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RESEARCH ARTICLE

Shade tree pruning effects on flowering and cacao yields in different cropping systems in a long-term trial in Bolivia

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Abstract

Light access is the primary factor affecting yields in cacao-based agroforestry systems (CAFS). While CAFS ecosystem services provision is extensively documented, research on improving light access in CAFS remains scarce. Shade canopy pruning, a developing technique in Latin America, is part of the long-term SysCom Bolivia trial. It is undertaken twice a year, at the start of the rainy and dry seasons. This paper presents the results of a 5-year study on the relationship between CAFS canopy cover, flowering levels, cocoa yields, and pruning events from this trial.

The seasonality and peak periods of flowering and pod production were independent from the cropping system, underlining both climatic- and genetically determined production patterns. Yet, flowering levels depended on canopy cover levels during the rainy season, which translated into different pod production levels in the following months. Average annual yields were 1300 kg ha^{-1} for full sun cacao, 780 kg ha^{-1} for agroforestry systems (AF), and 640 kg ha^{-1} for dynamic agroforestry systems (DAF), with rainy season canopy covers maintained at 25–35% for AF and 40–60% for DAF.

The relationships between canopy cover, flowering, and cocoa yield were found to be exponential, indicating that the lower the canopy cover, the greater the yield increase could be expected from pruning. The lower levels of cover obtained in AF after the ‘flowering’ pruning triggered better flowering levels in comparison to DAF. However, these did not systematically translate into significantly higher yields, underlining the probable significance of the ‘ripening pruning’ for DAF’s cocoa yield. Overall, our results show (i) the great potential of timely shade canopy pruning and (ii) the need to adapt such a technique to systems’ diversity and density to make it cost/labour-effective and support its scalability.

Keywords: agroforestry; canopy dynamics; pruning

Introduction

Cacao (*Theobroma cacao*) has traditionally been **cultivated** under the canopy of shade tree species (Zarrillo *et al.* 2018). As a late successional tree species in the riparian forests of the Amazon basin, cacao thrives in the understory. Its leaves lack a **cuticle**, making it highly susceptible to prolonged or intense sun exposure, strong winds, and water shortage. This explains the prevalence of **cocoa agroforestry systems (CAFS)** in the humid tropics (Almeida and Valle 2007). However, cacao can also **adapt** to full sun conditions and **produce high yields** for several decades using conventional and intensive practices (Mossu 1990; Wood and Lass 2001). In Africa, responsible for nearly 70% of global cocoa production, green revolution cultivation approaches during the 1950s and 1960s demonstrated the **higher annual cocoa yields** of full-sun, intensive cultivation compared to shaded, traditional systems (Ahenkorah *et al.* 1974, 1987). This led to the expansion of cacao monocultures and the drastic reduction or removal of shade trees in existing CAFS. Yet, the consequences of such an approach and the negative effects of current full sun systems are now widely recognised (Grohs *et al.* 2023; Higonnet *et al.* 2017).

Extensive scientific evidence demonstrates that **low-input, shaded CAFS** offer diversified, **longer-term, more stable production** (e.g. Cerda *et al.*, 2014; Saj *et al.*, 2017a); align better with the knowledge, socio-economic conditions, and investment capacities of cocoa farmers (Niether *et al.*, 2020; Saj *et al.*, 2017b); deliver a wide range of ecosystem services (ES); and enhance resilience to climate change (Aaron *et al.* 2024; Mortimer *et al.* 2018). The 2010s witnessed a surge in initiatives like payments for ES, certification standards, and niche markets to bolster the economic viability of CAFS for farmers (Lescuyer and Bassanaga 2021; Rapidel *et al.* 2011). Cocoa yields in CAFS have been shown to achieve or exceed regional/national averages (FAOSTAT 2024; Niether *et al.* 2020).

The potential of CAFS to achieve high, acceptable cocoa yields heavily depends on shade levels; low yields are consistent with heavy shade (Suárez Salazar *et al.* 2018a), and good yields are achieved under lightly shaded, medium-complexity shade canopies (Blaser *et al.* 2018; Hawkins *et al.* 2024; Orozco-Aguilar *et al.* 2024). Proper shade canopy design (botanical composition, population density, and spatiotemporal planting patterns) and management over the entire life cycle of a cacao plantation are mandatory for high cocoa yields. The use and value of temporary shade (e.g. bananas and other short-term crops) is a standard and long-recommended practice in cocoa cultivation (Braudeau 1969). The recruitment of valuable shade tree species from natural regeneration is now widely recognised and promoted (Kouassi *et al.*, 2023; Somarriba and López Sampson, 2018). However, farmers' constraints and objectives (e.g. land tenure, production of other goods, environmental or organic certifications, available labour, etc.) may translate into sub-optimal shade canopy design and management, resulting in inadequate shade levels for high cocoa yields (Andres *et al.* 2018; Asare *et al.* 2019).

Pollarding and pruning shade trees are key management practices to regulate canopy cover and shading (Estrada *et al.*, 2011). Designing an optimal shade tree pruning scheme requires the consideration of a variety of factors, including the botanical composition, planting density and spatiotemporal population dynamics of shade trees, pruning intensity (amount of biomass removed) and frequency (number of pruning events per year), and timing (to match the phenological phases of cocoa in a year cycle of production). Pruning criteria differ depending on whether a shade tree is meant to produce timber, fruit, mulch, or only for shade (Somarriba and López Sampson 2018).

In this article, we used data from a long-term trial in Bolivia (https://systems-comparison.fibl.org/) to explore the effects of shade tree pruning and canopy cover on flowering and yields of cocoa in monocropping and agroforestry systems. We hypothesised that low canopy cover results in higher flowering and yield levels and that the timely pruning of the shade canopy can partially close the yield gap between shaded and non-shaded systems.

Material and methods

Site description and experimental setup

The experimental trial was established in Sara Ana, Alto Beni, Bolivia (380 m altitude; 15° 27′36.60″S and 67°28′20.65″W; (https://systems-comparison.fibl.org/). The Sara Ana Research Centre operates its own manual weather station, recording daily rainfall and air temperatures (at 8 a.m., 2 p.m., and 6 p.m.) and daily minimum and maximum temperatures (data can be accessed at https://senamhi.gob.bo/index.php/inicio). Sara Ana's climate is humid tropical with a unimodal rainfall pattern. The dry season (months with less than 100 mm) typically lasts from May to October; the rainy period is between November and April. The average annual rainfall over the past 10 years (2013–22) is 1635 ± 83 mm, with an average annual temperature of 27°C. The extremes in temperature recorded were 9°C in June 2022 and 42°C in November 2020.

The trial began in 2008 with the clearing of an approximately 20-year-old secondary forest on the terrace of the Alto Beni River. The plots are 48 × 48 m (2304 m^2), with a net central plot of 24 × 24 m (576 m^2) where all measurements are taken. The trial investigates five distinct cacao cropping systems in an incomplete, randomised block design with four replicates, as detailed by Schneider *et al.* (2017). The systems include conventionally (herbicide and synthetic fertilisation use) and organically (manual weeding and compost use) managed cacao monocultures (MONO Conv and MONO Org); conventionally and organically managed agroforestry systems (AF Conv and AF Org); and dynamic agroforestry systems (DAF) without inputs (neither organic nor conventional). Dynamic agroforestry is inspired by natural forest succession. It uses high planting densities, diversity, and stratification, with regular pruning and selective weeding. In DAF, species (or crops) are grouped by lifespan into pioneer, secondary, and primary species, all planted simultaneously or allowed to regenerate naturally and managed accordingly (more details in Andres *et al.*, 2016). Cocoa is planted at 4 × 4 m (625 trees per hectare) in all systems, with 36 cocoa trees in the net plot. The cocoa stand is made up of 12 cacao genotypes randomly distributed in each plot, with three cocoa trees per genotype in the net plot. Four of these genotypes were locally selected by the cooperative clones: IIa22, IIa58, III-6, and III-13. Four are international clones: ICS-1, ICS-6, ICS-95, and TSH-565. Finally, the trial includes four full-sib families generated through the pollination of the four international clones by IMC-67 pollen: ICS-1 × IMC-67, ICS-6 × IMC-67, ICS-95 × IMC-67, and TSH-565 × IMC-67. All clones, but TSH-565, are self-compatibles. Self-compatibility is unknown for full sibs (Armengot *et al.* 2023).

Both AF Conv and AF Org have the same fixed layout of shade trees, initially planted (in 2009) with a density of >300 timber, fruit, and N-fixing trees ha^{-1}. The DAF system was initially planted (in 2009) at a density > 1100 trees ha^{-1} (for more details see Schneider *et al.*, 2016). AF contained between 13 and 14 associated shade species, the most numerous being *Erythrina* spp., *Inga* spp., and *Euterpe oleracea*. DAF contained between 40 and 47 associated shade species, with *Swartzia jorori*, *Myroxylon balsamum*, *Amburana cearensis*, *Guarea* spp., *Erythrina* spp., *Inga* spp., and *Euterpe oleracea* being the most numerous ones (depending on the plot). During the 5 years of the experiment, living shade tree densities in AF and DAF were on average 185 and 770 trees ha^{-1}, respectively. Following the management scheme in DAF, the gradual thinning of shade trees decreased their density with time, from 868 trees ha^{-1} in 2017 to 602 trees ha^{-1} in 2022. In AF systems, windy events induced the fall of numerous Ingas, involuntarily decreasing the total shade tree density from 191 to 170 trees ha^{-1}.

Canopy cover, flowering, and cocoa yields were evaluated over five cocoa cultivation cycles, from 2017 to 2022. Each production cycle follows the phenological cycle of cocoa in Sara Ana, starting 1st of October of year n and ending on September 31st of year n+1. Hence, cocoa production cycles are denoted as 2018–2018, 2018–2019, and so on.

Pruning of cocoa trees

During the study period, cocoa trees in all systems are pruned three times per year: in January (before the main flowering season), in March–April (pod filling), and in August–September (maintenance; after the harvest season). Pruning follows five criteria: (i) maintain a canopy height of a maximum of 4 m; (ii) avoid branch overlap between neighbour cocoa trees; (iii) maintain an ‘open’ crown to increase light transmission and stimulate flowering; (iv) eliminate suckers, low-hanging and/or diseased shoots; this criterion is also applied during weeding events; and (v) align to the within-year phenological phases of cocoa in Sara Ana.

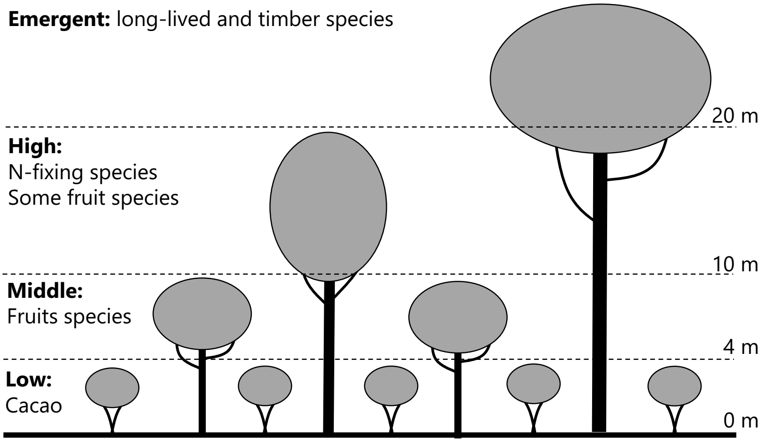

Figure 1. Diagram showing the height and tree species type by vertical strata.

Pruning of shade trees

The five cocoa cropping systems are conceived as having four vertical strata (Fig. 1). Tree pollarding and pruning followed the following criteria.

1) The main objective of shade tree pruning is to increase the access of cacao to light to ensure high yields; the production of tree products (fruits, timber, latex, etc.) is secondary.

2) Lower branches are constantly removed to avoid interfering with trees (cocoa or other shade trees) in adjacent strata. At least 3–4 m separation between tree canopy strata is aimed at.

3) Stratum- and species-specific pruning criteria:

- Timber tree species usually occupy the high or emergent strata (e.g. *Swietenia macrophylla, Myroxylon balsamum*) and are pruned by removing lower branches to favour them reaching the emergent stratum.
- Nitrogen-fixing species (e.g. *Inga* spp. and *Erythrina* spp.) are assigned to the high strata. Inga tree crowns are pruned to remove around 80% of foliage and branches, while maintaining the main structural branches of the crown. Erythrina trees are pruned so that their crowns clearly stand above the Ingas. These two species dominate in AF Org and AF Conv.
- Fruit tree species (e.g. *Citrus* spp., *Garcinia humilis*, *Nephelium lappaceum*, *Theobroma grandiflorum*) occupy the middle strata. Their lower branches are removed to avoid interfering with the crown of cocoa plants in the low stratum. Upper branches are pruned to prevent them from growing into the high stratum. Branches inside the crown are pruned/thinned lightly; unproductive or diseased wood is removed. In some cases, fruit trees can occupy the high strata in replacement of dead or fallen N-fixing trees.

The timing of tree pollarding/pruning is tuned to the phenological phases of cocoa (flowering period between January and March and fruit ripening between June and August), which are aligned with the local climate (cf. section 2.1). It usually consists of two events per cacao cycle:

- The first pruning event removes up to 80% of the crown of mulch-producing tree species (such as *Inga* spp. and *Erythrina* spp.). It takes place at the start of the rainy season (around November/December), just before cocoa starts flowering. This event is called ‘flowering pruning’, as it aims at stimulating cocoa flowering.
- The second pruning event mainly removes new shoots and branches crossing to the adjacent strata. It takes place after the end of the rainy season (typically in April) when the cocoa trees

are developing and filling their fruits. This event is called 'ripening pruning', as it aims at improving ventilation in the plots, thereby reducing the risk of fungal diseases and fruit losses. More incoming radiation is also likely to increase air temperature and accelerate fruit ripening.

Estimation of cocoa yields

Cocoa pods per tree were harvested fortnightly. Fresh weight of cocoa beans was determined in the field and later converted to dry, fermented bean weight using a conversion factor of 0.33 (Armengot *et al.* 2020; Vervuurt *et al.* 2022). For data analysis, fortnight yield data was accumulated monthly and per annual cycle (monthly cocoa yields between October of year n and September of year n+1).

Estimation of canopy cover

Canopy cover was estimated monthly with a GRS Densitometer™ and followed FAO (2015). Each month, eighty-four shade canopy cover measurements were taken per net plot (between cocoa rows and every 2 m), above the canopy of cocoa trees (Suppl. Material Fig. S1). Each canopy cover measurement was counted into one of five classes: 0 for 0% cover; 1 for]0–25]%; 2 for]25–50]%; 3 for]50–75]%; 4 for]75–100]% (Suppl. Material Fig. S2). Monthly average canopy cover per plot was calculated using class frequencies and the mid-point of each cover class (0.0%, 12.5%, 37.5%, 62.5%, 87.5%).

Estimation of flowering

Flowering of each cacao tree in the net plot was monitored fortnightly by visually inspecting and ranking the number of mature flowers (at anthesis or close to) on trunks and branches. The ranking includes five flower abundance classes: 0 = no flowers; 1 = very few (very few flowers in trunk and branches); 2 = few (few branches have a few flowers); 3 = medium (almost all branches have few flowers); 4 = many (almost all branches have many flowers) (Suppl. Material Fig. S3; Armengot *et al.* 2023). A monthly flowering index was calculated by summing the ranks per plant in the net plot. Flowering indexes were similarly calculated per annual cycle (12 months, from October to September, were added up) and per flowering (5 months, from December to April) and ripening period (5 months, from May to September of the year).

Statistical analyses

Preliminary analyses showed that cocoa yields were statistically similar between MONO Conv and MONO Org and between AF Conv and AF Org (Suppl. Material Tab. S1). For this reason, the data was pooled into only three cropping systems: MONO (eight plots), AF (eight plots), and DAF (four plots). Blocks were no longer taken as part of the experimental structure, resulting in a fully randomised experiment with five cycles, three treatments, and an uneven number of replicates (plots) per treatment.

Data analysis, by cycle and by period (flowering and ripening), was done in two steps. Each step included an analysis of variance and a regression analysis. In the first step, we performed a linear mixed model (LMM) analysis of variance using cropping system, annual cocoa cycle, and their interaction as fixed effects. Plots were taken as a random effect. Response variables used were annual (cycle) flowering index, canopy cover (average, maximum, minimum), and cocoa yield. When significant effects were detected, the MMA was followed by the Benjamini–Hochberg post hoc. Linear and exponential (non-linear) regression models were fitted to study the relationship between canopy cover variables and flowering index or cocoa yield. Regression analyses used plot data obtained by pooling cropping systems and cycles (i.e. 100 ‘plots’). In the second step, similar to MMA, post hoc and regression analyses were performed for period (flowering and ripening) data. All statistical analyses were performed in XLSTAT (Addinsoft, 2024); the significance level was set at $p < 0.05$.

Results

Cocoa yield, canopy cover, and flowering by cycle and by period

Both the cycle and cropping system significantly differed in terms of cocoa yield, canopy cover and flowering; interactions between these response variables were also statistically significant (Tab. 1). Cocoa yields were always statistically higher in MONO than in AF and DAF, and in general (in some cycles AF and DAF were statistically similar), yields in AF were 100–200 kg ha^{-1} $year^{-1}$ higher than in DAF. The same pattern was observed for flowering: MONO > AF > DAF. Canopy cover showed the inverse patterns observed for flowering, with consistently higher means in DAF than in AF (Tab. 1). The relationship between maximum, minimum, and average canopy cover and flowering was best fitted ($p < 0.01$) by linear regressions, with R^2 values between 0.685 and 0.732. (Fig. 2 a, b, c). Exponential regression models were the best fit for the relationship between canopy cover variables and cocoa yield, with R^2 values between 0.626 and 0.725 (Fig. 2 d, e, f). System-specific linear regressions are shown in Suppl. Material Tab. S2.

The same patterns observed by cycle were observed by period (flowering and ripening). In terms of yield and flowering, MONO > AF > DAF; the inverse pattern was observed for canopy cover with DAF > AF (Tab. 1). Exponential regression models were the best fit for the relationship between canopy cover variables by period and flowering, with R^2 values between 0.578 and 0.615 (Fig. 3 a, b). Exponential regression models were also the best fit for the relationship between canopy cover variables by period and cocoa yield, with R^2 values between 0.728 and 0.729 (Fig. 3 c, d). System-specific linear regressions are shown in Suppl. Material Tab. S3. In the flowering period, cocoa yields are positively related to flowering. The best-fit exponential regression model between these two variables explained 57% of the variation. System-specific linear regressions showed improved relationships with increasing yields (Fig. 4).

Pruning events

During the study period, four flowering and five ripening pruning events were done. The flowering pruning in November 2020 and the subsequent ripening pruning in May 2021, combined with the wind-induced fall of some of the associated trees in the agroforestry (AF) systems, severely reduced their canopy cover. As a result, no flowering pruning was carried out for the 2021–2022 cycle. On average, the four flowering pruning events reduced canopy cover to <30% in AF and <40% in DAF (Fig. 5).

During the flowering period, DAF reached, on average, a canopy cover of >60%, while AF cover was <40%. The maturation pruning events then reduced canopy cover to <25% in AF and <40% in DAF (Fig. 5).

Discussion

The relationship between shading (most times using canopy cover as a proxy) and cocoa yield is central to the design, management, and performance of cocoa agroforestry systems. Physiological models have shown that cocoa yields decrease with a reduction in light availability (Zuidema *et al.* 2005); other models recommend the use of light shade (Almeida and Valle 2007). Long-term field experiments have shown higher yields in open sun than in shaded

Table 1. Analysis of variance and treatment means of cocoa yield, flowering, and canopy cover by cycle and by period. MONO: monoculture. AF: agroforestry. DAF: dynamic agroforestry. ***: $p < 0{,}001$; **: $p < 0{,}01$; *: $p < 0{,}05$. Different letters after the mean values indicate significant differences

	Yield (kg ha^{-1})				Flowering index				Canopy cover (%)									
	Cycle		Ripening period		Cycle		Flowering period		Cycle maximum		Cycle minimum		Cycle average		Average flow. period		Average ripe. period	
F values																		
System	148.817	***	209.952	***	270.118	***	306.027	***	382.201	***	220.843	***	550.013	***	391.391	***	388.133	***
Cycle	4.290	**	7.834	***	32.007	***	78.279	***	0.607		27.156	***	16.470	***	6.275	***	82.726	***
System × Cycle	2.665	*	2.435	*	2.606	*	7.644	***	15.747	***	15.735	***	31.289	***	26.760	***	27.612	***
Means																		
2017–18																		
MONO	1249.3	AB	1082.8	AB	17.7	B	9.1	CD	–		–		–		–		–	
AF	768.3	E	650.5	DE	15.1	CD	7.8	E	44.6	C	26.6	CD	35.5	D	37.0	CD	33.9	B
DAF	618.2	E	508.2	DE	12.0	EF	6.0	F	60.3	B	30.2	BC	45.3	C	50.4	B	38.4	B
2018–19																		
MONO	1108.1	BCD	946.4	BC	18.3	B	9.5	BCD	–		–		–		–		–	
AF	669.3	E	546.1	DE	14.3	CD	7.3	E	42.6	C	26.9	C	36.3	D	32.7	DE	38.8	B
DAF	590.3	E	471.0	E	11.6	F	6.0	F	60.4	B	41.3	A	51.5	AB	48.8	B	54.5	A
2019–20																		
MONO	1231.5	ABC	946.4	BC	18.2	B	9.2	CD	–		–		–		–		–	
AF	916.6	CDE	546.1	DE	15.6	C	8.0	E	42.6	C	19.9	D	34.1	D	32.8	DE	38.8	B
DAF	796.2	DE	471.0	E	14.0	CD	7.4	E	57.5	B	28.8	C	45.1	C	40.3	C	54.5	A
2020–21																		
MONO	1492.0	A	1290.1	A	19.0	AB	10.1	B	–		–		–		–		–	
AF	790.2	DE	681.6	DE	15.4	C	7.3	E	40.8	C	7.8	E	21.7	E	28.6	EF	10.1	D
DAF	598.6	E	513.5	DE	13.5	DE	6.3	F	64.0	AB	29.4	C	47.1	BC	58.4	A	35.2	B
2021–22																		
MONO	1432.9	AB	1271.2	A	20.0	A	11.0	A	–		–		–		–		–	
AF	834.2	DE	723.8	CD	17.9	B	9.9	BC	32.5	D	11.9	E	19.8	E	23.7	F	18.7	C
DAF	594.2	E	461.1	E	15.3	C	8.8	D	71.7	A	36.7	AB	53.1	A	60.2	A	53.6	A

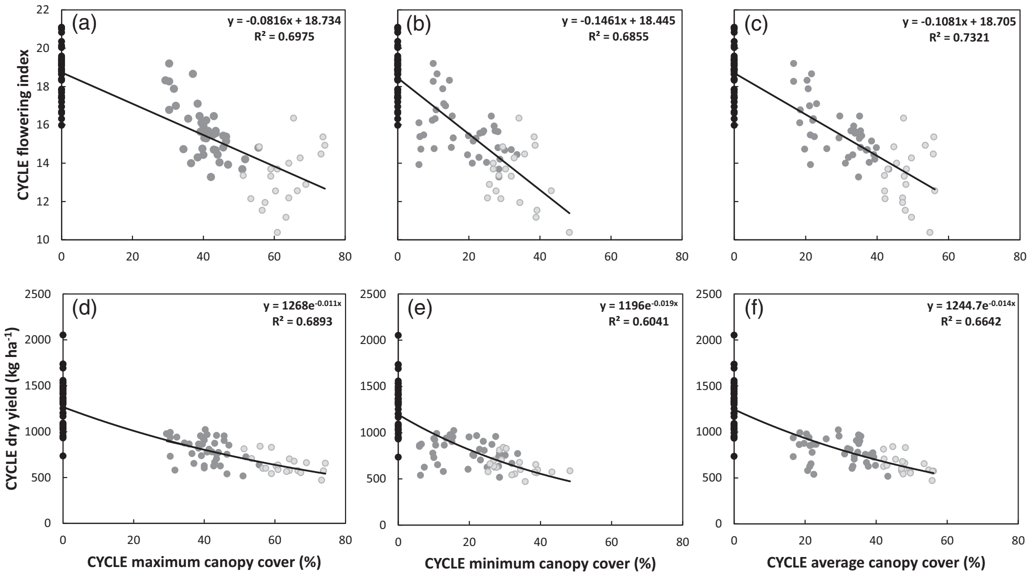

Figure 2. Linear and non-linear regressions between cocoa yield (a, b, c) and flowering index (d, e, f) with canopy cover variables (maximum, minimum, average) by cycle. Black dots represent monoculture (MONO), dark grey dots represent agroforestry systems (AF), and light grey dots represent dynamic agroforestry (DAF). R^2: determination coefficient.

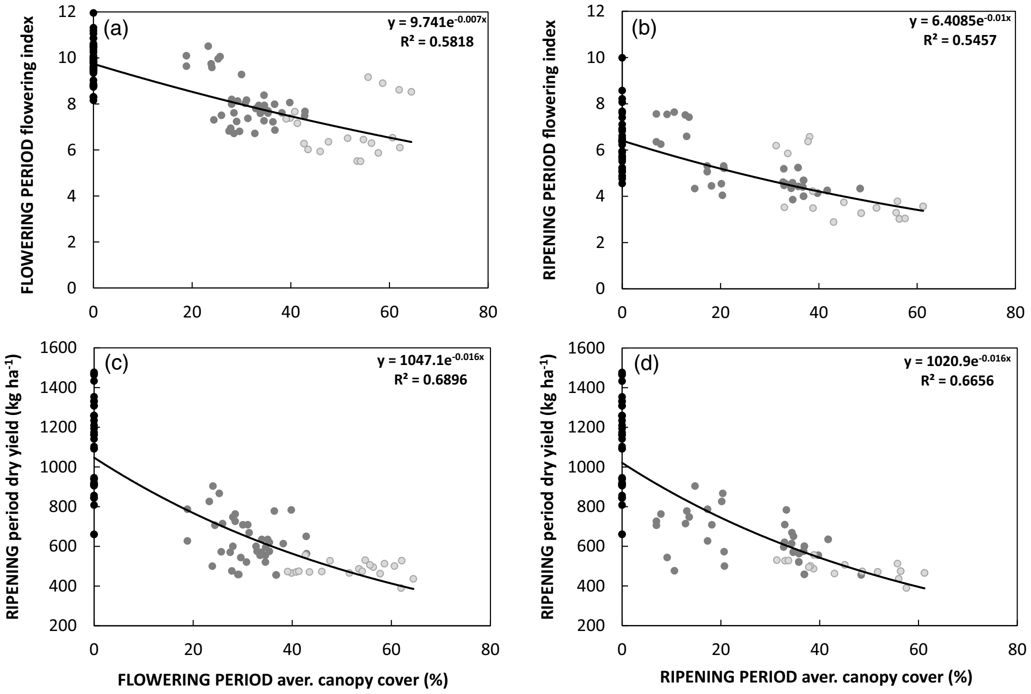

Figure 3. Non-linear regression between flowering index and cocoa yield with the average canopy cover of the flowering (a, c) and ripening periods (b, d). R^2: determination coefficient. Black dots represent monoculture (MONO), dark grey dots represent agroforestry systems (AF), and light grey dots represent dynamic agroforestry (DAF). R^2: determination coefficient.

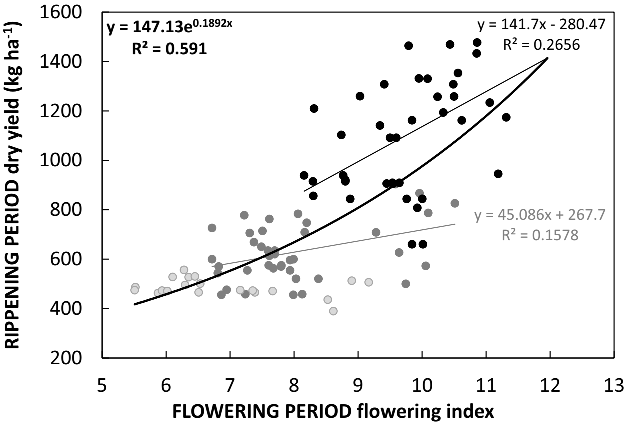

Figure 4. Non-linear regression between cocoa yield and flowering during the flowering period. Black dots represent monoculture (MONO), dark grey dots represent agroforestry systems (AF), and light grey dots represent dynamic agroforestry (DAF). R^2: determination coefficient. Significant system-specific regressions are shown in black (MONO) and dark grey (AF).

cocoa plots (Ahenkhora *et al.* 1987). But surveys of farmers' fields have shown that while heavy shade (high canopy cover) is consistent with low cocoa yields (Blaser *et al.* 2018; Clough *et al.* 2011; Wade *et al.* 2010), cocoa yield may not be adversely affected (and can even be improved) under light tree shade (Asare *et al.* 2019; Hernández-Nuñez *et al.* 2024; Suárez Salazar *et al.* 2018b). Canopy cover, a proxy for shading or reduction in light availability, doesn't fully capture the complex dynamics of shade and its impact on yields (Somarriba *et al.* 2024); crown shape and tree height, for a given canopy cover level, significantly alter the light regime influencing cocoa yield (Asante *et al.* 2022; Blaser-Hart *et al.* 2021). Our study shows that despite its limitations, canopy cover remains a valuable proxy. Canopy cover estimation is an easy, accessible, fast, and cheap technique to monitor the temporal evolution of light conditions in the field. The flowering indices constructed also demonstrated coherence within the study, backing up the use of such indicators in phenological studies (Wibaux *et al.* 2024).

Yearly flowering and yield levels are canopy cover level-dependent

The three cropping systems studied showed significant differences in terms of yield, flowering, and canopy cover. The regressions between yearly flowering indices and canopy cover variables support the hypothesis of a direct, negative effect of canopy cover on flower initiation (Asomaning *et al.* 1971) and the need to consider access to light as the first step of yield building (de Almeida and Valle 2010). Unsurprisingly, the full sun monocultures (MONO) presented the highest flowering indices, which translated into the highest cocoa yields. The agroforestry systems (AF) showed consistent higher annual flowering indices and lower canopy cover than the DAF. Yet, these differences did not systematically translate into statistically significant higher cocoa yields in AF. Our results support the hypothesis that a reduction in shade canopy cover in low-shade systems may result in a proportionally higher yield increase than the same level of reduction in shade canopy cover in heavily shaded systems (due to the exponential relationship found between cocoa yield and shade canopy cover). For instance, using the model found for the maximum canopy cover, a canopy cover reduction in maximum shade canopy cover from 60 to 40% would translate into a gain of approximately 161 kg.ha^{-1}, while a reduction from 40 to 20% in maximum shade canopy cover would translate into a gain of approx. 201 kg.ha^{-1}.

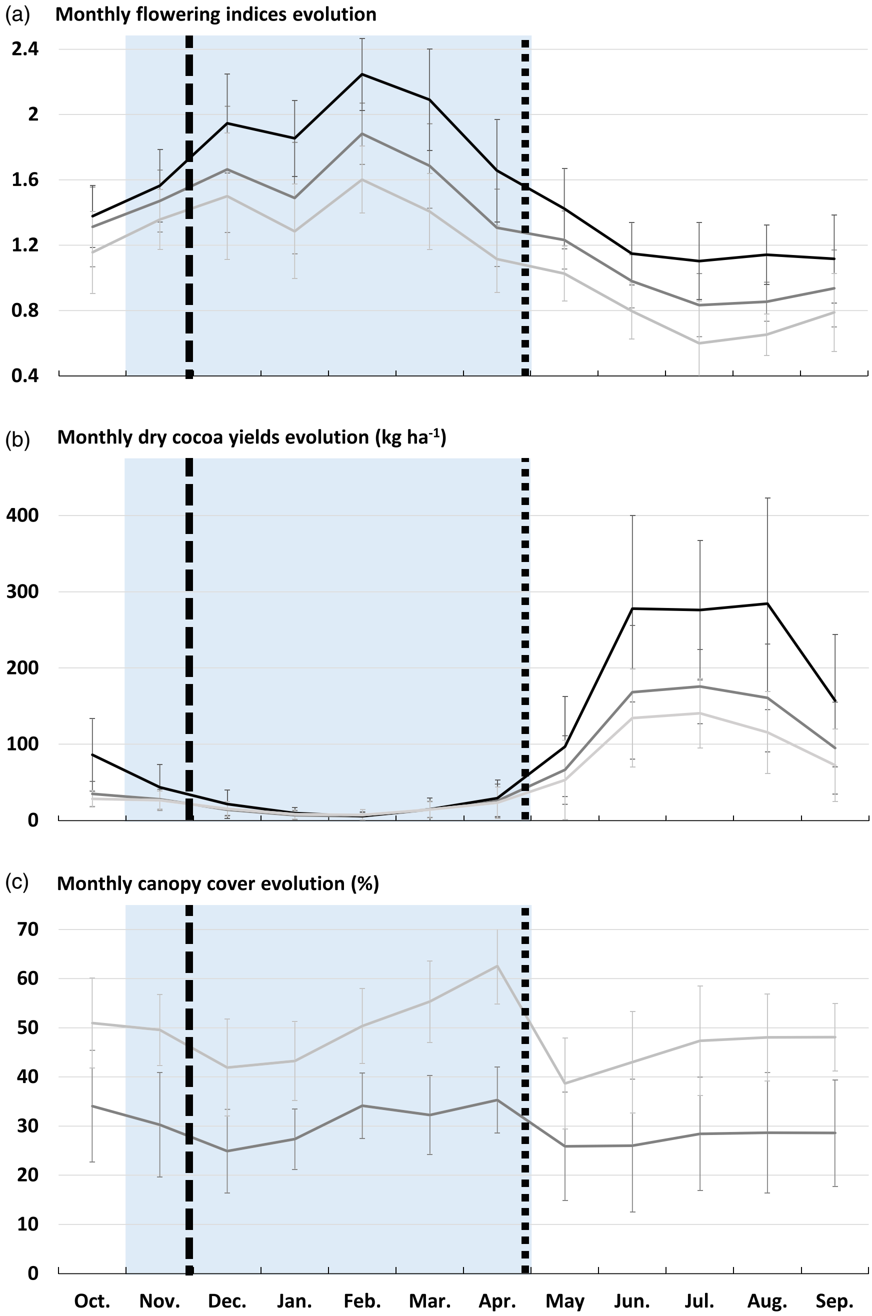

Figure 5. Five-year (2017–2022) mean (+/- S.E.) monthly flowering (a), cocoa yield (b), and canopy cover (c). Black line: monoculture (MONO). Dark grey line: agroforestry systems (AF). Light grey line: dynamic agroforestry (DAF). Vertical dashed lines indicate when pruning events take place. Long-dashed line = flowering pruning. Short-dashed line = ripening pruning. The blue zone demarcates the rainy season (monthly rainfall ≥ 100 mm).

Many internal and external factors may influence cacao reproductive growth (from flower initiation to pod harvest), and our study can't directly provide insights into them. However, Armengot *et al.* (2023) showed that in the same trial, there were no interactions between cocoa genotypes and cropping systems effects on cocoa yields, suggesting that those external conditions were the main drivers of the reproductive growth differences found in our study. Relative humidity, soil moisture, or air temperature were shown to differ between cropping systems in the same trial (Niether *et al.* 2017, 2018) and are long known for influencing flowering processes (Sale 1969, 1970). Besides, the community composition of flower-visiting insects was also shown to differ between cropping systems in the same trial (Herbas *et al.* 2020), and we may hypothesise that these also play a significant role in pollination success (Córdoba *et al.* 2013; Frimpong-Anin *et al.* 2014). On the contrary, soil quality did not differ between cropping systems in the same trial, despite the different natures and quantities of fertilisation and pruning residues transferred to the soil (Morales-Belpaire *et al.*, 2024; Schneidewind *et al.*, 2019). In our study, we did not find differences in either flowering or in cocoa yields between organic and conventional management in AF and MONO (see Suppl. Material Tab. S1). As a result, nutrient availability, which influences resource allocation and carbohydrate production within the cocoa trees, in turn influencing cherelle wilt (Alvim 1954; Valle *et al.* 1990), may not be a significant driver of the results observed in our study.

The seasonal dependency of flowering and cocoa yields

Flowering and fruit ripening in all cropping systems were strongly seasonal, emphasising the prominent effect of local climate on cacao phenology. On average, 80% of the total annual yield occurs between May and September (a period we call ‘ripening’). Similarly, 50% of flowering occurs between December and April (a period we call ‘flowering’), without differences between cropping systems. In regions with a strongly seasonal rainfall pattern, drought inhibits flowering, and rainfall distribution is known to determine cacao flowering onset and its distribution throughout the year (Restrepo *et al.* 2017; Wibaux *et al.* 2024). In our study site, rainfall is strongly seasonal, with only five ‘rainy months’ (months with more than 100 mm of rain) in the year. Flowering intensity began to increase in December, after the onset of rains, then increased and later decreased until it ended in April, clearly coinciding with the yearly rainy seasons. This 5-month flowering period translated into a peak of pod production between June and August, during the first part of the dry season. The 5-month range of flowering and ripening may point to the variability of the cocoa genetic pool used in this trial (Armengot *et al.* 2023). However, unfortunately, the design of the current study does not allow for assessing genotype-specific features.

The flowering and ripening pattern observed per cycle was also observed per flowering and ripening period. It is worth mentioning that 50% of total flowering occurs outside the 5-month flowering period. However, this flower production translates into only 20% of the yield in the annual cycle, probably because fruits set at the end of the rainy period will face water deficits that may diminish their probability to reach full maturity and harvest (Moser *et al.* 2010). The same applies if some rainy events trigger flowering during the dry season. Endogenous processes of resource partitioning between vegetative and reproductive growth are also probably at stake both when the trees are filling up their pods during the maturation period and after (de Almeida and Valle 2010; Melnick 2016; Valle *et al.* 1990). Moreover, the community of pollinators may also vary seasonally, influenced both by climatic conditions and by the phenology of plant species inside and/or surrounding the plots (Abrahamczyk *et al.* 2011). Fewer pollinators visit fewer flowers and result in a less successful pollination. All these issues may contribute to explaining why, in the same trial, the international clones (which are having their flowering peak later than the local ones) are low-producing in the local climatic context (Armengot *et al.*, 2023).

Finally, the cropping systems may also play a role in the level of flowering between May and November and yield between September and April (year N+1). But our results clearly underline that the agroforestry systems of the trial, despite triggering different microclimatic conditions and buffering some climatic effects (Niether *et al.* 2017, 2018), were not able to significantly play on the success rate of the reproductive growth in comparison to monoculture outside the main production period.

Pruning of the shade canopy

While traditional cocoa agronomy typically recommends a fixed shade canopy cover level (Jaimes-Suárez *et al.* 2022; Wilson *et al.* 1999; Wood and Lass 2001), our study demonstrates that pruning and shade canopy cover form a dynamic process capable of partially closing the yield gap between monocultures and agroforestry systems. Identifying indicators to guide pruning decisions is therefore crucial for maximising the agronomic and economic profitability of cocoa agroforestry systems (Esche *et al.* 2022).

The severity of tree canopy removal during the flowering pruning event determined the level from which the shade trees started their regrowth when the rains resumed. The lower this level, the lower the speed of regrowth, and the lower the canopy cover level reached at the end of April. This is exemplified by AF and DAF systems. On average, AF had a canopy cover level close to 25% after the flowering pruning event and gained approximately 2% of shade cover each month before the ripening pruning took place. DAF had initial cover levels close to 42% and gained approximately 4% of shade canopy cover per month. Such a dynamic explains the need for a much stronger ripening pruning in DAF than in AF systems. For both DAF and AF, the rate of regrowth of shade canopy cover after the ripening pruning was lower as the climatic conditions were getting drier.

Our best-fit regression models between yields or flowering and shade canopy cover, both per cycle and per period, were non-linear. Such results suggest that the yields of systems having a canopy cover greater than 40–45% over the entire annual cycle, like DAF, may not benefit from pruning as much as AF systems will do. Yet, our data shows that this was not systematically the case, except when the differences in canopy covers were higher than 30% (as in 2021–2022). This points to the fact that canopy cover does not inform precisely enough on the quality of shading (Somarriba *et al.* 2024). Yet, it also probably shows that some room is available in the management of the shade canopy, as underlined by the fitted regressions by cropping system. Indeed, the flowering indices and yield of AF showed a significant relationship with the canopy covers in both the flowering and ripening periods, which underlines the usefulness of both pruning events. In DAF, those relationships were only significant for the ripening period. Hence, it appears that while DAF's yield potential is impaired by their high canopy cover during the flowering season, their strong ripening pruning (>25% of the cover removed) may have allowed them to partially close the yield gap with AF.

Overall, these results suggest that if AF were more heavily pruned before the main flowering season (to reach minimum canopy cover close to 15%), it may be possible to skip the ripening pruning, thus reducing labour/input costs without impairing cocoa yields. In the case of DAF, a stronger flowering pruning (to reach a minimum canopy cover close to 25%) would increase flowering and cocoa yield, reducing the need for a strong ripening pruning event (also reducing some labour/input costs).

Conclusion

Our study highlighted the seasonal rainfall and temperature patterns that drive the flowering and yield building of cocoa cropping systems in the study site. It also showed the significant role of canopy cover on flowering and cocoa yield. The timely pruning of shade trees can adjust shade levels at the right moment in the within-year phenological cycle of cacao. The non-linear relationships between cocoa flowering or yield and canopy cover strongly suggest that the positive effects of pruning on flowering and cocoa yield will be higher in low-cover shade canopies than in high-cover shade canopies. Timing and intensity of pruning are therefore to be adapted to the systems' diversity and density in order to make such a practice cost/labour-effective and to support its scalability.

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References

Aaron, W., Amritbir, R., Stephane, S., Laura, A., Harun, C., Milka, K., Akanksha, S., Ingo, G. and Marc, C. (2024) The ecological and socioeconomic sustainability of organic agroforestry: a systematic review. *Agroforestry Systems* **98**(8), 2933–2949.

Abrahamczyk, S., Kluge, J., Gareca, Y., Reichle, S., and Kessler, M. (2011) The influence of climatic seasonality on the diversity of different tropical pollinator groups. *PLoS ONE* **6**(11), e27115.

Addinsoft (2024) XLStat version 2024 2. 2. Available at: http://www.xlstat.com. Lumivero Inc. Paris, France.

Ahenkorah, Y., Akrofi, G. S., and Adri, A. K. (1974) The end of the first cocoa shade and manurial experiment at the Cocoa research institute of Ghana. *Journal of Horticultural Science* **49**(1), 43–51.

Ahenkorah, Y., Halm, B. J., Appiah, M. R., Akrofi, G. S., and Yirenkyi, J. E. K. (1987) 20 years results from a shade and fertilizer trial on Amazon cocoa (Theobroma cacao) in Ghana. *Experimental Agriculture* **23**(1), 31–39.

Almeida, A.-A. F. de, and Valle, R. R. (2007) Ecophysiology of the cacao tree. *Brazilian Journal of Plant Physiology* **19**, 425–448.

Alvim, P. de T. (1954) Studies on the cause of cherelle wilt of cacao.

Andres, C., Blaser W.J., Dzahini-Obiatey H.K., Ameyaw G.A., Domfeh O.K., Awiagah M.A., Gattinger A., Schneider M., Offei S.K., and Six J.. (2018) Agroforestry systems can mitigate the severity of cocoa swollen shoot virus disease. *Agriculture, Ecosystems & Environment* **252**, 83–92.

Andres, C., Comoé, H., Beerli, A., Schneider, M., Rist, S., and Jacobi, J. (2016) Cocoa in Monoculture and Dynamic Agroforestry. In Lichtfouse E., (ed.), *Sustainable Agriculture Reviews: Volume 19*, Cham: Springer International Publishing, pp. 121–153.

Armengot, L., Ferrari, L., Milz, J., Velásquez, F., Hohmann, P., and Schneider, M. (2020) Cacao agroforestry systems do not increase pest and disease incidence compared with monocultures under good cultural management practices. *Crop Protection* **130**, 105047.

Armengot, L., Picucci, M., Milz, J., Hansen, J. K., and Schneider, M. (2023) Locally-selected cacao clones for improved yield: a case study in different production systems in a long-term trial. *Frontiers in Sustainable Food Systems* **7**, 1253063.

Asante, P.A., Rahn E., Zuidema P.A., Rozendaal D.M.A., Van der Baan M.E.G., Läderach P., Asare R., Cryer N.C., Anten, N. P. R. (2022) The cocoa yield gap in Ghana: a quantification and an analysis of factors that could narrow the gap. *Agricultural Systems* **201**, 103473.

Asare, R., Markussen, B., Asare, R. A., Anim-Kwapong, G., and Ræbild, A. (2019) On-farm cocoa yields increase with canopy cover of shade trees in two agro-ecological zones in Ghana. *Climate and Development* **11**(5), 435–445.

Asomaning, E. J. A., Kwaka, R. S., and Hutcheon, W. V. (1971) Physiological studies on an amazon shade and fertilizer trial at the Cocoa Research Institute of Ghana. *Ghana Journal of Agricultural Science* **4**, 47–64.

Blaser, W. J., Oppong, J., Hart, S. P., Landolt, J., Yeboah, E., and Six, J. (2018) Climate-smart sustainable agriculture in low-to-intermediate shade agroforests. *Nature Sustainability* **1**(5), 234–239.

Blaser-Hart, W. J., Hart, S. P., Oppong, J., Kyereh, D., Yeboah, E., and Six, J. (2021) The effectiveness of cocoa agroforests depends on shade-tree canopy height. *Agriculture, Ecosystems & Environment* **322**, 107676.

Braudeau, J. (1969) *Le cacaoyer*, Paris, France: Maisonneuve et Larose, 304p

Cerda, R., Deheuvels, O., Calvache, D., Niehaus, L., Saenz, Y., Kent, J., Vilchez, S., Villota, A., Martinez, C., and Somarriba, E. (2014) Contribution of cocoa agroforestry systems to family income and domestic consumption: looking toward intensification. *Agroforestry Systems* **88**(6), 957–981.

Clough, Y., Barkmann, J., Juhrbandt, J., Kessler, M., Wanger, T. C., Anshary, A., Buchori, D., Cicuzza, D., Darras, K., Putra, D. D., Erasmi, S., Pitopang, R., Schmidt, C., Schulze, C. H., Seidel, D., Steffan-Dewenter, I., Stenchly, K., Vidal, S., Weist, M., Wilegoss, A.C., Tscharntke, T. (2011) Combining high biodiversity with high yields in tropical agroforests. *Proceedings of the National Academy of Sciences of the United States of America* **108**(20), 8311–8316.

Córdoba, C., Cerda Bustillos, R., Deheuvels, O., and DeClerck, F. A. (2013) Polinizadores, polinización y producción potencial de cacao en sistemas agroforestales de Bocas del Toro, Panamá. *Agroforestería En Las Américas* 49.

de Almeida, A. A. F., and Valle, R. R. (2010) *Cacao: Ecophysiology of Growth and Production*, Hauppauge: Nova Science Publishers, Inc.

Esche, L., Schneider, M., Milz, J., and Armengot, L. (2022) The role of shade tree pruning in cocoa agroforestry systems: agronomic and economic benefits. *Agroforestry Systems* **97**(2), 175–185. doi: 10.1007/s10457-022-00796-x

Estrada, W., Romero, X., and Moreno, J. (2011) Guía técnica del cultivo de cacao manejado con técnicas agroecológicas. Confederación de Federaciones de La Reforma Agraria Salvadoreña.

FAO. (2015) Field guide for rapid assessment of forest protective function for soil and water. A scientifically sound, cost effective and easy-to-apply method for collecting data to promote forest management for protection of soil and water, *Global Forest Resources Assessment 2015*, 16p.

FAOSTAT. (2024) Food and Agriculture Organization of the United Nations FAOSTAT website. http://www.fao.org/faostat/en/#data/QC Accessed 21 February 2024.

Frimpong-Anin, K., Adjaloo, M. K., Kwapong, P. K., and Oduro, W. (2014) Structure and Stability of Cocoa Flowers and Their Response to Pollination. *Journal of Botany* **2014**, 6.

Grohs, H., Grumiller, J., and Peham, A. (2023) Potentials for improving the socioeconomic situation of Ghanaian cocoa farmers: The role of sustainability initiatives, ÖFSE, Austrian Foundation for Development Research.

Hawkins, J. W., Gallagher, E. J., van der Haar, S., Sevor, M. K., Weng, X., Rufino, M. C., and Schoneveld, G. C. (2024) Low-emissions and profitable cocoa through moderate-shade agroforestry: Insights from Ghana. *Agriculture, Ecosystems & Environment* **367**, 108961.

Herbas, L. J. Z., Cartagena, I. L., Naoki, K., and Armengot, L. (2020) Variación en la composición de visitantes florales de cacao (Theobroma cacao) entre cinco sistemas de producción en Sara Ana, Alto Beni, Bolivia. *Ecología En Bolivia: Revista Del Instituto de Ecología* **55**(3), 145–159.

Hernández-Nuñez, H. E., Suárez, J. C., Andrade, H. J., Acosta, J. R. S., Núñez, R. D., Gutiérrez, D. R., Gutiérrez, G. A., Gutiérrez-Montes, I., and Casanoves, F. (2024) Interactions between climate, shade canopy characteristics and cocoa production in Colombia. *Frontiers in Sustainable Food Systems* **8**, 1295992.

Higonnet, E., Bellantonio, M., and Hurowitz, G. (2017) Chocolate's dark secret. *Mighty Earth* 24.

Jaimes-Suárez, Y. Y., Carvajal-Rivera, A. S., Galvis-Neira, D. A., Carvalho, F. E., and Rojas-Molina, J. (2022) Cacao agroforestry systems beyond the stigmas: Biotic and abiotic stress incidence impact. *Frontiers in Plant Science* **13**, 921469.

Kouassi, A. K., Zo-Bi, I. C., Aussenac, R., Kouamé, I. K., Dago, M. R., N'guessan, A. E., Jagoret, P., and Hérault, B. (2023) The great mistake of plantation programs in cocoa agroforests – let's bet on natural regeneration to sustainably provide timber wood. *Trees, Forests and People* **12**, 100386

Lescuyer, G., and Bassanaga, S. (2021) Positive influence of certification on the financial performance of cocoa production models in Cameroon. *Frontiers in Sustainable Food Systems* **5**, 743079. doi: 10.3389/fsufs.2021.743079

Melnick, R. L. (2016) Cherelle wilt of cacao: a physiological condition. In *Cacao Diseases: A History of Old Enemies and New Encounters* pp. 483–499.

Morales-Belpaire, I., Alfaro-Flores, A., Losantos-Ramos, K., Palabral-Velarde, O., Amurrio-Ordoñez, P., and Armengot, L. (2024) Soil quality indicators under five different cacao production systems and fallow in Alto Beni, Bolivia. *Agroforestry Systems* **98**, 2517–2532.

Mortimer, R., Saj, S., and David, C. (2018) Supporting and regulating ecosystem services in cacao agroforestry systems. *Agroforestry Systems* **92**(6), 1639–1657.

Moser, G., Ch Leuschner, D. Hertel, D. Hölscher, M. Köhler, D. Leitner, B. Michalzik, E. Prihastanti, S. Tjitrosemito, Schwendenmann, L. (2010) Response of cocoa trees (Theobroma cacao) to a 13-month desiccation period in Sulawesi, Indonesia. *Agroforestry Systems* **79**(2), 171–187.

Mossu, G. (1990) *Le cacaoyer*, Maisonneuve et Larose, Paris, France.

Niether, W., Armengot, L., Andres, C., Schneider, M., and Gerold, G. (2018) Shade trees and tree pruning alter throughfall and microclimate in cocoa (Theobroma cacao L.) production systems. *Annals of Forest Science* **75**(2), 38.

Niether, W., Jacobi, J., Blaser, W. J., Andres, C., and Armengot, L. (2020) Cocoa agroforestry systems versus monocultures: a multi-dimensional meta-analysis. *Environmental Research Letters* **15**(10), 104085.

Niether, W., Schneidewind, U., Armengot, L., Adamtey, N., Schneider, M., and Gerold, G. (2017) Spatial-temporal soil moisture dynamics under different cocoa production systems. *CATENA* **158**, 340–349.

Orozco-Aguilar, L., Lopez-Sampson, A., Cerda, R.H., Casanoves, F., Ramirez-Argueta, O., Diaz Matute, J., Suárez Salazar, J.C., Rüegg, J., Saj, S., Milz, J., Schneidewind, U., Mora Garces, A., Baez Daza, E., Rojas Molina, J., Jaimes Suarez, Y., Agudelo-Castañeda, G.A., Deheuvels, O., Brito Sosa, E., Gómez, J.H., Jaimez, R.E., Reyes Espinoza, S., Bordeaux, M., Caicedo Vargas, C., Tinoco, L., Peña Monserrate, G., Perez Flores, J., Azpeitia Morales, A., Arevalo-Hernandez, C.O., Arevalo Gardini, E., Pocasangre, L.E., Araque, O., Koutouleas, A., Segura Magaña, E., Dominguez, O., Arenas, P., Sotopinto, L., Salgado-Mora, M., Gama-Rodrigues, A., Gama-Rodrigues, E., Holder, A., Ramtahal, G., Umaharan, P., Muller, M.W., Texeira Mendes, F., and Somarriba, E. (2024) CacaoFIT: the network of cacao field trials in Latin America and its contribution to sustainable cacao farming in the region. *Frontiers in Sustainable Food Systems* **8**, 1370275.

Rapidel, B., Le Coq, J. F., DeClerck, F. A. J., and Beer, J. (2011) Measurement and payment for ecosystem services from agriculture and agroforestry : new insights from the Neotropics. In Rapidel B., Le Coq J. F., DeClerck F. A. J., and Beer J., (eds.), *Ecosystem Services from Agriculture and Agroforestry: Measurement and Payment*, London, UK: Earthscan, pp. 377–396.

Restrepo, J. P. G., Leiva-Rojas, E. I., and Pisco, R. R. (2017) Phenology of cocoa tree in a tropical moist forest. *Científica* **45**(3), 240–252.

Saj, S., Durot, C., Mvondo-Sakouma, K., Tayo Gamo, K., and Avana-Tientcheu, M.-L. (2017a) Contribution of associated trees to long-term species conservation, carbon storage and sustainability: a functional analysis of tree communities in cacao plantations of Central Cameroon. *International Journal of Agricultural Sustainability* **15**(3), 282–302.

Saj, S., Jagoret, P., Etoa, L. E., Fonkeng, E. E., Tarla, J. N., Nieboukaho, J. D. E., and Sakouma, K. M. (2017b) Lessons learned from the long-term analysis of cacao yield and stand structure in central Cameroonian agroforestry systems. *Agricultural Systems* **156**, 95–104.

Sale, P. (1969) Extension growth of cacao under controlled temperature conditions. *Journal of Horticultural Science* **44**(2), 189–193.

Sale, P. (1970) Growth, flowering and fruiting of cacao under controlled soil moisture conditions. *Journal of Horticultural Science* **45**(2), 99–118.

Schneider, M., Andres C., Trujillo G., Alcon F., Amurrio P., Perez E., Weibel F., Milz, J. (2016) Cocoa and total system yields of organic and conventional agroforestry vs. monoculture systems in a long-term field trial in Bolivia. *Experimental Agriculture* 1–24.

Somarriba, E., and López Sampson, A. (2018) Coffee and cocoa agroforestry systems: pathways to deforestation, reforestation, and tree cover change. In: *Leveraging Agricultural Value Chains to Enhance Tropical Tree Cover and Slow Deforestation, LEAVES, Program on Forests (PROFOR)*, The World Bank. Washington, DC, USA. p. 51.

Somarriba, E., Saj, S., Orozco-Aguilar, L., Somarriba, A., and Rapidel, B. (2024) Shade canopy density variables in cocoa and coffee agroforestry systems. *Agroforestry Systems* **98**(3), 585–601

Suárez Salazar, J. C., Melgarejo, L. M., Casanoves, F., Di Rienzo, J. A., DaMatta, F. M., and Armas, C. (2018a) Photosynthesis limitations in cacao leaves under different agroforestry systems in the Colombian Amazon. *PLoS ONE* **13**(11), e0206149.

Suárez Salazar, J. C., Ngo Bieng, M. A., Melgarejo, L. M., Di Rienzo, J. A., and Casanoves, F. (2018b) First typology of cacao (Theobroma cacao L.) systems in Colombian Amazonia, based on tree species richness, canopy structure and light availability. *PLoS ONE* **13**(2), e0191003.

Valle, R. R., De Almeida, A.-A. F., and De O. Leite, R. M. (1990) Energy costs of flowering, fruiting, and cherelle wilt in cacao. *Tree Physiology* **6**(3), 329–336.

Vervuurt, W., Slingerland, M. A., Pronk, A. A., and Van Bussel, L. G. J. (2022) Modelling greenhouse gas emissions of cacao production in the republic of Côte d'Ivoire. *Agroforestry Systems* **96**(2), 417–434.

Wade, A. S. I., Asase, A., Hadley, P., . . . Norris, K. (2010) Management strategies for maximizing carbon storage and tree species diversity in cocoa-growing landscapes. *Agriculture, Ecosystems & Environment* **138**(3–4), 324–334.

Wibaux, T., Normand, F., Vezy, R., Durand, J.-B., and Lauri, P.-É. (2024) Does seasonal flowering and fruiting patterns of cacao only depend on climatic factors? The case study of mixed genotype populations in Côte d'Ivoire. *Scientia Horticulturae* **337**, 113529.

Wilson, P. J., Thompson, K., and Hodgson, J. G. (1999) Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist* **143**(1), 155–162.

Wood, G. A. R., and Lass, R. A. (2001) *Cocoa. Fourth edition.*, London: Longman.

Zarrillo, S., Gaikwad, N., Lanaud, C., Powis, T., Viot, C., Lesur, I., Fouet, O., Argout, X., Guichoux, E., Salin, F., Solorzano, R.L., Bouchez, O., Vignes, H., Severts, P., Hurtado, J., Yepez, A., Grivetti, L., Blake, M., and Valdez, F. (2018) The use and domestication of Theobroma cacao during the mid-Holocene in the upper Amazon. *Nature Ecology and Evolution* **2**(12), 1879–1888.

Zuidema, P. A., Leffelaar, P. A., Gerritsma, W., Mommer, L., and Anten, N. P. R. (2005) A physiological production model for cocoa (Theobroma cacao): model presentation, validation and application. *Agricultural Systems* **84**(2), 195–225.

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