Shade tree functional traits and their impact on cocoa yields across a gradient in environmental conditions in Cote d'Ivoire and Ghana

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MSc Thesis, Plant Production System

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Contact: office.pps@wur.nl for access to data, models and scripts used for the analysis.

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Summary

Cocoa (*Theobroma cacao* L.) is an understory plant often grown in agroforestry systems, where shade trees may help regulate the microclimate and enhance soil fertility. However, understanding how shade trees and their functional traits influence ecosystem services in cocoa systems remains crucial for optimizing agroforestry. This study analyses the relationships between shade tree density, shade tree functional traits, and cocoa yield across varying environmental conditions in Cote d'Ivoire and Ghana. Our dataset combines field measurements across 87 farms, with functional trait data from the TRY Plant Trait Database, climate variables from WorldClim, and soil properties from ISRIC SoilGrids. Using mixed-effects models, we examine (1) how environmental conditions influence the variation in shade levels and shade tree functional traits, (2) the effects of shade levels and shade tree traits on cocoa yield, and (3) whether these environmental factors modify the impact of shade levels and shade tree traits on cocoa yield.

Although shade tree density did not significantly vary with environmental conditions, our findings suggest that environmental conditions influence the variation in functional traits of shade trees. The shade tree species in the study area are planted by farmers. In drier conditions, shade tree communities were dominated by species with higher wood density, lower specific leaf area (SLA), and shorter tree height likely as an adaptation to water limitation. Conversely, species with lower wood density, higher SLA, and greater tree height dominated in wetter conditions. We also found that high shade tree density reduced cocoa yield, possibly due to increased competition for light and water.

Our results also revealed that environmental conditions modified the effect of shade on cocoa yield. In dry conditions, a higher shade tree basal area positively influenced cocoa yield by reducing drought stress. We also show that cocoa yield was highest with low shade tree wood density under high precipitation seasonality.

These findings emphasize the importance of shade tree selection and management strategies that integrate environmental conditions and functional traits for sustainable cocoa agroforestry.

Keywords: Cocoa agroforestry, shade tree functional traits, environmental conditions, mixed-effects models, Ghana, Cote d'Ivoire.

1. Introduction

Cocoa is a tropical understorey tree originating from Latin America that has become one of the leading agricultural commodities (Afoakwa, 2016). Currently, Cote d'Ivoire and Ghana are the two largest global cocoa producers (*Theobroma cacao* L.), with a market share of 60% of total world cocoa production (Daymond et al., 2022). Despite this significant market share, cocoa productivity on smallholder farms remains low, with average yields of only 300-600 kg ha^{-1} (Asante et al., 2021; Wessel & Quist-Wessel, 2015). The low yield is caused by several factors, such as the old age of cocoa farms, lack of soil nutrients, diseased trees, and climate change (Wessel & Quist-Wessel, 2015).

Climate change is a global threat that negatively impacts the agricultural sector (File et al., 2023; Ogunyiola et al., 2022). One of the primary consequences of climate change is the alteration of temperature and rainfall patterns. Trisos et al. (2022) projected that a 2°C increase in global warming would expose West Africa to a drier, more drought-prone, climate. As a result, the regions suitable for cocoa production may shift from Ghana and Cote d'Ivoire towards the eastern countries of Africa, such as Nigeria and Cameroon, while cocoa production within Ghana and Cote d'Ivoire may become more constrained to the southern areas (Asante et al., 2025). Climate change poses a significant risk of disrupting optimal growing conditions for cocoa (Afele et al., 2024). The main impact is expected on smallholder rainfed systems in the tropics, which currently produce about 95% of the world's cocoa (Daymond et al., 2022).

To ensure the sustainability of cocoa production under these changing conditions, effective land management strategies are required. One promising approach is agroforestry, where shade trees are incorporated into cocoa farms to mitigate environmental stress. There has been a concerted effort to promote the inclusion of shade trees in cocoa cultivation to sustain cocoa yield (Addo-Danso et al., 2024; Asare & David, 2011).

1.1. Cocoa agroforestry and its benefits

Agroforestry systems are integrated land-use systems that combine tree and annual or perennial crops in spatial arrangement or temporal sequence (Lorenz & Lal, 2018). When farmers select shade trees for cocoa agroforestry systems, they will prioritize specific ecosystem services or benefits provided by the trees (Kaba et al., 2020). In addition to reducing sunlight intensity, shade trees regulate microclimate (temperature and humidity) and improve environmental quality by improving soil nutrition by adding organic matter (Isaac et al., 2024). Including shade trees can also increase environmental resistance to pests and diseases such as mirid pests (Asitoakor et al., 2024). Moreover, agroforests are believed to contribute to climate change mitigation through increased carbon sequestration while also maintaining the diversity of associated species (Blaser et al., 2018). In some cases, shade trees can also provide income as a cash crop, through fruit production, or provide timber (Braga et al., 2019). In Ghana, tree species such as *Morinda lucida*, *Milicia* spp., and *Terminalia* spp. are the most prevalent shade trees in cocoa plantations (Kyereh, 2017). In Cote d'Ivoire, there are 176 plant species utilized by farmers as shade trees, which provide

additional products such as food sources, medicine, firewood, and other products (Yves et al., 2015).

Cocoa is a shade-tolerant crop and naturally grows under shade. A shade level of less than 30% has been found to not interfere with cocoa production (Blaser et al., 2018). The microclimatic conditions beneath shaded areas in agroforestry systems often align with the needs of cacao trees, making these areas favorable for cacao cultivation (Ramos et al., 2024). Cocoa agroforestry systems can moderate temperature, humidity, and reduce sun exposure (Konaté et al., 2024). Yield reductions with increasing shade tree cover are likely to occur as a consequence of competition for light, water, and nutrients (Blaser et al., 2018). The optimal density of shade trees may differ across environmental gradients. In drier conditions, where water availability is limited, moderate shade can help reduce heat stress by regulating the microclimate (Ramos et al., 2024). However, too much shade in such conditions may still reduce yield due to competition for light and water. In wetter conditions, where water is abundant, shade helps maintain suitable microclimatic conditions for cacao cultivation, but excessive shade could increase disease risk. Therefore, maintaining an optimal level of shade is essential for sustaining cocoa yield in agroforestry systems.

The impact of shade trees on cocoa can vary based on the traits of the shade trees. Tree functional traits include all morphological, anatomical, physiological, and phenotypic characteristics that can be measured at the individual plant level (Isaac et al., 2024; Kumar, 2024). In agroforestry systems, the functional traits of trees can be used to select and manage shade trees (Isaac et al., 2024), based on their ecological functions and benefits. For example, a shade tree canopy can affect rainfall dynamics in cocoa plantations (Isaac et al., 2024; Li et al., 2019; Nakamura et al., 2017). A canopy with a high leaf area index (LAI) can reduce throughfall amounts and increase throughfall kinetic energy (TKE) (Isaac et al., 2024). These interactions with rainfall dynamics have larger implications, as high TKE can create splash erosion of bare soils and pathogen dispersal from infected surfaces (Isaac et al., 2024).

Other key functional traits also play significant roles in shaping the microclimate of the agroforestry system. Specific leaf area (SLA) represents the ratio of leaf surface area to its dry weight, influencing light capture and photosynthetic efficiency. SLA serves as microclimate moderation where a buffered microclimate is favorable for litter decomposition throughout the year (Isaac et al., 2024). Wood density, a measure of wood mass per unit volume, has a positive function as drought resistance, with denser wood often associated with slower growth but greater water retention capacity. In addition, leaf habit also plays an important role in cocoa agroforestry systems. There are generally two types of trees: evergreen trees that retain their foliage throughout the year and deciduous trees that shed their leaves during the dry season. Shade tree species classified as complete deciduous trees during the dry season have been shown to positively influence soil moisture and microclimatic conditions, leading to improved cacao physiological functions and higher productivity (Abdulai et al., 2025). Lastly, leaf nitrogen (Leaf N) content reflects a tree's nutrient status and its role in soil nutrient cycling (Isaac et al., 2024). Higher leaf N content may enhance nitrogen cycling in the agroforestry system.

Given their potential importance, it is essential to understand which specific shade tree traits best support cocoa yield. There is a need to understand how the functional traits of shade trees affect cocoa yield. A functional trait-based approach helps to determine the suitability of a species and its benefits in cocoa agroforestry systems.

1.2. Research objectives

This study aims to analyze the effect of shade trees and functional traits of shade trees on cocoa yield in Ghana and Cote d'Ivoire (Figure 1). This study will determine whether environmental conditions such as temperature, precipitation, and soil property influence the variations of shade level and shade tree traits. This study also examines whether environmental conditions modify the effect of shade and shade tree traits on cocoa yield. The following research questions will be addressed:

1. How do shade tree density and functional traits vary with environmental conditions?
   Hypothesis: In dry conditions (low rainfall and high temperatures), shade tree density is expected to be lower to minimize competition for limited water resources. Shade tree species with high wood density are more likely to dominate in these conditions, as this trait enhances water retention and drought resilience. Specific leaf area (SLA) is expected to be lower in dry environments due to tree adaptation to environmental stress. Additionally, in conditions with high cation exchange capacity (CEC), shade tree communities are expected to be dominated by taller species with higher SLA.
2. What are the effects of shade levels and shade tree traits on cocoa yield?
   Hypothesis: High shade tree density will reduce cocoa yield because of competition for light and water. However, shade trees with low SLA and high wood density can reduce competition for water because they tend to have slower growth rates and more conservative water use strategies, potentially benefiting cocoa yield.
3. Do environmental conditions alter the effects of shade levels and shade tree traits on cocoa yield?
   Hypothesis: The effect of shade on cocoa yield is expected to change with environmental conditions. In dry conditions, characterized by high temperatures and low rainfall, shade can have positive effects by reducing heat stress. On the contrary, in wet conditions with high rainfall, shade may negatively affect cocoa yield by competing for light and creating a more favorable microclimate for diseases.

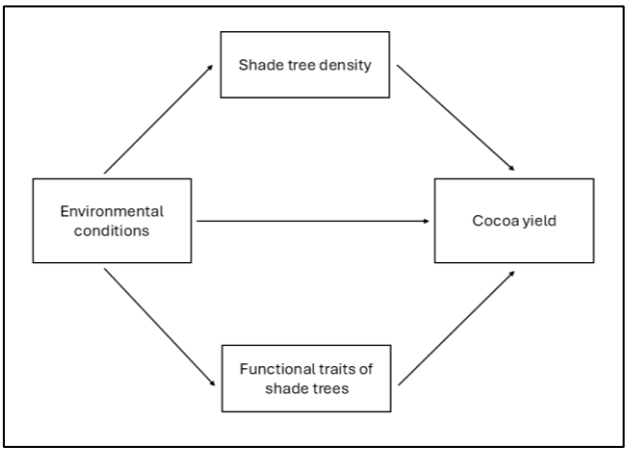

Figure 1 Conceptual model of the study

2. Material and Methods

2.1. Study site

This study was conducted in two West African countries, Cote d'Ivoire and Ghana. The regions covered in this research included three in Cote d'Ivoire (Sassandra-Marahoue, Bas-Sassandra, Goh-Djiboua) and five in Ghana (Ashanti, Western, Brong Ahafo, Central, and Eastern; Figure 2). These locations were chosen due to the high dependence of people on cocoa farming and the presence of a variety of shade trees on the farms. The shade tree species consists of a mix of deciduous and evergreen tree species, which may influence the microclimate and resource availability for cocoa. The study was conducted in plots established within the CocoaSoils Satellite Trial sites, where different treatments were applied (Vasquez-Zambrano et al., 2025).

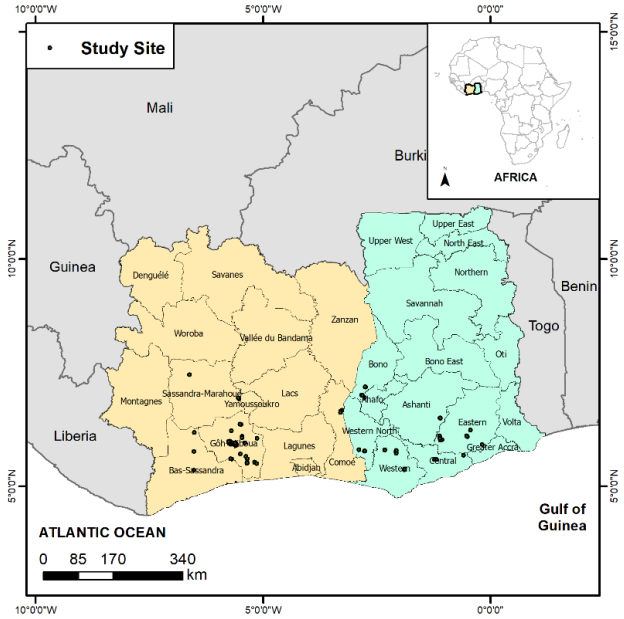

Figure 2 Distribution of research farms in Cote d'Ivoire and Ghana.

Both countries have a tropical climate with two distinct seasons. The rainy seasons occur from April to June and September to October, whereas the dry seasons extend from August to September and December through February (Afele et al., 2024). Annual rainfall in the region ranges from 1180 to 1720 mm, and average temperatures are between 24°C and 27°C throughout the year (Table 2). Additionally, the cation exchange capacity (CEC) ranges from 9.63 to 47.70 cmol (c) kg^{-1} (Table 2), indicating considerable variation in the capacity of the soil to retain and exchange nutrients.

Table 1 Environmental conditions in the cocoa agroforestry systems

Environmental variable	Unit	Mean ± S.E.	Minimum – Maximum
Annual temperature	ºC	25.92 ± 0.02	24.47 – 26.79
Annual precipitation	mm $year^{-1}$	1344.14 ± 8.84	1180 – 1719.00
Precipitation seasonality	-	54.79 ± 0.34	47.48 – 70.41
Cation exchange capacity	cmol(c) kg^{-1}	21.27 ± 0.47	9.63 – 47.70

Source: WorldClim (Fick & Hijmans, 2017).

2.2. Plot data

Data were collected to examine the effects of shade trees and their functional traits on cocoa yield under varying environmental conditions in agroforestry systems. The shade tree data collection in Ghana was conducted from March to April 2022, covering 38 farms across 24 villages. In Cote d'Ivoire, data collection took place from March to April 2023, including 49 farms across 25 villages. Per farm, four plots of 21 m x 21 m were established, resulting in a total of 313 plots surveyed across the two countries. In each plot, the diameter at breast height (DBH, measured in cm) of shade trees was measured at 1.3 meters from the ground. The height of shade trees was estimated. DBH was used to calculate the basal area of each tree using the following formula (Equation 1):

$$\text{Basal area } (\text{m}^2) = \pi \times \left(\frac{\text{DBH (cm)}}{200} \right)^2$$

The total basal area per plot was calculated as the sum of the basal area of all trees within the same plot. Tree density (the number of trees per ha) was calculated based on the number of trees recorded per plot. Both basal area and tree density were used as indicators of the level of shade in the plot. Cocoa yield data were obtained from these plots in 2022. The yield represents the total annual harvest of cocoa beans per plot, measured in kg ha^{-1} $year^{-1}$.

2.3. Functional trait data

To assess the potential effects of shade tree functional traits on cocoa yield, trait data for the shade tree species were obtained from the TRY Plant Trait Database (Kattge et al., 2020). This data included wood density (g cm^{-3}), specific leaf area (SLA, cm^2g^{-1}), nitrogen fixation, leaf habit (deciduous vs. evergreen), maximum tree height (m), and leaf nitrogen (leaf N, %). If multiple trait values were available for a species, then the mean values were calculated for traits with numeric values (such as wood density, SLA, leaf N, and maximum tree height), while categorical traits (such as leaf habit and nitrogen fixation) were summarized by aligning categories. For species with missing functional trait data, trait data at the genus level were included. Additional data were sourced from the Global Wood Density Database (Chave et al., 2009) for trees with unknown wood density in the TRY database.

2.4. Environmental data

Climate and soil characteristics data were obtained for each of the farms to account for environmental variability in cocoa agroforestry systems. Environmental data was extracted using the geographic coordinates of each farm. Climate data including maximum temperature (°C), minimum temperature (°C), annual mean temperature (°C), annual precipitation (mm $year^{-1}$), precipitation in the wettest month (mm), precipitation in the driest month (mm), and precipitation seasonality were obtained from the WorldClim database at a spatial resolution of approximately 1 km^2 (Fick & Hijmans, 2017). Soil properties were obtained from the ISRIC/SoilGrids database at a spatial resolution of 250 m (Hengl et al., 2017). The soil variables collected included cation exchange capacity (CEC, cmol(c) kg^{-1}), soil pH, soil organic carbon (SOC, %), total nitrogen (N, %), silt content (%), clay content (%), and sand content (%).

Climate data from WorldClim were accessed using the raster package in R (Hijmans et al., 2005). Soil properties from SoilGrids were obtained through the SoilGrids web interface and processed in R.

2.5. Statistical analysis

All data analyses were performed using R software (version 4.3.1). To account for differences in species abundance, functional traits of shade tree species were calculated at the community level for each plot through the Community Weighted Mean (CWM) (Equation 2):

$$\mathrm{CWM} = \sum_{i=1}^{N} bixi$$

Where *bi* is the relative biomass of the *i*- species, *xi* is the i- species trait value, and N is the total number of species observed in the plot. These CWM values represent the trait metrics used in the model analysis.

Prior to model fitting, all predictors were standardized by subtracting the mean and dividing by the standard deviation to improve numerical stability and facilitate effect size comparability. Pairwise correlations between variables were examined to identify potential multicollinearity issues. Variables with strong correlations (Pearson's $|r| > 0.6$) were not included in the same model to reduce redundancy. For example, tree density and basal area were strongly correlated, so they were included in separate models. Similarly, annual temperature was highly correlated with maximum temperature, and therefore only annual temperature was retained for the analysis. The final set of variables included annual temperature, annual precipitation, precipitation seasonality, and cation exchange capacity (CEC) as environmental predictors, and tree density, basal area, wood density (g cm^{-3}), specific leaf area (SLA, cm^2 g^{-1}), maximum tree height (m), leaf nitrogen content (leaf N, %), nitrogen fixation ability, and leaf habit as shade-related predictors.

First, mixed-effects models were fitted to assess how environmental conditions influenced variation in shade levels and shade tree functional traits, with environmental variables as fixed effects and farm as a random effect. Second, mixed-effects models were used to evaluate the effects of shade levels (tree density and basal area) and (shade) functional traits on cocoa yield. These shade-related variables were included as fixed effects, with the farm again treated as a random effect.

Next, to determine whether environmental conditions modified the effects of shade trees on cocoa yield, additional models were fitted that included interaction terms between environmental variables and shade levels and shade tree traits. Specifically, interactions were tested between (1) environmental variables (annual precipitation and precipitation seasonality) and shade intensity (tree density and basal area), and (2) environmental variables and functional traits (wood density, SLA, maximum tree height, leaf N, nitrogen fixation, and leaf habit). These analyses allowed us to assess whether the influence of shade trees on cocoa yield varied across different environmental contexts.

3. Results

3.1. The effect of environmental conditions on shade levels and shade tree traits

In this section, we examined whether shade levels and shade tree traits varied with environmental conditions such as temperature, precipitation, and soil properties. The shade tree composition consisted of a total of 1092 individuals from 108 different species (Table S1, Appendix). The dominant tree species were *Persea americana* (8.6%), *Morinda lucida* (7.2%), *Terminalia superba* (7.0%), and *Terminalia ivorensis* (6.0%). Some other species, such as *Citrus sinensis*, *Elaeis guineensis*, *Coffea arabica*, and *Mangifera indica*, each contributed about 5% to the total number of shade trees. Furthermore, more than 100 other tree species accounted for less than 3% of the total number of tree species.

Shade tree density ranged from 22 to 498 trees per hectare, while basal area varied between 0.01 and 60 m² per hectare. Shade levels in this cocoa agroforestry system did not vary with precipitation, temperature, or precipitation seasonality, thus showing no variation along the climate gradient. However, soil properties, such as cation exchange capacity (CEC), had a significant negative effect on basal area (Figure 3b), while tree density remained unchanged (Figure 3a).

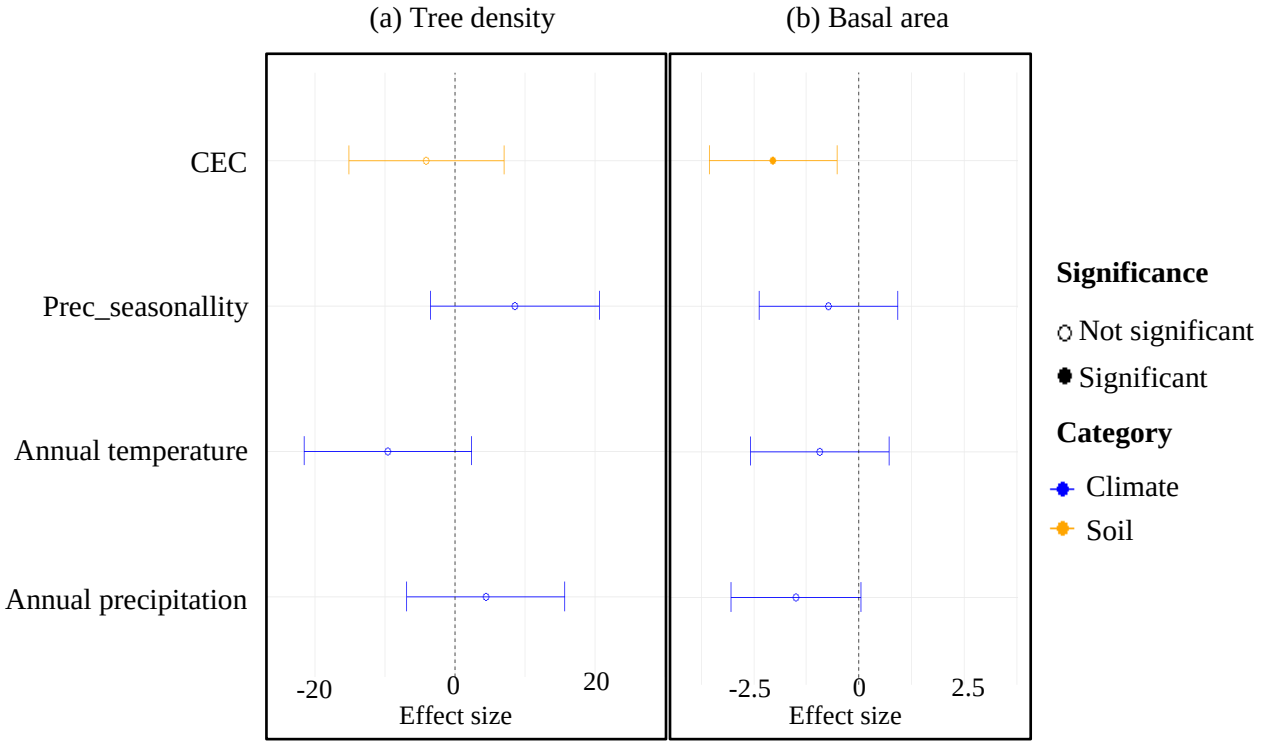

Figure 3 The effect of environmental conditions on (a) tree density and (b) basal area, based on results from a mixed-effects model.

To assess the variation in shade tree functional traits, the shade tree traits were summarised as Community Weighted Means (CWM) (Table 2). Several functional traits showed large variation, including CWM wood density with values of 0.28 – 0.78 g cm^{-3}, SLA of 7.58 – 43.73 cm^2 g^{-1}, and maximum tree height ranging from 2.01 – 45 m. The abundance of nitrogen-fixing trees was low, and evergreen species dominated the tree community.

Table 2 Community weighted mean

CWM of variable	Mean ± S.E.	Min – Max	CI of mean
Wood density (g cm^{-3})	0.51 ± 0.005	0.28 – 0.78	0.50 – 0.522
SLA (cm^2 g^{-1})	16.30 ± 0.29	7.58 – 43.73	15.72 – 16.89
Nitrogen fixation	0.04 ± 0.03	0 – 1	0.02 – 0.05
Maximum tree height (m)	21.72 ± 0.62	2.01 – 45	20.50 – 22.93
Leaf habit	0.69 ± 0.02	0 – 1	0.65 – 0.73
Leaf N (%)	24.54 ± 0.23	13.53 – 36.68	24.08– 25.00

Remarks: For nitrogen fixation, 0 = non-fixing, 1 = fixing. For leaf habit, 0 = deciduous, 1 = evergreen.

Environmental variables such as annual precipitation and CEC significantly influenced several functional traits of shade trees (Figure 5). The analysis shows that annual precipitation has a significant negative effect on wood density. This indicates that in dry conditions, high wood density species dominate (Figure 4a). On the other hand, annual precipitation had a positive effect on SLA and maximum tree height, which indicates that in wet conditions species with thinner leaves (high SLA) and taller trees dominate (Figures 4b and 4c). The level of cation exchange capacity (CEC) also influenced shade tree functional traits. High CEC had a positive impact on SLA and maximum tree height (Figures 6a and 6b). In contrast, CEC had a negative relationship with tree leaf habit (Figure 6c). This finding shows that plots with high CEC tended to have species that are thin-leaved (high SLA), grow taller, and are dominated by deciduous species.

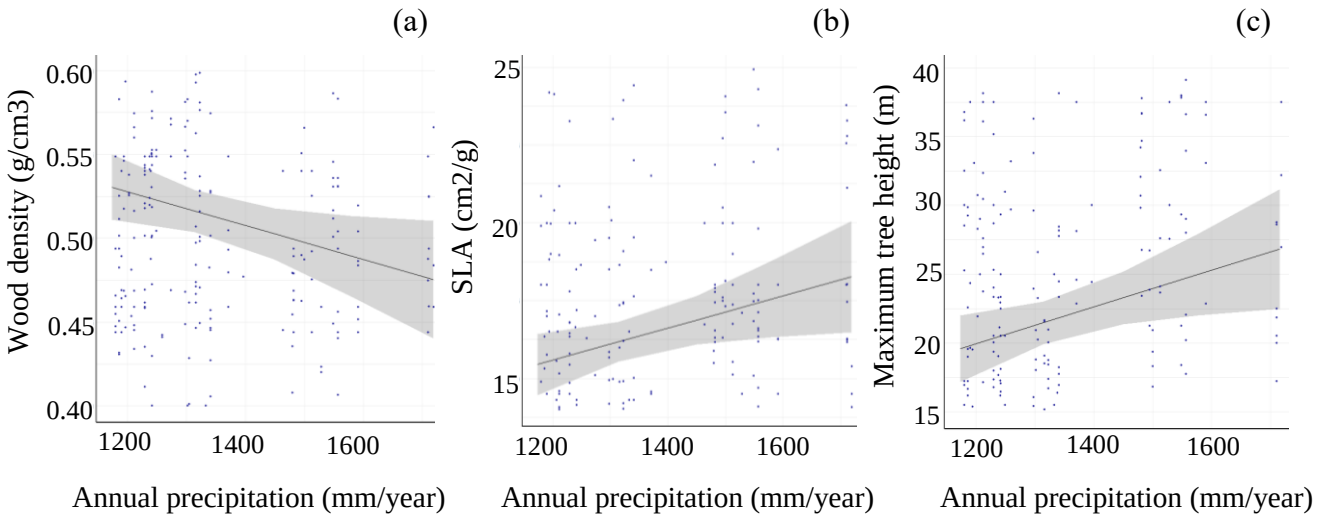

Figure 4 Relationship between annual precipitation and (a) wood density, (b) specific leaf area, and (c) maximum tree height. The data points represent the Community Weighted Mean values of traits per plot. The lines indicate the predicted effects of annual precipitation on each trait based on a linear mixed-effects model, with other predictors kept constant at the mean.

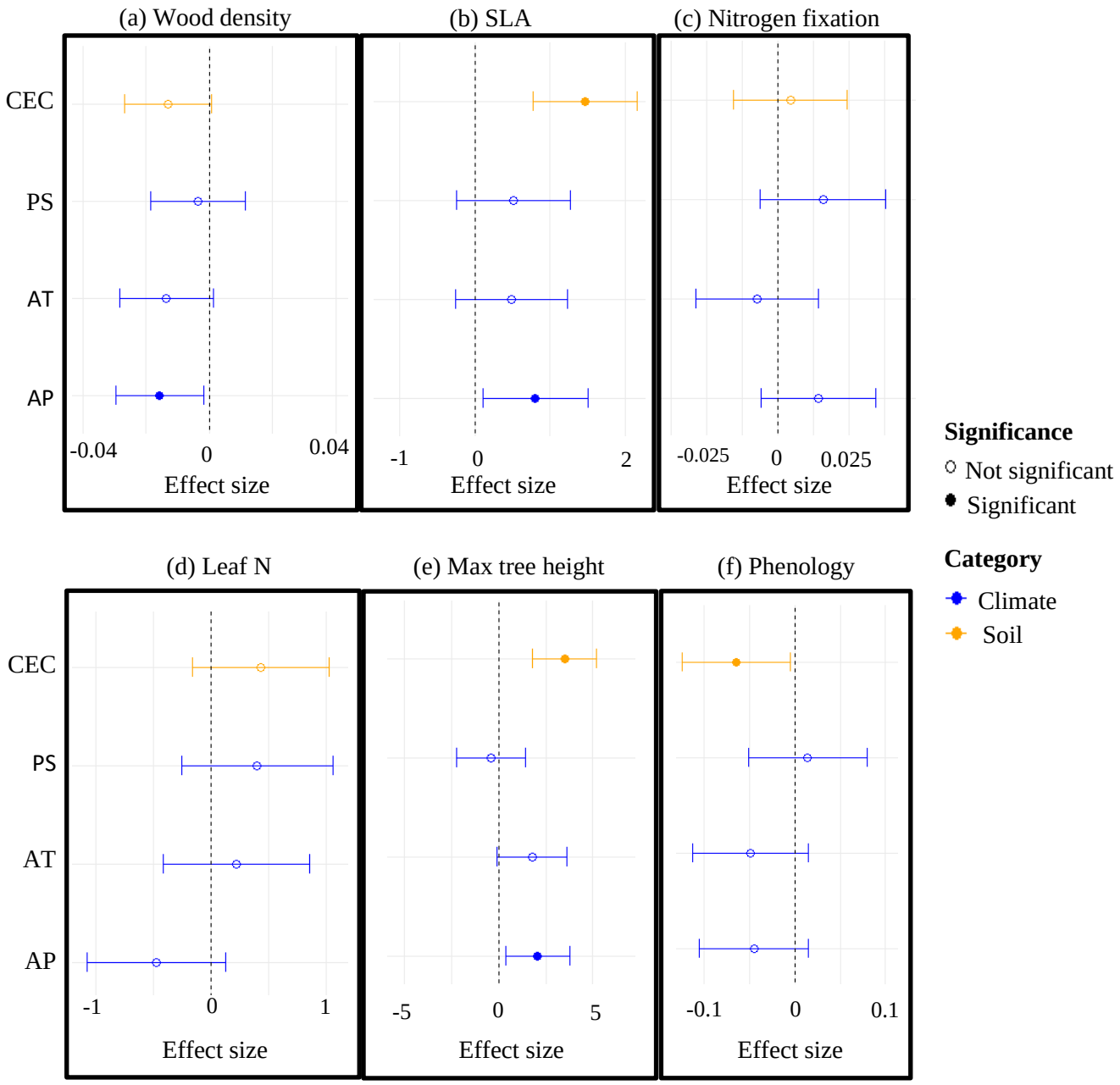

Figure 5 The effect of environmental conditions on (a) wood density, (b) specific leaf area, (c) nitrogen fixation, (d) leaf nitrogen content, (e) maximum tree height, and (f) leaf habit, based on results from a mixed-effects model. CEC: Cation exchange capacity (cmol(c) kg^{-1}), PS: precipitation seasonality, AT: Annual temperature (°C), AP: Annual precipitation (mm $year^{-1}$).

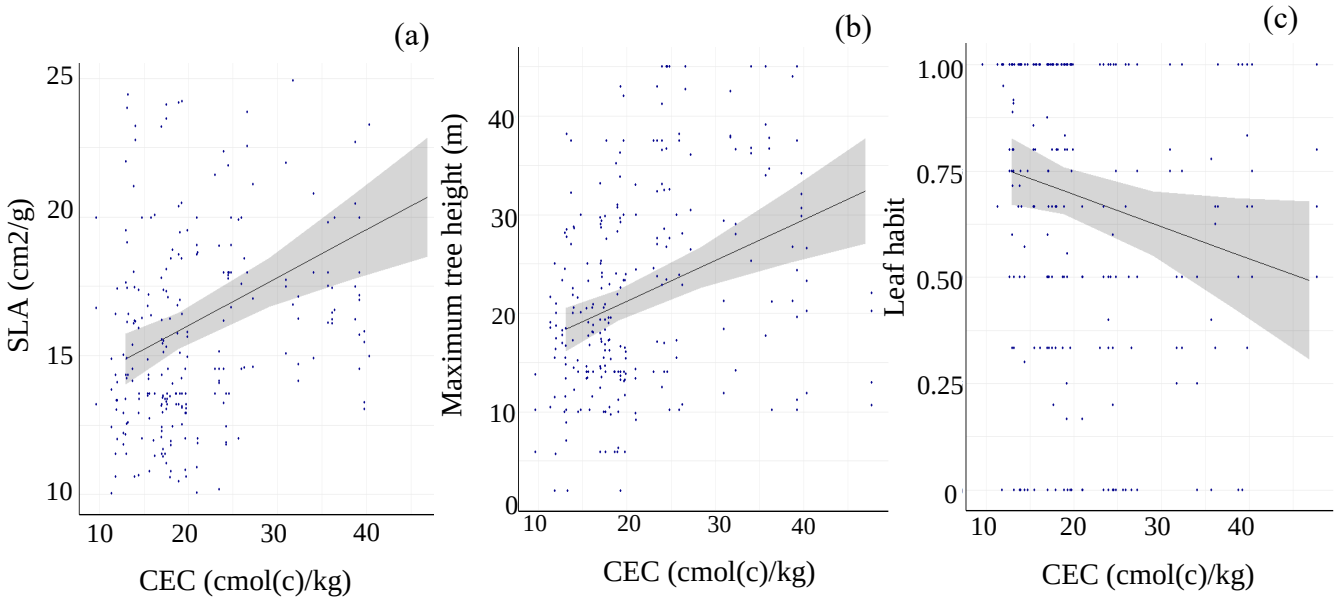

Figure 6 Relationship between CEC and (a) specific leaf area, (b) maximum tree height, and (c) leaf habit. For leaf habit, 0 = deciduous, 1 = evergreen. The data points represent the Community Weighted Mean (CWM) values of traits per plot. The lines indicate the predicted effects of CEC on each trait based on a linear mixed-effects model, with other predictors kept constant at the mean.

3.2. Effects of shade and shade tree traits on cocoa yield

This section aims to analyze the effect of shade trees and their functional traits on cocoa yield. We used mixed-effects models to examine the relationships between shade tree variables and cocoa yield. The analysis revealed that shade tree density significantly affected annual cocoa yield (Figure 7), with higher tree density associated with a reduction in cocoa yield (Figure 8). Additionally, when the basal area was included in a separate model, it showed no significant effect on annual cocoa yield (Figure A1, Appendix). Variations in basal area across plots did not correspond to changes in cocoa yield (Figure 9).

Next, the results showed that none of all functional traits tested had a significant relationship with cocoa yield (Figure 7, 10). This indicates that functional traits of shade trees such as wood density, specific leaf area (SLA), nitrogen fixation ability, leaf nitrogen (leaf N), maximum tree height and leaf habit are not the factors that determine yield outcomes in these agroforestry systems.

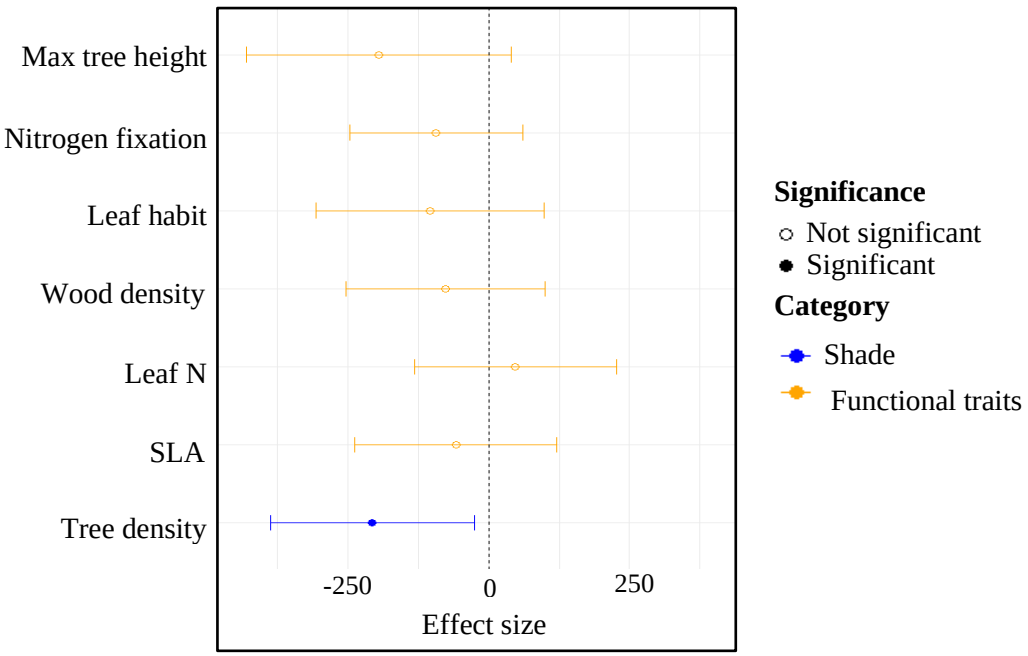

Figure 7 The effect of shade and functional traits on cocoa yield. SLA: Specific leaf area; Leaf N: Leaf nitrogen content; Max tree height: Maximum tree height. Results are based on a mixed-effects model.

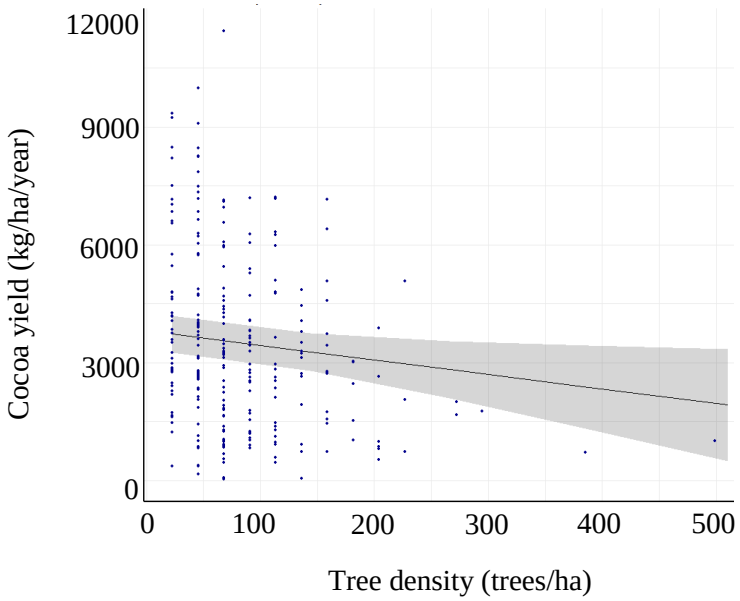

Figure 8 Relationship between cocoa yield and tree density. The data points represent the annual cocoa yield per plot. The line indicates the predicted effect of tree density on cocoa yield based on a linear mixed-effects model, with other predictors kept constant at the mean.

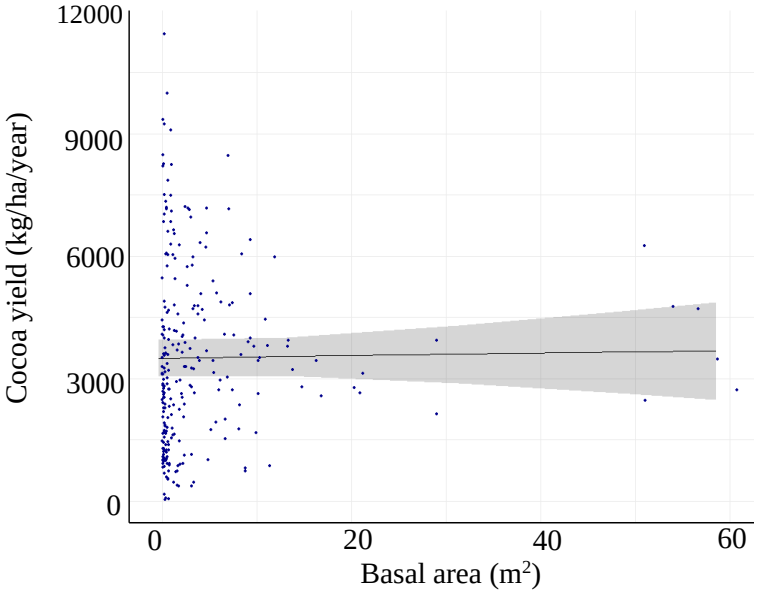

Figure 9 Relationship between basal area and cocoa yield. The data points represent the annual cocoa yield per plot. The line indicates the predicted effect of basal area on cocoa yield based on a linear mixed-effects model, with other predictors kept constant at the mean.

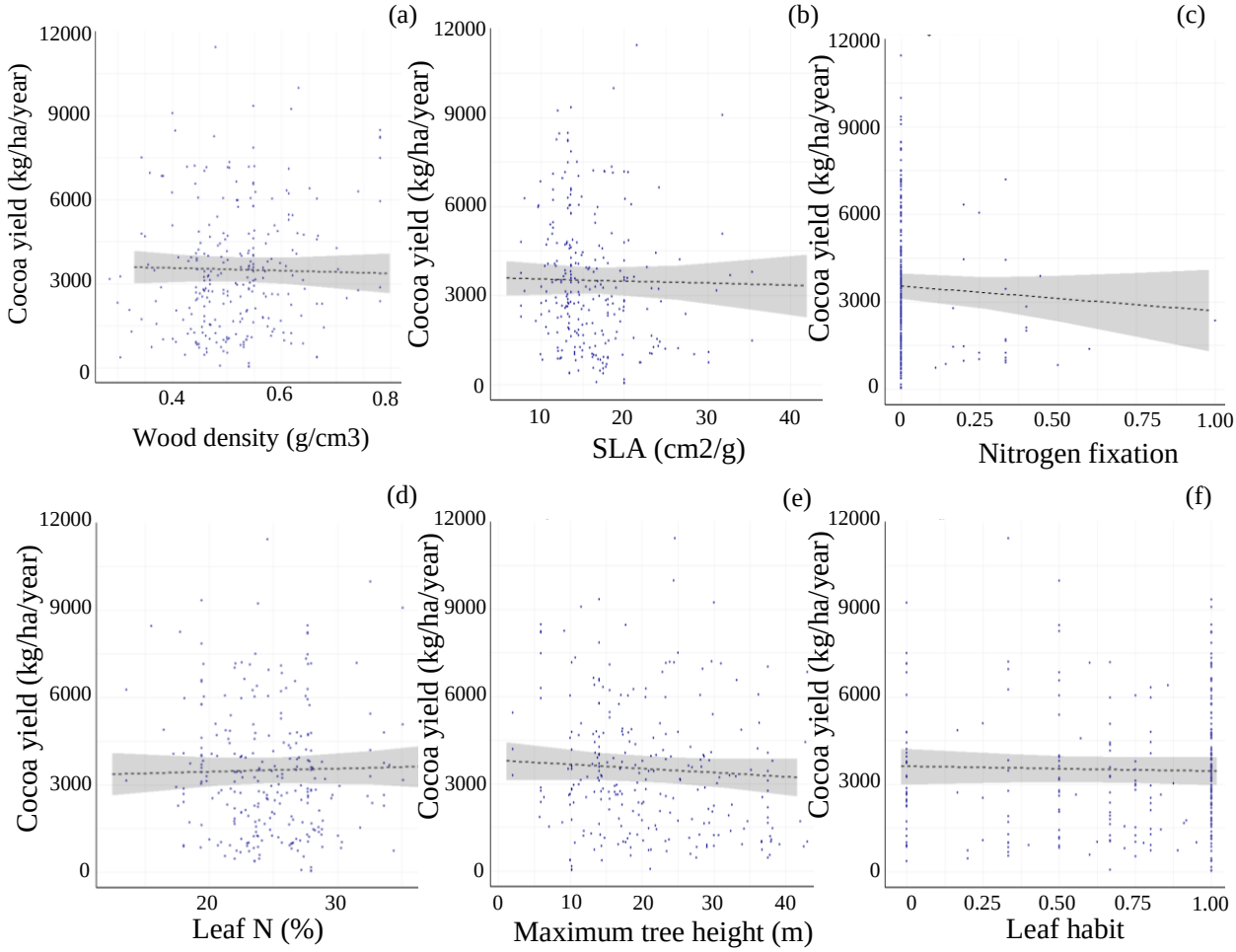

Figure 10 Relationship between cocoa yield and (a) Wood density, (b) Specific leaf area, (c) Nitrogen fixation, (d) Leaf nitrogen content, (e) Maximum tree height, and (f) Leaf habit. For

nitrogen fixation, 0 = non-fixing, 1 = fixing. For leaf habit, 0 = deciduous, 1 = evergreen. The data points represent the annual cocoa yield per plot. The lines indicate the predicted effects of each trait on cocoa yield based on a linear mixed-effects model, with other predictors kept constant at the mean.

3.3. Do environmental conditions change the effect of shade and shade tree traits on cocoa yield?

To assess whether environmental conditions modify the effect of shade trees on cocoa yield, we analyzed interactions between shade tree density, basal area, and climatic variables. The mixed-effects model results showed that environmental conditions did not significantly alter the effect of shade tree density on cocoa yield (Figure 11). In other words, the number of shade trees has the same impact on cocoa yields, regardless of whether the plots were in drier or wetter areas. However, when assessing shade levels based on shade tree basal area instead of shade tree density, the interaction between basal area and precipitation seasonality was positive and significant (Figure A2, Appendix). This finding indicates that in areas with more extensive precipitation fluctuations that have a clear contrast between dry and wet periods, a higher basal area may help maintain water availability for cocoa (Figure A3, Appendix).

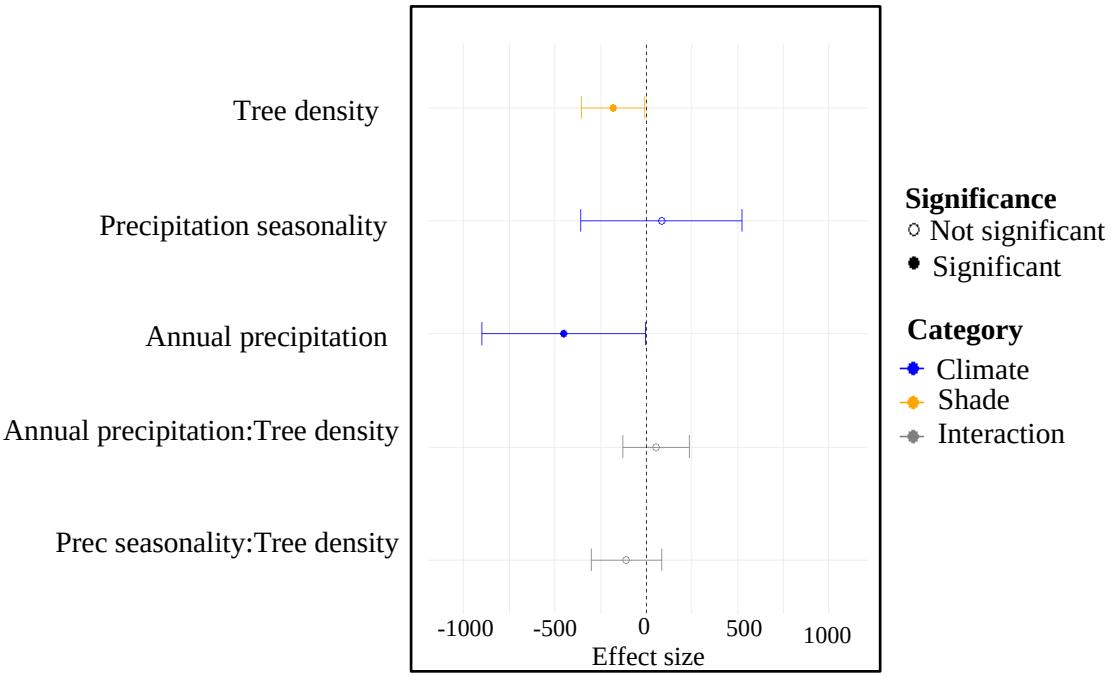

Figure 11 The role of climate in modifying the effects of tree density on cocoa yield. Results are based on a mixed-effects model.

To further examine how environmental conditions modify the effect of shade tree functional traits on cocoa yield, we analyzed the interaction between precipitation seasonality and shade tree traits (Figure 12). The results showed that precipitation seasonality significantly changed the effect of wood density on cocoa yield. In areas with higher precipitation seasonality, thus more contrasting wet and dry seasons, plots with low wood density had higher yields than plots with high wood density (Figure 13). In areas with lower precipitation seasonality, to the contrary, cocoa yield increased with wood density (Figure 13).

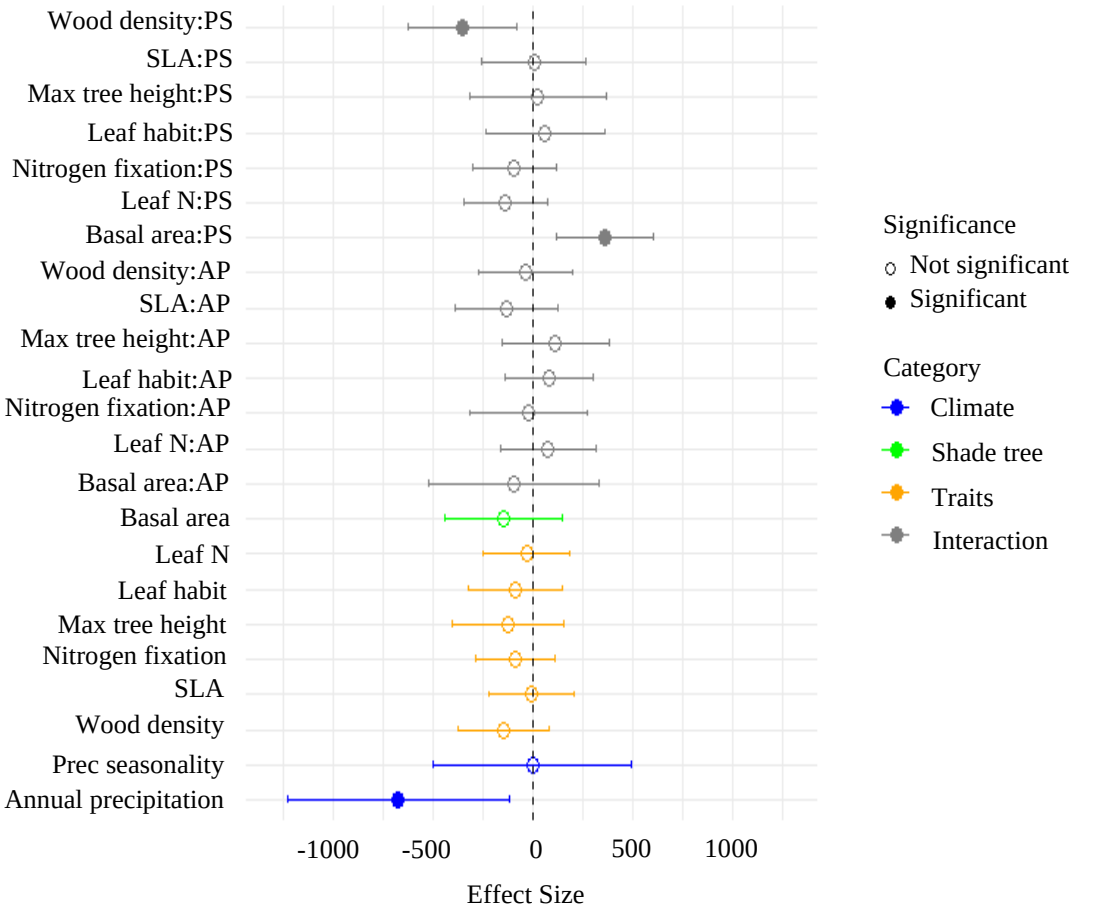

Figure 12 The role of climate in modifying the effects of functional traits on cocoa yield. Results are based on a mixed-effects model. PS: Precipitation seasonality, AP: Annual precipitation.

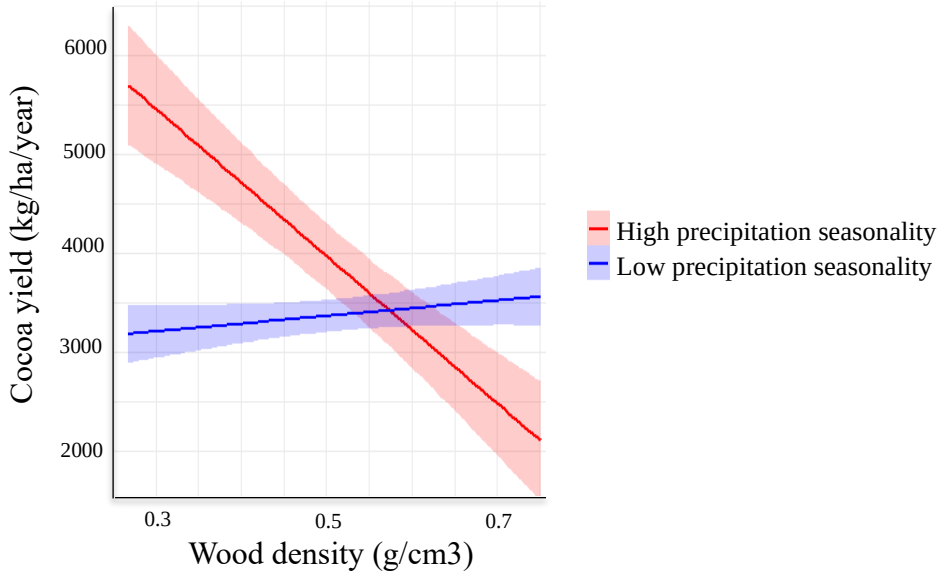

Figure 13 The impact of wood density on cocoa yield under varying levels of precipitation seasonality. The relationship between wood density and cocoa yield is examined at both low and high precipitation seasonality, based on mixed-effects models. All predictors were kept constant at their mean values for this analysis.

4. Discussion

4.1. Effects of environmental conditions on shade levels and shade tree traits

In this study, we examined how environmental conditions influence variation in shade levels and shade tree traits in cocoa agroforestry systems in Ghana and Cote d'Ivoire. Surprisingly, our results showed that shade tree density is not significantly affected by climatic conditions or soil fertility. This suggests that environmental conditions do not strongly drive variation in shade intensity. While we expected that farmers would plant fewer shade trees in drier areas to reduce competition for water, our findings indicate that this is not necessarily the case. It is worth noting that farmer interventions played a dominant role in shaping shade intensity. Farmers may regulate tree populations to optimize shade and maintain benefits such as fruit, timber, and other non-timber products (Kaba et al., 2020). Interestingly, we found that CEC levels were negatively correlated with shade when we used the basal area as a shading factor. This was an unexpected result because fertile soils are generally assumed to support tree growth by enhancing resource uptake (Achat et al., 2018;Soong et al., 2020). Poor-quality soils with low nutrient availability may result in more intense competition between trees (Coates et al., 2013). These discrepancies suggest that the relationship between soil fertility and tree growth may be influenced by additional factors such as species composition, competition intensity, and environmental stress, which may counteract the expected benefits of higher soil fertility (Soubeyrand et al., 2024).

Environmental conditions influenced the functional traits of shade trees. First, our results show that wood density (WD) was significantly lower under wet conditions than in dry conditions. The difference in WD between wet and dry conditions may reflect species adaptation to water availability (Nabais et al., 2018). In areas with low precipitation, species with high WD are more common, as species with denser wood tend to grow slowly and use water efficiently (Ibanez et al., 2017; Mo et al., 2024). High WD also improves resistance to cavitation, helping trees survive in dry conditions where hydraulic stress is frequent (Markesteijn et al., 2011). Conversely, species with lower WD tend to be more dominant in wet conditions, as they can allocate more resources toward rapid growth (Mendivelso et al., 2013; Mo et al., 2024). Nonetheless, shade trees with lower WD may offer other benefits to agroforestry systems. Low wood density tree species generally have fast growth, which is desirable to farmers because of higher wood production. In cocoa and coffee systems, fast-growing shade tree species are commonly used by farmers to generate additional income (Isaac et al., 2024).

Secondly, shade trees had a higher specific leaf area (SLA) in wet conditions than in dry conditions. In wet conditions, shade tree communities are dominated by species with high SLA with broader and thinner leaves (Gong et al., 2011). In contrast, shade trees in dry conditions have lower SLA with thicker and smaller leaves (Gong et al., 2011; Milla et al., 2008). Having thicker leaves is an adaptive strategy to reduce transpiration and water loss (Gong et al., 2011; Liu et al., 2017). In addition to climatic factors, our results show that higher CEC is associated with increased SLA in agroforestry systems. This relationship may be due to the role of fertile soils in providing nutrients like N, P, and K that support shade tree growth and increase SLA (Gong & Gao, 2019).

Lastly, our results show that water and nutrient availability positively influenced maximum tree height, as predicted in our hypothesis. Sufficient water availability in wet conditions favors stem elongation, which can increase tree height (Schippers et al., 2015). In wet conditions, species with broader leaves dominate, as these traits help optimize water use and support vertical growth (Lloyd & Farquhar, 2008; Zheng et al., 2022). Our results also suggest that a high level of CEC positively correlates with maximum tree height, indicating that soil fertility supports vertical growth by providing nutrients that facilitate stem growth (Cramer, 2012). In contrast, trees are shorter in drier conditions as they adapt to limited water availability (Elli et al., 2017; Koch et al., 2004; Lopez et al., 2019). Under dry conditions, water scarcity limits tree growth by reducing transpiration and photosynthesis (Schippers et al., 2015).

Our results indicate that deciduous species are more dominant in agroforestry systems on soils with higher cation exchange capacity (CEC). In contrast, evergreen species are more common on soils with lower CEC. While soil nutrient availability can influence species composition by favoring certain functional strategies, in this context, species composition is also strongly shaped by farmers' decisions on which tree species to plant. Deciduous trees can take advantage of soil nutrients to support rapid growth and seasonal leaf shedding (De Souza et al., 2007). In contrast, evergreen species may be more suitable for less fertile soils, as they are more efficient at retaining their leaves year-round to minimize excessive nutrient loss (Goldberg, 1982). At the same time, only a few shade tree species have nitrogen-fixing ability, and the presence of nitrogen-fixing species was not influenced by environmental conditions. The low proportion of these species likely reflects farmers' preferences for selecting shade trees that provide direct benefits, such as fruit and timber (Kaba et al., 2020).

4.2. Effects of shade levels and shade tree traits on cocoa yield

We hypothesized that high shade tree density would reduce cocoa yield due to increased competition for light and water. As we expected, our results showed that cocoa yield was highest at the lowest tree density and declined as tree density increased. Similar findings in coffee plantations indicate that excessive tree density significantly reduces productivity (Tran et al., 2021) because there is competition for nutrients and water (Asare & David, 2011). Moreover, dense canopy cover can reduce cocoa productivity by limiting the amount of sunlight reaching the understory (Lahive et al., 2019). According to Blaser et al. (2018), the optimal shade level for cocoa growth is around 30% of the total canopy cover in an agroforestry system. On the positive side, shade trees potentially increase cocoa yield because of more resistance to mirids (Asitoakor et al., 2022). Therefore, achieving optimal cocoa yield requires maintaining a shade level that balances the benefits without causing excessive competition for resources (Blaser et al., 2018; Blaser-Hart et al., 2021; Tran et al., 2021).

Beyond shade intensity, shade tree functional traits could also influence cocoa yield, yet our findings suggest that their effects are limited. Traits such as wood density (WD), specific leaf area (SLA), nitrogen fixation capacity, leaf nitrogen content, and maximum height did not influence cocoa yield. The effect of shade on cocoa production was overruled by management practices such as pruning activities (Niether et al., 2018). This is in line with

the findings of Asante et al. (2021), who showed that yield variability between fields was determined by agronomic practices applied by farmers, such as cocoa density and shade tree density. Therefore, shade intensity and land management practices may influence cocoa yield more strongly than the shade trees' functional traits.

4.3. Do environmental conditions alter shade tree effects on cocoa yields?

We hypothesized that the impact of shade would vary with environmental conditions, with positive effects in dry conditions by reducing heat stress and adverse effects in wet conditions due to increased disease pressure and competition for light. Our results present a mixed picture.

Climate conditions did not alter the effect of tree density on cocoa yield. However, when considering basal area instead of tree density, the results indicate that shade effects depend on environmental conditions, as expected. This difference may be due to basal area providing a more accurate proxy for actual shade levels than tree density alone, as it accounts for both the number and size of trees. In contrast, tree density does not reflect variation in tree size and canopy cover, which may explain why its effects do not vary with environmental conditions. At high precipitation seasonality (under drier conditions), we observed a positive effect of basal area on cocoa yield, but a negative effect under low precipitation seasonality (wetter conditions). In areas with low precipitation seasonality, the basal area is negatively associated with cocoa yield, possibly because increased shade limits light availability and increases disease risk for cocoa. Increased humidity under shade could have provided a favourable environment for fungal diseases such as *Phytophthora* spp., causing damage to cherelles and pods (Delgado-Ospina et al., 2021). High precipitation seasonality is characterized by intense rainfall but only in a few months, while the rest of the time there is drought or very low rainfall (Moustakis et al., 2021). During the dry season, high (shade) tree basal area can help regulate the microclimate by reducing soil evaporation (Isabelle et al., 2018), thereby mitigating drought stress in plots (Schwartz et al., 2022). Furthermore, in secondary dry forests, plots with higher basal area were cooler during the wet and dry seasons, but the cooling effects were stronger during the dry season (Schwartz et al., 2022). Agroforestry systems have been shown to buffer stress in cocoa sensitive to temperature fluctuations (Niether et al., 2018).

Although the basal area was positively associated with cocoa yield under high precipitation seasonality, this positive effect did not extend to belowground interactions. Contrary to our expectations, we observed a negative association between the wood density (WD) of shade trees and cocoa yield under high precipitation seasonality. This finding leads to the interpretation that shade may not fully prevent cocoa yield from declining under drought stress. While shade can reduce heat stress, it does not fully compensate for water deficits, especially during drought stress conditions (Abdulai et al., 2018; Mensah et al., 2023). This suggests that shade trees with high WD still have belowground competition for water during prolonged dry periods. In effect, cocoa trees being more sensitive to water stress, may experience increased water shortage, especially during high precipitation seasonality.

Our results highlight the complexity of tree–crop interactions in agroforestry systems. Selecting shade tree species should not only focus on aboveground contributions to shade but also consider belowground interactions between trees. A trade-off may exist where trees that provide valuable shade during the dry season also exacerbate competition for water.

4.4. Limitations

This study showed how environmental conditions influence shade levels and shade tree traits in cocoa agroforestry systems, and how shade levels and shade tree functional traits influence cocoa yield across a gradient in environmental conditions. However, there are limitations that need to be considered when interpreting the results. One of the main limitations is the incomplete trait data for some shade tree species in the study site. Not all species had trait data in the TRY Database and Global Wood Density Database, so traits for some species had to be estimated based on the same genus or excluded from the analysis. This incompleteness may affect the accuracy of calculations and interpretation of results.

The difference between the location of the functional trait data collection and the research site is also a factor that needs to be considered. The shade tree traits data used came from a database covering a wide range of locations (Kattge et al., 2020), and the methods of functional trait data collection may also differ across studies. As a result, there is a potential mismatch between the environmental conditions where the trait data were collected and the actual conditions at the study site. In addition, the same species can exhibit different growth characteristics depending on the growing location due to adaptation to local environmental conditions (Valor et al., 2024). Thus, future research should collect trait data directly from the research location to ensure compatibility between variables.

Another limitation is that this study focused only on a subset of functional traits, and did not include other potentially relevant traits such as leaf area index (LAI) or belowground traits. Analysing root traits to identify belowground resource acquisition strategies and linking them to aboveground traits may provide deeper insights (Abdulai et al., 2025). Including such traits could improve our understanding of the mechanisms behind resource-use efficiency and drought resilience in cocoa agroforestry systems, and thereby support the design of more climate-resilient production systems.

5. Conclusion

Our results clearly illustrate the interactions between shade trees, their functional traits, and cocoa yield across a gradient in environmental conditions in Ghana and Cote d'Ivoire. The effects of environmental conditions did not significantly influence shade tree density, suggesting that shade levels are shaped more by farmer management than by climatic or soil factors. However, denser shade reduced cocoa yield due to increased competition for light and water. While shade tree functional traits varied across the environmental gradient, they had no direct impact on cocoa yield compared to shade intensity.

Nevertheless, environmental conditions modified the effects of basal area and certain shade tree traits on cocoa yield. Under high precipitation seasonality, the impact of the basal area on cocoa yield became positive, suggesting that a larger shade tree basal area may help buffer environmental stress. Under the same conditions, our results show a negative association between shade tree wood density (WD) and cocoa yield. This indicates that while shade trees with high WD may provide structural stability and persist in dry environments, there is still belowground competition for water.

These findings emphasize the importance of shade tree selection and management strategies that integrate environmental conditions and functional traits for sustainable cocoa agroforestry. In areas prone to drought, farmers should consider maintaining shade trees with a larger basal area to provide more consistent shade and help buffer environmental stress during dry periods. Additionally, farmers may consider planting fast-growing tree species with low WD, which can be harvested for timber offering an additional source of income in the short term.

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7. Appendix

7.1. Species abundance

Table S1 Species abundance

Species	Genus	Abundance	Percentage (%)
Persea americana	Persea	94	8.61
Morinda lucida	Morinda	79	7.23
Terminalia superba	Terminalia	77	7.05
Terminalia ivorensis	Terminalia	66	6.04
Citrus sinensis	Citrus	55	5.04
Elaeis guineensis	Elaeis	55	5.04
Coffea arabica	Coffea	37	3.39
Mangifera indica	Mangifera	37	3.39
Newbouldia laevis	Newbouldia	35	3.21
Milicia excelsa	Milicia	34	3.11
Antiaris toxicaria	Antiaris	29	2.66
Cola nitida	Cola	28	2.56
Ficus exasperata	Ficus	25	2.29
Hevea brasiliensis	Hevea	24	2.20
Carica papaya	Carica	21	1.92
Holarrhena floribunda	Holarrhena	20	1.83
Ricinodendron heudelotii	Ricinodendron	20	1.83
Gliricidia sepium	Gliricidia	18	1.65
Ficus sur	Ficus	14	1.28
Tectona grandis	Tectona	14	1.28
Albizia zygia	Albizia	13	1.19
Alstonia boonei	Alstonia	13	1.19
Spathodea campanulata	Spathodea	13	1.19
Entandrophragma angolense	Entandrophragma	12	1.10
Spondias mombin	Spondias	11	1.01
Albizia adianthifolia	Albizia	10	0.92
Amphimas pterocarpoides	Amphimas	10	0.92
Cedrela odorata	Cedrela	10	0.92
Nesogordonia papaverifera	Nesogordonia	10	0.92
Xylopia aethiopica	Xylopia	9	0.82
Harungana madagascariensis	Harungana	8	0.73
Ceiba pentandra	Ceiba	7	0.64
Ficus mucuso	Ficus	7	0.64
Cecropia peltata	Cecropia	6	0.55
Lannea welwitschii	Lannea	6	0.55
Rauvolfia vomitoria	Rauvolfia	6	0.55

Syzygium malaccense	Syzygium	6	0.55
Anacardium occidentalis	Anacardium	5	0.46
Bombax buonopozense	Bombax	5	0.46
Celtis mildbraedii	Celtis	5	0.46
Ficus capensis	Ficus	5	0.46
Ficus vogeliana	Ficus	5	0.46
Psidium guajava	Psidium	5	0.46
Albizia ferruginea	Albizia	4	0.37
Sterculia tragacantha	Sterculia	4	0.37
Trichilia monadelpha	Trichilia	4	0.37
Vernonia amygdalina	Vernonia	4	0.37
Acacia mangium	Acacia	3	0.27
Anthocleista djalonensis	Anthocleista	3	0.27
Anthocleista nobilis	Anthocleista	3	0.27
Citrus grandis	Citrus	3	0.27
Citrus limon	Citrus	3	0.27
Citrus reticulata	Citrus	3	0.27
Cocos nucifera	Cocos	3	0.27
Daniellia ogea	Daniellia	3	0.27
Heritiera densiflora	Heritiera	3	0.27
Khaya ivorensis	Khaya	3	0.27
Mareya micrantha	Mareya	3	0.27
Pycnanthus angolensis	Pycnanthus	3	0.27
Artocarpus altilis	Artocarpus	2	0.18
Baphia pubescens	Baphia	2	0.18
Blighia sapida	Blighia	2	0.18
Bridelia micrantha	Bridelia	2	0.18
Celtis zenkeri	Celtis	2	0.18
Diospyros mespiIiformis	Diospyros	2	0.18
Dracaena mannii	Dracaena	2	0.18
Funtumia africana	Funtumia	2	0.18
Funtumia elastica	Funtumia	2	0.18
Lonchocarpus sericeus	Lonchocarpus	2	0.18
Macaritaria discopia	Macaritaria	2	0.18
Manihot esculenta	Manihot	2	0.18
Millettia zechiana	Millettia	2	0.18
Moringa oleifera	Moringa	2	0.18
Musanga cecropioides	Musanga	2	0.18
Myrianthus arboreus	Myrianthus	2	0.18
Pouteria altissima	Pouteria	2	0.18
Pterocarpus santalinoides	Pterocarpus	2	0.18
Solanum torvum	Solanum	2	0.18

Sterculia rhinopetala	Sterculia	2	0.18
Strombosia glaucescens	Strombosia	2	0.18
Triplochiton scleroxylon	Triplochiton	2	0.18
Albizia lebbeck	Albizia	1	0.09
Anonidium mannii	Albizia	1	0.09
Artocarpus heterophyllus	Artocarpus	1	0.09
Berlinia tomentella	Berlinia	1	0.09
Blighia unijugata	Blighia	1	0.09
Carapa procera	Carapa	1	0.09
Chrysophyllum sp	Chrysophyllum	1	0.09
Cola gigantea	Cola	1	0.09
Dialium dinklagei	Dialium	1	0.09
Dialium guineense	Dialium	1	0.09
Distemonanthus benthamianus	Distemonanthus	1	0.09
Entandrophragma candollei	Entandrophragma	1	0.09
Erythrina senegalensis	Erythrina	1	0.09
Jatropha curcas	Jatropha	1	0.09
Khaya anthotheca	Khaya	1	0.09
Mallotus oppositifolius	Mallotus	1	0.09
Margaritaria discoidea	Margaritaria	1	0.09
Milicia regia	Milicia	1	0.09
Napoleonaea vogelii	Napoleonaea	1	0.09
Nauclea diderrichii	Nauclea	1	0.09
Piliostigma thonningii	Piliostigma	1	0.09
Piptadeniastrum africanum	Piptadeniastrum	1	0.09
Pterygota macrocarpa	Pterygota	1	0.09
Raphia hookeri	Raphia	1	0.09
Sterculia oblongata	Sterculia	1	0.09
Terminalia mentaly	Terminalia	1	0.09
Vitex sp	Vitex	1	0.09

7.2. The effect of basal area and shade tree traits on cocoa yield

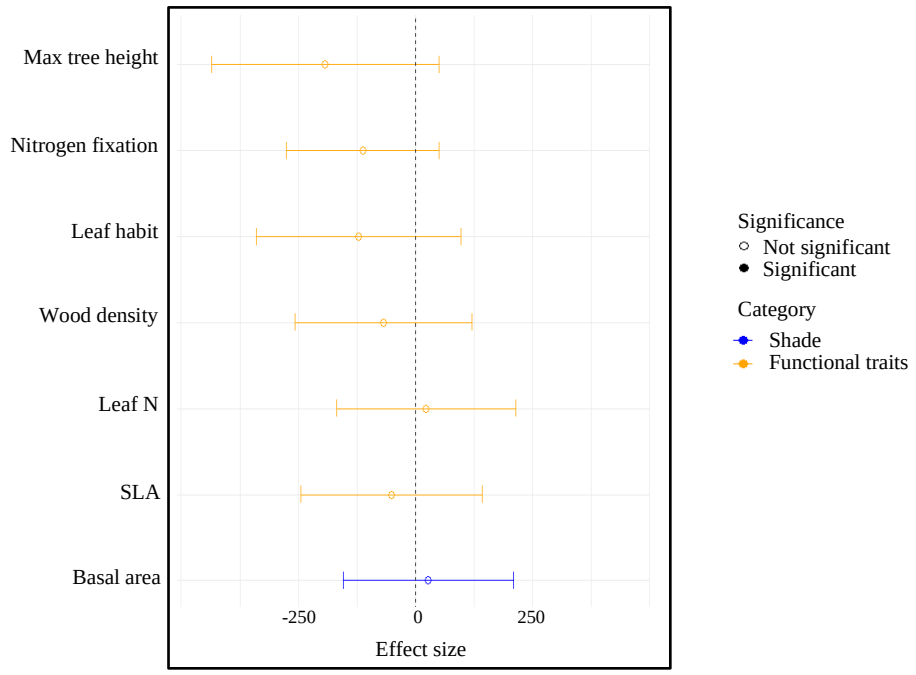

Figure A1 The effect of basal area and functional traits on cocoa yield. Results are based on a mixed-effects model.

7.3. The role of climate in modifying the effect of the basal area on cocoa yield

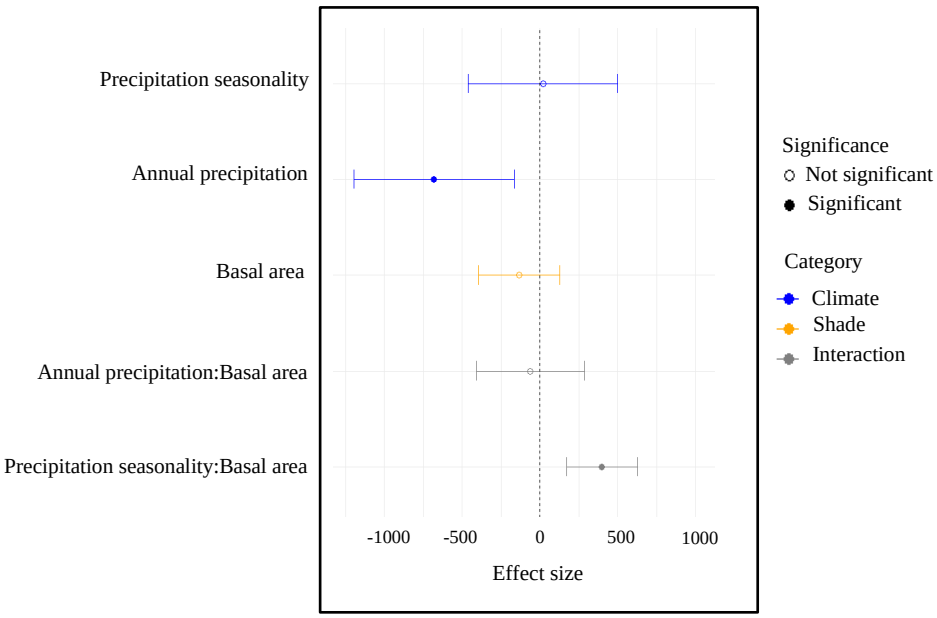

Figure A2 The role of climate in modifying the effects of the basal area on cocoa yield. Results are based on a mixed-effects model.

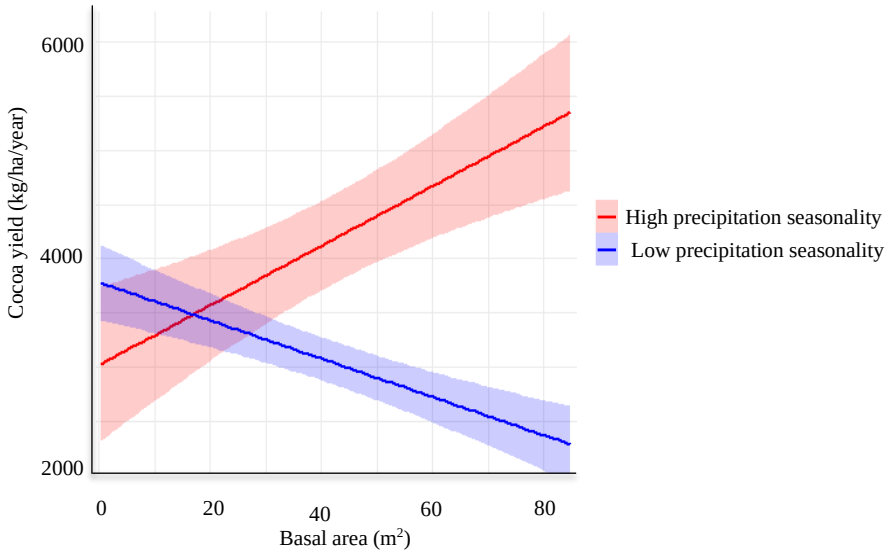

Figure A3 The impact of basal area on cocoa yield under varying levels of precipitation seasonality. The relationship between basal area and cocoa yield is examined at both low and high precipitation seasonality, based on mixed-effects models. All predictors were kept constant at their mean values for this analysis.