



Physiological performance of *Coffea arabica* cultivated in different shadings in the Brazilian semi-arid region

ANDRADE, Mateus Ferreira⁽¹⁾; SIQUEIRA, Tânia da Silva⁽²⁾; SIMPLICÍO, Josimar Bento⁽³⁾; SILVA, Monalisa Alves Diniz⁽⁴⁾

⁽¹⁾ 0000-0002-7012-782X; Universidade Federal Rural de Pernambuco. Serra Talhada, PE, Brasil. matheus.fandrade2013@gmail.com

⁽²⁾ 0000-0002-7502-4942; Universidade Federal Rural de Pernambuco. Serra Talhada, PE, Brasil. taniaasilva0315@gmail.com

⁽³⁾ 0000-0002-7669-0584; Universidade Federal Rural de Pernambuco. Serra Talhada, PE, Brasil. josimar.bento@ufrpe.br

⁽⁴⁾ 0000-0001-9052-7380; Universidade Federal Rural de Pernambuco. Serra Talhada, PE, Brasil. monaliza.diniz@ufrpe.br

O conteúdo expresso neste artigo é de inteira responsabilidade dos/as seus/as autores/as.

ABSTRACT

Coffee is one of the most consumed drinks in the world and its production comes from the work of approximately 100 million coffee farmers across the planet. For its cultivation in semi-arid regions, management is necessary to help mitigate possible abiotic and biotic stresses. An alternative to produce in these environments is the use of shading, as shading helps to reduce radiation damage and contributes to mitigating harmful effects in photosynthesis generated by light saturation. In this context, the objective of this study was to determine the influence of different shading on the photosynthetic characteristics of young coffee plants, under Brazilian semi-arid conditions. The experiment was carried out following a randomized block design, with 4 treatments and 8 replications, totaling 32 experimental units. The four treatments were: 1- Full sun; 2- 50% shading, 3- 70% shading and 4- 80% shading. The physiological variables evaluated were: net photosynthesis, transpiration, stomatal conductance and internal CO₂ concentration, using the infrared gas analyzer (IRGA-Ci340). Furthermore, carboxylation efficiency values were obtained; water use efficiency and intrinsic water use efficiency. The results showed that coffee shaded with 50 and 70% showed an increase in photosynthetic rate. Cultivation conditions in full sun and 80% shade specifically reduced the photosynthesis of *Coffea arabica* plants, var. Red catuai. Water use efficiency, carboxylation efficiency and intrinsic water use efficiency were not significantly influenced by shading. Relatively, the 50% shading condition favored greater water use efficiency and greater intrinsic water use efficiency.

RESUMO

O café é uma das bebidas mais consumidas no mundo e sua produção é oriunda do trabalho de aproximadamente 100 milhões de cafeicultores em todo o planeta. Para seu cultivo em regiões semiáridas é necessário manejo que ajude a mitigar possíveis estresses bióticos e abióticos, uma alternativa para se produzir nesses ambientes é a utilização de sombrites, pois, o sombreamento ajuda a reduzir os danos pela radiação e contribui na mitigação dos efeitos deletérios na fotossíntese gerados pela saturação por luz. Neste contexto, o objetivo deste estudo foi determinar a influência de diferentes sombreamentos nas características fotossintéticas de plantas jovens de café arábicas, sob condições de semiárido brasileiro. O experimento foi realizado seguindo o delineamento em blocos casualizados, com 4 tratamentos e 8 repetições, totalizando 32 unidades experimentais. Os quatro tratamentos foram: 1- Pleno sol; 2- 50% de sombreamento, 3- 70% de sombreamento e 4- 80% de sombreamento. As variáveis fisiológicas avaliadas foram: fotossíntese líquida, transpiração, condutância estomática e concentração de CO₂ interna, utilizando o analisador de gás por infravermelho (IRGA-Ci340). Além disso, foram obtidos os valores de eficiência da carboxilação; eficiência de uso da água e a eficiência intrínseca do uso da água. Os resultados mostraram que o café sombreado com 50 e 70 % apresentou aumento na taxa fotossintética. As condições de cultivo a pleno sol e a 80% de sombreamento reduziram de forma específica a fotossíntese das plantas de café arábica, var. Catuai vermelho. A eficiência do uso da água, a eficiência de carboxilação e a eficiência intrínseca do uso da água não sofreram influência significativa dos sombreamentos. De forma relativa, a condição de 50% de sombreamento favoreceu a maior eficiência do uso de água e a maior eficiência intrínseca do uso de água.

ARTICLE INFORMATION

Article Process:

Submetido: 07/05/2024

Aprovado: 14/03/2025

Publicação: 27/03/2025



Keywords:

Photosynthesis, water use efficiency, solar radiation.

Introduction

Coffee is one of the most consumed beverages in the world and its production comes from the work of approximately 100 million coffee farmers around the planet (Davis *et al.*, 2019). Due to climate change, coffee producing areas have had to adapt to different growing environments (Venancio *et al.*, 2020), and the environmental pressure of monoculture in the Brazilian coffee system (Matta *et al.*, 2019).

Coffea arabica, as an understory species, originates from mountainous forests of Ethiopia (Bez *et al.*, 2022; Hu *et al.*, 2022). At altitudes above 1,500 meters, characterized by an average annual temperature of 20°C Charrier and Berthaud, (1985), it normally requires greater care, especially in producing areas located in arid and semi-arid environments.

For its cultivation in semiarid regions, management is required to help mitigate possible abiotic and biotic stresses. Because these production environments often offer environmental conditions that are different from those of deep forests such as those in the centers of origin of coffee, these particularities make species shade-tolerant (Ayalew, 2018).

Thus, their seedlings are generally produced in nurseries with plastic mesh shades that block approximately 50 to 75% or more of the photosynthetically active radiation (PAR), reaching values between 400 and 700 $\mu\text{mol of photons m}^{-2}\text{s}^{-1}$, which corresponds to the light saturation point in coffee (Matiello *et al.*, 2010, Rakocevic *et al.*, 2021, León-Burgos *et al.*, 2022).

In general, light is one of the most important environmental factors for the commercial establishment of a crop, and its intensity can influence plant growth and development, as well as their foliar gas exchange and water use efficiency (Hatamian *et al.*, 2015; Thakur *et al.*, 2019). According to Moraes *et al.* (2010), seedlings in shaded conditions, compared to full sun, have larger and greener leaves, which may give a false impression of greater vigor. However, seedlings grown in the shade may present photooxidative damage when transplanted to the field, requiring acclimatization or a gradual reduction in the level of shade (Moraes *et al.*, 2010).

After transplantation, coffee seedlings are subjected to high air temperatures and high solar irradiation. This exposure can simultaneously cause leaf burns (Ulm and Jenkins, 2015; Santos *et al.*, 2016; Bernado *et al.*, 2021). Sunburn is expressed by symptoms of chlorosis and necrosis in one in several species (RACSKÓ *et al.*, 2010). In addition to these symptoms, sunburn can lead to reduced photosynthetic rates, decreased plant height, leaf area, shortening of the internode and the length of the coffee tree branches (Santos *et al.*, 2016).

Thus, shaded cultivation emerges as an alternative for crop production, as it helps to reduce radiation damage and contributes to mitigating deleterious effects on photosynthesis generated by light saturation, in addition to increasing water use efficiency, as leaves directly exposed to the sun have greater hydraulic conductance per unit of leaf area and consequently greater water demand (Carins Murphy *et al.*, 2012). As observed by Damatta (2004), due to

light saturation, the plant needs greater transpiration to maintain low leaf temperature, resulting in greater water consumption.

Therefore, the objective of this study was to determine the influence of different shading on the photosynthetic characteristics of young *Coffea arabica* plants, under Brazilian semiarid conditions.

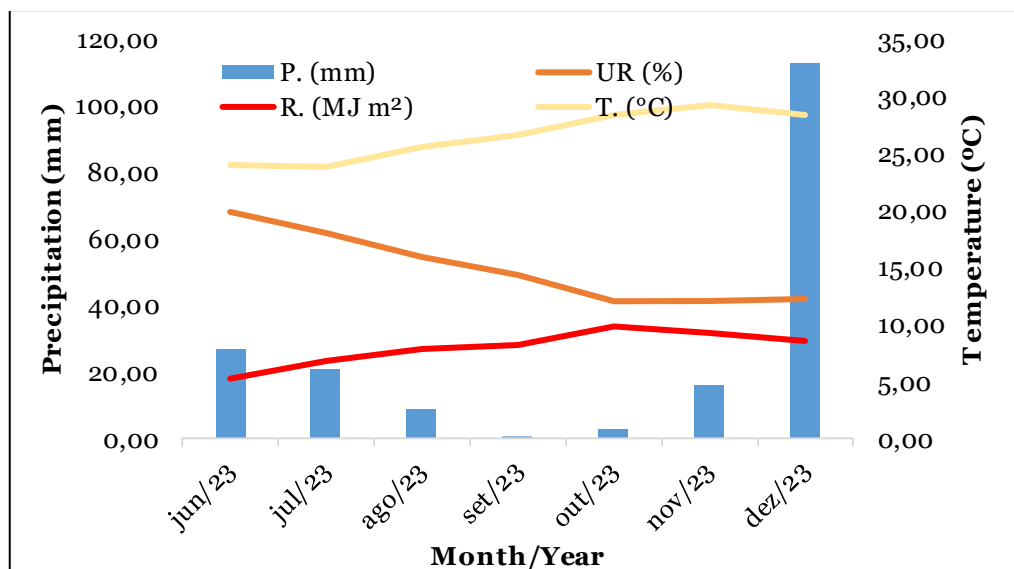
Materials and methods

Experiment location and plant material

The work was carried out from 06/18/2023 to 12/13/2023, in the experimental area of the Serra Talhada Academic Unit (UAST), linked to the Federal Rural University of Pernambuco (UFRPE), municipality of Serra Talhada, PE, Sertão do Pajeú microregion, located at the following geographic coordinates: Latitude: $-7.95^{\circ} 59' 7''$ South, Longitude: $38.29^{\circ} 17' 34''$ West and Altitude of 499 m. Climatic conditions during the study are presented in Table 1.

Figure 1.

Average monthly values of Precipitation (P, mm); Relative Humidity (RH, %); Global Solar Radiation (R, MJ m⁻²) and Temperature (T, °C), from June to December 2023. Serra Talhada, PE. 2023.



Source: INMET, 2023.

Seeds of *Coffea arabica* (variation Red *catuai*) were sown in plastic trays on 09/15/2022, approximately 65 days after sowing, when seedlings had expanded cotyledonary leaves. They were transplanted into a 2 kg plastic bag where they remained until 06/18/23,

when they were transferred to the soil, following a spacing of 2 x 1 m, in a population of 10 thousand plants per hectare. The chemical characteristics of the soil used in the study are shown in Table 1. After transplanting, the seedlings were separated into four groups corresponding to the shading levels. Each shade cloth was placed at a height of 1 m above the ground so as not to overlap the neighboring seedlings of each shaded experimental unit.

Table 1.
Chemical characteristics of the surface layer of the soil used in the experiment. Serra Talhada –PE, 2023.

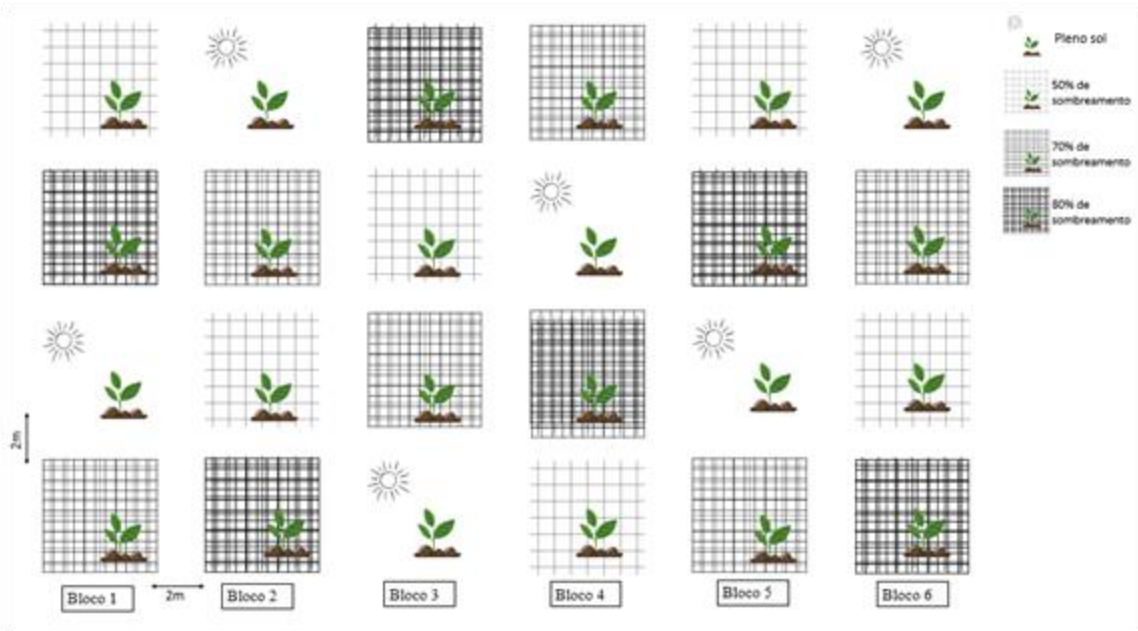
Layer (cm)	P	pH	Ca	Mg	Na	K	Al	H
	mg dm ⁻³	(H ₂ O)	-----cmolc dm ⁻³ -----					
0-40	252	6,4	4	1,5	0,03	0,7	0	0

Source: IPA laboratory.

Treatments and experimental design

The experiment was carried out following a randomized block design, with 4 treatments and 6 replicates, totaling 24 experimental units. The four treatments were: 1-Full sun; 2- 50% shade, 3- 70% shade and 4- 80% shade. Before the start of data collection, seedlings were maintained from 06/18/23 to 12/13/23 at shade levels corresponding to each treatment, figure 2.

Figure 2.
Sketch of the experimental area, coffee plants subjected to each level of shading. Serra Talhada, PE. 2024.



Source: Own authorship, 2024.

Treatments with fertilizers and agricultural inputs

Planting and growth fertilizations were carried out according to the soil analysis, table 1 and based on the fertilization recommendation manual of the State of Pernambuco, as recommended for the crop (Cavalcanti, 2008).

Weed control was carried out manually whenever necessary. During the experiment, 2 applications of insecticide based on (METHOMIL) 600 mL ha⁻¹ and fungicide based on (MANCONZEB) 1.5 kg ha⁻¹ were made to control insect pests and diseases that commonly occur in cultivation areas.

Irrigation was used daily based on crop evapotranspiration, following the model proposed by Penman-Monteith FAO 56:

$$E_{tc} = (E_{to} \cdot K_c) - P$$

In this:

E_{tc} = Crop evapotranspiration (mm dia⁻¹);

E_{to} = Reference evapotranspiration (mm dia⁻¹)

K_c = Cultivation coefficient

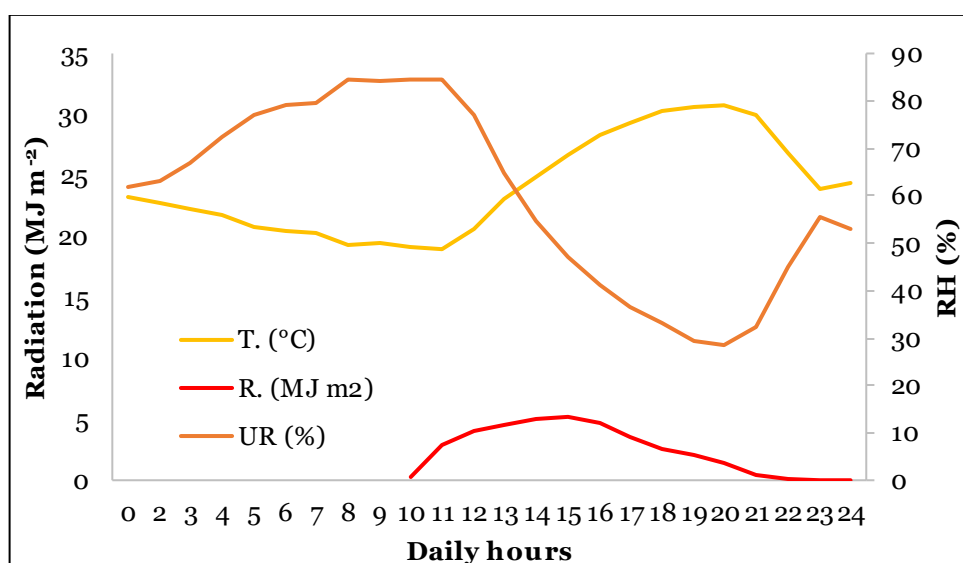
P = Precipitation (mm)

Measurements of gas exchange in young coffee plants

Measurements were carried out on December 13, 2023 between 10 and 11 am, on healthy leaves of the third plagiotropic branch, from the apex of each plant. The climatic conditions at the time of the measurements are shown in Figure 3, where measurements were carried out on six plants at each shading level, except for the two plants at the ends (borders). The physiological variables were: net photosynthesis (PN), transpiration (T), stomatal conductance (gs) and internal CO₂ concentration (Ci) using the infrared gas analyzer (IRGA-Ci340). In addition, the carboxylation efficiency ($EC = P_n / C_i$); water use efficiency ($EUA = P_n / T$) and intrinsic water use efficiency ($EIUA = P_n / g_s$) were obtained.

Figure 3.

Average temperature (T, °C); Global solar radiation (R, MJ m⁻²) and relative humidity (RH, %) on the day of assessment. Serra talhada, Pernambuco. 2023.



Source: INMET, 2023.

Statistical analysis

Results obtained were subjected to the normality of distribution test using the Shapiro-Wilk test with a significance level of 5% ($p < 0.05$), subsequently, analysis of variance (ANOVA) was performed, using the F test ($p < 0.05$). When significant, the Tukey test was performed at 5% probability ($p < 0.05$), using the statistical software R version 4.1.3 (R Core Team, 2020). Then, principal component analysis (PCA) was applied in order to examine the interrelationships between the physiological variables of *Coffea arabica* var. Red *catuai* in different shadings. Significant principal components (PCs) were selected according to the Kaiser criterion (1960), considering only eigenvalues greater than 1.0 for the validity of the application of the (PCA) (Lamichhane *et al.*, 2021). Principal component analysis was performed using PAST 4.03 software (Hammer *et al.*, 2001).

Results

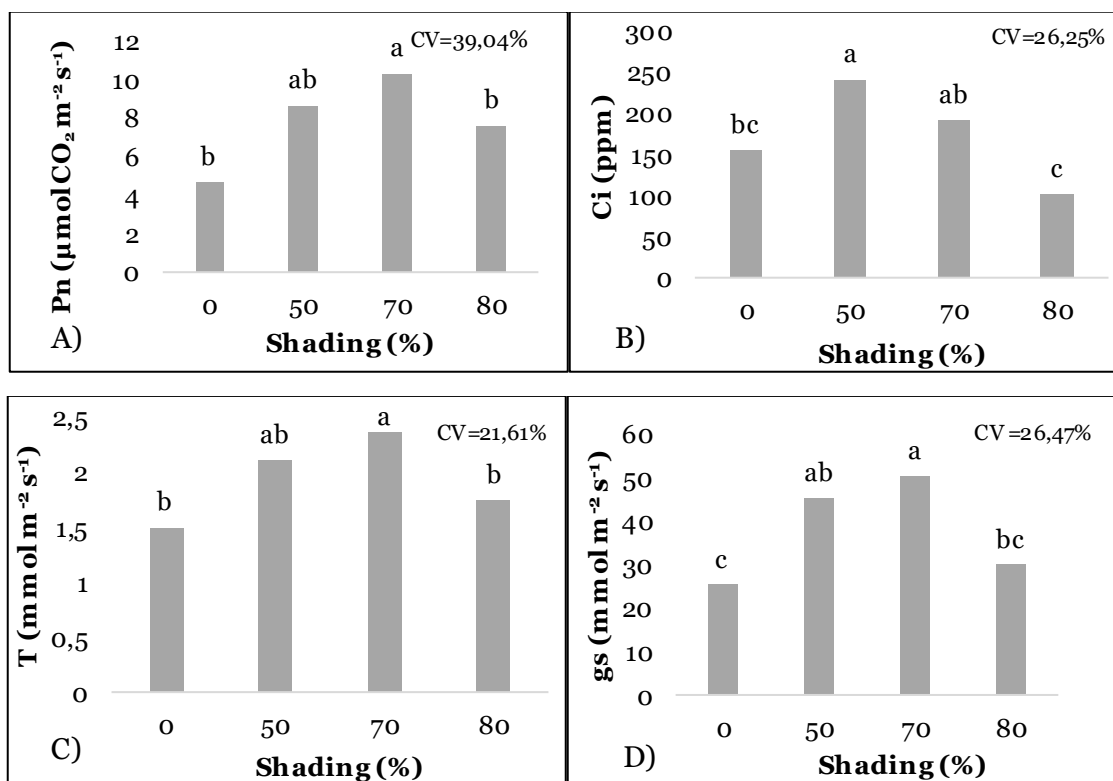
Results of net photosynthesis (Pn) were significantly influenced by different shading conditions, so that plants with 70% shading presented higher Pn values than when placed in full sun or 80% shade. In contrast, the full sun condition resulted in a reduction of more than 50% in net photosynthesis. These results suggest that young Catuí red coffee plants develop better in semiarid environments under shade between 50 and 70%. This suggestion is similar to the results found by (Tatagiba *et al.*, 2010, Córdova *et al.*, 2016), who observed better development in shade less than 60% compared to full sun.

Still in this context, Ribeiro *et al.* (2019) obtained similar results, since according to these authors, light restriction (at adequate levels) improves the photosynthetic mechanism and gas exchange of the *Coffea arabica* plant during initial growth, mainly due to the photosynthetic capacity being reduced when overloaded by excess light (Mathur *et al.*, 2018).

Some authors emphasize that leaves developed in full sun compared to leaves in shaded conditions are generally thicker and have a thicker palisade parenchyma, have greater stomatal density, and, as a rule, a higher nitrogen concentration per unit of leaf area. However, they have less chlorophylls A and B in their leaf mass, in addition to presenting higher photosynthesis rates and an increase in the content of photoprotective pigments (Martins *et al.*, 2014; Assis *et al.*, 2019; Venâncio *et al.*, 2019; Pérez-Molina *et al.*, 2021). However, our results suggest that plants in full sun and 80% shaded conditions reduced their photosynthetic rates, stomatal conductance, transpiration, and internal CO₂ concentration (Figures 4 (A; B; C and D), respectively).

Figures 4 (A; B; C e D).

Physiological parameters: A) Net photosynthesis (Pn); B) Internal carbon concentration (Ci); C) Transpiration (T) and D) Stomatal conductance (gs) in young plants of *Coffea arabica*, var. Red Catuaí subjected to four treatments: 1-Full sun; 2- 50% shading, 3- 70% shade and 4- 80% shading.



* Means followed by the same letter do not differ statistically from each other, according to the Tukey test at 5% probability ($p < 0.05$). CV = coefficient of variation.

In general, full sun and 80% shade treatments were statistically similar and resulted in the lowest rates of net photosynthesis, stomatal conductance, internal CO₂ concentration and transpiration. This fact was also observed by Zhu *et al.* (2017) who, studying the influence of light on pak-choi plants (*Brassica campestris* ssp. *Chinensis* Makino L. "ziyi"), found that the photosynthetic rate decreased significantly in plants subjected to low light (250 to 750 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$) compared to normal light (1000 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$), indicating that photosynthetic capacity is impaired in treatments with a certain level of shade.

Plants had higher transpiration values in the 50 and 70% shading treatments, while the lowest values were observed in the plants subjected to full sun and 80% shading. This may have occurred due to the weather conditions on the day of the measurements (Figure 3), where there was a large variation in relative humidity, with higher values in the early morning and decreasing throughout the day, generating an average below 50% RH. This condition, combined with the higher incidence of solar radiation, results in stresses capable of reducing transpiration, mainly due to stomatal closure (Figure 4B).

EC (Carboxylation efficiency), EUA (water use efficiency) and EIUA (intrinsic water use efficiency) values were not significantly influenced by the different shading levels (Figures 5A; B and C). However, higher relative values of carboxylation efficiency occurred due to coverage of 70 and 80%, respectively, showing that these shading levels promoted a favorable environment, reducing the stresses caused by radiation and temperature. According to Navarro *et al.* (2022), there are specific conditions for high carboxylation efficiency to occur, such as: availability of ATP and NADPH, amount of light, temperature level and CO₂ concentrations to be made available in the mesophyll for carboxylation to occur (Nobre *et al.*, 2023).

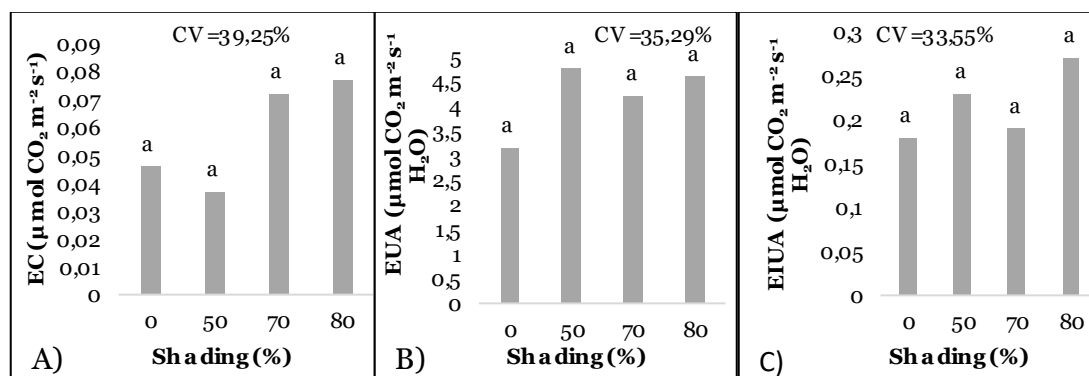
EUA refers to the amount of carbon fixed by the plant per water molecule and when plants have a net photosynthetic rate higher than the transpiration rate, there is a higher EUA (Chagas *et al.*, 2019).

These results suggest that in adequate shaded conditions, plants have greater agronomic efficiency, compared to those in full sun, which tend to have greater transpiration and, consequently, lower efficiency in water use, although no significant difference was observed in this study for this variable (Figure 5B).

It is worth observing, in particular, the behavior of coffee plants between treatments with 50% and 70% shade, although there was no significant difference between the treatments, it is important to highlight the greater efficiency of water use when in less shade (50%), ratifying the better environmental condition for better EC (Figures 5 A; B and C).

Figures 5 (A; B e C).

Physiological parameters: A) Carboxylation Efficiency (CE); B) Water Use Efficiency (WUE) and C) Intrinsic Water Use Efficiency (IWUE) of *Coffea arabica* var. Red *catuai* seedlings subjected to four treatments: 1-Full sun; 2- 50% shading, 3- 70% shading and 4- 80% shading.



* Means followed by the same letter do not differ statistically from each other, according to the Tukey test at 5% probability ($p < 0.05$). CV = coefficient of variation.

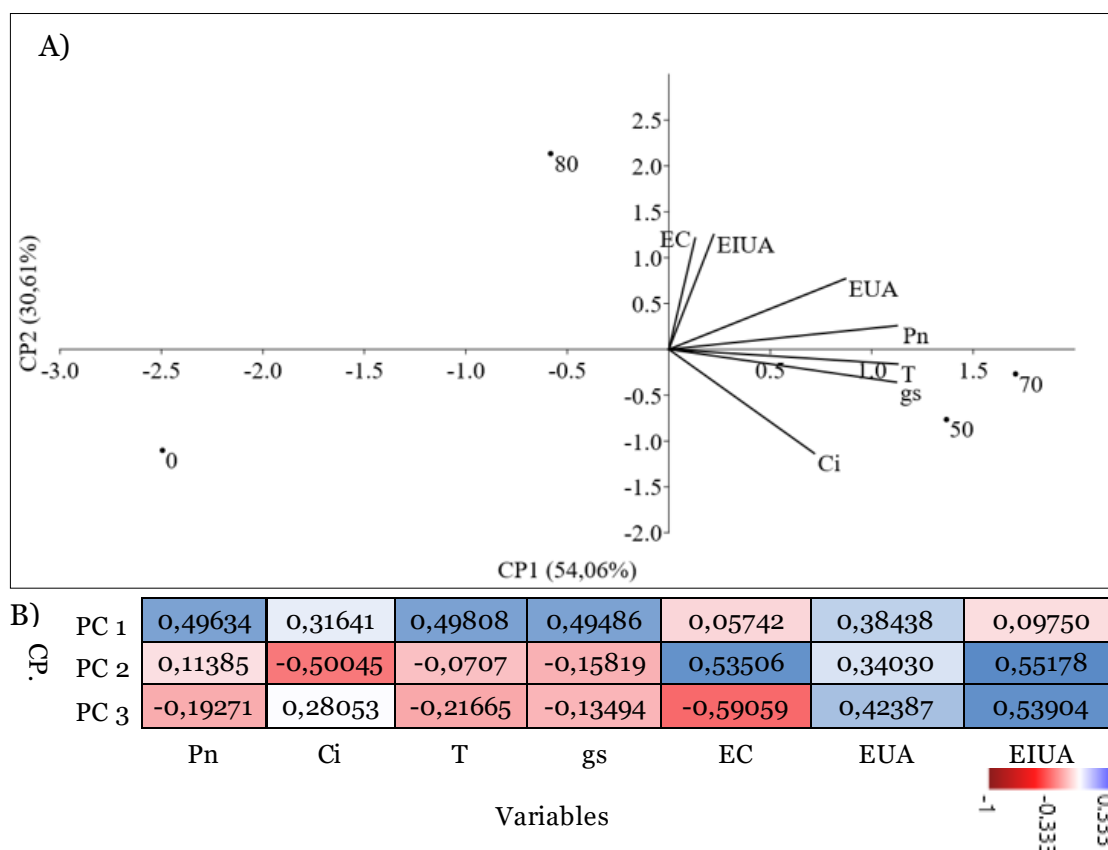
Figure 6 shows the principal component analysis (PCA) and the relationship between physiological variables of *Coffea arabica* var. Red *Catuaí* according to different shadings, suggesting that the two axes (CP1 and CP2) explain 84.67% of the data variation, with 54.06% explained by the first principal component (PC1) and 30.61% by the second principal component (PC2). The lines that connect the physiological variables to the center of origin of the graph are called vectors (Miroslavljevic *et al.*, 2018). Thus, angles formed between the vectors determine the relationship between shading levels, as well as between the physiological variables investigated and the shading levels. For example, variables that present an acute angle are positively correlated, while those that present obtuse angles are negatively correlated, and those that have a right angle (90°) between them are not correlated.

In this understanding, stomatal conductance (gs), transpiration (T) and liquid photosynthesis (Pn) are associated with the 70% coverage level, while internal carbon concentration revealed a better association with the 50% coverage treatment.

In Figure 6B, we observe variables that compose each principal component, with CP1 composed of variables with the highest loads, such as Pn (0.49634), T (0.49808), and gs (0.49486), while CP2 is composed of Ci (-0.50045) and EIUA (0.55178); finally, CP3 is composed of EC (-0.59059) and EUA (0.42387), respectively. Variable loads show that Pn, T, gs, EC, EUA, and EIUA are positively correlated, while Ci and EC are negatively correlated, evidencing that despite the high levels of internal CO₂, the plant ceased CO₂ assimilation due to the lower investment in proteins associated with Rubisco (Mendes *et al.*, 2017).

Figure 6 (A and B).

Principal component analysis (PCA) showing the relationship between physiological variables of *Coffea arabica* var. Red *Catuaí* subjected to four treatments: 1-Full sun; 2- 50% shading, 3- 70% shading and 4- 80% shading. A) Variable loadings on the first two axes and B) component matrix with loading factors for each variable on the first three PCs with eigenvalues greater than 1.0.



* Pn= liquid photosynthesis; Ci= internal carbon concentration; T= Transpiration; gs= stomatal conductance; EC= Carboxylation efficiency; EUA= water use efficiency; EIUA= intrinsic water use efficiency; CP1= main component 1; CP2= main component 2; CP= main components.

Conclusions

Different shading conditions influenced the physiological characteristics of young plants of *Coffea arabica* var. Red *Catuaí*;

Young plants of coffee var. Red *Catuaí* subjected to treatments of 50 and 70% shading increased their photosynthetic rates;

Growing conditions in full sun and 80% shading reduced the photosynthesis of young plants of *Coffea arabica* var. Red *Catuaí*;

Water use efficiency, carboxylation efficiency and intrinsic water use efficiency were not significantly influenced by shading.

BIBLIOGRAPHIC REFERENCES

- Assis, B. D. P., Gross, E., Pereira, N. E., Mielke, M. S., & Gomes Júnior, G. A. (2019). Growth response of four Conilon coffee varieties (*Coffea canephora* Pierre ex A. Froehner) to different shading levels. *Journal of Agricultural Science*, 11(7), 29. URL: <https://doi.org/10.5539/jas.v11n7p29>
- Bernado, W. D. P., Rakocevic, M., Santos, A. R., Ruas, K. F., Baroni, D. F., Abraham, A. C., ... & Rodrigues, W. P. (2021). Biomass and leaf acclimations to ultraviolet solar radiation in juvenile plants of *Coffea arabica* and *C. canephora*. *Plants*, 10(4), 640. <https://doi.org/10.3390/plants10040640>
- Bez, C., Esposito, A., Musonerimana, S., Nguyen, T. H., Navarro-Escalante, L., Tesfaye, K., ... & Venturi, V. (2023). 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. <https://doi.org/10.1016/j.rhisph.2022.100652>
- Carins Murphy, M. R., Jordan, G. J., & Brodribb, T. J. (2012). Differential leaf expansion can enable hydraulic acclimation to sun and shade. *Plant, Cell & Environment*, 35(8), 1407-1418. <https://doi.org/10.1111/j.1365-3040.2012.02498.x>
- Castanheira, D. T., Rezende, T. T., Baliza, D. P., Guedes, J. M., Carvalho, S. P., Guimarães, R. J., & Viana, M. T. R. (2016). Potential use of anatomical and physiological characteristics in the selection of coffee progenies. http://www.coffeescience.ufla.br/index.php/Coffeescience/article/view/1105/pdf_1105
- Cavalcanti, F. D. A. (1998). Recomendações de adubação para o Estado de Pernambuco: 2a. aproximacao. IPA.
- Chagas, W. F. T., Silva, D. R. G., Lacerda, J. R., Pinto, L. C., Andrade, A. B., & Faquin, V. (2019). Nitrogen fertilizers technologies for coffee plants. <http://dx.doi.org/10.25186/cs.v14i1>
- Chen, J., Wu, S., Dong, F., Li, J., Zeng, L., Tang, J., & Gu, D. (2021). Mechanism underlying the shading-induced chlorophyll accumulation in tea leaves. *Frontiers in Plant Science*, 12, 779819. <https://doi.org/10.3389/fpls.2021.779819>
- Companhia Nacional de Abastecimento - CONAB (2022). Safra brasileira de café. <https://www.conab.gov.br/info-agro/safras/café>.

- DaMatta, C.P.; Oliveira, M.; Maestri, R.S.; Barros. (2010). Café: Meio Ambiente e Fisiologia da Lavoura Ecofisiologia das Culturas Arbóreas Tropicais, *Nova Science Publishers*, 181-216.
- DaMatta, F. M. (2004). Ecophysiological constraints on the production of shaded and unshaded coffee: a review. *Field crops research*, 86(2-3), 99-114. <https://doi.org/10.1016/j.fcr.2003.09.001>
- Davis, A. P., Chadburn, H., Moat, J., O'Sullivan, R., Hargreaves, S., & Nic Lughadha, E. (2019). High extinction risk for wild coffee species and implications for coffee sector sustainability. *Science advances*, 5(1), eaav3473. <https://doi.org/10.1126/sciadv.aav3473>
- de Abreu, D. P., Roda, N. D. M., de Abreu, G. P., Bernado, W. D. P., Rodrigues, W. P., Campostrini, E., & Rakocevic, M. (2022). Kaolin film increases gas exchange parameters of coffee seedlings during transference from nursery to full sunlight. *Frontiers in Plant Science*, 12, 784482. <https://doi.org/10.3389/fpls.2021.784482>
- dos Reis, C. O., Magalhães, P. C., Avila, R. G., Almeida, L. G., Rabelo, V. M., Carvalho, D. T., ... & de Souza, T. C. (2019). Action of N-Succinyl and N, O-Dicarboxymethyl chitosan derivatives on chlorophyll photosynthesis and fluorescence in drought-sensitive maize. *Journal of Plant Growth Regulation*, 38, 619-630. <https://doi.org/10.1007/s00344-018-9877-9>
- Gokavi, N., Mukharib, D. S., Mote, K., Manjunatha, A. N., e Raghuramulu, Y. (2019). Estudos sobre geometria de plantio e métodos de poda para melhorar a produtividade e reduzir o trabalho pesado em café arábica cultivar Chandragiri. *J. Colheita. Erva daninha*.15, 58–64.
- Hammer, Ø.; Harper, D.A.T.; Ryan, P.D. (2001). PAST: Palaeontological statistics software package for education and data analysis. *Palaeontol. Electron.* 4, (9). https://palaeo-electronica.org/2001_1/past/spain.htm
- Hatamian, M., Arab, M., & Roozban, M. R. (2015). Stomatal behavior of two rose cultivar under different light intensities. *J. Agric. Crops Prod*, 17, 1-11. https://jci.ut.ac.ir/article_56490_fc658248223d8a01a295de3614e8bd8a.pdf?lang=en
- Hu, F., Bi, X., Liu, H., Fu, X., Li, Y., Yang, Y., ... & 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. <https://doi.org/10.1016/j.pld.2021.11.005>
- León-Burgos, A. F., Unigarro, C., & Balaguera-López, H. E. (2022). Can prolonged conditions of water deficit alter photosynthetic performance and water relations of coffee plants in central-west Colombia?. *South African Journal of Botany*, 149, 366-375. <https://doi.org/10.1016/j.sajb.2022.06.034>
- Lisboa, L. A. M., Cunha, M. L. O., Nakayama, F. T., de FIGUEIREDO, P. A. M., da Silva Viana, R., Ramos, S. B., & Ferrari, S. (2021). Morphophysiological characteristics of arabic coffee. *Nativa*, 9(1), 36-43. <https://doi.org/10.31413/nativa.v9i1.11066>
- Martins, S. C., Galmes, J., Cavatte, P. C., Pereira, L. F., Ventrella, M. C., & DaMatta, F. M. (2014). Understanding the low photosynthetic rates of sun and shade coffee leaves: bridging the gap on the relative roles of hydraulic, diffusive and biochemical constraints to photosynthesis. *PLoS One*, 9(4), e95571. <https://doi.org/10.1371/journal.pone.0095571>
- Matiello, J. B., Santinato, R., Garcia, A. W. R., ALMEIDA, S. D., & Fernandes, D. R. (2010). Cultura de café no Brasil: manual de recomendações. Rio de Janeiro: MAPA/Procafé.
- 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.
- Mendes, K. R., Marenco, R. A., & Nascimento, H. C. S. (2017). Velocidade de carboxilação da rubisco e transporte de elétrons em espécies arbóreas em resposta a fatores do ambiente na Amazônia Central. *Ciência Florestal*, 27, 947-959. <https://doi.org/10.5902/1980509828666>
- Mirosavljević, M., Momčilović, V., Jocković, B., Zorić, M., Aćin, V., Denčić, S., & Pržulj, N. (2018). Identification of Favourable Testing Locations for Barley Breeding in South Pannonian Plain. *Journal of Agricultural Sciences*, 24(3), 303-311. <https://doi.org/10.15832/ankutbd.451279>
- Nascimento, E. A. D., Oliveira, L. E. M. D., Castro, E. M. D., Delú Filho, N., Mesquita, A. C., & Vieira, C. V. (2006). Morphophysiological alternations in leaves of *Coffea arabica* L. plants in consort with *Hevea brasiliensis* Muell. Arg. *Ciência Rural*, 36, 852-857. <https://doi.org/10.1590/S0103-84782006000300019>
- Navarro, F. E., Santos, J. A., Martins, J. B., Cruz, R. I., Silva, M. M. D., & Medeiros, S. D. S. (2022). Physiological aspects and production of coriander using nutrient solutions prepared in different brackish waters. *Revista Brasileira de Engenharia Agrícola e*

Ambiental, 26(11), 831-839. <https://doi.org/10.1590/1807-1929/agriambi.v26n11p831-839>

- Nobre, R. G., Rodrigues Filho, R. A., Lima, G. S. de., Linhares, E. L. da R., Soares, L. A. dos A., Silva, L. de A., Teixeira, A. D. da S., & Macumbi, N. J. V.. (2023). Gas exchange and photochemical efficiency of guava under saline water irrigation and nitrogen-potassium fertilization . *Revista Brasileira De Engenharia Agrícola E Ambiental*, 27(5), 429–437. <https://doi.org/10.1590/1807-1929/agriambi.v27n5p429-437>.
- Pérez-Molina, J. P., de Toledo Picoli, E. A., Oliveira, L. A., Silva, B. T., de Souza, G. A., dos Santos Rufino, J. L., ... & Ferreira, W. P. M. (2021). Treasured exceptions: Association of morphoanatomical leaf traits with cup quality of *Coffea arabica* L. cv. “Catuaí”. *Food research international*, 141, 110118. <https://doi.org/10.1016/j.foodres.2021.110118>
- Racskó, J., Szabó, T., Nyéki, J., Soltész, M., & Nagy, P. T. (2010). Characterization of sunburn damage to apple fruits and leaves. *International Journal of Horticultural Science*, 16(4), 15-20. <https://doi.org/10.31421/IJHS/16/4/909>
- Rakocevic, M., Batista, E. R., Pazianotto, R. A., Scholz, M. B., Souza, G. A., Campostrini, E., & Ramalho, J. C. (2021). Leaf gas exchange and bean quality fluctuations over the whole canopy vertical profile of Arabic coffee cultivated under elevated CO₂. *Functional Plant Biology*, 48(5), 469-482. <https://doi.org/10.1071/FP20298>
- Rezaei, S., Etemadi, N., Nikbakht, A., Yousefi, M., & Majidi, M. M. (2018). Effect of light intensity on leaf morphology, photosynthetic capacity, and chlorophyll content in Sage (*Salvia officinalis* L.). *Horticultural Science and Technology*, 36(1), 46-57. <https://doi.org/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. <https://doi.org/10.9734/JEAI/2019/v32i630128>
- Rocha, O. C., Guerra, A. F., Silva, F. A. M., Machado Júnior, J. R. R., de ARAÚJO, M. C., & Silva, H. C. (2006). Programa para monitoramento de irrigação do cafeeiro no cerrado.
- Santos, L.A.; Lorenzetti, E.R.; Souza, P.E.; de Paula, P.V. A.A.; e Luz, A.L.F. (2016). Escaldamento no café: exposição facial e danos fotossintéticos. *Tecnol. Agropec.*10, 13–17.

- Sharma, R. R., Datta, S. C., & Varghese, E. (2018). Effect of Surround WP®, a kaolin-based particle film on sunburn, fruit cracking and postharvest quality of 'Kandhari' pomegranates. *Crop Protection*, 114, 18-22. <https://doi.org/10.1016/j.cropro.2018.08.009>
- Silva, E. A. Á. D. (2019). TROCAS GASOSAS, CRESCIMENTO E PRODUTIVIDADE DE CAFEZEIROS (*Coffea arabica*) IRRIGADOS EM CERES-GOÍÁS. <https://repositorio.ifgoiano.edu.br/handle/prefix/1780>
- Tadesse, M. (2021). Produção em massa e partição de biomassa em mudas de genótipos de café Harerghe sob irrigação deficitária em Jimma, sudoeste da Etiópia. *Revista Americana de Ciências da Vida*, 9(4), 67-72.
- Tang Xinglin, Jiang Jiang, Jin Hongping, Zhou Chen, Liu Guangzheng, & Yang Hua. (2019). Efeitos do sombreamento no teor de clorofila e propriedades fotossintéticas de *Phoebe bougainvillea*. *Yingyong Shengtai Xuebao*, 30(9).
- Taugourdeau S, Maire G, Avelino J, Jones JR, Ramirez LG, Quesada MJ, Charbonnier F, Gómez-Delgado F, Harmand J, Rapidel B, Vaast P, Roupsard O (2014) Leaf area index as an indicator of ecosystem services and management practices: An application for coffee agroforestry. *Agriculture, Ecosystems and Environment* 192:19-37. <https://doi.org/10.1016/j.agee.2014.03.042>
- Thakur, M., Bhatt, V., & Kumar, R. (2019). Effect of shade level and mulch type on growth, yield and essential oil composition of damask rose (*Rosa damascena* Mill.) under mid hill conditions of Western Himalayas. *PloS one*, 14(4), e0214672. <https://doi.org/10.1371/journal.pone.0214672>
- Ulm, R., & Jenkins, G. I. (2015). Q&A: How do plants sense and respond to UV-B radiation?. *BMC biology*, 13, 1-6. <https://doi.org/10.1186/s12915-015-0156-y>
- Venancio, L. P., Do Amaral, J. F. T., Cavatte, P. C., Vargas, C. T., Dos Reis, E. F., & Dias, J. R. (2019). Vegetative growth and yield of robusta coffee genotypes cultivated under different shading levels. *Bioscience Journal*, 35(5), 1490-1503. <http://www.seer.ufu.br/index.php/biosciencejournal/article/view/45039/27073>
- Venancio, L. P., Filgueiras, R., Mantovani, E. C., do Amaral, C. H., da Cunha, F. F., dos Santos Silva, F. C., ... & Cavatte, P. C. (2020). Impact of drought associated with high temperatures on *Coffea canephora* plantations: a case study in Espírito Santo State, Brazil. *Scientific Reports*, 10(1), 19719. <https://doi.org/10.1038/s41598-020-76713-y>

- 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).<https://doi.org/10.13287/j.1001-9332.202003.004>
- Zhu H, Li X, Zhai W, Liu Y, Gao Q, Liu J, Ren L, Chen H, Zhu Y. Effects of low light on photosynthetic properties, antioxidant enzyme activity, and anthocyanin accumulation in purple pak-choi (*Brassica campestris* ssp. *Chinensis* Makino). *PLoS One*. 2017 Jun 13;12(6):e0179305. doi: 10.1371/journal.pone.0179305. PMID: 28609452; PMCID: PMC5469474.