DOI: 10.5433/1679-0359.2023v44n2p721

Impact of intercropping on the photosynthetic activity of coffee

Impacto do cultivo consorciado na atividade fotossintética do café

Dionicio Belisario Luis Olivas[1]; Marcelo Antonio Tomaz[2]; José Francisco Teixeira do Amaral[2]; Fábio Luiz de Oliveira[2]; Paulo Cezar Cavatte[2]; Bruno Fardim Christo[3]; Wagner Nunes Rodrigues[4]; Lima Deleon Martins[5]; Amanda Dutra de Vargas[6]*

Highlights

Intercropping influenced the photosynthetic activity of coffee plants.
A atividade fotossintética das plantas de café foi influenciada pelo consórcio.
Intercropping with banana stood out for net assimilation rate.
Houve destaque no consórcio com bananeira para a variável taxa de assimilação líquida.
Intercropping with two crops negatively influenced water use by the coffee plant.
O consórcio com duas culturas influenciou negativamente o uso da água pelo cafeeiro.

Abstract

Conducting studies that assist in the evaluation of agroecosystems is essential for advancing biodiverse and sustainable agriculture. This study aimed to assess the impact of intercropping on the photosynthetic activity of Arabica coffee plants. The experiment was conducted in the municipality of Alegre, Espírito Santo, southeastern Brazil. Three coffee cropping systems were studied: Arabica coffee monoculture; Arabica coffee intercropped with Nanicon variety banana; and Arabica coffee intercropped with Nanicon variety banana and Juçara palm. The Arabica coffee variety used was Catuaí Vermelho IAC 44, planted in 1991, with a spacing of 3.0 m between rows and 2.0 m between holes, accommodating two plants per hole. In 2010, coffee trees underwent mid-height pruning (low-cutting pruning), and the Nanicon bananas were planted between rows with a spacing of 5.0 x 3.0 m. Three years later, palm seedlings

[1] Prof. Dr., Universidad Nacional José Faustino Sánchez Carrión, UNJFSC, Huacho, Lima, Peru. E-mail: dluis@unjfsc.edu.pe
[2] Profs. Drs., Universidade Federal do Espírito Santo, UFES, Alegre, ES, Brazil. E-mail: tomazamarcelo@yahoo.com.br; jftamaral@yahoo.com.br; fabiocapi@yahoo.com.br; cavattepc@hotmail.com
[3] Student of the Doctoral Course of the Graduate Program in Administration, Universidade Federal de Santa Catarina, UFSC, Florianópolis, SC, Brazil. E-mail: brunochristo@hotmail.com
[4] Prof. Dr., Centro Universitário UNIFACIG, Manhuaçu, ES, Brazil. E-mail: wagner.nunes@sempre.unifacig.edu.br
[5] Prof. Dr., Centro Universitário São Camilo, Cachoeiro de Itapemirim, ES, Brazil. E-mail: deleon_lima@hotmail.com
[6] Student of the Doctoral Course of the Graduate Program in Agronomy, UFES, Alegre, ES, Brazil. E-mail: amandadvargas@hotmail.com
* Author for correspondence

Received: Nov. 28, 2022 Approved: Apr. 30, 2023

were planted in the same rows as the banana plants, with a spacing of 5 x 3 m. Five experimental units were randomly selected for each cropping system. The evaluated variables included chlorophyll indexes (chlorophyll *a*, chlorophyll *b*, total chlorophyll, and chlorophyll *a/b* ratio) and gas exchange parameters (net CO_2 assimilation rate, stomatal conductance, intercellular CO_2 concentration, transpiration, intrinsic water use efficiency, instantaneous water use efficiency, and carboxylation efficiency). Regarding chlorophyll indexes, differences were observed only in chlorophyll *b*, with monoculture coffee displaying the highest values. In terms of gas exchange, intercropped coffee exhibited lower values of intrinsic and instantaneous water use efficiency, and higher values of stomatal conductance and transpiration. The highest net assimilation rate values were observed in coffee with banana intercropping, while the highest water use efficiency was found in coffee in monoculture. In summary, monoculture coffee showed the highest values for most of the variables related to photosynthetic activity, followed by Arabica coffee intercropped with banana, which stood out for achieving the highest net assimilation rate.
Key words: *Coffea arabica. Musa* sp. var Nanicon. *Euterpe edulis.* Intercrop. Gas exchange.

Resumo

Realizar estudos que auxiliem na avaliação de agroecossistemas são de vital importância para avançar no desenvolvimento de uma agricultura biodiversa e sustentável. Desta forma, o objetivo da pesquisa foi avaliar o impacto do consórcio na atividade fotossintética de plantas de cafeeiro arábica. O experimento foi desenvolvido no município de Alegre, Espírito Santo, sudeste do Brasil. O estudo foi realizado em plantações de café sob três sistemas de cultivo: café Arábica em monocultura; café Arábica consorciado com banana variedade Nanicon; e café Arábica consorciado com banana variedade Nanicon e palmito Juçara. A variedade de café Arábica usada nos sistemas de cultivo foi o Catuaí Vermelho IAC 44, plantada em 1991, com espaçamento de 3,0 m entre linhas e 2,0 m entre covas, com duas plantas por cova. Em 2010, as árvores de café foram podadas na altura média (poda de baixo corte) e as bananas da variedade Nanicon foram plantadas entre as fileiras a 5,0 x 3,0 m de espaçamento. Três anos depois, as mudas de palmito foram plantadas na mesma linha que a banana a 5 x 3 m de espaçamento. Em cada sistema foram estabelecidas cinco unidades experimentais, selecionadas aleatoriamente. As variáveis avaliadas foram índices de clorofila (clorofila *a*, clorofila *b*, clorofila total e razão clorofila *a/b*) e trocas gasosas (taxa de assimilação líquida de CO_2, condutância estomática, concentração subestomática de CO_2, transpiração, eficiência intrínseca do uso da água, eficiência instantânea do uso da água e eficiência da carboxilação). Para os índices de clorofila, as diferenças são observadas apenas na clorofila *b*, onde o café em monocultura obteve os maiores índices. No caso das trocas gasosas, os menores valores de eficiência intrínseca e instantânea do uso da água, e os maiores valores de condutância estomática e transpiração, foram encontrados no café com consórcio, em que os maiores valores líquidos taxa de assimilação correspondeu ao café consorciado com banana, enquanto maior eficiência no uso da água, ao café em monocultura. Desta forma, observou-se que o café em monocultivo obteve os maiores valores para a maioria das variáveis envolvidas na atividade fotossintética, seguido pelo consórcio de café Arábica com banana, que se destacou por obter a maior taxa de assimilação líquida.
Palavras-chave: *Coffea arabica. Musa* sp. var Nanicon. *Euterpe edulis.* Consórcio. Trocas gasosas.

Introduction

The coffee plant, an understory species originating from the highland forests of Ethiopia (Bez et al., 2022; Hu et al., 2022), holds significant importance in the global agribusiness sector. It also plays a prominent role in Brazil, with a production of over 50 million 60-kg bags and cultivation spanning more than 2.2 million hectares across different regions of the country (Companhia Nacional de Abastecimento [CONAB], 2022). The species *Coffea arabica* is cultivated in various tropical countries, both in full sun and shaded environments (Boreux et al., 2016).

Due to increasing concerns regarding the environmental aspect of agricultural production, conservation of natural resources, and biodiversity preservation (DaMatta & Rena, 2002), the adoption of alternative systems to coffee monoculture has become more prevalent. These systems involve the association of different species, enabling the extraction of multiple agricultural products from the same area. Moreover, they contribute to the creation of diverse agroecosystems that enhance nutrient cycling, microclimate, and morphophysiological regulation (Ohse et al., 2012; Li et al., 2018).

Furthermore, coffee cultivation is experiencing the adverse effects of rising temperatures resulting from climate change. Intercropping coffee with shade-providing crops has been recognized as a strategy to mitigate the impact of extreme climatic conditions, creating a more favorable and sustainable environment for coffee production (Jesus et al., 2012). In Brazil, several tree and fruit crops, including banana, coconut, and heart palm, among others, are being used in consortia with coffee (Pezzopane et al., 2007).

The availability of radiation is a crucial factor influencing the growth of coffee plants. The presence of taller plants within the plantation creates shade, modifying the microclimate and influencing vegetative and reproductive growth (Campanha et al., 2007). Consequently, variations in light intensity occur in these environments, prompting plants to adjust their photosynthetic apparatus to enhance the absorption and transfer of energy for photosynthetic processes (Souza et al., 2011).

Some indicators provide insights into the photosynthetic capacity and efficiency of plants; most notably, the amount of chlorophyll per unit of leaf area and the net assimilation rate (García et al., 2005). These parameters are used to determine biomass production under different exploitation conditions. The quantification of these variables and the study of their dynamics over time contribute to a better understanding of plant behavior throughout the developmental cycle, which is closely linked to the utilization of light energy, CO_2, water, and nutrients. Such knowledge could also be valuable for designing effective management systems (Fortes et al., 2009). In this context, the objective of this study was to determine which photosynthetic characteristics are influenced by intercropping in coffee plants in the Caparaó region, located in the southern part of Espírito Santo state, Brazil.

Material and Methods

The experiment was conducted in Lagoa Seca, a rural area within the municipality of Alegre, located in the state of Espírito Santo, Brazil. The study site is a typical Arabica coffee-producing property situated at an altitude of 740 m above sea level, with the following geographical coordinates: 20° 53'30'' south latitude and 41° 28' west longitude. The region exhibits a rugged undulating topography, and the soils are classified as Red-Yellow Latosols. Based on the Köppen classification, the climate of the area is Cwa, characterized by rainy summers and dry winters. Precipitation and temperature data for the 2016/2017 crop season were collected using an E5000 automatic weather station installed at the study site. The average annual temperature was 21.34 °C, and the annual rainfall was 1,616.29 mm (Figure 1). These climatic conditions are suitable for coffee cultivation (Mesquita et al., 2016).

The study involved three cropping systems in coffee plantations: a) Arabica coffee monoculture (CM); b) Arabica coffee intercropped with Nanicon variety banana (CB); and c) Arabica coffee intercropped with Nanicon variety banana and Juçara palm (CBP). The Arabica coffee variety used in all cultivation systems was Catuaí Vermelho IAC 44, which was planted in 1991, with contour lines oriented westward. The spacing between rows was 3.0 m, and there were two plants per hole. In 2010, the coffee trees underwent mid-height pruning (low-cutting pruning), and the Nanicon variety bananas were planted between the rows with a spacing of 5.0 x 3.0 m. Three years later, palm seedlings were planted in the same rows as the bananas, with a spacing of 5 x 3 m.

The characteristics of the three cropping systems were as follows: a) coffee in monoculture (CM) - cultivated species *C. arabica* L. var Catuaí Vermelho IAC-44; average number of 3,333 coffee plants/ha; the average height of coffee plants was 2.40 m; solar radiation measured at noon was 1625 photon m^{-2} s^{-1}; b) coffee intercropped with banana (CB) - cultivated species *C. arabica* L. var Catuaí Vermelho IAC-44 and *Musa* sp. var. Nanicon; average number of 3,333 coffee plants ha^{-1} and 666 banana plants ha^{-1}; the average height of the coffee plants was 2.40 m and the average height of the banana plants was 5.0 m; solar radiation measured at noon was 196 µmol photon m^{-2} s^{-1}; c) coffee intercropped with banana and palm heart (CBP) - cultivated species *C. arabica* L. var Catuaí Vermelho IAC-44, Musa sp. var Nanicon, and *Euterpe edulis*; average number of 3,333 coffee plants ha^{-1}, 666 banana plants ha^{-1}, and 666 palm plants ha^{-1}; the average height of the coffee plants was 2.40 m, the average height of the banana plants was 5.0 m, and the average height of the palm plants was 3.0 m; solar radiation measured at noon was 162 µmol photon m^{-2} s^{-1}. The radiation measurement was performed at a single point within each cultivation system (Figure 2).

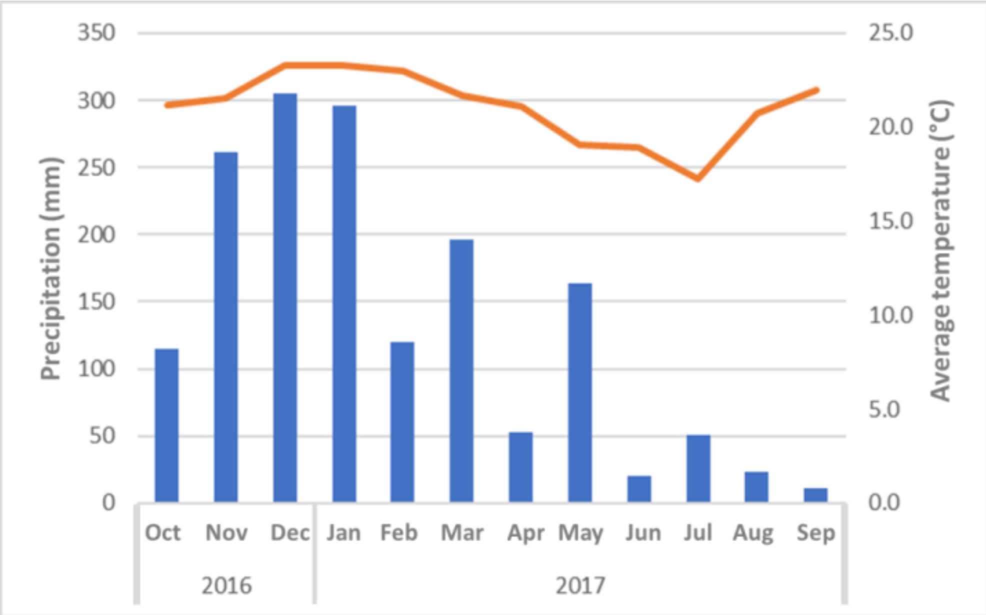

Figure 1. Meteorological data of the area in the experimental period. Alegre, Espírito Santo, Brazil. 2016/2017.

The tillage management practices in this study followed the recommendations proposed for Arabica coffee by Reis and Cunha (2010). In October 2016, soil acidity was adjusted by liming, and one month later, the first application of macro- and micronutrients was carried out. Two additional applications of macronutrients were made subsequently in December 2016 and February 2017, following the nutritional management recommendation for Arabica coffee (Prezotti et al., 2007).

The crops were cultivated under dryland conditions without the use of chemicals for pest and disease control. Weed control was achieved by mechanical cutting with a sickle, with the plant residues left on the soil as ground cover. The experimental units consisted of randomly selected 30-m^2 areas within each cropping system. Five replications were used, and the mean values of the plots were estimated based on evaluations of all central plants in each plot.

At the stage when the fruits reached their maximum growth expansion (granation stage), the following physiological characteristics were evaluated: (a) chlorophyll indexes (chlorophyll *a, b,* and total chlorophyll content), measured using a portable chlorophyll meter ("ChlorofiLOG" Falker model CFL1030); (b) gas exchange parameters, (CO_2 assimilation rate (*A*, μmol CO_2 m^{-2} s^{-1}), transpiration rate (*E*, mmol H_2O m^{-2} s^{-1}), stomatal conductance (*gs*, mol H_2O m^{-2} s^{-1}), and intercellular CO_2 concentration (*Ci*, ppm)), measured using a portable infrared gas analyzer (IRGA Licor 6800XT). Photosynthetically active radiation was standardized with artificial light, with a photon saturation of 1000 μmol m^{-2} s^{-1}, and the chamber CO_2 concentration was set at 420 ppm; and (c) estimates of instantaneous water use efficiency (A/E, μmol CO_2 $mmol^{-1}$ H_2O), intrinsic water use efficiency (*A/gs*, μmol CO_2 mol^{-1} H_2O), and instantaneous carboxylation efficiency (*A/Ci,* mol CO_2 m^{-2} s^{-1}).

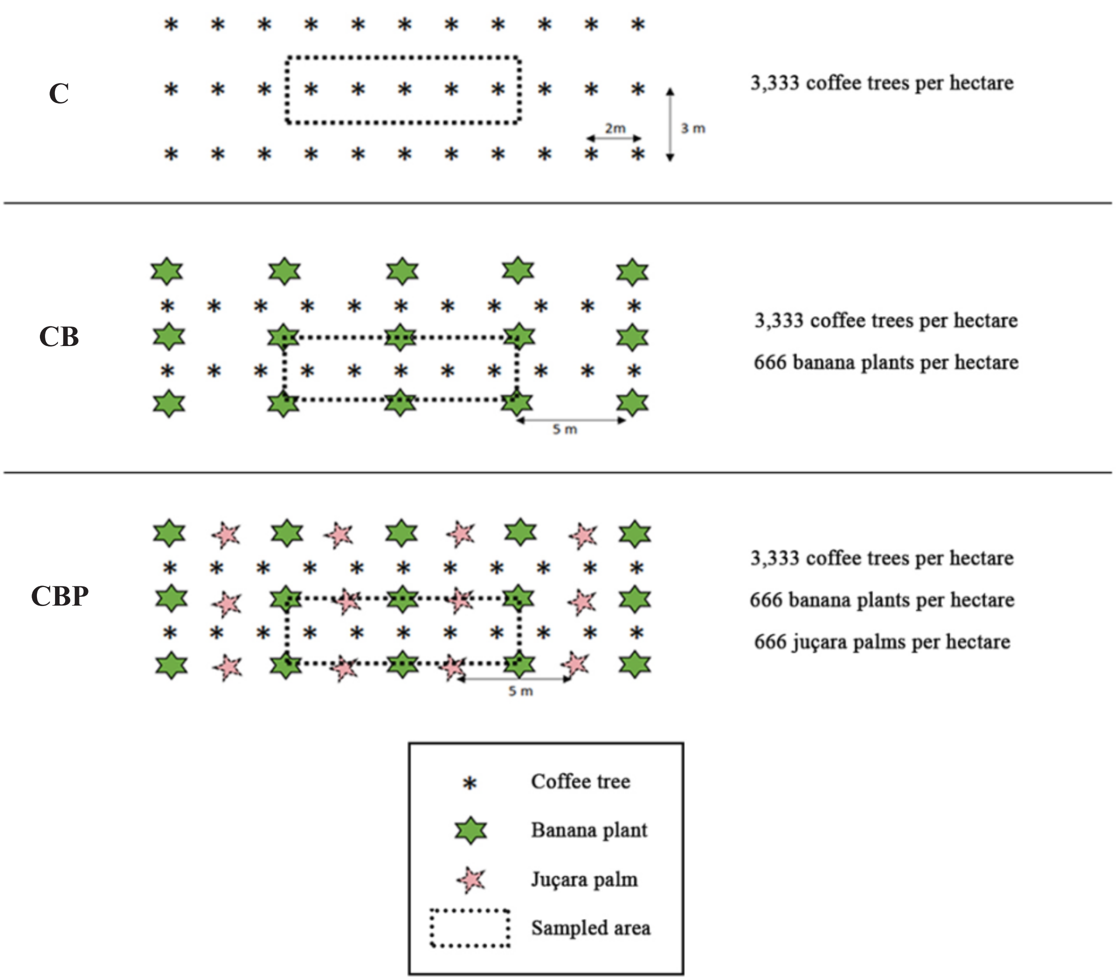

Figure 2. Schematic representation of the experiment. Alegre, Espírito Santo, Brazil. 2016/2017.

These traits were evaluated in fully expanded leaves of the third or fourth pair, starting from the apex of the plagiotropic branches and reaching the average height of the plant. Three central plants were selected for each sampled area, and measurements were taken between 08h00 and 11h00. Two plagiotropic branches per plant, one on each side of the cultivation row, were evaluated. Results were expressed as mean values per plant for each experimental plot.

Descriptive statistical analyses were performed using the obtained results. For each variable, the mean, standard deviation, maximum value, minimum value, and coefficient of variation were calculated. The normality of data distribution was assessed using the Shapiro-Wilk test at a significance level of 5%. The symmetry and kurtosis coefficients of the distributions were estimated using benchmark values of 0 and 3, respectively. Data analyses were conducted using the SISVAR statistical program (Ferreira, 2019). Means and 95% confidence intervals were used to compare the means between cropping systems, considering them similar when the confidence intervals overlapped (Payton et al., 2000).

Results and Discussion

Chlorophylls

Upon observing the results, it is evident that the average chlorophyll *a* content did not differ significantly between the cultivation systems (Table 1). However, when analyzing chlorophyll *b* and total chlorophyll content, the CM and CB systems exhibited the highest means and did not differ from each other (Table 1). In contrast, the CBP and CB systems had the highest means for the chlorophyll *a/b* ratio (Table 1). Overall, the CB cultivation system demonstrated greater prominence in most of the evaluated chlorophyll characteristics, except for chlorophyll *a*, for which no significant differences in the means were observed between the systems (Table 1).

Table 1
Chlorophyll *a* (CL*a*), chlorophyll *b* (CL*b*), total chlorophyll (CLT), and chlorophyll *a/b* ratio (CL*a/b*) indexes of Catuaí Vermelho IAC 44 coffee under three cropping systems: coffee monoculture (CM), coffee intercropped with banana (CB), and coffee intercropped with banana and heart palm (CBP), 2016/2017 harvest, Alegre - Espírito Santo

Cultivation system	CL*a*	CL*b*	CLT	CL*a/b*
Mean: CM	44.41 ± 0.57a	21.74 ± 1.32a	66.14 ± 1.73a	2.05 ± 0.11b
Mean: CB	43.99 ± 0.88a	19.56 ± 2.58ab	63.54 ± 3.21ab	2.28 ± 0.27ab
Mean: CBP	43.91 ± 1.45a	17.78 ± 2.60b	61.69 ± 3.14b	2.51 ± 0.35a
Maximum	45.55	23.08	68.13	2.96
Minimum	42.20	15.40	58.40	1.91
Overall mean	44.10	19.69	63.79	2.28
$CV_{experimental}$ (%)	2.23	13.55	5.01	13.66
$W_{calculated}$	0.93^{N}	0.93^{N}	0.93^{N}	0.93^{N}
Coefficient of asymmetry	-0.53	-0.28	-0.44	0.72
Coefficient of kurtosis	2.43	1.80	1.99	2.59

The sample originates from a population with normal distribution, using the Shapiro-Wilk test at 5% probability. The benchmark values for the asymmetry and kurtosis estimators are 0 and 3, respectively. Means followed by the same letter between rows, within each column, do not differ according to Payton et al. (2000). Each mean is followed by its respective standard deviation (±).

Photosynthesis can be influenced by both shading and excessive light, requiring adjustments to enhance light capture efficiency or photoprotection, respectively (Imru et al., 2015). Such adjustments are commonly observed in morphophysiological adaptation mechanisms and changes in photosynthetic responses (Slattery et al., 2018). Some studies have established a direct relationship between light intensity and leaf-related characteristics (Cogliatti-Carvalho et al., 1998; Deng et al., 2012a,b; Holcman & Sentelhas, 2013).

The intensity of light reaching plants can result in morphological changes such as a reduction in photosynthetic pigment content (chlorophyll *a, b,* and total) and accumulation of photo-assimilates (Coelho et al., 2014). Increases in ultraviolet radiation can lead to the degradation and synthesis of these pigments, whereas reduced ultraviolet radiation can result in higher levels of chlorophyll *a* and *b* in plant tissues (Kataria et al., 2013). This adaptability of plants, effectively influencing the photochemical reactions of photosynthesis, represents a mechanism to adjust to lower light intensities (Ruberti et al., 2012).

The chlorophyll content of coffee leaves can be modified by shading (Partelli et al., 2014; A. V. Araújo et al., 2016). Typically, leaves exposed to direct sunlight exhibit lower chlorophyll content per reaction center, a higher ratio of chlorophyll *a* to *b*, and increased carotenoid amounts compared with shaded leaves (Rochaix, 2014; Taiz et al., 2017). Mayoli and Gitau (2012) and A. V. Araújo et al. (2015) found higher chlorophyll levels in shaded coffee plants intercropped with Cordia africana (*Cordia abyssinica*) and banana trees, respectively. Cavatte et al. (2012) and Ribeiro et al. (2019) also observed higher total chlorophyll content in shaded coffee trees compared with those grown in full sun. Bonfim et al. (2010) reported higher levels of total chlorophyll in shade-grown arabica coffee trees with adequate nutritional conditions compared with coffee trees grown in full sun.

Studies by Quevedo-Rojas et al. (2018) on rainforest seedlings and Poorter et al. (2019) on woody plants revealed higher total chlorophyll content in shadier environments compared with areas with higher photosynthetically active radiation. Numerous studies conducted in various crops have reported higher chlorophyll content in shaded plants compared with those grown in full sun (Mayoli & Gitau, 2012; Rezai et al., 2018; Tang et al., 2019; Wang et al., 2020; Chen et al., 2021a). According to Brisolara (2013), an increase in chlorophyll b content is likely to occur in shaded environments as an adaptation to reduced light intensity.

However, the fact that the CBP system (with lower luminosity) exhibited lower chlorophyll *b* and total chlorophyll content compared with the other systems (with higher radiation) indicates that this response depends on variables other than just the amount of light received by the leaf. These disproportionate results arise because chlorophylls respond differently to stress situations (Kramer & Kozlowski, 1979). In conilon coffee shaded by rubber trees, A. V. Araújo (2013) found similar levels of chlorophyll *a*, chlorophyll *b*, and total chlorophyll between coffee trees grown in the shade and those in the sun during summer. Nonetheless, during winter, coffee trees in the shade showed lower levels of chlorophyll *b* and total chlorophyll. These findings demonstrate that not only luminosity levels but also the evaluation timing influence the results.

When shading increases, the chlorophyll *a* to *b* ratio decreases due to the higher concentration of chlorophyll *b*, enabling plants to maximize light capture (Dalmolin et al., 2015). A low ratio indicates increased chlorophyll *b* content and better utilization of the available low light (A. V. Araújo et al., 2016). Ribeiro et al. (2019) observed a decreasing linear effect on the chlorophyll *a* to *b* ratio with increasing levels of light restriction, implying that the chlorophyll a to b ratio decreases as the percentage of light restriction increases. This adjustment assists plants in capturing light energy in shaded environments (Chen et al., 2021b). In contrast, in the present study, the system with greater light restriction (CBP) exhibited lower chlorophyll levels (*b* and total), resulting in a higher chlorophyll *a/b* ratio. These findings corroborate the results reported by Casierra et al. (2012), who found that marigold leaves under shade had a higher chlorophyll *a* to *b* ratio compared with leaves exposed to full sun.

Gas exchange

The results, the net CO_2 assimilation rate (*A*) of the CB system differed from that of the other systems, exhibiting the highest mean for this variable (Table 2). This finding is consistent with Ribeiro et al. (2019), who observed that light restriction enhanced the photosynthetic mechanism and leaf gas exchange of Arabica coffee during early growth. However, Zhu et al. (2017) noted that the photosynthetic rate decreased significantly under low-light treatment compared with normal light, indicating impaired photosynthetic capacity in pak-choi plants subjected to shade treatment.

In C3-type plants, such as coffee trees, low levels of radiation can saturate the photosynthetic apparatus (Larcher, 2006), which could explain the higher assimilation rate obtained. On the other hand, in the CM system, excessive radiation can lead to photooxidative damage to the photosynthetic apparatus, increasing the photorespiratory process and reducing the net CO_2 assimilation rate (Cavatte et al., 2012). In the CBP system, excessive shading may have reduced radiation levels, reducing the net CO_2 assimilation rate (Baliza et al., 2012).

Various factors, including environmental conditions, light, temperature, oxygen, and CO_2 concentrations, as well as plant tissue characteristics, can affect the respiration rate of plants (Taiz et al., 2017). The net CO_2 assimilation rate (*A*) values obtained in this study ranged from 7 to 12 μmol CO_2 m^{-2} s^{-1}, which are considered low compared to most woody plants (W. L. Araújo, 2006). This difference could be attributed to the resistance to CO_2 diffusion from the atmosphere to the carboxylation sites.

Table 2

Net CO_2 assimilation rate (*A*), stomatal conductance (*gs*), intercellular CO_2 concentration (*Ci*), and transpiration (*E*) of Catuaí Vermelho IAC 44 coffee under three cropping systems: coffee monoculture (CM), coffee intercropped with banana (CB), and coffee intercropped with banana and palm heart (CBP), 2016/2017 harvest, Alegre - Espírito Santo

Cultivation system	*A* (μmol CO_2 m^{-2} s^{-1})	*gs* (mol H2O m^2s^{-1})	*Ci* (ppm)	*E* (mmol H_2O m^2s^{-1})
Mean: CM	7.31 ± 0.43b	0.13 ± 0.02b	303.74 ± 17.90b	1.79 ± 0.32a
Mean: CB	8.84 ± 1.25a	0.19 ± 0.02a	318.79 ± 8.33b	2.26 ± 0.34a
Mean: CBP	6.32 ± 0.95b	0.24 ± 0.08a	332.90 ± 8.67a	2.10 ± 0.35a
Maximum	10.47	0.37	342.47	2.83
Minimum	5.17	0.11	286.77	1.36
Overall mean	7.49	0.18	318.49	2.05
$CV_{experimental}$ (%)	18.45	35.62	5.30	18.08
$W_{calculated}$	0.95^N	0.85	0.94^N	0.94^N
Coefficient of asymmetry	0.54	1.51	-0.46	0.47
Coefficient of kurtosis	2.99	5.57	2.24	3.34

The sample originates from a population with normal distribution, by the Shapiro-Wilk test at 5% probability. The benchmark values for asymmetry and kurtosis estimators are 0 and 3, respectively. Means followed by the same letter between rows, within each column, do not differ according to Payton et al. (2000). Each mean is followed by its respective standard deviation (±).

Stomatal conductance and the resistance that the CO_2 finds to enter and spread through the substomatal cavities are determined by the intensity of stomatal opening. Thus, the behavior of the stomata is essential for both photosynthesis and transpiration; when closed, they conserve water and reduce the risk of dehydration, but consequently also reduce the absorption of CO_2, and when open, they allow the assimilation of this carbon dioxide gas and the transpiration of water (Jones, 2014). This behavior is influenced by the interaction between soil, plants, and the atmosphere, with environmental conditions playing a significant role in stomatal opening and closure and affecting plant physiological responses (Huntingford et al., 2015). Stomatal conductance values serve as indirect indicators of soil moisture, with values above the optimum range (0.20 to 0.30 mmol m^{-2} s^{-1}) indicating luxury water consumption and values below causing stress (Vega & Mejía, 2017).

In the studied culture systems, the CB and CBP systems exhibited higher stomatal conductance (*gs*) values (Table 2). Taiz et al. (2017) suggest that gs is influenced by the availability of water, which allows for prolonged stomatal opening. The higher gs values observed in intercropped coffee plants can be attributed to the shading conditions that help maintain soil moisture. Additionally, as Wei et al. (2016) pointed out, water scarcity in the soil reduces gs, which could explain the lower value found in the monoculture system. In intercropping systems, the creation of a microclimate helps maintain soil moisture. However, reduced gs leads to increased water use efficiency but inevitably results in decreased CO_2 uptake (Avila et al., 2017). Similar findings were reported by Baliza et al. (2012), Cunha et al. (2012), Christo (2017), and Ribeiro et al. (2019), who found lower gs values in coffee trees exposed to full sun.

The highest intercellular CO_2 concentration (*Ci*) was observed in the CBP system (Table 2). When *Ci* is high, the photosynthetic rate decreases, showing an inversely proportional relationship between the two variables (Concenço et al., 2013). Regarding transpiration (*E*), the intercropped systems lost more water than the CM system, although no significant differences were found (Table 2). Ribeiro et al. (2019) reported a similar result in the analysis of leaf gas exchange in young coffee trees subjected to light restriction. The authors observed a direct relationship between increasing light restriction levels and the E of coffee trees, indicating that transpiration rate increased with greater shading.

In terms of intrinsic water use efficiency (*A/gs*), the CM and CB systems demonstrated higher efficiency in water use (Table 3). Higher *A/gs* values indicate better water utilization in plant biomass production (Medrano et al., 2007). A similar trend was observed for instantaneous carboxylation efficiency, with CB and CM systems exhibiting higher means than CBP (Table 3). The higher carboxylation efficiency in CB and CM can be attributed to the higher net CO_2 assimilation rate and intercellular CO_2 concentration, as these variables are closely related (Ferraz et al., 2012). Likewise, Almeida et al. (2018) found low carboxylation efficiency under 80% shading, associated with reduced photosynthetic rate, likely due to low radiation.

Table 3

Intrinsic water use efficiency (*A/gs*), instantaneous carboxylation efficiency (*A/Ci*), and instantaneous water use efficiency (*A/E*) of Catuaí Vermelho IAC 44 coffee under three cropping systems: coffee monoculture (CM), coffee intercropped with banana (CB), and coffee intercropped with banana and palm heart (CBP), 2016/2017 harvest, Alegre - Espírito Santo

Cultivation system	*A* (µmol CO_2 m^{-2} s^{-1})	*gs* (mol H2O m^2s^{-1})	*Ci* (ppm)
Mean: CM	58.39 ± 7.35a	0.024 ± 0.002a	4.20 ± 0.90a
Mean: CB	47.25 ± 5.41a	0.028 ± 0.004a	3.94 ± 0.44a
Mean: CBP	27.67 ± 5.09b	0.019 ± 0.003b	3.04 ± 0.36b
Maximum	69.64	0.034	5.71
Minimum	20.75	0.015	2.68
Overall mean	44.44	0.024	3.73
$CV_{experimental}$ (%)	32.14	20.28	20.66
$W_{calculated}$	0.95^{N}	0.98^{N}	0.92^{N}
Coefficient of asymmetry	-0.13	0.35	0.97
Coefficient of kurtosis	2.04	2.86	4.08

The sample comes from a population with normal distribution, by the Shapiro-Wilk test at 5% probability. The benchmark values for the asymmetry and kurtosis estimators are 0 and 3, respectively Means followed by the same letter between rows, within each column, do not differ according to Payton et al. (2000). Each mean is followed by its respective standard deviation (±).

Consistent with the above two variables, instantaneous water use efficiency also showed higher values for the CM and CB systems compared with CBP (Table 3). Increasing shading reduces efficiency, as the assimilation of carbon dioxide from the external environment leads to water loss in leaves, and reduced loss restricts CO_2 uptake (Shimazaki et al., 2007). Estimates of water use efficiency indicate how much water is lost via transpiration for each molecule of CO_2 assimilated into organic compounds by the plant (Oliveira et al., 2011).

Conclusions

Based on the conditions of the study, the cultivation system can influence certain variables related to the photosynthetic activity of coffee. The intercropping system involving coffee, banana, and heart palm led to a reduction in chlorophyll *b* and total chlorophyll content. Additionally, this intercropping system exhibited lower water use efficiency. On the other hand, the net assimilation rate was higher in coffee intercropped with banana. Overall, the coffee-banana intercropping system (CB) showed promising results for most of the studied variables, except for chlorophyll *a*, intercellular CO_2 concentration, and transpiration. These findings demonstrate the considerable potential of this specific intercropping system.

Acknowledgments

The authors thank FAPES for the financial support for the study; and CAPES for the doctoral fellowship granted to the first author.

References

Almeida, E. I. B., Corrêa, M. C. M., Mesquita, R. O., Queiroz, R. F., Cajazeira, J. P., & Amorim, F. F. V. R. (2018). Growth and gas exchanges of red pitaya under different shading conditions. *Revista Brasileira de Ciências Agrárias, 13*(3), 1-8. doi: 10.5039/agraria.v13i3a5554

Araújo, A. V. (2013). *Microclima e características fisiológicas do cafeeiro conilon consorciado com seringueira e bananeira.* Dissertação de mestrado. Universidade Federal do Espírito Santo, São Mateus, ES, Brasil. https://repositorio.ufes.br/handle/10/5189

Araújo, A. V., Partelli, F. L., Oliveira, M. G., Pezzopane, J. R. M., Falqueto, A. R., & Cavatte, P. C. (2015). Microclima e crescimento vegetativo do café conilon consorciado com bananeiras. *Coffee Science, Lavras, 10*(2), 214-222. https://ainfo.cnptia.embrapa.br/digital/bitstream/item/131325/1/PROCI-2015.00049.pdf

Araújo, A. V., Partelli, F. L., Oliosi, G., & Pezzopane, J. R. M. (2016). Microclimate, development and productivity of robusta coffee shaded by rubber trees and at full sun. *Revista Ciências Agronômicas, 47*(4), 700-709. doi: 10.5935/1806-6690.20160084

Araújo, W. L. (2006). *Limitações da fotossíntese e metabolismo do carbono em folhas de diferentes posições da copa do cafeeiro* (Coffea arábica L.). Dissertação de mestrado, Universidade Federal de Viçosa, Viçosa, MG, Brasil. https://www.locus.ufv.br/bitstream/123456789/4302/1/texto%20completo.pdf

Avila, R. G., Silva, E. M., Magalhães, P. C., Alvarenga, A. A., & Lavinsky, A. O. (2017). Drought changes yield and organic and mineral composition of grains of four maize genotypes. *Journal of Agricultural Research, 5*(9), 243-250. doi: 10.15413/ajar.2017.0517

Baliza, D. P., Cunha, R. L., Castro, E. M., Barbosa, J. P. R. A. D., Pires, M. F., & Gomes, R. A. (2012). Trocas gasosas e características estruturais adaptativas de Cafeeiros cultivados em diferentes níveis de radiação. *Coffee Science, 7*(3), 250-258. http://www.sbicafe.ufv.br/bitstream/handle/123456789/7921/Coffee%20Science_v7_n3_p250-258_2012.pdf?sequence=1&isAllowed=y

Bez, C., Esposito, A., Musonerimana, S., Nguyen, T. H., Navarro-Escalante, L., Tesfaye, K., Turello, L., Navarini, L., Piazza, S., & Venturi, V. (2022). A comparative study of the rhizosphere microbiome of *Coffea arabica* grown in different countries reveals a small set of prevalent and keystone taxa. *Rhizosphere, 25*, 100652. doi: 10.1016/j.rhisph.2022.100652

Bonfim, J. A., Matsumoto, S. N., Lima, J. M., César, F. R. C., & Santos, M. A. F. (2010). Fungos micorrízicos arbusculares (fma) e aspectos fisiológicos em cafeeiros cultivados em sistema agroflorestal e a pleno sol. *Bragantia, 69*(1), 201-206. doi: 10.1590/S0006-87052010000100025

Boreux, V., Vaast, P., Madappa, L. P., Cheppudira, K. G., Garcia, C., & Ghazoul, J. (2016). Agroforestry coffee production increased by native shade trees, irrigation, and liming. *Agronomy for Sustainable Development, 36*(3), 1-9. doi: 10.1007/s13593-016-0377-7

Brisolara, C. V. (2013). *Sombreamento e utilização da fluorescência da clorofila na detecção de sementes esverdeadas de soja.* Tese de doutorado, Universidade Federal de Pelotas, Pelotas, RS, Brasil. http://repositorio.ufpel.edu.br:8080/bitstream/prefix/3093/1/tese_cristiane_velleda_brisolara.pdf

Campanha, M. M., Santos, R. H. S., Freitas, G. B., Martinez, H. E. P., Jaramillo-Botero, C., & Garcia, S. L. R. (2007). Análise comparativa das características da serapilheira e do solo em cafezais (*Coffea arabica* L.) cultivados em sistema agroflorestal e em monocultura, na Zona da Mata MG. *Revista Árvore, 31*(5), 805-812. doi: 10.1590/S0100-67622007000500004

Casierra, F., Avila, O., & Riascos, D. (2012). Cambios diarios del contenido de pigmentos fotosintéticos en hojas de caléndula bajo sol y sombra. *Temas Agrarios, 17*(1), 60-71. doi: 10.21897/rta.v17i1.697

Cavatte, P. C., Oliveira, Á. A. G., Morais, L. E., Martins, S. C. V., Sanglard, L. M. V. P., & DaMatta, F. M. (2012). Could shading reduce the negative impacts of drought on coffee? A morphophysiological analysis. *Physiologia Plantarum, 144*(2), 111-122. doi: 10.1111/j.1399-3054.2011.01525.x

Chen, J. M., Wu, S. H., Zeng, L. T., Dong, F., & Gu, D. C. (2021a). Research progress on the influence of shading on tea (*Camellia sinensis*) quality and yield. *China Tea, 5*, 1-10. doi: 10.3969/j.issn.1000-3150.2021.05.001

Chen, J., Wu, S., Dong, F., Li, J., Zeng, L., Tang, J., & Gu, D. (2021b). Mechanism underlying the shading-induced chlorophyll accumulation in tea leaves. *Frontiers in Plant Science, 12*, 779819. doi: 10.3389/fpls. 2021.779819

Christo, B. F. (2017). *Análise fotossintética e econômica de cafeeiro arábica em sistemas consorciados e a pleno sol.* Monografia, Curso de Especialização em Educação Ambiental e Sustentabilidade, Instituto Federal do Espírito Santo, Ibatiba, ES, Brasil. https://repositorio.ifes.edu.br/bitstream/handle/123456789/437/MONOGRAFIA_An%c3%a1lise_fotossint%c3%a9tica_e_econ%c3%b4mica_de_cafeeiro_ar%c3%a1bica.pdf?sequence=1&isAllowed=y

Coelho, D. S., Marques, M. A. D., Silva, J. A. B., Garrido, M. S., & Carvalho, P. G. S. (2014). Respostas fisiológicas em variedades de feijão caupi submetidas a diferentes níveis de sombreamento. *Revista Brasileira de Biociências, 12*(1), 14-19. https://www.seer.ufrgs.br/index.php/rbrasbioci/article/view/114852

Cogliatti-Carvalho, L., Almeida, D. R. de, & Rocha, C. F. D. (1998). Phenotypic response of Neoregelia johannis (Bromeliaceae) dependent on light intensity reaching the plant microhabitat. *Selbyana, 19*(2), 240-244. https://www.academia.edu/22589016/PHENOTYPIC_RESPONSE_OF_NEOREGELIA_JOHANNIS_BROMELIACEAE_DEPENDENT_ON_LIGHT_INTENSITY_REACHING_THE_PLANT_MICROHABITAT

Companhia Nacional de Abastecimento (2022). *Safra brasileira de café.* https://www.conab.gov.br/info-agro/ safras/cafe

Concenço, G., Motta, I. S., Correia, I. V. T., Silva, F. M., & Salomão, G. B. (2013). Infestação de plantas espontâneas em cafeeiro solteiro ou consorciado em sistema agroecológico. *Revista Agrarian, 6*(19), 22-28. https://ojs.ufgd.edu.br/index.php/agrarian/article/view/1846

Cunha, D. P., Castro, R. L. E. M., Barbosa, J. P. R. A. D., Pires, M. F., & Gomes, R. A. (2012). Trocas gasosas e características estruturais diferentes adaptativas de cafeeiros cultivadas níveis de radiação. *Coffee Science, 7*(3), 250-258. http://www.sbicafe.ufv.br/bitstream/handle/123456789/7921/Coffee%20Science_v7_n3_p250-258_2012.pdf?sequence=1&isAllowed=y

Dalmolin, A. C., Oliveira, S. E., Almeida, B. C., & Ortíz, C. E. (2015). Alterações morfofisiológicas de plantas jovens de *Curatella americana* L. submetidas ao sombreamento. *Revista Brasileira de Biociências, 13*(1), 41-48. https://www.academia.edu/65536878/Altera%C3%A7%C3%B5es_morfofisiol%C3%B3gicas_de_plantas_jovens_de_Curatella_americana_L_submetidas_ao_sombreamento

DaMatta, F. M., & Rena, A. B. (2002). Ecofisiologia de cafezais sombreados e a pleno sol. In L., Zambolim (Ed.), *O estado da arte de tecnologias na produção de café* (pp. 93-135). Viçosa, MG: Universidade Federal de Viçosa.

Deng, Y., Li, C., Shao, Q., Ye, X., & She, J. (2012a). Differential responses of double petal and multi petal jasmine to shading: I. Photosynthetic characteristics and chloroplast ultrastructure. *Plant Physiology and Biochemistry, 55*, 93-102. doi: 10.1016/j.plaphy.2012.03.006

Deng, Y., Shao, Q., Li, C., Ye, X., & Tang, R. (2012b). Differential responses of double petal and multi petal jasmine to shading: II. Morphology, anatomy and physiology. *Scientia Horticulturae, 144*, 19-28. doi: 10.1016/j.scienta.2012.06.031

Ferraz, R. L. S., Melo, A. S., Suassuna, J. F., Brito, M. E. B., Fernandes, P. D., & Nunes, E. S. N. Jr. (2012). Trocas gasosas e eficiência fotossintética em ecótipos de feijoeiro cultivados no semiárido. *Pesquisa Agropecuária Tropical, 42*(2), 181-188. doi: 10.1590/S1983-406320 12000200010

Ferreira, D. F. (2019). Sisvar: a computer analysis system to fixed effects split plot type designs. *Revista Brasileira de Biometria, 37*(4), 529-535. doi: 10.28951/rbb.v37i4.450

Fortes, D., Herrera, R. S., González, S., García, M., Romero, A., & Cruz, A. M. (2009). Comportamiento de los pigmentos fotosintéticos, según la edad de rebrote después del pastoreo de *Pennisetum purpureum* vc. Cuba CT-115 en la estación poco lluviosa. *Revista Cubana de Ciencia Agrícola, 43*(2), 183-186. https://www.researchgate.net/publication/237027962_Comportamiento_de_los_pigmentos_fotosinteticos_segun_la_edad_de_rebrote_despues_del_pastoreo_de_Pennisetum_purpureum_vc_Cuba_CT-115_en _la_estacion_poco_lluviosa

García, X., García, E., Rascón, Q., Herrera, L., & Aguado, G. A. (2005). Chlorophyll accumulation is enhanced by osmotic stress in graminaceous chlorophyllic cells. *Journal of Plant Physiology, 162*(6), 650-661. doi: 10.1016/j.jplph.2004.09.015

Holcman, E., & Sentelhas, P. C. (2013). Bromeliads production in greenhouses associated to different shading screens. *Horticultura Brasileira, 31*(3), 386-391. doi: 10.1590/S0102-05362013000300008

Hu, F., Bi, X., Liu, H., Fu, X., Li, Y., Yang, Y., Zhang, X., Wu, R., Li, G., Lv, Y., Huang, J., Luo, X., & Shi, R. (2022). Transcriptome and carotenoid profiling of different varieties of *Coffea arabica* provides insights into fruit color formation. *Plant Diversity, 44*(3), 322-334. doi: 10.1016/j.pld.2021.11.005

Huntingford, C., Smith, D. M., Davies, W. J., Falk, R., Sitch, S., & Mercado, L. M. (2015). Combining the (ABA) and net photosynthesis-based model equations of stomatal conductance. *Ecological Modelling, 300*, 81-88. doi: 10.1016/j.ecolmodel.2015.01.005

Imru, N. O., Wogderess, M. D., & Gidada, T. V. (2015). A study of the effects of shade on growth, production and quality of coffee (*Coffea arabica*) in Ethiopia. International *Journal of Agricultural Sciences, 5*(5), 748-752. https://www.internationalscholarsjournals.com/articles/a-study-of-the-effects-of-shade-on-growth-production-and-quality-of-coffee-coffea-arabica-in-ethiopia.pdf

Jones, H. G. (2014). *Plants and microclimate: a quantitative approach to environmental plant physiology.* Cambridge University Press.

Jesus, W. C. Jr., Martins, L. D., Rodrigues, W. N., Moraes, W. B., Amaral, J. F. T., Tomaz, M. A., & Alves, F. R. (2012). Mudanças climáticas globais e seus potenciais impactos sobre a cafeicultura brasileira. In M. A. Tomaz, J. F. T. Amaral, W. C. de Jr., Jesus, A. F. A. da, Fonseca, R. G. Ferrão, M. A. G. Ferrão, (Eds.), *Tecnologias para a sustentabilidade da cafeicultura* (pp. 263-294). Alegre, ES.

Kataria, S., Guruprasad, K. N., Ahuja, S., & Singh, B. (2013). Enhancement of growth, photosynthetic performance and yield by exclusion of ambient UV components in C3 and C4 plants. *Journal of Photochemistry and Photobiology B: Biology, 127,* 140-152. doi: 10.1016/j.jphotobiol.2013.08.013

Kramer, P. J., & Kozlowski, T. (1979). *Physiology of wood plants.* Academic Press.

Larcher, W. (2006). *Ecofisiologia vegetal.* RiMa.

Li, J., Zhou, L. J., & Lin, W. F. (2018). Competitive characteristics related to nitrogen utilization and calla lily growth in rubber-calla lily intercropping systems. *Industrial Crops and Products, 125*, 567-572. doi: 10.1016/j.indcrop.2018.09.032

Mayoli, R. N., & Gitau, K. M. (2012). The effects of shade trees on physiology of arabica coffee. *African Journal of Horticultural Science, 6*, 35-42. https://www.semanticscholar.org/paper/THE-EFFECTS-OF-SHADE-TREES-ON-PHYSIOLOGY-OF-ARABICA-Mayoli-Gitau/5e12377b100b4d3b277e431af7fdd9775e6b27e0

Medrano, H., Bota, J., Cifre, J., Flexas, J., Carbó, M. R., & Gulías, J. (2007). Eficiencia en el uso del agua por las plantas. *Investigaciones Geográficas, 43*, 63-84. doi: 10.14198/INGEO2007.43.04

Mesquita, C. M., Melo, E. M., Rezende, J. E., Carvalho, J. S., Fabri, M. A., Jr., Moraes, N. C., Dias, P. T., Carvalho, R. M., & Araújo, W. G. (2016). *Manual do café: implantação de cafezais* (*Coffea arábica* L.). EMATER.

Ohse, S., Rezende, B. L. A., Silveira, L. S., & Cortez, M. G. (2012). Viabilidade agronômica de consórcios de brócolis e alface estabelecidos em diferentes épocas. *Idesia, 30*(2), 29-37. doi: 10.4067/S0718-34292012 000200004

Oliveira, E. C. A., Freire, F. J., Oliveira, A. C., Simões, D. E., Neto, Rocha, A. T., & Carvalho, L. A. (2011). Produtividade, eficiência energética de uso da água e qualidade de qualidade de diferentes regimes. *Pesquisa Agropecuária Brasileira, 46*(6), 617-625. doi: 10.1590/S0100-204X2011000600007

Partelli, F. L., Araujo, A. V., Vieira, H. D., Dias, J. R. M., Menezes, T., Fernando, L., & Ramalho, J. C. (2014). Microclimate and development of 'Conilon' coffee intercropped with rubber trees. *Pesquisa Agropecuária Brasileira, 49*(11), 872-881. doi: 10.1590/S0100-204X2014001100006

Payton, M. E., Miller, A. E., & Raun, W. R. (2000). Testing statistical hypotheses using standard error bars and confidence intervals. *Communications in Soil Science and Plant Analysis, 31*(5-6), 547-551. doi: 10.1080/00103620009370458

Pezzopane, J. R. M., Gallo, M. J. P. B., Carmargo, M. P. B., & Fazuoli, L. C. (2007). Avaliações fenológicas e agronômicas em café arábica cultivado a pleno sol e consorciado com banana 'Prata Anã'. *Bragantia, 66*(4), 701-709. doi: 10.1590/S0006-87052007000400021

Poorter, H., Niinemets, Ü., Ntagkas, N., Siebenkäs, A., Mäenpää, M., Matsubara, S., & Pons, T. (2019). A meta-analysis of plant responses to light intensity for 70 traits ranging from molecules to whole plant performance. *New Phytologist, 223*(3), 1073-1105. doi: 10.1111/nph.15754

Prezotti, L. C., Gomes, J. A., Dadalto, G. G., & Oliveira, J. A. (2007). *Manual de recomendação de calagem e adubação para o Estado do Espírito Santo: 5ª aproximação.* Seea/Incaper/Cedagro.

Quevedo-Rojas, A., García-Núñez, C., Jerez-Rico, M., Jaimez, R., & Schwarzkopf, T. (2018). Leaf acclimation strategies to contrasting light conditions in saplings of different shade tolerance in a tropical cloud forest. *Functional Plant Biology, 45*(9), 968-982. doi: 10.1071/FP17308

Reis, P. R., & Cunha, R. L. (2010). *Café Arábica do plantio à colheita.* U.R. Epamig SM.

Rezai, S., Etemadi, N., Nikbakht, A., Yousefi, M., & Majidi, M. M. (2018). Effect of light intensity on leaf morphology, photosynthetic capacity, and chlorophyll content inSage (*Salvia officinalis* L.). *Horticultural Science and Technology, 36*(1), 46-57. doi: 10.12972/kjhst.20180006

Ribeiro, A. F. F., Matsumoto, S. N., Pereira, L. F., Oliveira, U. S., Teixeira, E. C., & Ramos, P. A. S. (2019). Content of photosynthetic pigments and leaf gas exchanges of young coffee plants under light restriction and treated with Paclobutrazol. *Journal of Experimental Agriculture International, 32*(6), 1-13. doi: 10.9734/JEAI/2019/v32i630128

Rochaix, J. D. (2014). Regulation and dynamics of the light-harvesting system. *Annual Review of Plant Biology, 65*, 287-309. doi: 10.1146/annurev-arplant-050213-040226

Ruberti, I., Sessa, G., Ciolfi, A., Possenti, M., Carabelli, M., & Morelli, G. (2012). Plant adaptation to dynamically changing environment: the shade avoidance response. *Biotechnology Advances, 30*(5), 1047-1058. doi: 10.1016/j.biotechadv.2011.08.014

Shimazaki, K., Doi, M., Assmann, S. M., & Kinoshita, T. (2007). Light regulation of stomatal movement. *Annual Review of Plant Biology, 58*(1), 219-247. doi: 10.1146/annurev.arplant.57.032905.105434

Slattery, R. A., Walker, B. J., Weber, A. P. M., & Ort, D. R. C. (2018). The impacts of fluctuating light on crop performance. *Plant Physiology, 176*(2), 990-1003. doi: 10.1104/pp.17.01234

Souza, G., Castro, E., Soares, A., Santos, A., & Alves, E. (2011). Teores de pigmentos fotossintéticos, taxa de fotossíntese e estrutura de cloroplastos de plantas jovens de *Mikania laevigata* Schultz Bip. ex Baker cultivadas sob malhas coloridas. *Semina: Ciências Agrárias, 32*(1), 1843-1854. doi: 10.5433/1679-0359.2011v32Suplp1843

Taiz, L., Zeiger, E., Møller, I. M., & Murphy, A. (2017). *Fisiologia e desenvolvimento vegetal.* Artmed.

Tang, X. L., Jiang, J., Jin, H. P., Zhou, C., Liu, G. Z., & Yang, H. (2019). Effects of shading on chlorophyll content and photosynthetic characteristics in leaves of Phoebe bournei. *Ying Yong Sheng Tai Xue Bao, 30*(9), 2941-2948. doi: 10.13287/j.1001-9332.201909.002

Vega, E., & Mejía, J. (2017). Desempeño del Phaseolus vulgaris bajo riego parcial cultivado en un sistema de respuesta hidrogravitrópica. *Scientia Agropecuaria, 8*(2), 137-147. doi: 10.17268/sci.agropecu.2017.02. 06

Wang, Y. N., Dong, L. N., Ding, Y. F., Li, H., Song, P., Cai, H., & Xu, Z. H. (2020). Effects of shading on photosynthetic characteristics and chlorophyll fluorescence parameters of four Corydalis species. *Ying Yong Sheng Tai Xue Bao, 31*(3), 769-777. doi: 10.13287/j.1001-9332.202003.004

Wei, Z., Du, T., Zhang, J., Xu, S., Cambre, P. J., & Davies, W. J. (2016). Carbon isotope discrimination shows a higher water use efficiency under alternate partial root-zone irrigation of field-grown tomato. *Agricultural Water Management, 165*, 33-43. doi: 10.1016/j.agwat.2015.11.009

Zhu, H., Li, X., Zhai, W., Liu, Y., Gao, Q., Liu, J., Ren, L., Chen, H., & Zhu, Y. (2017). Effects of low light on photosynthetic properties, antioxidant enzyme activity, and anthocyanin accumulation in purple pak-choi (*Brassica campestris* ssp. Chinensis Makino). *PLoS One, 12*(6), e0179305. doi: 10.1371/journal.pone.0179305