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Agroforestry Shading Mitigates Light Stress in Cocoa (*Theobroma cacao* L.) by Improving Photosystem II Efficiency Assessed via Chlorophyll Fluorescence (Fv/Fm)

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Authors' contributions

This work was carried out in collaboration among all authors. Author GSH carried out the conceptualization, study design, field data collection, data analysis, and drafting of the manuscript. Authors SS, MKAA, DSR, EDK and CM contributed to the methodology, participated in the interpretation of results, critically revised the manuscript, and approved the final version. All authors read and approved the final manuscript.

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Abstract

Background: Cocoa is a shade-tolerant species. Excessive light can induce photo-oxidative stress and photosystem II (PSII) photoinhibition in cocoa. In agroforestry, the tree canopy plays a key role in modulating the light microclimate and could therefore contribute to cocoa photoprotection.

Aims: This study evaluates the effect of different agroforestry shading levels on PSII efficiency, estimated from the maximum photochemical yield (Fv/Fm) measured after dark adaptation.

Study Design: Field experiment comparing three light environments on mature cocoa trees (O0: full sun; O1: moderate shade; O2: dense shade).

Place of Study: Experimental cocoa agroforestry sites in Côte d'Ivoire (Azaguie, Soubré, and Blé/Divo).

Methodology: Three light environments were implemented on mature cocoa trees: full direct light (O0), partial shade (approximately 30%, O1), and dense shade (30–60%, O2). The effect of shade on Fv/Fm was assessed using a Kruskal–Wallis test complemented by post hoc analyses ($\alpha = 5\%$).

Results: Shade had a significant effect on PSII efficiency (p-value = 0.009). Cocoa trees under full sunlight showed a reduced Fv/Fm ratio (0.752 ± 0.015), indicating strong photoinhibition, whereas trees under moderate shade (0.796 ± 0.003) and dense shade (0.785 ± 0.005) exhibited markedly higher values. O1 and O2 did not differ significantly, suggesting that a moderate shade level is sufficient to provide effective protection against light stress.

Conclusion: These results indicate that agroforestry shade reduces light stress in cocoa while increasing PSII performance. They highlight the value of moderate shade as a management approach to prevent photoinhibition. It is recommended that future studies should assess long-term yield and physiological resilience under optimised shade regimes.

Keywords: Theobroma cacao; agroforestry; shading; photoinhibition; chlorophyll fluorescence (Fv/Fm).

1. Introduction

Cocoa (*Theobroma cacao* L.) is a tropical species originating from the forest understory of the Amazon, where it naturally develops beneath tree cover. Its optimal growth conditions include an elevation of approximately 300 meters above sea level, with an annual rainfall of 1500-2000 mm and temperatures ranging from 15-39°C. Adequate humidity levels are crucial for its cultivation (Mohanalakshmi et al., 2024). Cocoa trees are relatively small, reaching heights of 8-12 meters, with simple, shiny, dark green leaves, small cauliflorous flowers, and an indehiscent fruit encasing 20-60 seeds enveloped in sweet mucilage (Jegadeeswari et al., 2024). This ecological origin explains its shade tolerance and its sensitivity to excess solar radiation (Acheampong et al., 2015; Arévalo-Gardini et al., 2021). Several studies have shown that the photosynthetic light-saturation threshold of cocoa generally ranges between 400 and 700 µmol m^{-2} s^{-1}, whereas irradiance under tropical conditions may exceed 1500 µmol m^{-2} s^{-1} at midday (Baker, 2008; Daymond et al., 2011; Suárez Salazar et al., 2018). This imbalance leads to excess light energy absorbed by the light-harvesting antennae of photosystem II (Hieke et al., 2003; Keren et al., 1997).

Photoinhibition is defined as the light-induced loss of photosynthetic activity and is an unavoidable consequence of the light reactions (Keren & Krieger-Liszkay, 2011; Sonoike, 2025). When absorbed energy exceeds the capacity for photochemical use, it promotes the formation of reactive oxygen species (ROS), which can damage PSII components, notably the D1 protein in the reaction centre (Foyer & Hanke, 2022). This phenomenon, known as photoinhibition, results in a reduction in the maximum photochemical efficiency of PSII (Keren et al., 1997). This efficiency is commonly assessed using the chlorophyll fluorescence ratio Fv/Fm (Maxwell & Johnson, 2000), determined after a dark period that allows full reopening of reaction centres (Murchie & Lawson, 2013; Osorio Zambrano et al., 2021). In cocoa, several studies have documented reductions in Fv/Fm under high irradiance, with values potentially dropping to 0.70–0.75 under full-sun conditions (Acheampong et al., 2015; Jaimez et al., 2018).

Shade trees are commonly used to partially shade cocoa, thereby reducing light stress through microclimate regulation (Agele et al., 2016; Kohl et al., 2024; Niether et al., 2018). This buffering of environmental constraints may reduce PSII photoinhibition, improve cocoa photochemical efficiency, and consequently support photosynthetic activity. The present study, therefore, evaluates the effect of different shading levels on the maximum quantum yield Fv/Fm in cocoa, in order to identify the optimal shade level that limits light stress while maintaining efficient photosynthetic function.

2. Material and Methods

2.1 Study Sites

The study was conducted in 1,000 m² experimental cocoa plots established within traditional agroforestry sites across three locations in Côte d'Ivoire: Azaguie (5°37′ N, 4°05′ W) in a forest–savanna transition zone in the south; Divo (5°50′ N, 5°21′ W) in an intermediate subequatorial zone; and Soubré (5°46′ N, 6°36′ W) in a humid forest zone in the southwest. These sites, among the country's main cocoa-producing regions, present contrasting agroecological conditions. Azaguie has a tropical savanna climate with approximately 1,466 mm of annual rainfall and a mean temperature of 26.7 °C. Divo has a subequatorial climate (approximately 1,200 mm annual rainfall; 26.5 °C mean temperature). In contrast, Soubré experiences a humid tropical climate (approximately 1,069 mm annual rainfall; 26.1 °C mean temperature). These climatic differences create diverse environmental conditions, enabling a comprehensive assessment of the relationship between shade and cocoa performance (Fig. 1).

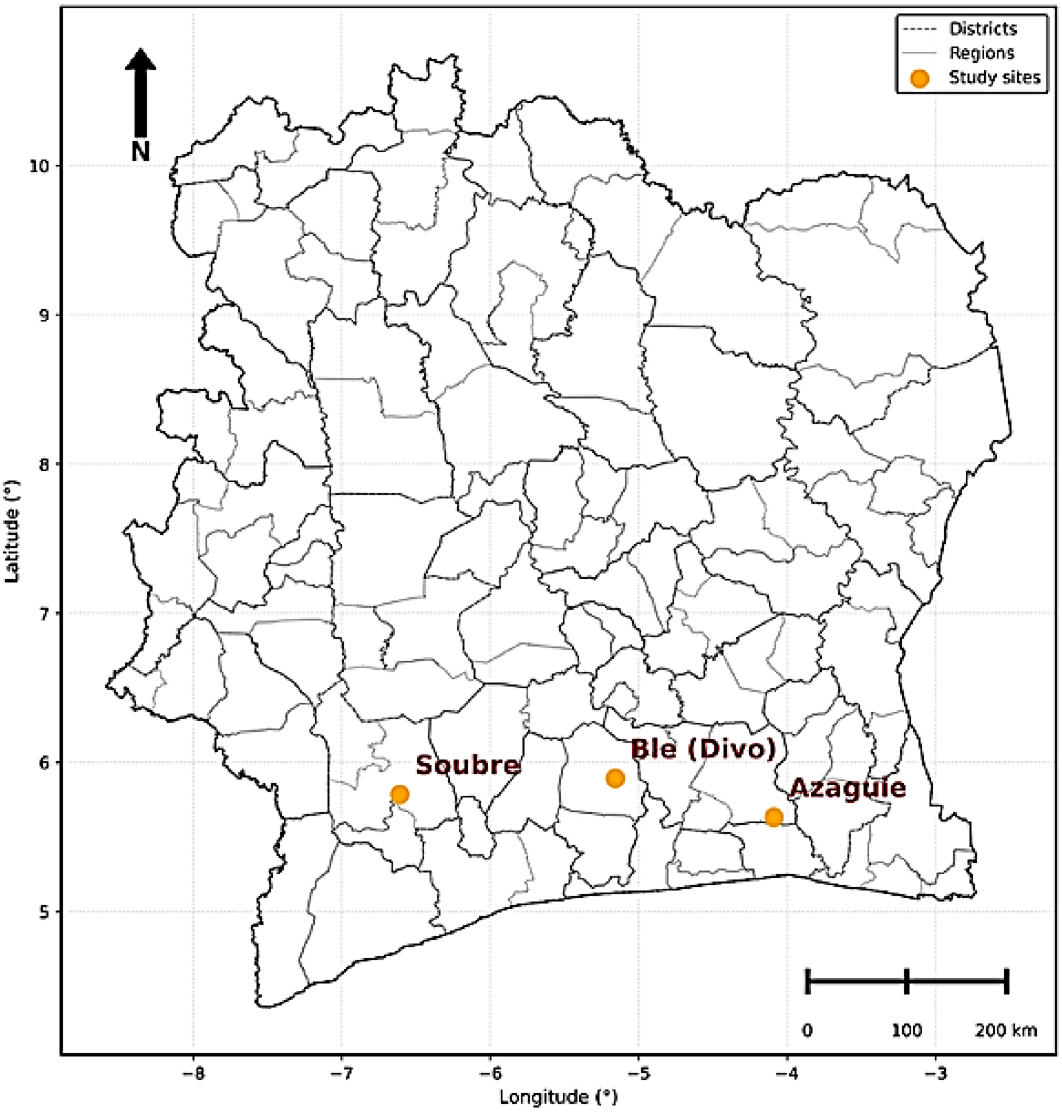

Fig. 1. Location map of study sites in Côte d'Ivoire

2.2 Shade Mapping and Quantification

Upper-canopy shade was measured using a LI-191R quantum sensor (LI-COR) on a regular grid of 25 points spaced 8 m apart, covering each 1,000 m² plot (Fig. 2). Photosynthetically active radiation (PAR) measurements were taken inside the plot just below the shade-tree canopy (PARi) and outside the plot in full sun (PARe) between 12:00 and 14:00 under clear-sky conditions to minimise variation due to solar angle or cloud cover. The shade percentage (TO) at each grid point was calculated as follows (Monteith & Unsworth, 2013):

$$TO = 1 - (PARi / PARe)$$

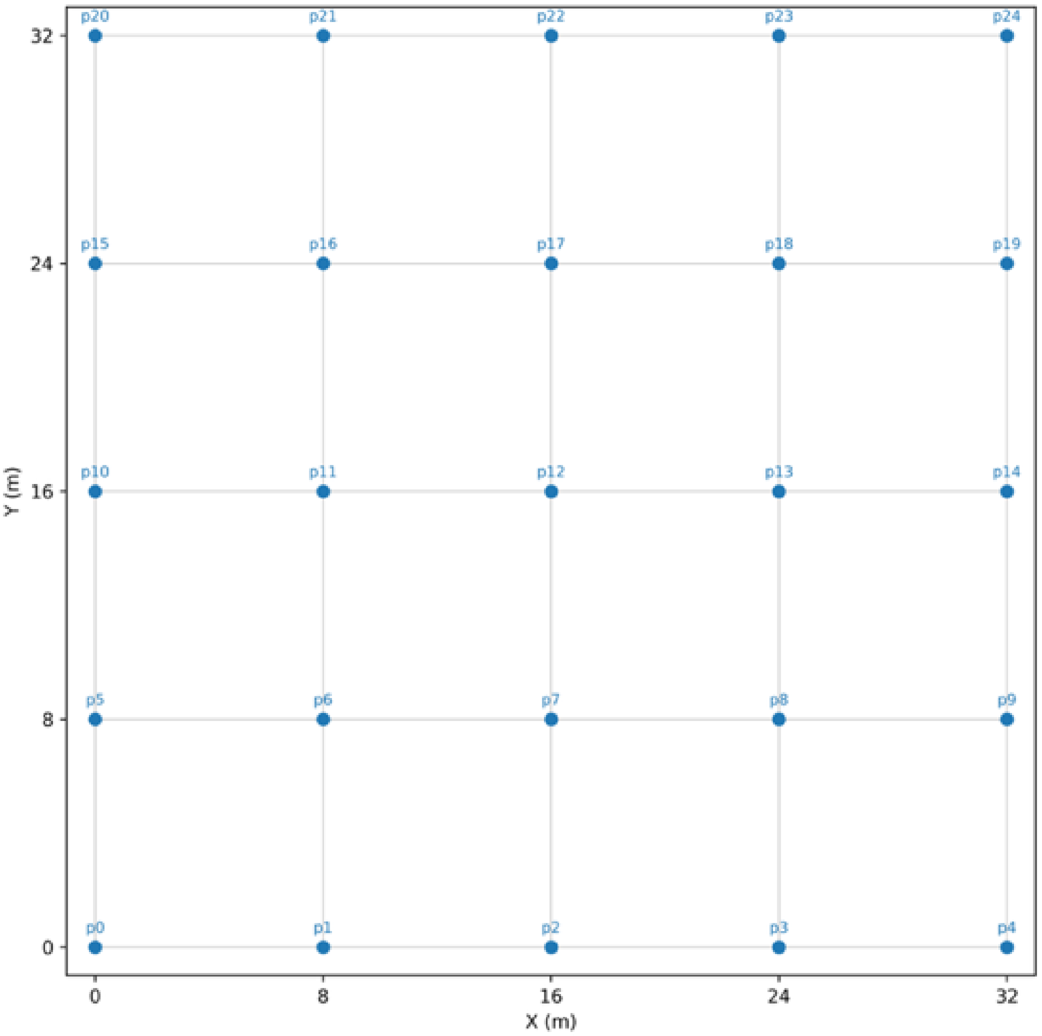

Fig. 2. Regular 25-point sampling grid (8 m spacing) used for shade measurements in 1,000 m² plots

This value represents the fraction of incident light intercepted by the shade-tree canopy. The TO values were then used to characterise shade conditions within the study plots using the ordinary kriging continuous interpolation method (Goovaerts, 1997; Gratton, 2002; Webster & Oliver, 2007). Using a variogram model, the exponential function provided the best descriptive fit of the spatial dependence of shade (TO) data. The resulting map provides a local estimate of TO (with kriging variance) at any location within the plot. All geospatial analyses were performed in Python 3.10 using the PyKrige library. A key processing step relied on the Python Geopandas library to automate the extraction of shade values at each measurement point. The shade level received by cocoa trees was subsequently extracted based on their GPS positions.

2.3 Chlorophyll Fluorescence Measurements (Fv/Fm)

Chlorophyll fluorescence measurements were conducted using a CIRAS-4 photosynthetic gas analyser equipped with the CFM-4 fluorimetry module (Pulse-Amplitude Modulated, PAM) integrated into a compatible leaf chamber (Schreiber, 2004). The CFM-4 is a pulse-modulated fluorometer that generates the fluorescence signal. The maximum PSII quantum yield (Fv/Fm) was measured on leaves that had been dark-adapted for 20 minutes (He et al., 2024; Kalaji et al., 2017). For each leaf, the minimum (Fo) and maximum (Fm) fluorescence signals were obtained under modulated measuring light (Fo) and following a saturating pulse (Fm), respectively. Variable fluorescence was calculated as $Fv = Fm - Fo$, and maximum PSII yield as:

$$Fv/Fm = (Fm - Fo) / Fm$$

These equations correspond to the calculations implemented in the CIRAS-4 for fluorescence parameters.

2.4 Statistical Analysis

Processed Fv/Fm data were analysed using non-parametric statistical methods. First, a global Kruskal–Wallis test was applied to assess the effect of shading treatment on the median Fv/Fm. When a significant difference was detected ($p < 0.05$), pairwise comparisons were performed using the Least Significant Difference (LSD) test to determine which treatments differed significantly. All analyses were performed in Python 3.1.3.

3. Results and Discussion

3.1 Results

Effect of shading on Fv/Fm: depending on shade regime, dawn Fv/Fm values varied markedly (Fig. 3). The Kruskal–Wallis analysis indicated a highly significant effect of shade ($H = 9.32$; $p = 0.009$) on maximum PSII performance (Fv/Fm). Under full sunlight (O0), cocoa leaves displayed the lowest mean Fv/Fm (0.752 ± 0.015). In contrast, leaves under moderate shade (O1) showed the highest mean Fv/Fm (0.796 ± 0.003), while those under dense shade (O2) had a mean Fv/Fm of 0.785 ± 0.005. Thus, both shaded treatments produced Fv/Fm values approximately 4–5 percentage points higher than the full-sun condition.

Post hoc analyses confirmed that shading significantly increased Fv/Fm compared with full sun. A statistically significant difference was observed between O0 and both shaded treatments ($p < 0.05$): on average, Fv/Fm increased by approximately +0.04 under shade (moderate or dense). Conversely, the difference in Fv/Fm between moderate (O1) and dense shade (O2) was small (+0.011) and not significant (LSD, $p > 0.05$). In other words, O1 and O2 provided a comparable benefit in PSII protection, both outperforming the full-sun condition.

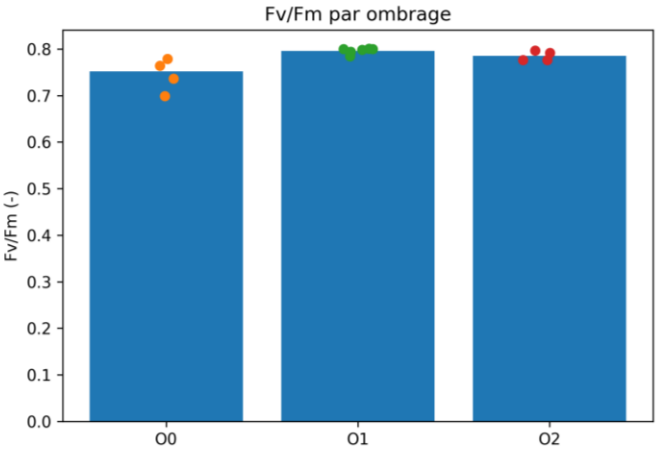

Fig. 3. Effect of shade regimes (O0: full sun, O1: shade < 30%, O2: shade 30–60%) on maximum PSII yield (Fv/Fm) measured in cocoa

3.2 Discussion

The data indicate that direct exposure to sunlight causes marked photosystem II (PSII) photoinhibition in cocoa, as evidenced by a reduction in maximum quantum yield Fv/Fm to around 0.75. According to ecophysiological criteria, an ideal Fv/Fm value for non-stressed leaves ranges from 0.80 to 0.83, whereas values below 0.80 reflect residual photochemical stress (Maxwell & Johnson, 2000; Baker, 2008).

These observations are consistent with previous research on cocoa. Cocoa genotypes exposed to high irradiance show a marked decline in Fv/Fm at midday, followed by partial recovery during periods of lower light (Jaimez et al., 2018). Similarly, strong daytime photoinhibition has been reported under full sun, while shade-grown leaves maintained values closer to the optimum (Baker, 2008). These findings support the idea that cocoa, as a forest species, has a limited capacity to tolerate high irradiance levels (Daymond et al., 2011).

The decline in Fv/Fm under high light results from an imbalance between photo-oxidative damage and PSII repair processes. Excess light enhances ROS production, leading to degradation of the D1 protein in the reaction center (Baker, 2008). When the rate of degradation exceeds the rate of repair, photochemical efficiency decreases (Takeuchi et al., 2025). The temperature increase commonly associated with full-sun exposure further intensifies this process by limiting D1 resynthesis and exacerbating oxidative damage (Murchie & Niyogi, 2011).

Cocoa trees under moderate (O1) and dense shade (O2) exhibited Fv/Fm values around 0.79–0.80, indicating an almost complete absence of persistent photoinhibition. This is consistent with Maxwell & Johnson (2000), who associate values close to 0.83 with fully functional PSII. In this context, shade acts as a microclimate regulator by reducing incident radiation and leaf temperature, two key drivers of photochemical stress (Blaser et al., 2018; Niether et al., 2018). By intercepting a substantial fraction of photosynthetically active radiation, the shade canopy modulates light flux to match the intrinsic photosynthetic capacity of cocoa, thereby preventing PSII saturation.

A notable result of this study is the absence of a significant difference between moderate shade (≈30%) and dense shade (30–60%) for Fv/Fm. This suggests a threshold beyond which additional shade provides no further benefit for PSII protection. Likewise, Daymond et al. (2011) reported that excessive shade can reduce overall photosynthetic capacity without necessarily improving photoprotection further.

From an agronomic perspective, these results are particularly relevant in the context of climate change. Agroforestry systems are recognised for their potential to reduce climatic extremes, stabilise microclimates, and enhance crop resilience over the long term (Schroth et al., 2016; Tscharntke et al., 2011). By maintaining functional PSII and minimising recurrent photo-oxidative damage, moderate shade may support more stable photosynthesis throughout the day while reducing the physiological costs associated with PSII repair (Murchie & Niyogi, 2011). This could ultimately contribute to longer leaf lifespan, an increase in active photosynthetic area, and more stable production.

Overall, the evidence supports the idea that moderate shade represents an optimal balance: insufficient shade exposes cocoa trees to chronic photoinhibition, whereas excessive shade does not necessarily provide further gains in PSII efficiency and could constrain productivity.

4. Conclusion

This study shows that agroforestry shade significantly reduces light stress in cocoa by limiting PSII photoinhibition. Based on Fv/Fm, maximum PSII quantum efficiency was clearly higher under shaded conditions than under direct sunlight, indicating a more favourable photochemical status of leaves in shade. A moderate shade level (approximately 30%) was sufficient to raise Fv/Fm to values close to the optimum (~0.80), nearly eliminating the persistent photoinhibition observed without shade. Denser shade did not further increase Fv/Fm, suggesting an optimal shade threshold beyond which benefits plateau. Practically, these findings support agroforestry management as a means of improving cocoa resilience to extreme light and temperature conditions in open systems. Maintaining adequate tree cover in tropical cocoa farms helps preserve photosynthetic efficiency. In summary, moderate shade is a key agronomic factor for combining physiological performance with sustainable cocoa production in tropical regions. Future studies should assess long-term yield and physiological resilience under optimised shade regimes.

Disclaimer (Artificial Intelligence)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of this manuscript.

Competing Interests

Authors have declared that they have no known competing financial interests OR non-financial interests OR personal relationships that could have appeared to influence the work reported in this paper.

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