were characterized. The influence of radiation levels on CO₂ assimilation (A) were evaluated. Measurements were made on the fourth leaf of mature branches using a portable infrared analysis of gas exchange (Ciras-3 PP SYSTEM®) equipment with a light unit (universal PLC3 -RGBW), and simultaneously the soil moisture was recorded every 5 min. The A/PAR curves were created, and photosynthesis models were evaluated. The fittest models for A/PAR curves to estimate the parameters Amax, light saturation point, light compensation point, dark respiration, and photosynthetic yield (Φ) were selected. It was found that photosynthesis increased consistently when PAR increased but each clone at different rates. The highest A and (Φ) in CCN51, and the lowest in LK40 were shown. The best-fit models for A were that of Kaipainen (2009), Smith (1935), and Ye (2007). The appropriate light range was set with relation 0.5 A max up to A max. For CCN51, it was 500–1500. For FSV41, it was 250–750. Finally, for LK40, it was 546–1000 μmol photons m² s⁻¹.

Keywords: CO₂ assimilation, maximum photosynthesis, PAR, LCP, LSP

RESUMEN

Cientos de artículos tratan sobre luz, agua, CO₂ y clorofila participan en el proceso maravilloso de la fotosíntesis, sin embargo, es necesario determinar las condiciones que optimizan la asimilación de CO₂ en el cultivo del cacao, tema en el cual se presentan divergencias conceptuales debido a su origen de sotobosque. Se caracterizó la fotosíntesis en clones de cacao para establecer sus necesidades de luz, en CCN 51, FSV 41 y LK 40 se estudió la influencia de la radiación sobre la asimilación de CO₂ (A), las mediciones se realizaron en la cuarta hoja de ramas maduras, utilizando un equipo portátil de análisis de intercambio de gases por infrarrojos (Ciras-3 PP SYSTEM®) con una unidad de luz (universal PLC3 -RGBW) y simultáneamente se registró la humedad del suelo cada cinco minutos. Se elaboraron las curvas A/PAR, y se probaron modelos de fotosíntesis. Se seleccionaron los modelos de mayor ajuste A/PAR para estimar los parámetros A máxima, punto de saturación de luz, punto de compensación de luz, respiración y rendimiento fotosintético(Φ). Se encontró que la fotosíntesis aumentó con el incremento de la PAR, pero con tasas distintas en cada clon. La A y (Φ) más altas se presentaron en CCN51 y las más bajas en LK40. Los modelos de mejor ajuste para A fueron los de Kaipainen (2009), Smith (1935) y Ye (2007). El rango de luz apropiado a los niveles de radiación con los que se logra 0.5 Amax hasta Amax, para CCN51 está entre 500 y 1500 μmol fotones m² s⁻¹. Para FSV41, es de 250 a 750 μmol fotones m² s⁻¹. Finalmente, para LK40, fue de 546 a 1000 μmol de fotones m² s⁻¹.

Palabras clave: asimilación de CO₂, fotosíntesis máxima, PAR, PCL, PSL

Received: February 1st, 2023

Accepted: July 12th, 2024

Introduction

The cocoa plant (*Theobroma cacao* L.) is one of the most critical perennial crops worldwide, given its participation in the economies of many countries (Lahive *et al.*, 2019). It is native to tropical America (Thomas *et al.*, 2012) and has traditionally been cultivated under a light canopy of trees. Nonetheless, the intensification of cultivation and the selection of high-yield clones have motivated a revision of the conditions under which they express their full productive potential.

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A high variability has been observed while measuring photosynthesis in cocoa leaves, ranging from 1.3 to 12 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Acheampong *et al.*, 2013; Almeida *et al.*, 2014; Ávila *et al.*, 2016; Daymond *et al.*, 2011; Jaimez *et al.*, 2018). Extrinsic factors explain such measurements, such as different light levels and soil moisture, in addition to ambient temperature changes (Araque *et al.*, 2012; Lambers *et al.*, 2008; Tezara *et al.*, 2020a). This photosynthetic process derives in dry matter. In cocoa trees, the observed accumulated biomass is between 8.5 and 9.1 Mg ha per year (Moser *et al.*, 2010).

Eight-year-old trees can reach 20.75 kg of dry biomass (Isaac *et al.*, 2007), and 35-year-old trees obtain values between 24.4 and 45.4 kg (Norgrove and Hauser, 2013), up to 62.4 kg per tree (Madountsap *et al.*, 2018), distributed across their structure and fruit production.

Photosynthesis is a biophysical process in which plants use solar energy to convert simple substances, such as water and carbon dioxide, which are poor in energy, into complex, energy-rich organic materials (Skillman *et al.*, 2011). The photosynthetic capacity of a tree is affected by factors such as temperature and soil water, which can decrease carbohydrate synthesis or even cause damage to the photosynthetic apparatus (Zhou *et al.*, 2014). The performance and efficiency of photosynthesis condition the growth and development of crops (Woittiez *et al.*, 2017), which is also spatially and temporally affected by cumulative predecessor edaphoclimatic factors (Connor *et al.*, 2011).

Limitations in photosynthetic productivity are related to the state and characteristics of the leaves, their location in the canopy, and their genotype (intrinsic aspects). These factors are subject to the variation and accumulation of environmental resources and stress factors (external aspects). These regulated interactions can limit the photosynthetic productivity of plants (Kaipiainen, 2009; Liao *et al.*, 2020; Skillman *et al.*, 2011).

Analyzing photosynthetic light response curves (A/PAR) allows determining the parameters that characterize the photosynthesis of cocoa in a given environment. By establishing the adjusted model of CO_2 assimilation and the photosynthetically active radiation curve (A/PAR), the efficiency of the reaction to light is obtained, and the light compensation point (LCP) can be identified. The LCP corresponds to the photosynthetically active radiation (PAR), wherein the rate of photosynthesis (CO_2 intake) equals that of respiration (CO_2 release). Above the LCP, the photosynthetic rate increases in response to an increase in photonic flux assimilation. The CO_2 incorporation rate is stabilized with an increase in PAR, reaching its maximum capacity (maximum photosynthesis) when it reaches the light saturation point (LSP). The LSP occurs when an increase in PAR does not affect the rate of CO_2 incorporation during photosynthesis (Duan and Zhang, 2009; Liao *et al.*, 2020; Lobo *et al.*, 2013; Kaipiainen, 2009; Ye, 2007).

Characterizing photosynthesis for different cocoa clones provides guidance regarding the appropriate light conditions for production, as well as for improving the space distribution of cocoa trees and other species. This research aims to determine the photosynthetic parameters of three cocoa clones and apply the models presented by Lobo *et al.* (2013) to determine their light intensity requirements and photosynthetic yield.

Materials and methods

CO_2 assimilation was studied in the clones CCN51 (Castro Naranjal Collection 51) while fully exposed to sunlight, and in FSV 41 (Federacion San Vicente 41) and LK40 (Luker 40) under the shade of *Cedrela odorata* L (Meliaceae) in eight-year-old crops (Table 1). These clones generally exhibit high yield and good agronomic performance. Due to their characteristics, they have gained considerable acceptance among producers, which is why we selected them for this study.

Table 1. Agronomic characteristics of the cocoa clones CCN51, FSV41, and LK40

Characteristics	CCN51 ⁽¹⁾	FSV41 ⁽²⁾	LK40 ⁽³⁾
Origin	Ecuador	San Vicente de Chucurí, Santander, Colombia	Palestina, Caldas, Colombia
Compatibility	SC*	SC	SC
Cob index	15	13	18
Grain index	1.60	2.10	1.40
Seeds/fruits	48.3 ± 2.20	39.2 ± 2.69	39.7 ± 2.00
Yield kg ha ⁻¹ year ⁻¹	2200	1474	2000
Pedigree	ICS95 x IMC67	Hybrid x Trinitario ICS1 x IMC6	
Germplasm	Castro Naranjal Collection	Federación San Vicente	Granja Luker

SC: self-compatible

Source: Perea Villamil *et al.* (2013), Espinosa *et al.* (2006), and Granja Luker (2015)

Traditionally, cocoa has been planted under the shade. However, it is known that CCN51 is highly productive under full sunlight. Therefore, the crops were established in both ways – although the regional clones were still planted under the shade.

Measurements of the photosynthetic rate (A) were taken from 9:00 to noon. The fourth leaf of the cocoa trees was selected from mature branches (Hernández, 2020; Espinosa *et al.*, 2006; Almeida and Valle, 2007), exposed to light, located in the middle third of the tree canopy, and put under self-shading leaves inside the tree, a methodology similar to

that of Tezara *et al.* (2015). Portable infrared gas exchange analysis equipment (Ciras-3 PP SYSTEM) was used with a universal LED light unit (PLC3 RGBW). A total of 11 radiation levels were selected, from 0 to 2200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. Three measurements were taken for each flashlight level. A 5 min acclimatization period before the measurement and a 3 min one between each flash of light were considered. Simultaneously, the volumetric moisture content in the soil was obtained with a Delta T-Devices Theta Probe ML3.

Data analysis

A/PAR curves were elaborated, and LCP, LSP, and A_{max} were determined with a graphic scale using the R Studio software (RCORE TEAM, 2017). The photosynthesis data (A/PAR) were tested on 11 models with the calculation system presented by Lobo *et al.* (2013). The models with the most significant fit for each clone were selected under the criterion of a lower mean square error (MSE). The parameters A_{max} , LSP, LCP, respiration (R_d), and photosynthetic efficiency (Φ PAR) were estimated with the equations presented in (Table 2).

Table 2. Models selected for their fit to the A/PAR curve

Model	Functional form
Kaipiainen (2009)	$P_N = [I \times P_{g\text{max}} / (I + I_{(50)})] - R_D$
Smith (1935)	$P_N = [\varphi_{(I_0)} \times I \times P_{g\text{max}} / (\varphi_{(I_0)}^2 \times I^2 + P_{g\text{max}}^2)^{0.5}] - R_D$
Ye (2007)	$A = \varphi_{(I_0, I_{\text{comp}})} \times [(1 - \beta \times I) / (1 + \gamma \times I)] \times (I - I_{\text{comp}})$

Source: Lobo *et al.* (2013)

Results

CO_2 assimilation and PAR

In the CCN51 clone, the rate of A increased with the progressive increase in PAR. This occurred until the maximum value of 7.4, with a PAR value of 1500, was reached in the trees under free exposure. Under the shade, A obtained up to 5.3, with a PAR of 1500 (Figures 1a and 1b). The LCP was observed at 50 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ in leaves under direct radiation and with a volumetric soil moisture of 40% (matric potential of less than 0.5 bars). In leaves of trees under shade, the LCP value was 100 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. These values are within the range reported in other studies for creole and foreign cultivars (Almeida *et al.*, 2014; Ávila *et al.*, 2016; Tezara *et al.*, 2016). The LSP was observed at 1500 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ in both situations (Figure 1a).

In the FSV 41 clone, the LCP was at 50 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, and the LSP was reached at 750 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, with a maximum A of 3.8 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Figure 2a). LK40 had an LCP value of 100 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, and its LSP was at 1000 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, with an average A of 3.6 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Figure 2b). In these clones under the shade, the volumetric soil moisture was 45% (matric potential of less

than 0.3 bars). It is worth noting that, above the LSP value, the capacity of the photosynthetic apparatus is limited (Xu and Shen, 2002).

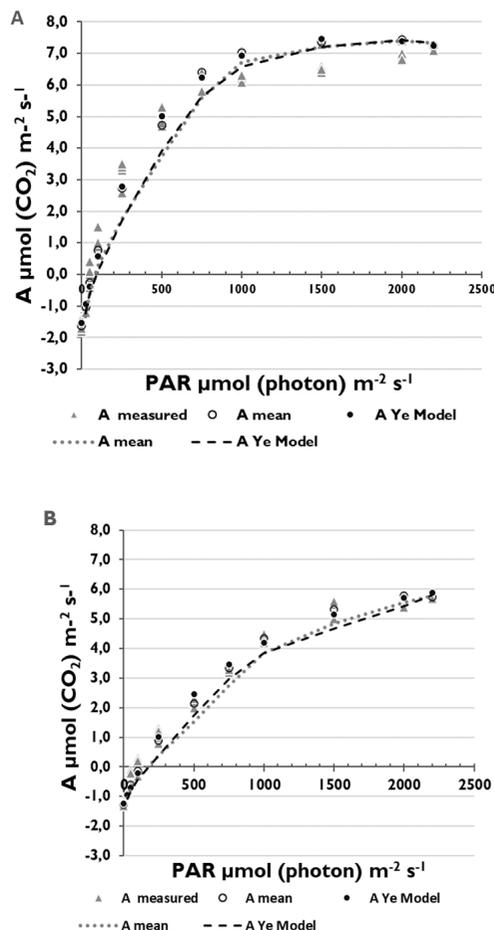
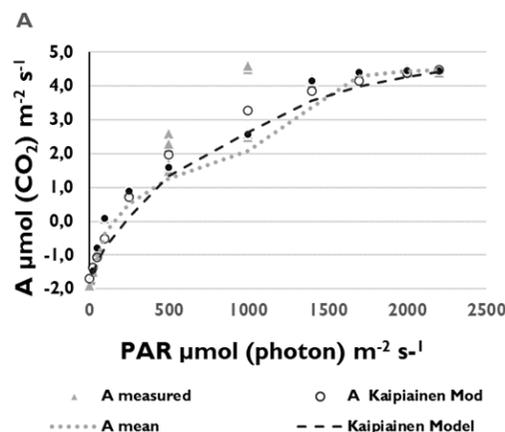


Figure 1. Photosynthetic light response curves for CCN51: a) trees exposed to full sunlight, b) trees shaded by cedar (*C. odorata* L.)
Source: Authors



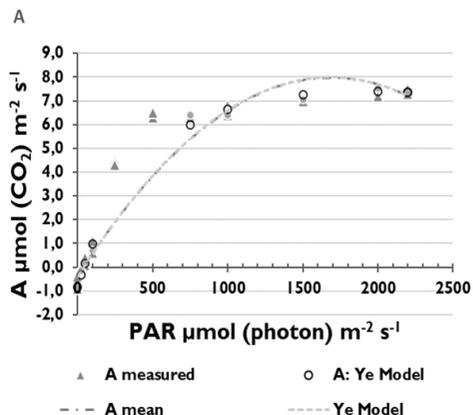
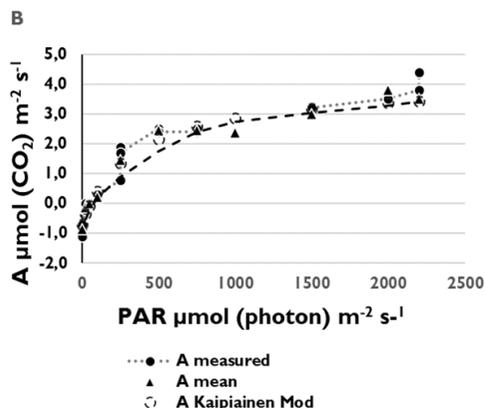


Figure 2. Photosynthetic light response curve (A/PAR): a) FSV41, b) LK40
Source: Authors

CO₂ assimilation and leaf location

For the mature leaves located inside the canopy, the LCP was at 50 μmol photons m⁻² s⁻¹, the maximum A was 2.4 μmol CO₂ m⁻² s⁻¹, the LSP was at 500 μmol photons m⁻² s⁻¹.

For the leaves exposed to light, the LCP was at 25 μmol photons m⁻² s⁻¹, the LSP was at 1000 μmol photons m⁻² s⁻¹, and the maximum A was 6.8 μmol CO₂ m⁻² s⁻¹. The A of the shaded leaves reached 30% of that of the leaves exposed to direct sunlight (Figures 3a and 3b).

The highest A was observed in the leaves under full sunlight. There was a decrease in photosynthesis when the leaves received less radiation (Lima *et al.*, 2010; Suárez *et al.*, 2018).

Photosynthetic models and parameters for A/PAR

The A in response to radiation (A/PAR) was represented as a rectangular hyperbola described by several models in cocoa leaves. The models selected for these conditions, considering their greater fit and low SME, were those by Kaipiainen (2009), Smith (1935), and Ye (2007) (Table 3).

Table 3. Models selected for each cocoa clone

Model	Clone	MSE	R ²
Ye ZP	CCN51 (S)	0.193	0.999
Ye ZP	CCN51 (sh)	0.253	0.997
Ye ZP	CCN51 (Lsh)	0.434	0.964
Kaipiainen, E. L	FSV41	0.716	0.972
Kaipiainen, E. L	LK40	1.576	0.975
Smith, E. L	CCN51 (LS)	0.262	0.998

(S) Tree under full sunlight, (sh) tree under shade, (Lsh) leaf located inside the canopy, (LS) leaves receiving direct sunlight

Source: Authors

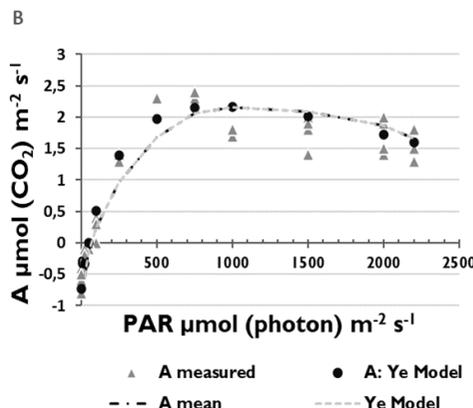


Figure 3. Photosynthetic light response curves (A/PAR): a) leaves under full sunlight, b) shaded leaves inside the canopy
Source: Authors

The photosynthetic parameters were estimated using the selected models and are shown in Table 4.

Table 4. Photosynthetic parameters for cocoa clones CCN51, LK40, and FSV41

Parameter	CCN51 (S)	CCN51 (sh)	CCN51 (Lsh)	FSV41	LK40	CCN51 (LS)
R _D	1.5	1.2	0.7	0.7	1.7	0.7
LCP	69.3	122.7	49.9	56.3	155.7	45
LSP	1134	1558	461	448	867	1037
A _{max}	7.2	5,2	1.9	3.4	4.3	6.7
Φ _(I₀_comp)	0.0221	0.0100	0.0146	0.0121	0.0108	0.0162

(S) Tree under full sunlight, (sh) tree under shade, (Lsh) leaf located inside the canopy, (LS) leaves receiving direct sunlight. LCP and LSP in μmol photons m⁻² s⁻¹; Φ (I₀_comp) mol (CO₂) mo⁻¹ (photons).

Source: Authors

The models adjusted to the studied conditions are as follows. For the CCN51 clone crop with trees exposed under full sunlight, see Equation (1). For shaded CCN51 trees, refer to Equation (2). For leaves of CCN51 that grew shaded inside the canopy, see Equation (3), and, for leaves that grew exposed to the sun, consider Equation (4). For the shaded FSV41 trees, see Equation (5), and for LK40 shaded trees, refer to Equation (6).

$$A = (0,0221) \times \left[\frac{1 - 0.00014 \times I}{1 + 0.0015 \times I} \right] \times (I - 69.3) \quad (1)$$

$$A = (0,01) \times \left[\frac{1 - 0.00004 \times I}{1 + 0.001 \times I} \right] \times (I - 122.7) \quad (2)$$

$$A = (0,0146) \times \left[\frac{1 - 0.0002 \times I}{1 + 0.0039 \times I} \right] \times (I - 49.9) \quad (3)$$

$$A = \left[\frac{0.0163 \times I \times 8.3}{(0.0163^2 \times I^2 + 8.3^2)^{0.5}} \right] - 0.7 \quad (4)$$

$$A = \left[I \times \frac{4.7}{I + 335.4} \right] - 0.7 \quad (5)$$

$$A = \left[I \times \frac{4.7}{I + 335.4} \right] - 0.7 \quad A = \left[I \times \frac{7.8}{I + 555.8} \right] - 1.7 \quad (6)$$

The model-estimated A and LCP parameters were similar to those obtained with the A/PAR curves. However, the LSP was underestimated (Duan, 2009; Ye, 2010) by 40% for FSV41 and by 15% for LK40. This happened because, in this model, the mathematical definition of LSP is the irradiance at which 50% of the maximum photosynthesis value is obtained. We calculated the maximum photosynthesis with the rate of change of the asymptotic curve (Kaipiainen, 2009). Still, the LSPs calculated for CCN51 were significantly fitted because the equation from the model by Ye (2010) had a straight segment function correction module aimed at defining the saturation irradiance associated with the maximum photosynthesis point. This function was a modified rectangular and asymptotic convergent.

The highest photosynthetic yield (ϕ) was obtained in CCN51 (S). It was reduced by 55% when the trees grew shaded. For FSV41 and LK40, the photosynthetic yield decreased by 45% compared to CCN51 (S).

FSV41 showed a low LSP, a low respiratory rate (R_o), and low CO_2 assimilation (A). The photosynthetic efficiency of the shaded trees, i.e., FSV41, LK40, and CCN51 (sh), was similar (0.0121, 0.0108, and 0.0100 $\mu mol CO_2/\mu mol photons m^2 s^{-1}$, respectively) and within the values reported by Daymond *et al.* (2011) for different genotypes under the shade.

Discussion

The CCN51 clone exhibited the highest CO_2 assimilation rate (A_{max}) under full sunlight. Under the shade, A_{max} decreased, the LCP increased, and the LSP decreased. The same behavior was observed in the leaves that grew under full sunlight and those that developed within the canopy (under the shade). In contrast, the shaded FSV41 clone exhibited an LCP value equal to that of the CCN51 tree under full sunlight, as well as an LSP typical of cacaos that are productive at low radiation (under shade). For these traditional conditions of different cacao genotypes, a LSP of 400 has been reported (Almeida *et al.*, 2016; Almeida and Valle, 2007).

The LK40 clone showed a high LCP, like that of the shaded CCN51, and a high LSP, in the middle between the two clones. This clone may have achieved physiological acclimatization, and, given its LCP and LSP, it could be exposed to higher radiation, with an expected increase in A (CO_2 assimilation rate), as has occurred with other clones, such as the Nacional type and CCN51 (Jaimez *et al.*, 2018). In this sense, photosynthesis models can be tested to estimate the level of luminosity to which LK40 and other clones could be exposed, combining A, PAR, and photosynthetic efficiency. Given that increasing light exposure can increase A but decrease the efficiency and generate reversible photodamage depending on the intensity of the radiation and the availability of water in the soil (Tezara *et al.*, 2016; Acheampong *et al.*, 2013), it is important to regulate these parameters. In this study, we always ensured that the soil water content remained within the matric potentials that favor cacao photosynthesis (Leiva-Rojas *et al.*, 2017; Leiva *et al.*, 2024). It is known that water depletion slows the electron transport rate, which would partly explain the low CO_2 assimilation rate of this species (Tezara *et al.*, 2015a).

Each clone exhibited a unique photosynthetic profile, in addition to changes depending on the light environment. This behavior is related to physiological characteristics and genotypic and morpho-anatomical variations (Tezara *et al.*, 2020b; Ávila-Lovera *et al.*, 2021; Daymond *et al.*, 2011; Skill *et al.*, 2011), which explain why some clones are more suitable for growth and production under the shade, while others perform better under higher light exposure conditions (Daymond *et al.*, 2011; Connor *et al.*, 2011).

The placement of leaves within the canopy plays a crucial role in radiation interception and, consequently, in the production of assimilates. A_{max} decreases due to acclimation to the light gradient (Skillman *et al.*, 2011; Connor *et al.*, 2011). In cocoa trees, as one moves from leaf to canopy, it is essential to achieve balanced solar radiation reception both above and within the canopy (Niether *et al.*, 2018) in order to enhance photosynthetic efficiency and utilize light for progressive tissue formation in the tree (Banguero-García *et al.*, 2015). This, in turn, promotes fruit development and formation, leading to higher agronomic yields (Lee *et al.*, 2000; Leiva *et al.*, 2019).

With the increase in radiation (from 400 to 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$), the CCN51 clone showed significant increments (by over 50%) in A . Jaimez *et al.* (2018) reported a 35% increase associated with a higher electron transport rate and a photosynthetic yield, as observed in this study. These results suggest that providing the crop with 'optimal' light conditions can enable its maximum photosynthetic expression, making it feasible to consider cultivation under full exposure. According to the model applied to CCN51, radiation values between 600 and 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ appear to be an appropriate range.

The higher rates of A and ϕ in CCN51 are reflected in its reported productivity, among the highest in commercial cocoa: 2200 $\text{kg ha}^{-1} \text{ year}^{-1}$ of dry beans. Combining an A_{max} of 7.7 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and a canopy management with a leaf area index (LAI) of 2.19 boosts its yield to 4 to 5 kg of dry beans per tree (5000 $\text{kg ha}^{-1} \text{ year}^{-1}$) (Leiva *et al.*, 2019). This, while including an adequate water supply (Köhler *et al.*, 2014) and nutrients, which can be higher in fully exposed cocoa. This confirms the importance of agronomic management in relation to physiology.

In LK40 and FSV41, with A values of 3.8 and 3.6 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively, and a low ϕ , the yield ranges between 1474 and 1900 $\text{kg ha}^{-1} \text{ year}^{-1}$. In the case of LK40, this could be increased with higher foliage luminosity, as estimated by the model, and with the photosynthetic contribution of cocoa stems and green branches (Ávila-Lovera *et al.*, 2020).

FSV41 and LK40 were evaluated under the shade conditions of traditional planting, where photosynthetic activity may be limited by the light environment. It is known that the lifespan of the leaves is longer under these conditions than under full sunlight, but the balance between C per leaf and biomass construction could increase if A_{max} increased. This is the reason why the 'optimal' radiation conditions of each clone are determined (Skillman, 2011). There are reports in Ecuador showing the morphoanatomical and photochemical characteristics of clone acclimatization to different light conditions (Tezara *et al.*, 2015). Such acclimatization seems related to soil moisture and can be modified (Köhler *et al.*, 2014).

In cocoa, the criteria to define light requirements for optimal tree performance are not well established, as each genotype exhibits a distinct photosynthetic behavior. Based on A/PAR response models (Ye, 2007, 2010) and Duan and Zhang's concept of *low light* (2009), the light range for maximizing the physiological potential of a tree could be inferred. The lower point is determined as the inflection point of the A/PAR curve (from measured data), corresponding to the point identified using Ye's geometric analysis for the development of his mathematical model (2010). The upper radiation value is established as the point where 0.9 A_{max} is achieved (Ye *et al.*, 2010; Duan and Zhang, 2009), *i.e.*, the level just below the photosynthetic suppression point (Duan and Zhang, 2009; Ye, 2010). With these determinations, the proposed range for CCN51 is between 350 and 1300 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. For FSV41, it is between 336 and 750, and, for LK40,

between 546 and 1000 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. However, it is advisable to validate these ranges under full sunlight, as the variability in A values and the increasing trend after the estimated saturation point suggest a response to higher radiation levels.

When scaling from leaf to canopy photosynthesis, the arrangement of the cocoa tree crown must tend to a higher number of light-exposed leaves, given the low photosynthesis of shaded leaves (Ávila-Lovera *et al.*, 2016; Tezara, 2016). Respiratory rates could hinder the total balance of photo-assimilate production in the tree. Pruning has been shown to improve the light distribution at the treetop and as well as the yield (Leiva *et al.*, 2019), thus confirming the importance of agronomic management.

Conclusion

In cocoa, certain genotypes showed increased photosynthesis with increasing radiation, reflecting the specific physiological responses for each clone and their optimal radiation range. For CCN51, the required light range was established from the radiation needed to achieve its A_{max} down to 50% of this value, ranging between 350 and 1300 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. For FSV41, the optimal range was from 336 to 750 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, and for LK40, it was 546-1000 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. These intervals were achieved under adequate soil moisture conditions.

The highest photosynthetic rates and efficiencies were recorded in CCN51. For trees of this clone, minimizing self-shaded leaves is advisable to optimize performance.

The use of mathematical models representing the photosynthetic A/PAR curve is useful for obtaining the parameters that guide light recommendations for cocoa cultivation.

CRedit author statement

All authors: conceptualization, methodology, software, formal analysis, investigation, data curation, writing (original draft, review, and editing).

Conflicts of interest

The authors of this paper declare that they have no conflicts of interest.

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