

Effect of Lighting in the Canopy of *Hevea brasiliensis* on the Establishment and Development of *Thaumatococcus daniellii*

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Received: December 1, 2025

Accepted: January 20, 2026

Online Published: February 15, 2026

doi:10.5539/jas.v18n3p43

URL: <https://doi.org/10.5539/jas.v18n3p43>

Abstract

This study aims to identify the optimal lighting conditions under rubber tree canopy to promote the establishment and growth of *Thaumatococcus daniellii*, a plant of high economic value. Five rubber tree stands, differentiated by their metabolism (slow, medium, fast) and age (IRCA 18 at 4 and 5 years, IRCA 41 at 5 years, and PB 217 at 2 and 4 years), were evaluated. *T. daniellii* was planted at a density of 3.17 plants/m² (70 × 44 cm) in the inter-rows of the rubber trees. Establishment was monitored through emergence and tillering rates, while the light conditions in the understory were assessed by canopy closure and trunk circumference measured at 1 m above the ground. The results show that moderate shading supports the emergence of *T. daniellii* seedlings, whereas excessive shade limits their development. The germination rate, which ranged from 7 to 66%, was strongly correlated with the level of light available under the canopy. Thirty months after planting, *T. daniellii* produced between 50 and 70 leaves/m², and the first fruits appeared in plots that successfully completed their establishment phase, particularly those with the IRCA 18 (4 years) and IRCA 41 (5 years) clones. The IRCA 18 clone recorded the highest production, with 73 fruits/m², followed by the IRCA 41 clone with 68 fruits/m², performances associated with favorable light conditions. This research highlights the positive interactions between rubber cultivation and biodiversity and suggests that integrating *T. daniellii* into rubber plantations could serve as a lever to enhance food security in Côte d'Ivoire.

Keywords: lighting, rubber tree canopy, *Thaumatococcus daniellii*, Côte d'Ivoire

1. Introduction

Rubber cultivation, by restoring dense forest cover from the fifth year of planting onwards, severely limits the possibilities for long-term intercropping, unlike other perennial crops such as cocoa or coffee (Kouadio et al., 1997). This characteristic raises concerns about the long-term impact of rubber tree expansion on food security in Côte d'Ivoire. Indeed, rubber cultivation has experienced remarkable growth over the past two decades, with more than 10,000 hectares planted each year (Obouayeba et al., 2015). This fast development isn't without consequences: it increases pressure on land and sometimes encourages people to go into protected forests, making deforestation worse. For some people, this situation feeds the perception that rubber cultivation is slowing down the development of food crops, which are essential for food security. Some analysts even believe that rubber could gradually replace other crops, particularly food crops (Koulibaly, 2014). This concern is even more justified given that rubber trees occupy the land for more than 40 years and that, after the fourth year of planting, the density of the canopy severely limits the introduction of food species due to the shade it creates (Obouayeba et al., 2015). In this context, it is crucial to develop agroforestry systems that sustainably integrate rubber trees with species that are useful to humans, to reconcile latex production, food security and biodiversity

conservation. During the first three years after planting, rubber trees are often combined with food crops, industrial crops or cover crops, as shown by several studies and experiments carried out in research stations and on farms (Obouayeba et al., 1995; Kéli et al., 2005; Boko et al., 2010). Moreover, in several rubber-growing regions, intercropping accounts for more than 75% of new plantations. According to a report by Boko et al., (2010), 62% of plantations, out of a total of 9,263 plots sampled, had hosted or were still hosting food crops associated with young rubber trees. In this context, *T. daniellii* (Benn) was introduced, as a plant native to the tropical rainforests of Africa, known for its fruits containing a natural protein with a sweetening power 3,000 times greater than that of sucrose: thaumatin (N'Guessan & Zouzou, 1997; Mangara, 2000). Thaumatin is used as a sweetener and flavors enhancer in many food products, including chewing gum, drinks and desserts. Its leaves, known in Côte d'Ivoire as 'attiéké leaves', are used for packaging (e.g., attiéké in Ivorian language, cassava semolina) and cooking certain foods (Kedjenou, Biokosseu, etc.) and medicines. Its growing economic importance is opening new prospects for domestication. Although this species is naturally adapted to shaded undergrowth environments, the optimal conditions for its cultivation in the inter-rows of rubber plantations remain to be evaluated. The first trials combining *Hevea brasiliensis* and *T. daniellii* were conducted in 1997 at the Anguédédou Experimental Station in Côte d'Ivoire. This work showed that vegetative propagation by rhizomes allowed *T. daniellii* to establish itself better than nursery seedlings (Boko et al., 2010), corroborating observations in the literature. However, although this plant is a shade species, the conditions for its optimal growth under rubber tree canopy and its impact on the growth, production and structure of rubber tree stands still require further study. This study therefore aims to evaluate the effect of light in the undergrowth of *Hevea brasiliensis* on the establishment and development of *T. daniellii*, with a view to contributing to the development of sustainable and economically viable agroforestry systems.

2. Material and Methods

2.1 Study Environment

The study was conducted in the rubber plantations of the National Agricultural Research Centre (CNRA), located in Anguédédou in south-eastern Côte d'Ivoire in the District of Abidjan, specifically in the commune of Songon, between 5°22' and 5°25' North latitude and 4°8' and 4°10' West longitude (Figure 1). This municipality is characterized by an average annual temperature of 28.8 °C. This municipality has an average annual temperature of 28.8 °C. Total annual rainfall is 1,545 mm, with a long dry season from December to February, followed by a long rainy season from March to July, a short dry season in August, and finally a short rainy season from September to November (SODEXAM, 2023). The soil is Ferralsol (Brou, 2005).

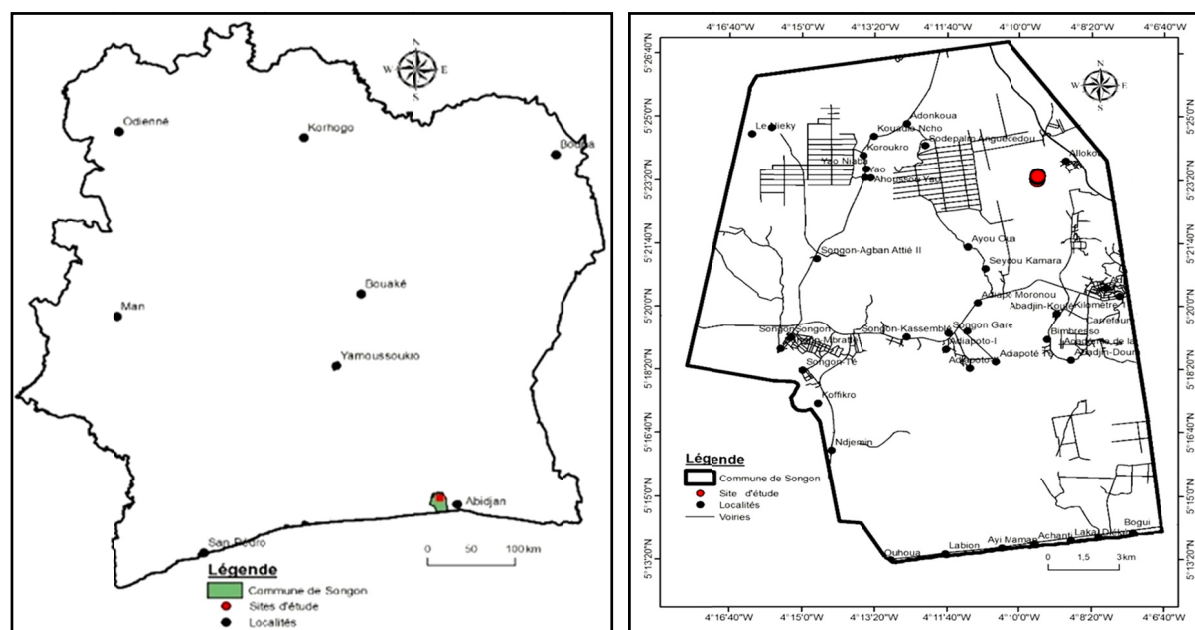


Figure 1. Location of the study site

Source: CNRA, 2022.

2.2 Experimental Design

The study was conducted on three clones of rubber tree: PB 217, IRCA 18 and IRCA 41, selected based on their age and foliage density, two parameters that significantly influence transmitted radiation under canopy cover and a determining factor for the growth of *T. daniellii*. These clones were planted at a density of 510 trees per hectare, with a spacing of 7×2.8 m. The PB 217 and IRCA 18 clones have relatively low coverage, while the IRCA 41 clone has average coverage. The experimental design is structured according to a Fischer block design, with five (5) treatments corresponding to different experimental plots (Table 1). The treatments were repeated four (4) times in plots B1, B3, C5 and D8, and three (3) times in plot H0. Each plot corresponds to a level of transmitted radiation and constitutes an experimental unit. A basic plot consists of three (3) rows of six (6) rows of rubber trees, including a central row and two inter-rows, *i.e.*, five (5) usable rows. *T. daniellii* is planted 1.5 m from the rubber tree row, at a density of 3.17 plants/m² (spacing of 70×44 cm), according to the recommendations of TALIN FOOD. Planting was carried out using rhizomes to reduce variability related to plant material. Within each plot, the following parameters were monitored to evaluate the performance of *T. daniellii* under different levels of transmitted radiation: transmitted radiation (TR), germination rate, tillering and number of leaves per square meter.

Table 1. Characteristics of plots, age and ground coverage of rubber tree clones

N° of plot	Rubber clone	Age of plantation (year)	Characteristic of ground coverage of the tree	Metabolic class of the clone	Genetic origin of clone
B1	PB 217	4	Low ground coverage	Slow	PB5/51 $\times$ PB6/9, in Malaysia, 1955
B3	PB 217	2	Very low ground coverage	Slow	
C5	IRCA 41	5	Medium ground coverage	Medium	GT 1 $\times$ PB 5/51, in Côte d'Ivoire, 1974
D8	IRCA 18	5	Very high ground coverage	Rapid	GT1 $\times$ PB 5/51, in Côte d'Ivoire, 1990
H0	IRCA 18	4	Medium ground coverage	Rapid	

2.3 Soil Sampling

Soil samples were taken using an auger in the 0-30 cm horizon before the trial was set up. For each elementary plot, three (03) soil samples were taken and then homogenized to form a composite sample. Physicochemical analyses of the soil (particle size, pH, organic matter content, adsorbing complex) were carried out at the Soil Analysis Laboratory of Ecole Supérieure de Agronomie (ESA) in Côte d'Ivoire.

2.4 Measurement of Transmitted Radiation

The assessment of radiation transmitted in the plots was carried out using a portable digital lux meter, model LX1010B, recognized for its accuracy in measuring illuminance in natural environments (Yao et al., 2018). This device, which is easy to transport and use, is particularly suitable for field surveys. Before each measurement session, the lux meter was calibrated in accordance with the manufacturer's recommendations to ensure the reliability of the recorded data (Brou, 2005). At the same time, a portable GPS device (Garmin) was used to record the geographical coordinates of each plot, thus ensuring the spatial traceability of light measurements (Kouadio et al., 2017). Light intensity measurements were taken at three key times of the day to account for natural variations in sunlight (Kouamé et al., 2019): in the morning (between 8:00 a.m. and 9:00 a.m.), at midday (between 12:00 and 13:00) and in the late afternoon (between 4:00 p.m. and 5:00 p.m.). At each moment, five (05) measurement points were selected in each plot: one in the center and four at the corners of the plot, arranged in a cross pattern, to accurately assess the spatial variability of light intensity (Soro et al., 2016). For each point, three successive readings were taken, and their average was calculated to obtain a representative value. All measurements were taken only in clear weather, without rain or significant cloud cover, to limit biases related to weather conditions (Brou, 2005). In case of unfavorable weather, the readings were postponed.

2.5 Measures of Agronomic Data

Sampling of *T. daniellii* was carried out using a stratified plot method to consider the variability of light penetration in the undergrowth (Soro et al., 2016). A grid was established on each plot to enable precise location of the plants. All *T. daniellii* individuals located within the plot boundaries were recorded. Each plant was marked with colored and numbered tape to ensure individual monitoring over time (Kouamé et al., 2019). Only plants with at least two fully developed leaves were selected for growth monitoring, in accordance with the vigor criteria defined by Yao et al. (2018). Monitoring, carried out every 30 days over a period of thirty (30) months,

focused on the germination and tillering rates, and the number of leaves and fruits produced. These parameters were measured as follows:

2.5.1 Germination rate and plant height

Germination rate was considered effective as soon as the seedling appeared on the soil surface. The germination rate (%) was determined 45 days after sowing. The height of the seedlings that emerged was measured at the same time. This height, expressed in cm, corresponds to the distance between the soil and the apex of each seedling. The germination rate was calculated using the following formula:

$$\text{Germination rate (\%)} = \frac{\text{Number of seedlings emerged}}{\text{Total number of rhizomes planted}} \times 100 \quad (1)$$

2.5.2 Tillage

Tillage (number and location) was assessed by manually counting the number of stems (tillage) produced per plant 45 days after sowing. This parameter provides information on the plant's vegetative vigor and its ability to multiply.

2.5.3 Number of Leaves and Fruits per Unit Area

Leaf counts were carried out on a one-square-meter area (1×1 m) in each experimental plot. Only visible, well-developed leaves were counted. In addition, fruiting was assessed at plant maturity by counting the number of fruits produced per square meter of surface area. This agronomic parameter makes it possible to estimate the potential productivity of the species.

2.6 Statistical Data Processing

Data relating to undergrowth light intensity, growth and production of *T. daniellii* were entered into Excel 2016 for quality control, including correction of duplicates and management of outliers. A descriptive analysis was conducted for each variable measured (light intensity, number of leaves, emergence and tillering rates, number of fruiting) to calculate means and standard deviations, coefficients of variation, with the aim of assessing the heterogeneity between the different plots. To compare the effect of light intensities on the growth and survival parameters of *T. daniellii*, comparative statistical tests were applied. A one-way analysis of variance (ANOVA) was used to compare means between groups (plots with different light levels) when the conditions of normality (Shapiro-Wilk test) and homogeneity of variances (Levene's test) were met. If these conditions were not met, the non-parametric Kruskal-Wallis test was used. When significant differences ($p < 0.05$) were observed, Tukey's HSD test was performed following ANOVA, or Dunn's test following Kruskal-Wallis, to identify statistically distinct groups. All statistical analyses were performed using R software version 4.2.1 (R Core Team, 2022), which offers great flexibility in the application of parametric and non-parametric tests, as well as effective visualization of results in graphical form (boxplots, scatter plots).

3. Results

3.1 Physical and Chemical Characteristics of Soils of Rubber Plantation

Table 2 presents the physical and chemical characteristics of the top 0 - 30 cm layer of soil in the experimental plots prior to the start of the trial. The grain size proportions (clay, fine and coarse silt, fine and coarse sand) reveal a certain textural homogeneity between the plots, with a sandy dominance (67 to 73%) characteristic of a sandy-clay texture (SA). The soil pH is between 4.0 and 4.3, indicating high soil acidity. Organic matter (OM) content varies from 3.0 to 3.7%. Nitrogen (N) content in the soil ranges from 0.05 to 1.53% for plots H0 and B1 respectively. The carbon/nitrogen (C/N) ratio, an indicator of organic matter decomposition dynamics, gives values ranging from 9.1 to 20.3. In terms of the absorbent complex, the CEC values obtained vary between 6.9 and 7.4 cmol(+)/kg across all sites.

3.2 Transmitted Incident Radiation Under Rubber Canopy

The study of transmitted incident radiation (TIR) under rubber tree canopy reveals significant variations depending on the age of the plantation and canopy density. After the introduction of *T. daniellii*, the rates of radiation transmitted under the trees measured vary from 3.7 to 73.2% of incident radiation (Table 3). Among the plots studied, B3, which has been used for rubber cultivation for two years, has the highest rate of transmitted radiation, reaching 73.3%. Conversely, plot D8, which has been in operation for more than five years, has the lowest rate of incident radiation (3.7%).

3.3 Germination Rate and Tillage of *T. daniellii* as a Function of Transmitted Radiation

The evaluation of the germination rate of *T. daniellii* based on transmitted light radiation reveals significant differences ranging from 7 to 66% between rubber tree plots (Table 4). Plots H0 and D8 of the IRCA 18 rubber tree clone recorded the highest germination rates, reaching 66%. In contrast, plots B1 and B3 of the PB 217 clone showed significantly lower rates of 7% and 32%, reflecting less favorable conditions for germination. Tillage, a key indicator of vegetative development, also shows significant disparity between rubber tree plots. Plots H0, D8 and C5 stand out with an average of 6 tills per location, while plots B3 and B1 of clones PB 217 show lower values, with 3 and 4 tills per location respectively.

3.4 Number of *T. daniellii* Leaves per m²

Figure 2 shows the number of *T. daniellii* leaves emitted in rubber tree plots as a function of transmitted radiation. Statistical analysis reveals considerable variability in the number of leaves for each treatment, as illustrated by the wide whisker boxes. Plot B1 stands out with the highest number of leaves, with a median value of 46 leaves, followed by plot H0 with an average of 40 leaves. Treatments B3, C5 and D8 have relatively low median values, ranging from 25 to 30 leaves.

Table 2. Initial physical and chemical characteristics of the soil

N° of plot	Rubber clones	Particle size (%)			Organic matter				P-ass (mg/kg)	Absorbing complex (cmol+/kg)		
		Clay	Silt	Sand	pH	OM (%)	N (%)	C/N		CEC	Ca ²⁺	Mg ²⁺
B1	PB 217	18.5	4.8	73.3	4.3	3.4	1.5	13.7	112.5	7.4	0.17	0.17
B3	PB 217	22.7	5.1	70.2	4.0	3.2	0.11	18.6	96.5	6.6	0.17	0.03
C5	IRCA 41	25.7	5.1	67.7	4.0	3.0	0.16	11.2	76.5	6.7	0.16	0.04
D8	IRCA 18	20.8	4.7	71.9	4.1	3.7	0.12	9.1	95.4	5.8	0.13	0.06
H0	IRCA 18	23.4	5.1	70.2	4.2	3.5	0.05	20.3	58.0	5.9	0.21	0.07

Table 3. Transmitted radiation (%IR) in the trial plots

N° of plot	Rubber clones	Age (year) of rubber trees at the time of planting <i>T. d.</i>	Transmitted radiation (%IR*) after planting
B1	PB 217	4	43,3 ± 9,4 ^b
B3	PB 217	2	73,2 ± 9,3 ^a
C5	IRCA 41	5	21,9 ± 6,6 ^c
D8	IRCA 18	5	3,7 ± 2,6 ^e
H0	IRCA 18	4	10,5 ± 3,3 ^d

Table 4. Rate of germination and tillage of *T. daniellii* according to transmitted radiation (TR)

N° Plot	Rubber clones	Age (year) of rubber trees at the time of planting <i>T. d.</i>	Germination rate (%)	Tillage (number/location)
B1	PB 217	4	32 ^c	4 ^b
B3	PB 217	2	7 ^d	3 ^b
C5	IRCA 41	5	60 ^b	6 ^a
D8	IRCA 18	5	65 ^a	6 ^a
H0	IRCA 18	4	66 ^a	6 ^a

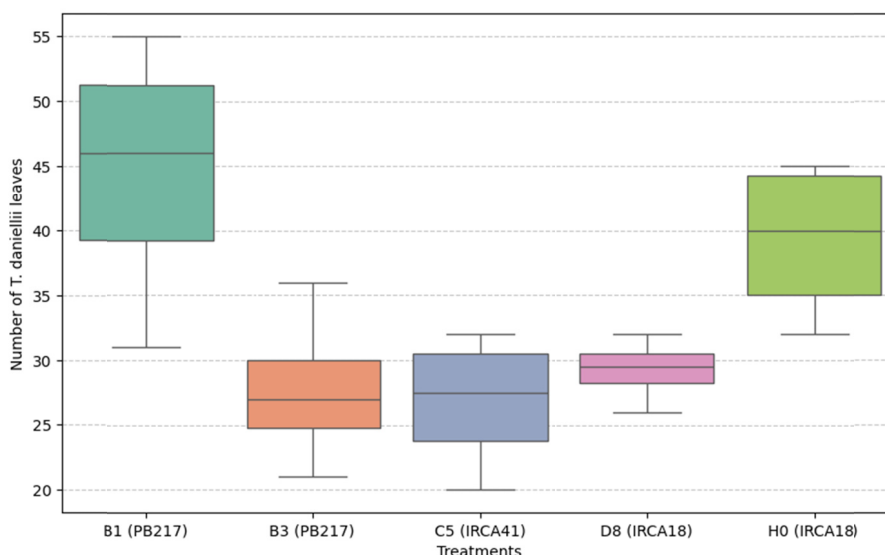


Figure 2. Number of leaves per m² of *T. daniellii* as a function of transmitted radiation

3.5 Number of *T. daniellii* Fruits per m²

Analysis of the fruit production of *T. daniellii* under rubber tree canopy reveals significant variations depending on the age of the plantation and canopy density. These two factors strongly influence fruit production per square meter, thereby affecting the growth dynamics and productivity of this species. The results obtained show significant disparities between rubber tree plots and clones (Table 5). Plot H0 of clone IRCA 18 recorded the highest production with 73 fruits/m², indicating particularly favorable ecological conditions. It is followed by plot C5 of clone IRCA 41, with an equally high yield of 68 fruits/m², close to that observed in H0. In contrast, plot B3 of clone PB 217 had the lowest production with 40 fruits/m².

Table 5. Number of fruits produced per square meter thirty (30) months after planting *T. daniellii*

N° plot	Rubber clone's	Age (year) of rubber trees at the time of planting <i>T. d</i>	Number of fruits produced per square meter
B1	PB 217	4	51 ^d
B3	PB 217	2	40 ^e
C5	IRCA 41	5	68 ^b
D8	IRCA 18	5	58 ^c
H0	IRCA 18	4	73 ^a

Note. * Values followed by the same letter are not statistically different.

3.6 Relationship Between Circumference and Germination Rate of *T. daniellii*

Figure 3 shows the variation in the germination rate of *T. daniellii* (%) as a function of the trunk circumference (cm) of rubber trees, regardless of clone. Analysis of the graph shows that the germination rate increases gradually from 30% at 20 cm circumference to a maximum of 65% at 40 cm circumference. Beyond 40 cm, there is a gradual decrease in germination rate (60% at 45 cm and 55% at 50 cm), indicating that excessively high circumferences do not promote germination. Thus, a circumference of 40 cm appears to be the optimal value for maximizing the germination rate of *T. daniellii*.

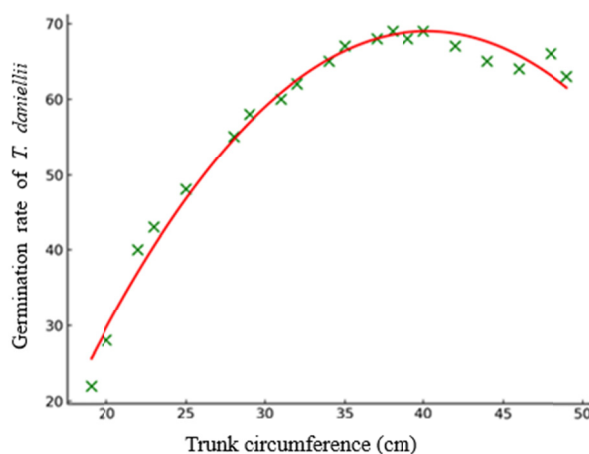


Figure 3. Relationship between rubber tree trunk circumference and germination rate of *T. daniellii*

3.7 Relationship Between Rubber Tree Trunk Circumference and Germination Rate of *T. daniellii*

The figure shows the results of the study on the relationship between trunk circumference (cm) and uncovered interline width (m). The results show an inverse relationship between these two parameters, with a decrease in uncovered interline width as trunk circumference increases (Figure 4). The width of the understory not directly covered by tree crowns is indicative of the level of light reaching the understory. When crowns touch the understory, this value is zero. There is a significant linear relationship ($P = 0.001$) between the circumference of the rubber tree trunk and this value. The smaller the circumferences, the less their foliage covers the interline spacing. The regression in *T. daniellii* emergence rates, at least six months after planting, by rubber tree circumferences shows that there is a highly significant quadratic relationship ($P < 0.001$) between these two variables, with the following parameters:

$$L = -0.09CIR^2 + 7.02CIR - 69.6 \text{ with } R^2 = 0.97 \quad (2)$$

This model accounts for 71.9% of the observed variations in germination rates.

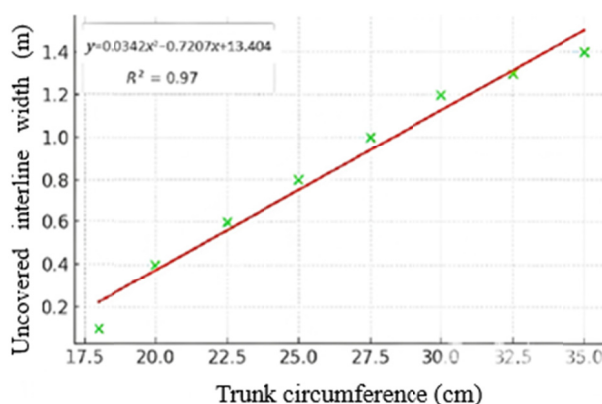


Figure 4. Relationship between trunk circumference and canopy cover

4. Discussion

The granulometric analysis of the soils studied reveals a silty-clayey-sandy texture, dominated by a high proportion of sand. These results show that the soils studied, although relatively homogeneous in terms of granulometry, present major chemical constraints for agricultural productivity, mainly due to their high acidity and low nutrient retention capacity. This acidity can compromise the bioavailability of nutrients, requiring possible amendments to optimize crop growth. Indeed, the study plots are covered with rubber trees aged between 2 and 5 years. At these ages, the vegetation cover is moderate, which could expose these soils to erosion and the effects of temperature, which partially destroys the physical structure of the soil (Martin, 1983). The effects of the bulldozers used to clear the plots should also be noted.

The work of Brad (2005), and Gerson and Gnamba-Yao (2020) has shown the harmful effect of bulldozer tracks on soil structure and texture. Furthermore, Bassolé et al. (2023), in their studies on tropical soils, also observed that silty-clay-sandy textures are common in West Africa, but that the high proportion of sand exacerbates nutrient leaching problems, especially in humid climates. The study of radiation transmitted under rubber tree canopies shows that light transmission varies greatly depending on the age of the plantation and the density of the canopy. Young plots, such as B3 (two years of exploitation), have high light transmission, while older plantations, such as D8 (more than five years), have much lower transmission, indicating denser canopy cover. This dynamic confirms that the increase in the age of rubber plantations is correlated with a significant reduction in light penetration due to the gradual thickening of the canopy.

These results confirm the known link between canopy growth dynamics and the reduction of light available at ground level, a phenomenon that is well documented in agroforestry systems. According to Rouspard et al. (2021), in tropical agroforestry plantations, vegetation cover density becomes a key factor in regulating the microclimate at ground level after 3 to 5 years of growth, with reductions in direct radiation comparable to our observations. Furthermore, Epron et al. (2020) observed that in young rubber tree plantations in West Africa, light transmission remains high during the first 2 to 3 years (above 60% of IR), before falling to less than 10% after 5 years, which is entirely consistent with the results of this study. The assessment of the germination rate of *T. daniellii* as a function of transmitted radiation shows significant variations between plots. Plots H0 and D8 show the best emergence rate results, above 66%, reflecting good adaptation to local light conditions.

However, plots B1 and B3 show much lower rates of between 7 and 32%, indicating less favorable conditions for germination. Tillering, which measures vegetative development, follows a similar pattern. Plots H0, D8 and C5 recorded an average of 6 tillers per location, indicating robust growth, while plots B1 and B3 recorded an average of 3 to 4 tillers, indicating more limited growth. These results confirm the decisive importance of the light microclimate on the emergence and growth of *T. daniellii*. According to Ndoeye et al. (2021), moderate radiation is optimal for the germination of many species under forest cover, while excess or insufficient light can significantly reduce germination rates. The best performance observed at H0 and D8 could be explained by an optimal balance between light and soil moisture, two factors essential for establishment.

Furthermore, the results obtained on tillering corroborate the observations of Kouadio et al. (2022), who showed that under semi-open canopy cover, *T. daniellii* develops a more vigorous vegetative system thanks to better availability of diffuse light, thus promoting tillering. Conversely, the poor performance of plots B1 and B3 could be linked either to excessive direct radiation (water stress effect) or to unfavorable soil conditions, as highlighted by Yao et al. (2020) in their work on the sensitivity of species under heliophilous canopy cover. Analysis of the number of leaves according to the different treatments reveals notable disparities in leaf development. Plot B1 stands out with the highest number of leaves, while plot H0 has the lowest. Treatments B3, C5 and D8 show a certain homogeneity in their leaf response. These results confirm that leaf development is strongly influenced by the specific conditions of each treatment, particularly the light environment and the nutritional status of the plots.

Indeed, Fofana et al. (2021) demonstrated that light and nutrient availability are determining factors in leaf development in tropical agroforestry systems. The best performance observed for B1 could be attributed to an optimal combination of light and nutrients, promoting leaf multiplication. Furthermore, Diallo et al. (2022) pointed out that differences in leaf number may also reflect morphological adaptation of plants to environmental stresses (water deficiency, soil acidity, low fertility). This would explain the more modest performance observed at H0, where probable stress may have limited leaf expansion. The study of *T. daniellii* fruiting under rubber tree cover reveals significant variations influenced by the age of the plantation and canopy density. Fruit production per square meter is strongly impacted by these parameters.

Thus, the results confirm that the availability of light under the canopy is a determining factor in fruiting, as shown by Lemmens et al. (2021), who emphasize that *T. daniellii* is a semi-heliophilous species, requiring a balance between moderate shade and diffuse light to optimize its productivity. In comparison, Yao et al. (2022) observed that in intercropping systems under tropical forests, a reduction in photosynthetically active radiation leads to a significant decrease in flowering and fruiting. The superior performance of plot H0 can be attributed to a relatively open canopy, allowing better light penetration, unlike B3, where greater foliage density appears to restrict photosynthesis and therefore fruit set. These observations corroborate those of Agyeman et al. (2023), who demonstrated that in agroforestry systems, excessive canopy cover not only reduces vegetative growth but also the reproduction of understory species. Analysis of the relationship between rubber tree trunk circumference and *T. daniellii* germination rate reveals an interesting trend.

The results show that the germination rate of *T. daniellii* initially increases with trunk circumference, reflecting a positive effect of increased shading provided by more developed trees. However, this relationship follows a bell curve, as beyond a certain threshold of circumference (and therefore shading), the germination rate begins to decline. This confirms that *T. daniellii* requires an optimal balance of diffuse light for successful germination. This dynamic is comparable to the observations of Lemmens et al. (2021), who showed that semi-shaded species in tropical environments thrive under moderately dense canopy cover, but their establishment is inhibited under excessive shade. Similarly, Sarr et al. (2022) noted that excessive canopy density drastically reduces the photosynthesis necessary for the establishment of young plants. The upward phase of the curve illustrates that shade protects young seedlings from water and heat stress (Jones et al., 2020), promoting better emergence. On the other hand, when light becomes insufficient, growth and emergence are limited, as also demonstrated by Agyeman et al. (2023) on other tropical understory species.

The study explores the relationship between the circumference of rubber tree trunks and the width of the interline spacing not covered by the leaf canopy. The results show a highly significant linear inverse relationship ($P = 0.001$): as trunk circumference increases, the width of the uncovered inter-row space decreases. This means that foliage development gradually closes the inter-row spaces, reducing ground light. These results confirm that canopy development strongly influences ground light conditions, which are essential for the establishment of understory species such as *T. daniellii*. The study is consistent with the work of Schroth and Sinclair (2021), who demonstrated that progressive shading in agroforests gradually limits direct light, affecting the germination and growth of associated plants. Furthermore, the quadratic relationship identified is reminiscent of the observations of Kwesiga and Boffa (2020), which show that for many understory species, moderate light levels are optimal: too little light limits photosynthesis, while too much light can induce water or heat stress.

The strong quadratic correlation ($R^2 = 71.9\%$) between circumference and emergence rate also confirms the conclusions of Caron et al. (2023), who indicate that canopy architecture is a powerful predictor of the dynamics of understory species.

5. Conclusion

The results obtained from our various analyses show the determining importance of environmental parameters (soil pH, organic matter content and transmitted radiation) on the growth and productivity dynamics of crops grown under rubber tree cover, particularly *T. daniellii*. On the one hand, the soil study reveals a predominantly silty-clay-sandy texture, pronounced acidity (pH between 4.0 and 4.3) and average organic matter content, influencing the availability of essential nutrients.

On the other hand, analysis of the radiation transmitted under the rubber tree canopy reveals a close correlation between the age of the plantations and light attenuation, with the gradual densification of the canopy significantly reducing the amount of light reaching the ground. This light dynamic directly impacts the germination rate, vegetative development (tillage and number of leaves) and fruiting of *T. daniellii*.

The significant quadratic relationship observed between the circumference of rubber tree trunks and the germination rate confirms that *T. daniellii* benefits from moderate light levels for optimal establishment. Our results therefore highlight the need for rational light management to optimize production in integrated agroforestry systems, particularly that of *T. daniellii*. In this sense, extending this investigation to farming communities across different agroecological zones would allow for a more representative assessment of the impact of rubber tree canopy cover on the development of this species.

The development of *T. danielli* cultivation offers farmers the opportunity to develop an agroforestry system, a means of agricultural intensification and diversification of income sources.

References

- Agyeman, K. O., Osei Owusu, P., & Antwi, E. K. (2023). Effect of agroforestry practices on soil properties and farmers' livelihood in Sub-Saharan Africa. *Agriculture, Ecosystems & Environment*, 348, 108441. <https://doi.org/10.1016/j.agee.2023.108441>
- Bassole, Z., Yanogo, I. P., & Idani, F. T. (2023). Caractérisation des sols ferrugineux tropicaux lessivés et des sols bruns eutrophes tropicaux pour l'utilisation agricole dans le bas-fond de Goundi-Djoro (Burkina Faso). *Revue Internationale des Sciences Biologiques et Chimiques*, 17(1), 247-266. <https://doi.org/10.4314/ijbcs.v17i1.18>
- Boko, C., Keli, J. Z., Okoma, M., Tahouo, O., & Obouayeba, S. (2010). *Associer des cultures vivrières à l'hévéa pour diversifier les sources de revenu en Côte d'Ivoire* (p. 52). Rapport annuel (Le CNRA en 2010), CNRA-Direction des Innovations et des systèmes d'information.

- Brad, J. (2005). The harmful effects of bulldozer tracks on soil structure and texture. *Soil Science Journal*, 170(2), 101-110. <https://doi.org/10.1016/j.ssj.2005.02.007>
- Brou, Y. T. (2005). Évaluation des instruments de mesure de l'éclairement dans les systèmes agroforestiers. *Bulletin de la Société de Géographie d'Abidjan*, 27(2), 14-21.
- Caron, M., Kouassi, K. P., & Ouattara, D. (2023). Rôle de la structure du couvert forestier dans la régénération des espèces herbacées. *Journal Ouest-Africain d'Écologie Appliquée*, 15(1), 33-41.
- Diallo, A., Sow, M., Traoré, S., & Keita, M. (2022). Effet de la gestion des cultures sur la fertilité du sol et la production agricole en Afrique de l'Ouest. *Journal of Agricultural Science and Technology*, 22(1), 65-77.
- Epron, B., Rounsard, O., Follain, S., Le Maire, G., Bonnefond, J. M., & Harmand, J. M. (2020). Influence de la densité du couvert végétal sur les flux de carbone et l'architecture du sol en milieu tropical. *Agriculture, Ecosystems & Environment*, 295, 106899. <https://doi.org/10.1016/j.agee.2020.106899>
- Fofana, M., Traoré, K., & Camara, M. (2021). Évaluation de la fertilité des sols dans les paysages cultivés du Mali : cas du bassin du Niger supérieur. *African Crop Science Journal*, 29(3), 401-414.
- Gerson, Y. L., & Gnamba-Yao, J. B. (2020). Analyse des contraintes et stratégies du développement de la riziculture dans la Sous-préfecture de Kouibly à l'Ouest de la Côte d'Ivoire. *Espace Géographique et Société Marocaine* (pp. 33-34).
- Jones, A., Smith, B., & Taylor, C. (2020). The role of shade in protecting young seedlings from water and heat stress. *Journal of Plant Ecology*, 13(5), 345-356. <https://doi.org/10.1093/jpe/rya123>
- Keli, J. Z., Omont, H., Assiri, A. A., Boko, K. A., Abouayebe, S., Dea, B. G., & Doumbia, A. (2005). Associations culturales à base d'hévéa : bilan de 20 années d'expérimentations en Côte d'Ivoire. Partie 1: Comportement végétatif. *Agronomie africaine*, 17(1), 37-52. <https://doi.org/10.4314/aga.v17i1.1656>
- Kouadio, A. M.-C., Kéli, Z. J., Assiri, A. A., & Déa, G. B. (1997). *Study of the intercropping of rubber trees and food plants: Vegetative growth and changes in the environmental parameters* (p. 27). Séminaire STD III, 8-9 Juillet, 1997, Sembawa, Indonesia.
- Kouadio, E. K., Yao, C. Y., & N'Guessan, K. F. (2017). Application des outils de géolocalisation dans la caractérisation des parcelles agroécologiques. *Journal Africain de Géomatique*, 9(1), 22-30.
- Kouadio, E. K., Koffi, B. Y., & Adou Yao, C. Y. (2022). Impact de la déforestation sur les propriétés physiques et chimiques des sols en Côte d'Ivoire. *African Journal of Agricultural Research*, 17(4), 542-550.
- Kouamé, D. E., Traoré, A., & N'Dri, K. J. (2019). Influence des variations journalières de l'ensoleillement sur la photosynthèse des cultures vivrières en Côte d'Ivoire. *Revue Africaine d'Agronomie*, 13(2), 78-86.
- Kwesiga, F., & Boffa, J. M. (2020). Agroforestry and soil fertility management: A synthesis of African experiences. *Agroforestry Systems*, 94(2), 265-278. <https://doi.org/10.1007/s10457-020-00443-0>
- Lemmens, R., Vanacker, V., Lejeune, P., & De Wulf, R. (2021). Monitoring the changes in soil carbon stocks under different land uses in tropical regions. *Geoderma Regional*, 25, e00365. <https://doi.org/10.1016/j.geodrs.2021.e00365>
- Mangara, A. (2000). *Contribution à l'étude de la biologie de la reproduction chez Thaumatooccus daniellii (Benn.) Benth. et Hook. (Marantaceae)* (p. 71, Diplôme d'Etudes Approfondies de Botanique, Université de Cocody, Abidjan).
- N'Guessan, A., & Zouzou, A. (1997). Introduction du thaumatin, une protéine sucrante d'origine végétale. *Journal des Sciences de l'Alimentation*, 12(3), 123-130. <https://doi.org/10.1016/j.jsa.1997.03.001>
- Ndoye, F., Diatta, M., Faye, A., & Guisse, A. (2021). Dynamique de la matière organique du sol sous différents systèmes d'utilisation des terres au Sénégal. *Journal of Soil Science and Environmental Management*, 12(1), 1-8.
- Obouayeba, S. (1995). Récolte de latex de l'hévéa en milieu non industriel. Document de formation des encadreurs du milieu hévéicole non industriel. *Projet Hévéa*, 5.
- Obouayeba, S., Boko, A. M. C. K., Soumahin, E. F., Elabo, A. A. E., Dea, G. B., N'guessan, B. E. A., & Kéli, Z. J. (2015). *Les systèmes de cultures intercalaires à base de caoutchouc naturel en Côte d'Ivoire: Bilan de quarante années de travaux* (pp. 211-226).

- Roupsard, O., Audebert, A., Ndour, A. P., Clermont-Dauphin, C., Agbohessou, Y., Sanou, J., ... Leroux, L. (2021). Jusqu'où va l'arbre affecter la culture en agroforesterie ? Nouvelles méthodes d'analyse spatiale dans un parc à Faidherbia. *Agr. Écosystème. Environ.*, 296, 106928, <https://doi.org/10.1016/j.agee.2020.106928>
- Schroth, G., & Sinclair, F. L. (2021). Impacts of agroforestry on soil quality: A review of the evidence. *Agroforestry Systems*, 95(5), 933-950. <https://doi.org/10.1007/s10457-021-00636-x>
- Soro, D., Koné, M., & Djè, K. M. (2016). Méthodologie d'échantillonnage lumineux dans les études de sous-bois. *Cahiers de Recherche Forestière*, 44(1), 12-20.
- Yao, C. Y., N'Guessan, K. F., & Kouadio, K. E. (2022). Influence de l'ombrage des plantations agroforestières sur la dynamique du carbone du sol en Côte d'Ivoire. *Tropical Agriculture Journal*, 99(3), 255-264.
- Yao, K. F., Koffi, B. Y., & Kouadio, E. K. (2018). Évaluation de la lumière incidente en milieu agroforestier à l'aide de capteurs portatifs. *Revue Ivoirienne des Sciences et Technologies*, 32(1), 45-52.
- Yao, K. F., Koffi, Y. B., & N'Guessan, K. F. (2020). Analyse de la variabilité des caractéristiques physiques des sols dans les zones agroforestières du Centre de la Côte d'Ivoire. *International Journal of Environmental and Rural Development*, 11(1), 38-44.

Acknowledgments

The authors acknowledge the Fund for Agricultural Research and Advice (FIRCA) and the Association of Natural Rubber Professionals (APROMAC) of Côte d'Ivoire for their contributions to this study.

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Ms. Chantal BOKO, project coordinator, is currently Head of Agricultural Operations at APROMAC. She led the project activities alongside Dr. Samuel OBOUAYEBA. Dr. Jean Lopez ESSEHI and Dr. Antoine KOFFI were responsible for drafting the manuscript. Dr. Djézou KONAN, head of the Agronomy and Physiology Unit of the rubber tree research program, and Dr. Guy Fernand YAO reviewed the document. All authors have read and approved the final manuscript.

Funding

This work was supported by Fund for Agricultural Research and Advice (FIRCA), reference: amendment No. 001 agreement No. 77 FIRCA-Research/Hevea.

Competing Interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Informed Consent

Obtained.

Ethics Approval

The Publication Ethics Committee of the Canadian Center of Science and Education.

The journal's policies adhere to the Core Practices established by the Committee on Publication Ethics (COPE).

Provenance and Peer Review

Not commissioned; externally double-blind peer reviewed.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

Data Sharing Statement

No additional data are available.

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