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Ecophysiological plasticity of *Theobroma cacao* L. clones in response to the structure and microclimate of agroforestry systems in Mexico

Plasticidad ecofisiológica de clones de *Theobroma cacao* L. como respuesta a la estructura y el microclima de sistemas agroforestales en México

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Abstract

Background: Cocoa is a species commonly cultivated under agroforestry systems (AFs), when microclimate conditions are adequate, it achieves high growth rates and seed yield.

Questions and Hypotheses: How do four cocoa varieties respond to open (OC) and closed (CC) shade tree canopy conditions within AFs? We hypothesized that cocoa functional traits values correlate with microclimate conditions in the CC.

Studied species: *Theobroma cacao* L. (Malvaceae).

Study site and dates: Papantla, Nautla, Veracruz; San Pedro, Oaxaca. Rainy season, 2018.

Methods: Three AFs were selected; either one with OC and CC zones, photosynthetically active radiation (PAR), vapor pressure deficit (VPD), air temperature (T_a) and relative humidity (RH) were registered. Cocoa tree and leaves functional traits were evaluated in four regional cocoa varieties, in ten individuals per variety, canopy condition and AFs.

Results: Higher values of PAR, VPD and T_a, and lower RH were recorded under OC than in CC. Cocoa tree height, stem diameter, fruit production, SLA (Specific Leaf Area), LWC (Leaf Water Content) and SS (Stomatal Size) were higher for Nautla. Only the cocoa clone Inifap8 displayed higher height and fruit production than the other varieties.

Conclusions: Veracruz and Oaxaca states have AFs with microclimatic conditions where cocoa cultivation can potentially develop. However, it is essential to incorporate our understanding of the adaptive responses of cocoa to particular shade trees canopy structure. Cocoa leaf traits, SLA, LWC and SS, may be used as indicators for enhancing management and sustainability in AFs in the face of climate change.

Keywords: canopy transmissivity, leaf relative water content, photosynthetic active radiation, specific leaf area, stomatal size, vapor pressure deficit.

Resumen

Antecedentes: El cacao se cultiva comúnmente en sistemas agroforestales (SAF), cuando las condiciones microclimáticas son adecuados, logra altas tasas de crecimiento y rendimiento.

Preguntas e Hipótesis: ¿Cómo responden diferentes clones locales de cacao a las condiciones microclimáticas de tres SAF distintos? Se sugiere que los valores de los atributos funcionales del cacao se relacionan con el microclima del dosel cerrado.

Especies de estudio: *Theobroma cacao* L. (Malvaceae).

Sitio y años de estudio: Papantla y Nautla, Veracruz; San Pedro, Oaxaca. Estación lluviosa, 2018.

Métodos: Se seleccionaron tres SAF, considerándose zonas de dosel abierto (DA) y cerrado (DC). Se midió la radiación fotosintéticamente activa (RFA), déficit de presión de vapor (DPV), temperatura del aire (T_a) y humedad relativa. Se evaluaron los atributos funcionales de cuatro variedades clonales de cacao, en cada condición de dosel y SAF.

Resultados: En todos los SAF se obtuvieron valores mayores de RFA, DPV y T_a en condiciones de DA. Para Nautla, el DC mostró mayor la altura del cacao, diámetro del tallo, producción de frutos, área foliar específica (AFE), contenido de agua foliar (CAF) y tamaño de estomas (TE), en comparación con los demás SAF.

Conclusiones: Los estados de Veracruz y Oaxaca tienen SAF con microclimas donde se puede desarrollar el cultivo del cacao. Sin embargo, es esencial incorporar las respuestas adaptativas del cacao a las condiciones microclimáticas del dosel. Los atributos funcionales del cacao, AFE, CAF y TE, pueden usarse como indicadores para mejorar el manejo y sostenibilidad de SAF frente al cambio climático.

Palabras clave: área foliar específica, déficit de presión de vapor, contenido relativo de agua de la hoja, radiación fotosintética activa, tamaño estomatal, transmisividad del dosel.

Cocoa (*Theobroma cacao* L.), also called cacao, is a symbolic and significant crop in Mexico since pre-Hispanic times, where native cultures domesticated Mesoamerican criollo varieties (Gómez-Pompa *et al.* 1990, Caso 2016). This crop has an essential role in tropical rural economies and environmental services when cultivated in agroforestry systems (AFs) (Avendaño-Arrazate *et al.* 2011, Armengot *et al.* 2016, Hipólito-Romero *et al.* 2019). Cocoa provides economic and environmental benefits and represents a low land-use alternative to face deforestation and climate change (Tscharntke *et al.* 2011, Harvey *et al.* 2014, Somarriba *et al.* 2018, World Cocoa Foundation: worldcocoafoundation.org).

Nowadays, cocoa production in Mexico stands at a crossroad since the country occupies the fourteenth place worldwide. During the last two decades, the surface planted with cocoa has been diminished by almost 30 % and the production by 44 %. Furthermore, the low prices in the local market and lack of governmental interest in this sector have hindered the development of agroecological management of cocoa AFs and the establishment of this crop in other areas (Espinosa-García *et al.* 2015, Rojas & Rodríguez 2019). The leading cocoa producing states are Tabasco and Chiapas (Díaz-José *et al.* 2013, Hipólito-Romero *et al.* 2019); however, it is crucial to evaluate cocoa in potential sites for its cultivation, such as Veracruz and Oaxaca.

The diversity, botanical composition and canopy complexity of cocoa AFs vary widely within and between geographical regions due to smallholder's manipulation of shade trees population density, as well as spatial and temporal patterns of tree cover in the plantation (Somarriba *et al.* 2018, Saavedra *et al.* 2020). The shade trees canopy of cocoa AFs modifies and regulates microclimatic conditions by buffering light, vapor pressure deficit (VPD), temperature, humidity and rain (Köhler *et al.* 2014, Armengot *et al.* 2016, Niether *et al.* 2018, Somarriba *et al.* 2018). It also captures and recycles water and nutrients in the above and below-ground biomass and soil, enabling agricultural diversification that improves food security and competitive business opportunities for smallholders (Harvey *et al.* 2014, Jacobi *et al.* 2014, Niether *et al.* 2018). In this context, it is relevant to enhance sustainable productivity in new areas for cocoa production and to face climate change through the design and management of optimal cocoa AFs (Tscharntke *et al.* 2011, Harvey *et al.* 2014, Somarriba *et al.* 2018, Cerda *et al.* 2019, Hipólito *et al.* 2019).

Cocoa is a species adapted to shade conditions. When cultivated at suitable irradiation levels, it achieves high water use efficiency, overall growth and seed yield (Daymond *et al.* 2011, Köhler *et al.* 2014, De Almeida *et al.* 2018, Jiménez-Pérez *et al.* 2019). The saturating irradiance for photosynthesis of cocoa seedlings and saplings correspond to 20-30 % of photosynthetic active radiation (PAR) at full sunlight; while mature tree leaves could reach 70-80 % (Isaac *et al*. 2007, Almeida & Valle 2008, Baligar *et al.* 2008, Ávila-Lovera *et al.* 2015, De Almeida *et al*. 2018, Suárez *et al.* 2018). Adequate estimation of optimal PAR agroecological conditions under shade trees canopy of AFs must consider the heterogeneity of canopy openness and PAR transmissivity (Carr & Lockwood 2011, Phillips *et al.* 2013, Köhler *et al.* 2014, Vaast *et al.* 2016, Somarriba *et al.* 2018).

To understand the processes that make cocoa AFs sustainable should be considered cocoa features such as ecophysiology of clones and shade sensitivity, as well as microclimate variations within AFs (Almeida & Valle 2008, De Almeida *et al*. 2018, Lahive *et al.* 2019). In general, plant responses to environmental conditions determine changes in functional traits; thus, the expression of different phenotypes by the same genotype is associated with plant fitness in diverse environments and regulates adaptation through their plasticity (Ackerly *et al.* 2000, Rozendaal *et al.* 2006, Pérez-Ramos *et al.* 2019). Improved cocoa clones can significantly increase production and exhibit resilience to stressful climate conditions, like droughts and flooding (Hipólito-Romero *et al.* 2017). Valuable insights into the adaptive value of specific leaf area (SLA), leaf water content (LWC), stomatal size (SS) and stomatal density (SD) responses of different cocoa cultivars in relation to PAR, VPD, temperature and humidity have been published elsewhere (Rozendaal *et al.* 2006, Daymond *et al*. 2011, Ávila-Lovera *et al*. 2015, De Almeida *et al*. 2018, Saavedra *et al*. 2020, Sauvadet *et al*. 2021). In cocoa AFs, shade conditions diminish PAR and VPD, increasing the SLA and LWC in cocoa leaves due to lower evaporative demand (Daymond *et al.* 2011, Saavedra *et al.* 2020). There is a wide variation of SS and SD responses due to light conditions. Higher values have been associated with closed canopy conditions that increase CO_2 assimilation, evapotranspiration and water use efficiency (Daymond *et al*. 2011, Ávila-Lovera *et al*. 2015).

In light of the above considerations, this study evaluates the ecophysiological plasticity of four regional cocoa clones growing in three AFs in Veracruz and Oaxaca, Mexico. Here, in each AFs, we analyzed the relationship between the cocoa tree and leaf functional traits with microclimate conditions under open canopy (OC) and closed canopy (CC) shade tree conditions. We propose that cocoa leaves display traits such as high SLA, LWC, SS, and SD under CC conditions related to the increase of growth rate and seed yield. Under CC conditions, shade-tolerant plants are physiological active due to sunlight received, displaying leaf traits that increase photosynthetic rate (Smith & Huston 1990). On the other hand, OC conditions represent stressful conditions for cocoa tree growth and development due to the lack of tolerance to high PAR and VPD values; therefore, we predicted cocoa traits values that avoid water loss, such as low SLA and LWC levels, smaller SS, and lower SD (De Almeida *et al.* 2018).

Materials and methods

Study sites. This study was carried out in three traditional AFs, in Veracruz and Oaxaca states of Mexico, during the rainy season (June to September) of 2018. The environmental summary of the different municipalities where the AFs are located is shown in Table 1 and Figure 1 (Thornton *et al.* 2016, Climate-data.org 2018).

Experimental design. Three cocoa experimental plots (0.5 ha) were established in the rainy season of 2012 within each of the AFs mentioned above. Four regionally developed cocoa clones: Inifap1, Inifap8, Inifap9, and Neocriollo (INIFAP 2011) were planted randomly in lines at 3 × 3 m and edaphic bacterial inoculants as biofertilizers were applied at the time of planting (Hipólito-Romero *et al.* 2017). Crop management consisted of annual weeding, pruning (formation and maintenance), pest control and no additional fertilizer was applied.

In 2018, for each AFs experimental plot, ten six-year-old cocoa trees were randomly selected for each clone (*i.e.* five trees in open canopy conditions and five more in closed canopy conditions). A CC condition was defined if at least half of the cocoa tree crown was beneath the canopy cover of a shade tree. On the other hand, an OC condition was established if the entire cocoa tree crown was out of the shade tree's canopy cover.

The experimental design was a randomized complete block in a 4 × 3 factorial arrangement of four cocoa clones, with five repetitions for every clone in three AFs experimental plots (Nautla, Papantla and San Pedro), and two canopy conditions (open and closed). In total, 120 cocoa trees were measured during the 2018 rain season: June-July for San Pedro, July-August for Nautla and August-September for Papantla municipalities.

Table 1. Environmental characteristics of three agroforestry systems in Oaxaca and Veracruz states of Mexico (Thornton *et al*. 2016, Climate-data.org 2018).

	Agroforestry systems		
Municipality	Nautla	Papantla	San Pedro
State	Veracruz	Veracruz	Oaxaca
Coordinates	20° 28' 42" N 96° 23' 08" W	20° 28' 17" N 97° 23' 32" W	18° 09' 13" N 96° 34' 55" W
masl	77	185	342
Mean annual precipitation (mm)	1,500	1,200	1,274
Mean daily solar radiation (W/m^2/day)	379	392	365
Mean annual temperature (°C)	25.6	24.2	23.7
Mean daily maximum temperature (°C)	30.5	30.9	29.7
Mean daily minimum temperature (°C)	20.8	19.9	17.9
Soil	Luvisol, vertisol	Cambisol, Regosol	Leptosol, luvisol

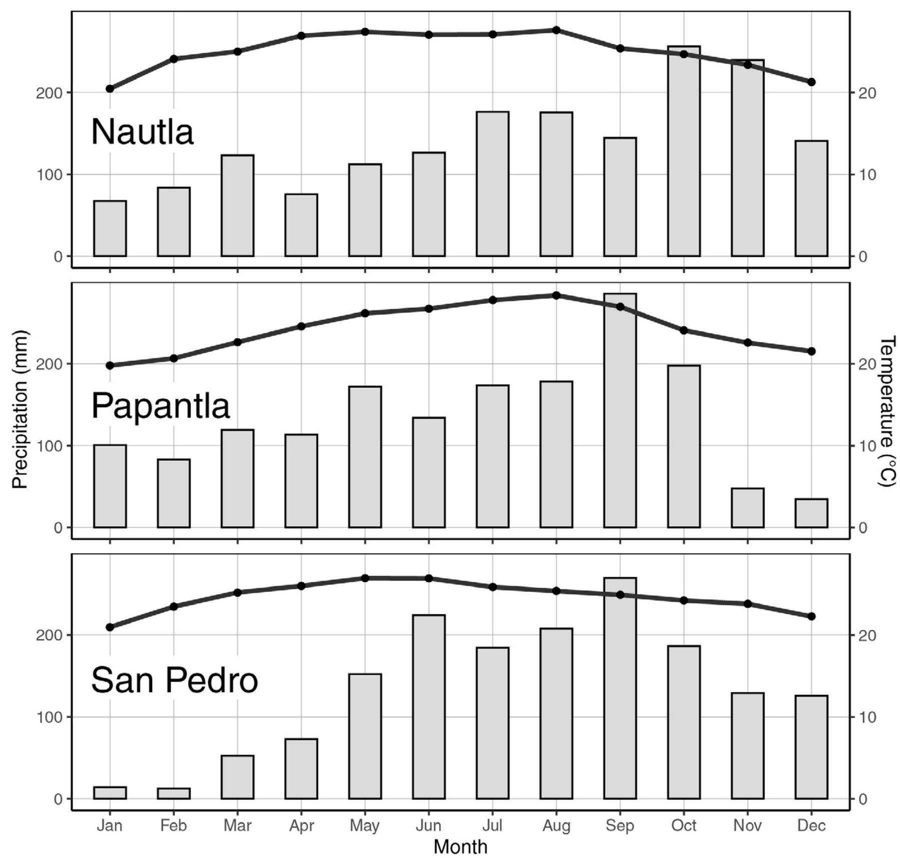

Figure 1. Average monthly temperature and rainfall for three agroforestry systems in Oaxaca and Veracruz states of Mexico (Thornton *et al.* 2016, Climate-data.org 2018).

Agroforestry system canopy structure. The canopy structure of shade trees for each AFs experimental plot was assessed by species composition, richness, tree density, canopy cover and vertical stratification following Somarriba *et al.* (2018) method. Shade individual tree species were taxonomically identified, tagged, and height, diameter at breast height (DBH), and canopy cover-density were measured at the beginning of the experiment.

Microclimatic conditions. Microclimatic conditions were recorded during 40 days for each AFs experimental plot. Measurements were made in the open sky in adjacent grasslands to AFs; it was considered as the reference. Measurements were also carried out above each cocoa tree clone's crown and for each AFs shade tree cover category (Monteith & Unsworth 2013, García-Arellano 2016, De Almeida *et al.* 2018, Niether *et al.* 2018, Pabello 2019). The sampling period ranged from June-July for San Pedro AFs, July-August for Nautla AFs and August-September for Papantla AFs. The PAR, air temperature (T_a) and air relative humidity (RH) were recorded with three data loggers HOBO H21-002 (Onset Computer Corporation, Bourne, Massachusets). The PAR (µmol cm^{-2} s^{-1}), T_a (°C) and RH (%) were measured with quantum sensors (SQ-420, Apogee Instruments, Logan, Utah) and temperature-humidity sensors (S-THB-M008, Onset Computer Corporation, Bourne, Massachusets). The VPD was calculated following Monteith & Unsworth (2013) equations.

Data logger stations were set hourly for the microclimate variables during daylight hours (7-19 h). One station was placed in the reference (adjacent grassland). The other station was located in the AF experimental plot; the sensors were positioned above (3 m) of cocoa tree crown (García-Arellano 2016, De Almeida *et al.* 2018, Niether *et al.* 2018, Pabello-Vega 2019).

We calculated the PAR percentage transmitted by the shade trees canopy (PAR_{st}) based on the PAR registered in the reference (PAR_{op}) and the PAR registered above the crown of cocoa trees (PAR_{ac}).

$$*PAR_{st} = (PAR_{ac} \times 100 / PAR_{op}) \quad (1)$$

Cocoa functional traits. The cocoa tree functional traits considered here were tree height, crown area, stem diameter and number of fruits. The tree height (m) was determined with a measuring pole. Crown area (m^2) was estimated using measurements of maximum and minimum crown diameters (m). Stem diameter (cm) was determined at 0.3 m height, and only healthy ripe fruits were considered for production over the 40 days measurement period (Somarriba *et al.* 2018, Utomo *et al.* 2016, Kongor *et al.* 2019). To estimate cocoa leaf functional traits, a random sample of five healthy, fully expanded leaves per cocoa tree were selected from the outer leaf layer halfway the crown to determine specific leaf area (SLA, measured in cm^2/g), leaf water content (LWC, measured in %), stomatal size (SS, measured in µm) and stomatal density (SD, stomata per mm^2).

SLA was calculated as leaf area (LA) divided by leaf dry weight (LDW, oven-dry mass 60 °C, 48 h; Perez-Harguindeguy *et al.* 2013, Saavedra *et al.* 2020). The LA was determined by scanning the leaves with a flatbed scanner and analyzing the pictures with the software ImageJ (Rozendaal *et al.* 2006, Rasband 2019). To calculate LWC, the difference between leaf fresh weight (LFW) and LDW was divided by the LFW and multiplied by 100 % (LFW-LDW/LFW) × 100 (Perez-Harguindeguy *et al.* 2013). To measure the SS and SD a thin layer of nail polish was applied on the abaxial surface of leaves; the dry layer of nail polish was removed with a double adherent surface tape. Three microphotographs of each polish layer were taken to determine the SD and five stomata per visual field were randomly selected to assess the SS. The SS was considered the product of the guard cell length and guard cell pair width (Kröber *et al.* 2015, Cocoletzi *et al.* 2019).

Statistical analysis. Two-way ANOVAs were performed to assess the microclimatic variables between shade trees canopy conditions (open and closed), and AFs experimental plots (Nautla, Papantla and San Pedro). For shade trees, two-way ANOVAs were performed for tree height, canopy cover and DBH to determine differences in canopy conditions (open and closed) and AFs experimental plots (Nautla, Papantla and San Pedro). For cocoa clones, three-way ANOVAs were performed for tree height, crown area, stem diameter, number of fruits, SLA, LWC, SS and SD to determine the difference between clones (Inifap1, Inifap8, Inifap9, and Neocriollo), shade tree canopy conditions (open and closed), and AFs experimental plots (Nautla, Papantla and San Pedro). Post-hoc Tukey means comparisons were made between levels of the factors (clones, canopy conditions and AFs experimental plots). Pearson correlation matrix was performed between cocoa functional traits and PAR_{ac}, VPD, T_a, RH. For all statistical analysis and graphs, R software ver. 4.0.3 was used (R Core Team 2020). The frequency of normality in data distribution for each variable was checked with the Shapiro-Wilk test ($P < 0.05$). When it was necessary, data were normalized by using a Box-Cox transformation (the λ value was adjusted as the base value). All results were indicated as the mean ± standard error of the mean.

Results

Agroforestry systems canopy structure. The summary of shade tree species, richness, tree height, canopy cover, DBH, density, and vertical canopy stratification for three AFs in Veracruz and Oaxaca states of Mexico are shown in Table 2. The average shade trees height in AFs experimental plots was higher in Nautla than in Papantla and San Pedro ($F = 3.17$, $P < 0.05$). The average tree height in closed conditions (10.75 ± 0.32 m) was higher than in open conditions (8.36 ± 0.29 m, $F = 40.78$, $P < 0.001$). The average shade trees canopy cover was statistically different between AFs experimental plots ($F = 11.93$, $P < 0.001$), Nautla were higher than Papantla and San Pedro, which showed similar values. The shade trees canopy cover between open (27.5 ± 3.5 m^2) and closed (42.3 ± 4.8 m^2) for all AFs differed significantly ($F = 37.58$, $P < 0.001$). The DBH of shade trees differed between AFs experimental plots ($F = 11.93$, $P < 0.001$), the highest was for Nautla compared to Papantla and San Pedro. No significant differences were found between open and closed conditions for DBH ($F = 0.88$, $P = 0.35$).

Microclimate conditions. Daily patterns of microclimatic conditions in three AFs experimental plots under open and closed shade trees canopy conditions are shown in Figure 2 and Table 3. Total daily PAR_{op} was significantly higher for Papantla than Nautla and San Pedro; the last two AFs experimental plots showed similar values. The same tendency was registered for maximum PAR_{op} values, which were reached during 11:00-16:00 hs; the highest values were recorded for Papantla (1,000-1,600 µmol m^{-2} s^{-1}), followed by Nautla (800-1,200 µmol m^{-2} s^{-1}) and the lowest for San Pedro (600-800 µmol m^{-2} s^{-1}).

Average total daily PAR_{ac} values were the highest in Papantla (40.1 ± 1.6 mol m^{-2} day^{-1}) followed by San Pedro (32.1 ± 3.4 mol m^{-2} day^{-1}) and Nautla with the lowest values (21.1 ± 1.3 mol m^{-2} day^{-1}). Total daily PAR_{ac} in OC (38.2 ± 3.4 mol m^{-2} day^{-1}) was 63 % higher than for CC (24.1 ± 1.3 mol m^{-2} day^{-1}) (Figure 2). The proportion of total daily PAR_{st} differs between AFs experimental plots ($F = 14.61$, $P < 0.001$); the highest average value was recorded for San Pedro (71.7 %), followed by Papantla (53.4 %) and Nautla with the lowest (48.6 %). PAR_{st} was also different between the open (63.9 %) and closed (51.9 %) shade tree canopy conditions ($F = 10.66$, $P < 0.01$).

Table 2. Shade tree species, richness, tree height, canopy cover, DBH, density, and vertical canopy stratification for three agroforestry systems experimental plots in Oaxaca and Veracruz states of Mexico.

	Agroforestry systems experimental plots		
Municipality	**Nautla**	**Papantla**	**San Pedro**
Overstorey dominant species	*Fraxinus uhdei*, *Guazuma ulmifolia*, *Populus alba*, *Leucaena leucocephala*, *Spondias mombin*, *Bursera simaruba*	*Swietenia macrophylla*, *Cedrela odorata*, *Mangifera indica*, *Acronomia mexicana*, *Pimienta dioica*	*Cedrela odorata*, *Acronomia mexicana*
Shade tree species richness	14	10	6
Average overstorey tree height (m)	10.7 ± 0.2	8.4 ± 0.4	9.4 ± 0.4
Average canopy cover of overstorey trees (m^2)	48.1 ± 3.1	31.7 ± 2.8	31.1 ± 2.7
Average DBH of overstorey trees (cm)	14.9 ± 0.4	13.1 ± 0.4	13.3 ± 0.5
Overstorey tree density (trees/ha)	220	257	217
Understory species	-	*Citrus sinensis*	*Musa paradisiaca* *Coffea arabica*
Average understory species height (m)	-	5.2	4.6

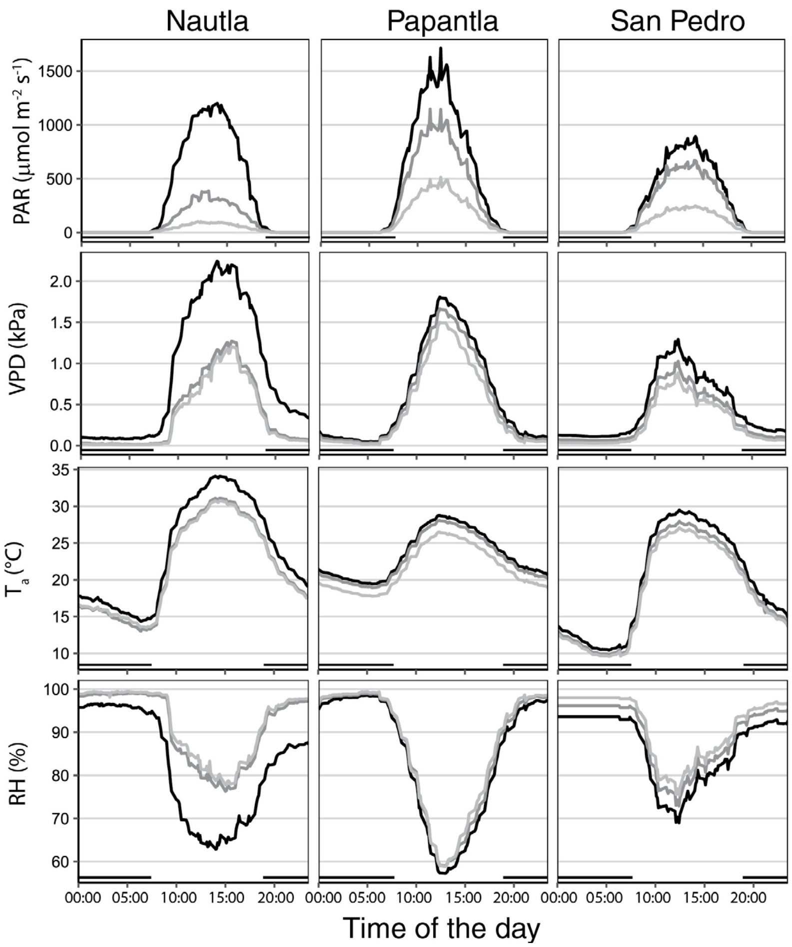

Figure 2. Daily pattern of microclimatic conditions in three agroforestry systems experimental plots. PAR = photosynthetic active radiation, VPD = vapor pressure deficit, T_a = air temperature and RH = relative humidity. Solid black lines represent reference values, the open sky in adjacent grasslands to AFs. Gray lines are values recorded above cocoa tree crowns in open shade tree canopy conditions. Light gray lines are values recorded above cocoa tree crowns in closed shade tree canopy conditions.

The VPD recorded in the reference reached maximum values from 11:00-16:00 h, with differences between AFs experimental plots (higher for Nautla), followed by Papantla and San Pedro that showed similar values (Figure 2, Table 3). We found differences for daily average maximum T_a in the reference between AFs experimental plots (4-5 ºC higher for Nautla with respect to Papantla and San Pedro). As expected for all AFs, the average T_a was lower above the cocoa crown than the reference (1.7-4.4 °C lower for OC and CC conditions, respectively) (Figure 2, Table 3). The RH in the reference was inversely related to PAR_{oc} and T_a, with the highest values for San Pedro, followed by Nautla and Papantla with similar values (Figure 2, Table 3). During the study period, the average RH above the cocoa crown was about 13 % higher than the RH in the reference, reaching mean values of 85.3 % for Nautla and 80.2 % for San Pedro; the lowest values were recorded for Papantla (65.9 %). Under CC conditions, the RH was 8 % higher (80.5 %) than OC conditions (Figure 2, Table 3).

Cocoa functional traits. Most functional traits analyzed for the four cocoa clones showed similar responses between AFs experimental plots, except for tree height and the number of fruits for the rainy season (Figures 3 and 4). Among AFs experimental plots, the cocoa tree height, crown area, stem diameter, and the number of fruits for the rainy season were higher for Nautla than San Pedro and Papantla, which showed similar values (Figure 3). The Inifap8 exhibited the highest tree height (Figure 3). The number of fruits was higher for Inifap8, ranging from 1-17 (average

Table 3. Microclimatic conditions in three agroforestry systems experimental plots under open and closed shade trees canopy conditions. Reference values represent open canopy conditions in adjacent grasslands. PAR_{ac} = total daily photosynthetic active radiation above cocoa tree crowns, VPD = daily average maximum vapor pressure deficit, T_a = daily average maximum air temperature, RH = daily average minimum air relative humidity and PAR_{st} = proportion of photosynthetic active radiation transmitted by shade trees (available for cocoa trees). Maximum values were obtained with records between 12:00-16:00 hr. Data are the average ± standard error. Different letters indicate significant differences (α = 0.05) between canopy conditions.

Microclimatic variables	Agroforestry systems experimental plots	Open		Closed		Reference
PAR_{ac}	Nautla	23.13 ± 1.7	b	19.16 ± 1.11	a	47.55 ± 4.05
(mol m^2 day^{-1})	Papantla	49.94 ± 2.94	b	30.22 ± 3.51	a	75.83 ± 3.03
	San Pedro	41.54 ± 2.63	b	22.53 ± 0.9	a	46.83 ± 2.76
VPD (kPa)	Nautla	1.02 ± 0.04	b	0.31 ± 0.01	a	2.04 ± 0.05
	Papantla	1.45 ± 0.03	b	1.11 ± 0.03	a	1.59 ± 0.03
	San Pedro	0.77 ± 0.02	b	0.61 ± 0.01	a	1.01 ± 0.03
T_a (°C)	Nautla	30.14 ± 0.13	b	26.64 ± 0.08	a	33.1 ± 0.17
	Papantla	27.41 ± 0.14	b	24.47 ± 0.14	a	28.07 ± 0.15
	San Pedro	27.07 ± 0.06	b	25.31 ± 0.06	a	28.59 ± 0.09
RH (%)	Nautla	78.96 ± 0.61	a	91.69 ± 0.3	b	63.76 ± 0.71
	Papantla	63.47 ± 0.65	a	68.26 ± 0.82	b	61.38 ± 0.62
	San Pedro	79.03 ± 0.57	a	81.41 ± 0.3	b	75.43 ± 0.59
PAR_{st} (%)	Nautla	48.64 + 4.2	b	40.31 + 3.31	a	
	Papantla	65.86 + 3.78	b	39.86 + 4.05	a	
	San Pedro	88.71 + 6.53	b	48.12 + 4.28	a	

6.1 ± 5.7), followed by Inifap9, from 1-14 fruits (average 4.3 ± 4.3), Neocriollo from 9-13 fruits (average 4.0 ± 4.0), while Inifap1 showed a range 1-11 fruits (average 3.8 ± 3.5) (Figure 3). Despite the similar traits responses between the clones and AFs experimental plots, we identify differences in traits between canopy conditions. Stem diameter and fruit production showed higher values for CC conditions (Figure 3). Furthermore, only the Inifap8 clone showed higher plasticity for stem diameter and fruit production under CC conditions than the other clones studied.

The SLA, LWC and SS were higher for San Pedro and Nautla than for Papantla. Foliar traits plasticity between canopy conditions was higher for Inifap8 than for other clones. Higher average SLA, LWC and SS values were recorded for all clones in CC than OC conditions (Figure 4). No differences were identified for SD.

Relationship of functional traits and microclimate. The AFs experimental plots provide low total daily PAR_{ac} levels (10-30 mol m^{-2} day^{-1} above the cocoa crown). These conditions were negatively related to cocoa tree functional traits: tree height, crown area, stem diameter and the number of fruits for all cocoa clones (Table 4). Nevertheless, above 40-50 mol m^{-2} day^{-1}, the cocoa tree functional traits values decrease significatively (Figure 4, Tables 3 and 4). A similar negative relation response was found between PAR_{ac} and cocoa leaf functional traits, lower PAR_{ac} levels around 20-30 mol m^{-2} day^{-1} lead to the highest SLA, LWC and SS (Figure 4, Tables 3 and 4).

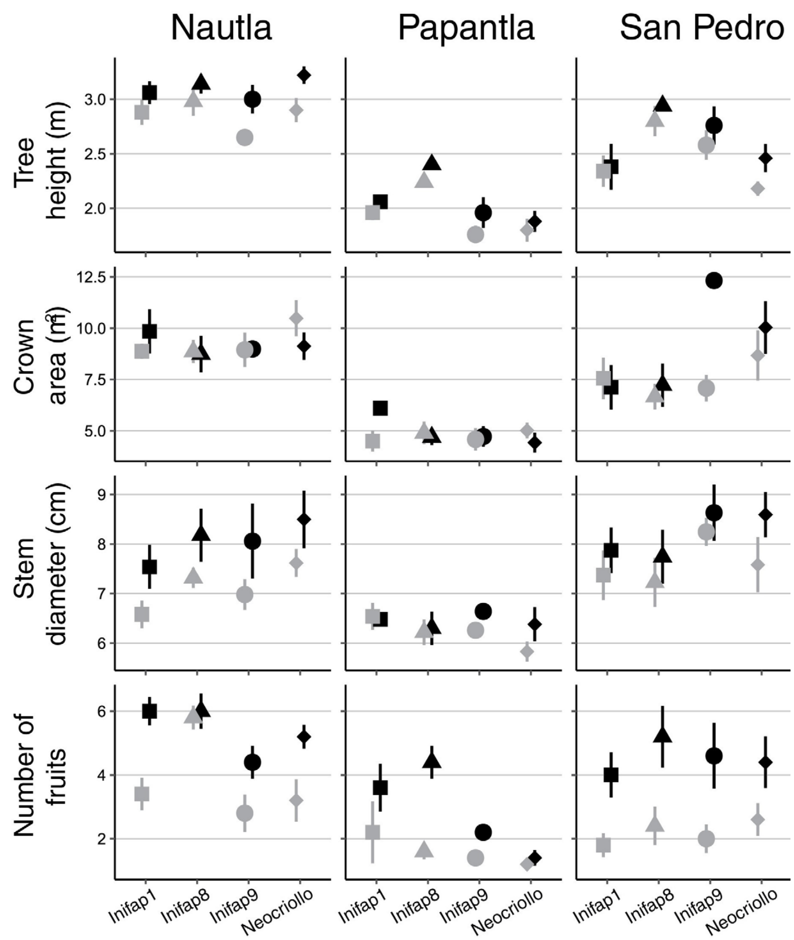

Figure 3. Average values and standard errors of cocoa trees functional traits for three agroforestry systems experimental plots, four cocoa clones and two AFs shade trees canopy conditions. Gray shapes represent open canopy conditions. Black shapes represent closed canopy conditions.

Table 4. Results of linear correlations between microclimatic conditions with functional traits of cocoa trees and leaves. R^2 is the correlation coefficient and P is the probability value. Specific leaf area = SLA, leaf water content = LWC, stomatal size = SS and stomatal density = SD.

Cocoa functional traits	PAR_{ac} (mol m^{-2} day^{-1})		VPD (kPa)		T_a (°C)		RH (%)	
	R^2	P	R^2	P	R^2	P	R^2	P
Tree height (m)	-0.49	< 0.0001	-0.41	< 0.0001	0.15	0.11	0.50	< 0.0001
Crown area (m²)	-0.43	< 0.0001	-0.34	< 0.0001	0.17	0.06	0.40	< 0.0001
Stem diameter (cm)	-0.24	< 0.01	-0.36	< 0.0001	0.02	0.83	0.39	< 0.0001
Number of fruits	-0.50	< 0.0001	-0.39	< 0.0001	-0.04	0.64	0.42	< 0.0001
SLA (cm² g)	-0.26	< 0.01	-0.39	< 0.0001	-0.22	< 0.05	0.36	< 0.0001
LWC (%)	-0.28	< 0.01	-0.45	< 0.0001	-0.17	0.07	0.45	< 0.0001
SS (μm²)	-0.35	< 0.0001	-0.41	< 0.0001	-0.09	0.33	0.42	< 0.0001
SD (per mm²)	-0.04	0.67	-0.12	0.19	-0.04	0.66	0.17	0.07

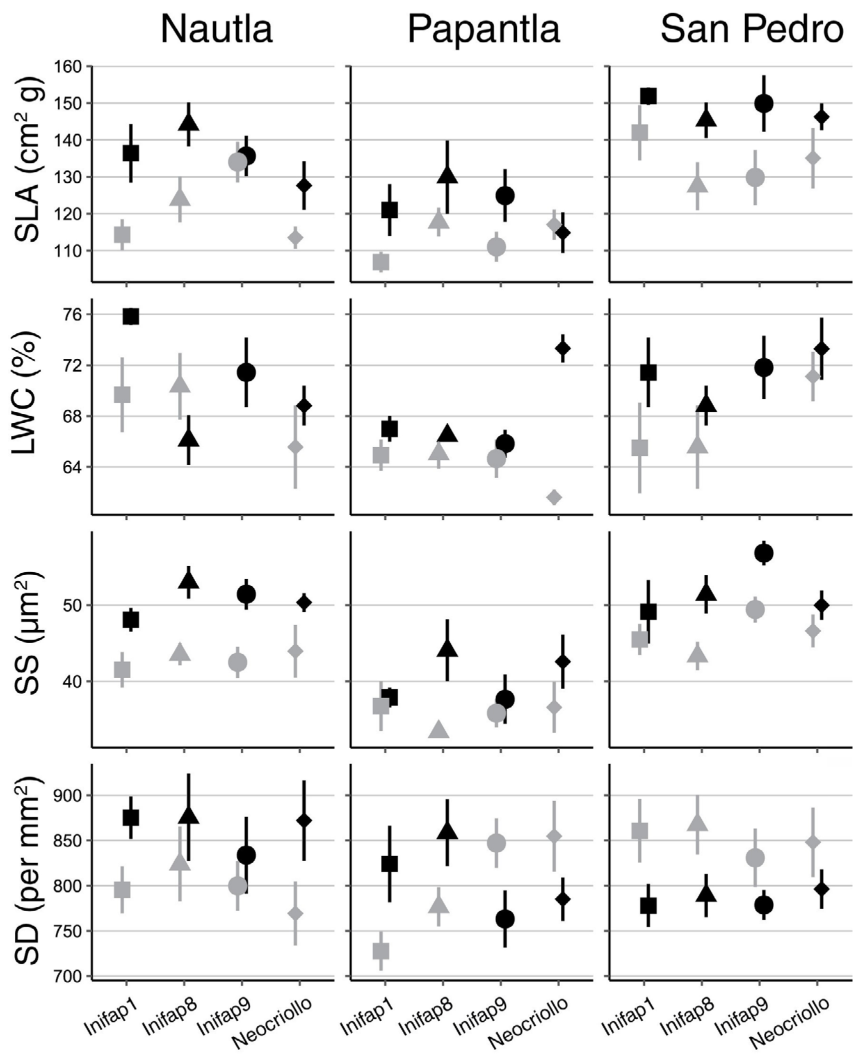

Figure 4. Average values and standard errors of cocoa leaves functional traits for three agroforestry systems experimental plots, four cocoa clones and two AFs shade trees canopy conditions. Gray shapes represent open canopy conditions. Black shapes represent closed canopy conditions. Specific leaf area = SLA, leaf water content = LWC, stomatal size = SS, stomatal density = SD.

The highest functional traits values for all clones were observed in a VPD range of 1.1-0.3 kPa, while above 1.4 kPa, most functional traits diminished (Figure 4, Tables 3 and 4). On the other hand, SD showed no correlation with any microclimatic conditions in this study (Table 4). The T_a was only negatively correlated with SLA. The RH was linearly related to all cocoa functional traits, except to SD.

Discussion

Agroforestry systems canopy structure. Our results of canopy cover for Oaxaca and Veracruz were similar to those obtained from other cocoa AFs studies in Tabasco and Chiapas, Mexico (Jiménez-Pérez *et al.* 2019, López-Juárez *et al.* 2019). About 54 % of shade trees show a dense shade tree cover (60-95 %), 36 % have a moderate cover (40-60 %) and 10% have a sparse cover (less than 40 %).

It has been estimated that the canopy height of shade trees modifies the cocoa yield. The lower the canopy height of the shade trees, the productivity of the crop could be negatively limited because of light competition (Blaser-Hart *et al.* 2021). In Nautla, the shade tree height and canopy diameter were higher than in the other two AFs experimental plots. Shade trees was higher in the CC than in the OC conditions. This corresponded with cocoa productivity; cocoa trees in Nautla in closed canopy conditions produced the highest number of fruits, particularly the Inifap8 clone.

Adequate agronomic management in the AFs, around 40-60 % shade tree cover, leads to an increase of average productivity and income of local farmers (Valenzuela & Alcudia 2010, Schneider *et al.* 2017, Saavedra *et al.* 2020). Sustainable agriculture requires native species and a tree canopy comprising at least two strata (Vaast & Somarriba 2014). We identified a stratum consisting of six to 14 native tree species in the overstorey of the three cocoa Afs. While in Nautla and San Pedro, it was registered a stratum in the understory comprised of fruit trees. These two tree strata are required to maintain cocoa shade conditions that provide a wide range of environmental services and products, common to other cocoa AFs (Zuidema *et al.* 2005, Somarriba *et al.* 2018).

Microclimate conditions. Our results extend the notion that cocoa AFs in Latin America show a wide range of topographic, climate and microclimate conditions. Particularly solar radiation, temperature and humidity vary greatly when interact with the complex shade canopy structure of AFs (Niether *et al.* 2018, Somarriba *et al.* 2018). The results we obtained were similar to those reported in cocoa AFs in Mexico, Colombia and Brazil; the open canopy increases PAR, VPD and T_a, but RH decreases in this condition (Niether *et al.* 2018, Jiménez-Pérez *et al.* 2019, López-Juárez *et al.* 2019).

Suitable conditions for cocoa occur at about 50 % of PAR_{st} (Acheampong *et al*. 2013, Niether *et al.* 2018). A closed canopy with stressful conditions for cocoa comprises around 4.9-3.6 % of PAR_{st}; it reduces transpiration and photosynthesis (Jiménez-Pérez *et al.* 2019). We found optimal PAR levels for cocoa growth given by the shade tree canopy management in a spatial-temporal distribution framework. Shade trees density and cover play an essential role in reducing stressful microclimatic conditions for cocoa trees, both for high and low PAR_{st} (Zuidema *et al.* 2005, Agele *et al.* 2016, Suárez *et al.* 2018).

Depending on the season, some microclimate factors can limit the physiological characteristics of cocoa. Acheampong *et al.* (2013) found in cocoa under various shade regimens in West Africa that high VPD values increase evapotranspiration and limit photosynthesis in the dry season. In contrast, low radiation may limit photosynthetic performance in the rainy season due to the cloudy conditions and closed canopy. In the rainy season, the VPD in West Africa ranged 1.5-1.3 kPa (Acheampong *et al.* 2013), while we recorded average VPD values of 1.1-0.6 kPa in OC and CC, respectively. Therefore, in our study, the VPD was not a limiting factor for cocoa in CC. Still, high radiation may reduce photosynthesis in OC conditions, particularly for Papantla since measurements were performed in the rainy season.

We found that the PAR_{op} varies significantly between AFs experimental plots due to different climatic and meteorological conditions. When adjusting and designing cocoa AFs canopy structures, it should be considered to avoid PAR levels above maximum light saturation levels for cocoa crowns (300-1,000 µmol m^{-2} s^{-1}). It was the case for Papantla that both OC and CC represented more stressful conditions for cocoa. PAR below minimum light saturation levels (200-300 µmol m^{-2} s^{-1}) should be avoided (Baligar *et al.* 2008, Daymond *et al.* 2011, García-Arellano 2016, Tezara *et al.* 2016, Jaimez *et al.* 2018).

Although cocoa is considered a shade species, it has been shown that some cultivars have a higher performance of physiological and functional traits when cultivated in open areas, locations with cloudy climates throughout the year, and low evaporative demand (Ávila-Lovera *et al.* 2015, Suárez *et al*. 2018). These environmental conditions can be found in the Colombian Amazon with average solar radiation values of 766 µmol m^{-2} s^{-1} (Ávila-Lovera *et al.* 2015, Agudelo-Castañeda *et al.* 2018).

We registered maximum PAR_{op} values around 1,000 to 1,500 µmol m^{-2} s^{-1} for AFs experimental plots; in these conditions, the Inifap8 had a higher tree height and more fruits than the other clones. This information suggests that Veracruz and Oaxaca are places where cocoa cultivation can potentially take place. Due to this, a case-by-case yearly and daily PAR evaluation is necessary to establish optimal cocoa growth conditions, considering a given geographic region (Somarriba *et al.* 2018, Jiménez-Pérez *et al.* 2019).

Cocoa functional traits. The cocoa trees we monitored showed no traits of intensive cocoa production systems. We registered that the mean cocoa tree height was 2.51 m, while the mean tree height in productive systems is around 6 m (Blaser-Hart *et al.* 2021). Intensive systems are more than 10 years old, while the plants we monitored were approximately 6 years old. However, the cocoa trees height in CC conditions indicates that these will achieve an intensive production system structure in some years. The cocoa crown cover differed between sites; the higher values corresponded to Nautla and San Pedro, the AFs experimental plots with higher shade canopy trees conditions.

The cocoa crown cover reflects the interaction with AFs; it can be modified by species, stage of maturity, and density of shade trees; and can be related with the stem diameter (Vaast & Somarriba 2014, Asare *et al.* 2017). We identified variations in cocoa tree height and the number of fruits between shade trees canopy conditions and cocoa clones. Foliar variation between cocoa clones under different shade conditions was due to leaf size and thickness (Jaimez *et al.* 2018). It indicates that cocoa clones can have a differential resource allocation (Daymond *et al.* 2011, Köhler *et al.* 2014, Tezara *et al.* 2016).

Our results for SLA were 9.52 % higher in CC than OC conditions; it was consistent with Suárez *et al.* (2018) findings for cocoa SLA values (24.4 % higher in CC than OC conditions). Suárez *et al.* (2018) found that SLA was inversely proportional to the incident PAR; the SLA was higher in AFs with low light conditions, while the SLA was lower in cocoa monocultures with higher light conditions. High SLA in cocoa maximizes photon capture efficiency by improving photosynthesis capacity, carbon gain and investment in photosynthetic tissues (Rozendaal *et al.* 2006). Saavedra *et al.* (2020) found that SLA and LRWC proportionally increase with the canopy cover percentage in cocoa varieties from South America.

We identify the same tendency in CC conditions; SLA, LWC and SS were negatively related to PAR_{ac} and VPD. We found differences for LWC between AFs experimental plots and canopy conditions but not for cocoa clones. Higher LWC in the CC conditions has been negatively related PAR and VPD, but positively associated with soil moisture (Lahive *et al.* 2019). In AFs, shade trees reduce light conditions and increase water content in the uppermost soil layer, making water available for plants (Niether *et al.* 2017).

Cocoa trees are sensitive to soil water availability; for this reason, the soil must have retention properties and good drainage (Kongor *et al.* 2016). Regosol in Papantla could prevent water penetration and limit the establishment of plants. While luvisol in Nautla and San Pedro, has properties that facilitate good water drainage. The soil type could determine differences in cocoa traits between the AFs, since soil type enables or limits cocoa cultivation.

The SS for all cocoa clones was significantly higher in CC than in OC conditions. Larger stomata in the CC increase transpiration rates to achieve the highest photosynthetic rates (Monteiro *et al.* 2016). Since cocoa is shade-adapted, the highest photosynthesis rate is performed at low radiation levels; this is possible due to photosynthetic enzymes and large occlusive cells with large pores for gas exchange (Gómez-Yarce *et al.* 2020). Therefore, plants that grow in CC conditions can have thinner leaves and large SS, taking advantage of the available PAR and thus increasing the water use efficiency (Rozendaal *et al.* 2006, Daymond *et al.* 2011, Saavedra *et al.* 2020). The SD was not modified; this variable has less plasticity in different environmental conditions (Saavedra *et al.* 2020).

Final thoughts. Local climate, topography and canopy management of AFs determine microclimatic variables for cocoa trees and influence differences in functional traits response of the four cocoa regional clones studied. Since most cocoa functional traits in three AFs were higher for CC conditions, they show high plasticity in response to radiation and humidity. The higher plasticity of functional traits for Inifap8 indicates that genotypic differences may be identified through phenotypic studies and can be interpreted as a differential partition of photosynthates in response to microclimate conditions.

Still, it is essential to incorporate our understanding of the adaptive responses of cocoa to these microclimatic conditions, particularly PAR_{st} and VPD, when discussing the implications of climate change on the design of resilient cocoa AFs canopy structure. It is worth mentioning that shade tree functional traits could be included to complement future studies, *i.e.,* a detailed analysis of canopy architecture since it influences cocoa production by buffering temperatures and VPD.

The design and management of shade trees canopies should consider the tradeoffs between optimizing cocoa growth and productivity, mainly when the aim is to maintain multi-species and multi-strata canopies. Systematic studies that relate management of space-time shade trees canopy structure with PAR transmissivity and VPD measurements are needed to assess cocoa optimum ecophysiological conditions.

Also, complementary studies of soil water and nutrient availability related to cocoa ecophysiological plasticity in the dry season will help further understand the potential for AFs to mitigate plant stress and improve cocoa trees' performance and resilience in the face of climate change.

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Literature cited

Acheampong K, Hadley P, Daymond AJ. 2013. Photosynthetic activity and early growth of four cacao genotypes as influenced by different shade regimes under west african dry and wet season conditions. *Experimental Agriculture* **49**: 31-42. DOI: http://doi.org/10.1017/S0014479712001007

Ackerly DD, Dudley SA, Sultan SE, Schmitt J, Coleman JS, Linder CR, Sandquist DR, Geber MA, Evans AS, Dawson TE, Lechowicz MJ. 2000. The evolution of plant ecophysiological traits: Recent advances and future directions: New research addresses natural selection, genetic constraints, and the adaptive evolution of plant ecophysiological traits. *BioScience,* **50**: 979-995. DOI: https://doi.org/10.1641/0006-3568(2000)050[0979:TEOPET]2.0.CO;2

Agele S, Famuwagun B, Ogunleye A. 2016. Effects of shade on microclimate, canopy characteristics and light integrals in dry season field-grown cocoa (*Theobroma cacao* L.) seedlings. *Journal of Horticultural Sciences* **11**: 47-56. DOI: https://jhs.iihr.res.in/index.php/jhs/article/view/105

Agudelo-Castañeda GA, Cadena-Torres J, Almanza-Merchán PJ, Pinzón-Sandoval EH. 2018. Desempeño fisiológico de nueve genotipos de cacao (*Theobroma cacao* L.) bajo la sombra de tres especies forestales en Santander, Colombia. *Revista Colombiana de Ciencias Hortícolas* **12**: 223-232. DOI: https://doi.org/10.17584/rcch.2018v12i1.7341

Almeida AA, Valle RR. 2008. Ecophysiology of the cacao tree. *Brazilian Journal of Plant Physiology* **19**: 425-448. DOI: http://doi.org/10.1590/S1677-04202007000400011

Armengot L, Barbieri P, Andres C, Milz J, Schneider M. 2016. Cacao agroforestry systems have higher return on labor compared to full-sun monocultures. *Agronomy for Sustainable Development* **36**: 1-10. DOI: http://doi.org/10.1007/s13593-016-0406-6

Asare R, Asare RA, Asante WA, Markussen B, Raebild A. 2017. Influences of shading and fertilization on on-farm yields of cocoa in Ghana. *Experimental Agriculture* **53**: 416-431. DOI: http://doi.org/10.1017/S0014479716000466

Avendaño-Arrazat CH, Villarreal-Fuentes JM, Campos-Rojas EG, Méndez-Richar A, Mendoza-López A, Aguirre-Medina JF, Sandoval-Esquivez A, Espinosa-Zaragoza S. 2011. Diagnóstico del cacao en México. México: Secretaría de Agricultura y Desarrollo Rural (SAGARPA)-
Universidad Autónoma Chapingo. https://acortar.link/zhXOZ3

Ávila-Lovera E, Coronel I, Jaimez R, Urich R, Pereyra G, Araque O, Chacón I, Tezara W. 2015. Ecophysiological traits of adult trees of criollo cocoa cultivars (*Theobroma cacao* l.) from a germplasm bank in Venezuela. *Experimental Agriculture* **52**: 137-153. DOI: http://doi.org/10.1017/S0014479714000593

Baligar V, Bunce J, Machado R, Elson M. 2008. Photosynthetic photon flux density, carbon dioxide concentration, and vapor pressure deficit effects on photosynthesis in cacao seedlings. *Photosynthetica* **46**: 216-221. DOI: https://doi.org/10.1007/s11099-008-0035-7

Blaser-Hart WJ, Hart SP, Oppong J, Kyereh D, Yeboah E, Six J. 2021. The effectiveness of cocoa agroforests depends on shade-tree canopy height. *Agriculture, Ecosystems & Environment* **322**: 107676. DOI: https://doi.org/10.1016/j.agee.2021.107676

Carr MKV, Lockwood G. 2011. The water relations and irrigation requirements of cocoa (*Theobroma cacao* L.): A review. *Experimental Agriculture* **47**: 653-676. DOI: http://doi.org/10.1017/S0014479711000421

Caso BL. 2016. *Cacao. Producción, consumo y comercio. Del período prehispánico a la actualidad en América Latina.* Madrid: Iberoamericana-Vervuet, ISBN 9788484899242

Cerda BR, Orozco AL, Carreño RG, Ordóñez JC, Amores CFM, Caicedo AWJ, Oblitas GPS, Somarriba CE. 2019. Tropical agroforestry and ecosystem services: tradeoff analysis for better design strategies. *In*: Mosquera-Losada MR, Prabhu R eds. *Agroforestry for sustainable agriculture*. Cambridge: Burleigh Dodds Science Publishing, UK. ISBN: 9781786762207

Climate-data.org. 2018. Public database. Mexico Climate: Average Temperature in Mexico, Weather & Mexico Weather by Month - Climate-Data.org. https://en.climate-data.org/north-america/mexico-179/ (accessed December 31, 2018).

Cocoletzi E, Contreras-Varela X, García-Pozos MJ, López-Portilla L, Gaspariano-Machorro MD, García-Chávez J, Fernandes GW, Aguirre-Jaimes A. 2019. Incidence of galls on fruits of *Parkinsonia praecox* and its consequences on structure and physiology traits in a Mexican semi-arid region. *Revista Mexicana de Biodiversidad* **90**: e902758. DOI: https://doi.org/10.22201/ib.20078706e.2019.90.2758

Daymond AJ, Tricker PJ, Hadley P. 2011. Genotypic variation in photosynthesis in cacao is correlated with stomatal conductance and leaf nitrogen. *Biologia plantarum* **55**: 99-104. DOI: https://doi.org/10.1007/s10535-011-0013-y

De Almeida J, Herrera A, Tezara W. 2018. Phenotypic plasticity to photon flux density of physiological, anatomical and growth traits in a modern criollo cocoa clone. *Physiologia Plantarum* **166**: 821-832. DOI: https://doi.org/10.1111/ppl.12840

Díaz-José O, Aguilar-Ávila J, Rendón-Medel R, Santoyo-Cortés VH. 2013. Current state of and perspectives on cocoa production in Mexico. *Ciencia e Investigación Agraria* **40**: 279-289. DOI: http://dx.doi.org/10.4067/S0718-16202013000200004

Espinosa-García JA, Uresti-Gil J, Vélez-Izquierdo A, Moctezuma-López G, Inurreta-Aguirre HD, Góngora-González SF. 2015. Productividad y rentabilidad potencial del cacao (*Theobroma cacao* L.) en el trópico mexicano. *Revista Mexicana de Ciencias Agrícolas* **6**: 1051-1063.

García-Arellano D. 2016. *Caracterización agroclimática de un sistema agroforestal y evaluación de la morfología de cuatro variedades de cacao (Theobroma cacao L.) en la comunidad de Cerro Camarón, municipio de San Pedro Ixcatlán, Oa*xaca. BSc Thesis. Universidad Veracruzana.

Gómez-Pompa A, Flores JS, Fernández MA. 1990. The sacred cacao groves of the Maya. *Latin American Antiquity* **1**: 247-257. DOI: https://doi.org/10.2307/972163

Gómez-Yarce JP, Mompotes-Largo ER, López-Castro A, Hernández-Arredondo JD, Córdoba-Gaona OJ. 2020. Gas exchange efficiency in Cocoa - Spanish elm agroforestry system in the northwest Antioquia, Colombia. *Revista Facultad Nacional de Agronomía Medellín* **73**: 9283-9291. DOI: https://doi.org/10.15446/rfnam.v73n3.85278

Harvey CA, Chacón M, Donatti CI, Garen E, Hannah L, Andrade A, Bede L, Brown D, Calle A, Chara J, Clement C, Gray E, Hoang, MH, Minang P, Rodríguez AM, Seeberg-Elizabeth C, Semroc B, Shames S, Smukler S, Somarriba E, Torquebiau, E, Van Etten J, Wollenber E. 2014. Climate-smart landscapes: opportunities and challenges for integrating adaptation and mitigation in tropical agriculture. *Conservation Letters* **7**: 77-90. DOI: https://doi.org/10.1111/conl.12066

Hipólito-Romero E, Ramos-Prado JM, Ricaño-Rodríguez J, Ortega-Pineda G. 2019. Sistemas agroforestales para el trópico mexicano en el manejo y la conservación de especies bioculturales. *In*: Del Amo RS, Vergara-Tenorio MC eds. *La restauración ecológica productiva: El camino para recuperar el patrimonio biocultural de los pueblos mesoamericanos*. Veracruz, México: Universidad Veracruzana: ISBN: 978-607-502-761-6

Hipólito-Romero E, Carcaño-Montiel MG, Ramos-Prado JM, Vázquez-Cabañas EA, López-Reyes L, Ricaño-Rodríguez J. 2017. Efecto de inoculantes bacterianos edáficos mixtos en el desarrollo temprano de cultivares mejorados de cacao (*Theobroma cacao* L.) en un sistema agroforestal tradicional del norte de Oaxaca, México. *Revista Argentina de Microbiología* **49**: 356-365. DOI: https://doi.org/10.1016/j.ram.2017.04.003

INIFAP [Instituto Nacional de Investigaciones Forestales, Agrícolas y pecuarias]. 2011. *Paquete tecnológico de cacao (Theobroma cacao L.): Producción de planta*. México: Secretaría de Agricultura Ganadería y Pesca, SAGARPA. https://acortar.link/TbxRAa (accessed January 18, 2022).

Isaac ME, Timmer VR, Quashie-Sam SJ. 2007. Shade tree effects in an 8-year-old cocoa agroforestry system: biomass and nutrient diagnosis of *Theobroma cacao* by vector analysis. *Nutrient Cycling in Agroecosystems* **78**: 155-165. DOI: http://doi.org/10.1007/s10705-006-9081-3

Jacobi J, Andres C, Schneider M, Pillco M, Calizaya P, Rist S. 2014. Carbon stocks, tree diversity, and the role of organic certification in different cocoa production systems in Alto Beni, Bolivia. *Agroforestry Systems* **88**: 1117-1132. DOI: http://doi.org/10.1007/s10457-013-9643-8

Jaimez RE, Amores PF, Vasco A, Gastón LR, Tarqui O, Quijano G, Jimenez JC, Tezara W. 2018. Photosynthetic response to low and high light of cacao growing without shade in an area of low evaporative demand. *Acta Biológica Colombiana* **23**: 95-103. DOI: https://doi.org/10.15446/abc.v23n1.64962

Jiménez-Pérez AJ, Cach-Pérez M, Valdez-Hernández M, de la Rosa-Manzano E. 2019. Effect of canopy management in the water status of cacao (*Theobroma cacao*) and the microclimate within the crop area. *Botanical Sciences* **97**: 701-710. DOI: http://doi.org/10.17129/botsci.2256

Köhler M, Hanf A, Barus H, Hendrayanto, Hölscher D. 2014. Cacao trees under different shade tree shelter: effects on water use. *Agroforestry Systems* **88**: 63-73. DOI: http://doi.org/10.1007/s10457-013-9656-3

Kongor JE, Boeckx P, Vermeir P, Van de Walle D, Baert G, Afoakwa EO, Dewettinck K. 2019. Assessment of soil fertility and quality for improved cocoa production in six cocoa growing regions in Ghana. *Agroforestry Systems,* **93**:1455-1467 https://doi.org/10.1007/s10457-018-0253-3.

Kröber W, Plath I, Heklau H, Bruelheide H. 2015. Relating stomatal conductance to leaf functional traits. *Journal of Visualized Experiments* **104**: e52738. DOI: https://doi.org/10.3791/52738

Lahive F, Hadley P, Daymond AJ. 2019. The physiological responses of cacao to the environment and the implications for climate change resilience. A review. *Agronomy for Sustainable Development* **39**: 1-22. DOI: https://doi.org/10.1007/s13593-018-0552-0

López-Juárez SA, Hipólito-Romero E, Cerdán-Cabrera CR, Ortiz-Ceballos GC, Reyes-López D. 2019. Association between cocoa (*Theobroma cacao* l.) and vanilla (*Vanilla planifolia* jacks. Ex andrews) crops in an agroforestry system in Comalcalco, Tabasco. *Tropical and Subtropical Agroecosystems* **22**: 613-629.

Monteiro MV, Blanuša T, Verhoef A, Hadley P, Cameron RW. 2016. Relative importance of transpiration rate and leaf morphological traits for the regulation of leaf temperature. *Australian Journal of Botany* **64**: 32-44. DOI: https://doi.org/10.1071/BT15198

Monteith JL, Unsworth MH. 2013. *Principles of Environmental Physics - Plants, Animals, and the Atmosphere*. Poland: Elsevier. ISBN: 978-0-12-386910-4.

Niether W, Armengot L, Andres C, Schneider M, Gerold G. 2018. Shade trees and tree pruning alter throughfall and microclimate in cocoa (*Theobroma cacao* L.) production systems. *Annals of Forest Science* **75**: 1-16. DOI: http://doi.org/10.1007/s13595-018-0723-9

Niether W, Schneidewind U, Armengot L, Adamtey N, Schneider M, Gerold G. 2017. Spatial-temporal soil moisture dynamics under different cocoa production systems. *CATENA* **158**: 340-349. DOI: https://doi.org/10.1016/j.catena.2017.07.011

Pabello-Vega EA. 2019. *Caracterización agroecológica de tres sistemas agroforestales con cultivares de Theobroma cacao L.* BSc Thesis. Universidad Veracruzana.

Perez-Harguindeguy N, Diaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte M, Cornwell WK, Craine JM, Gurvich DE, Urcelay C, Veneklaas EJ, Reich PB, Poorter L, Wright IJ, Ray P, Enrico L, Pausas JG, de Vos AC, Buchmann N, Funes G, Quétier F, Hodgson JG, Thompson K, Morgan HD, ter Steege H, Sack L, Blonder B, Poschlod P, Vaieretti MV, Conti G, Staver AC, Aquino S, Cornelissen JHC. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* **61**: 167-234. DOI: https://doi.org/10.1071/BT12225_CO

Pérez-Ramos IM, Matias L, Gomez-Aparicio L, Godoy O. 2019. Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions. *Nature Communications* **10**: 1-11. DOI: https://doi.org/10.1038/s41467-019-10453-0

Phillips-Mora W, Arciniegas-Leal A, Mata-Quirós A, Motamayor-Arias JC. 2013. *Catálogo de clones de cacao seleccionados por el CATIE para siembras comerciales*. Manual técnico. 105. Turrialba, Costa Rica, Centro Agronómico Tropical de Investigación y Enseñanza (CATIE). ISBN 978-9977-57-571-1

R Core Team. 2020. R: A language end environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. http://www.R-project.org/

Rasband WS. 2019. ImageJ. Image Processing and Analysis in Java. 1.49e. National Institutes of Health. http://imagej.nih.gov/ij/

Rojas FJ, Rodríguez MFD. 2019. Experiencias del Plan Cacao Nestlé, en México. Creación de valor compartido en sistemas agroforestales de cacao, café y vainilla. Una propuesta empresarial. *In*: Del Amo RS, Vergara TMC eds. *La restauración ecológica productiva: El camino para recuperar el patrimonio biocultural de los pueblos mesoamericanos.* Veracruz, México: Universidad Veracruzana, ISBN: 978-607-502-761-6

Rozendaal DMA, Hurtado VH, Poorter L. 2006. Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. *Functional Ecology* **20**: 207-216. DOI: https://doi.org/10.1111/j.1365-2435.2006.01105.x

Saavedra F, Jordan Peña E, Schneider M, Naoki K. 2020. Effects of environmental variables and foliar traits on the transpiration rate of cocoa (*Theobroma cacao* L.) under different cultivation systems. *Agroforestry systems* **94**: 2021-2031. DOI: http://doi.org/10.1007/s10457-020-00522-5

Sauvadet M, Dickinson AK, Somarriba E, Phillips-Mora W, Cerda RH, Martin AR, Isaac ME. 2021. Genotype–environment interactions shape leaf functional traits of cacao in agroforests. *Agronomy for Sustainable Development* **41**: 1-12. DOI: https://doi.org/10.1007/s13593-021-00690-3

Schneider FD, Morsdorf F, Schmid B, Petchey OL, Hueni A, Schimel DS, Schaepman ME. 2017. Mapping functional diversity from remotely sensed morphological and physiological forest traits. *Nature Communications* **8:** 1-12. DOI: http://doi.org/10.1038/s41467-017-01530-3

Smith T, Huston M. 1990. A theory of the spatial and temporal dynamics of plant communities. *In*: Grabherr G, Mucina L, Dale M, Ter Braak C eds. *Progress in theoretical vegetation science*. Dordrecht: Springer. DOI: https://doi.org/10.1007/978-94-009-1934-1

Somarriba E, Orozco Aguilar L, Cerda Bustillos R, López Sampson A, Cook J. 2018. Analysis and design of the shade canopy of cocoa-based agroforestry systems. *In*: Umaharan P. ed. *Achieving sustainable cultivation of cocoa*. Cambridge, UK: Burleigh Dodds Science Publishing, ISBN: 9781786761682

Suárez-Salazar JC, Ngo-Bieng MA, Melgarejo LM, Di Rienzo JA, Casanoves F. 2018. First typology of cacao (*Theobroma cacao* L.) systems in Colombian Amazonia, based on tree species richness, canopy structure and light availability. *Plos One* **13**: e0191003. DOI: http://doi.org/10.1371/journal.pone.0191003

Tezara W, Urich R, Jaimez R, Coronel I, Araque O, Azocar C, Chacón I. 2016. Does Criollo cocoa have the same ecophysiological characteristics than Forastero? *Botanical Sciences* **94**: 563-574. DOI: https://doi.org/10.17129/botsci.552

Thornton PE, Thornton MM, Mayer BW, Wei Y, Devarakonda R, Vose, RS, Cook RB. 2016. Daymet: Daily surface weather data on a 1-km grid for north america. DOI: http://doi.org/10.3334/ORNLDAAC/1328

Tscharntke T, Clough Y, Bhagwat SA, Buchori D, Faust H, Hertel D, Hölscher D, Juhrbandt J, Kessler M, Perfecto

I, Sherber C, Schroth G, Veldkamp E, Wanger TC. 2011. Multifunctional shade tree management in tropical agroforestry landscapes-a review. *Journal of Applied Ecology* **48**: 619-629. DOI: http://doi.org/10.1111/j.1365-2664.2010.01939.x

Utomo B, Prawoto AA, Bonnet S, Bangviwat A, Gheewala SH. 2016. Environmental performance of cocoa production from monoculture and agroforestry systems in Indonesia. *Journal of Cleaner Production,* 134(Part B), 583-591. https://doi.org/10.1016/j.jclepro.2015.08.102

Vaast P, Harmand JM, Rapidel B, Jagoret P, Deheuvels O. 2016. Coffee and cocoa production in agroforestry - A climate-smart agriculture model. *In*: Torquebiau E ed. *Climate Change and Agriculture Worldwide*. Dordrecht: Springer Netherlands, ISBN: 978-94-017-7462-8

Vaast P, Somarriba E. 2014. Tradeoffs between crop intensification and ecosystem services: the role of agroforestry in cocoa cultivation. *Agroforestry systems* **88**: 947-956. DOI: http://doi.org/10.1007/s10457-014-9762-x

Valenzuela-Que FG. 2010. *Manejo, producción y moniliasis en cacaotales con sombra mono y multi-específica en la Chontalpa, Tabasco, México.* BSc Thesis. Instituto Tecnológico de la Zona Olmeca, México.

World Cocoa Foundation. 2020. http://worldcocoafoundation.org

Zuidema PA, Leffelaar PA, Gerritsma W, Mommer L, Anten NP. 2005. A physiological production model for cocoa (*Theobroma cacao*): model presentation, validation and application. *Agricultural Systems* **84**: 195-225. DOI: https://doi.org/10.1016/j.agsy.2004.06.015

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