

**Relação de trocas gasosas em diferentes fases fenológicas com a produtividade de  
cafeeiros no Cerrado**

**Relationship of gas exchanges in different phenological phases with coffee productivity  
in the Cerrado**

**Relación del intercambio de gases en diferentes fases fenológicas con la productividad de  
cafetos del Cerrado**

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## Resumo

A cafeicultura vem expandindo no Cerrado brasileiro. Visando identificar genótipos adaptados às condições, em 2015, implantou-se um experimento com 35 genótipos de *Coffea arabica*, irrigados, em Ceres, Goiás, Brasil, latitude 15°21'00.67", longitude: 49°35'56.98", altitude de aproximadamente 570 m. Os cafeeiros apresentaram diferenças no crescimento, e na primeira safra, foram agrupados em baixa, média e alta produtividade. Buscando entender as divergências de crescimento e de produtividade entre os cafeeiros, avaliou-se as trocas gasosas entre 9:00 - 10:00 h; 12:00 - 13:00 h e 15:00 - 16:00 h, em cinco fases fenológicas da segunda safra (formação do fruto, enchimento do fruto, maturação, após a colheita e fase vegetativa), de três cafeeiros (Sarchimor MG 8840, Catucaí Amarelo 2SL e IBC – Palma 2) com alta, média e baixa produtividade, respectivamente, na primeira safra. Os genótipos apresentaram o mesmo padrão de produtividade na primeira e na segunda safra. As trocas gasosas em cafeeiros, com diferente potencial produtivo, cultivados no cerrado, sob irrigação, variaram entre os genótipos e as fases fenológicas. Os melhores resultados predominaram nas fases de formação e de enchimento dos frutos. Observou-se variação dos genótipos entre as fases fenológicas. Apesar das diferenças encontradas, as trocas gasosas não explicam as divergências nas respostas de crescimento e produtivas dos genótipos estudados, indicando o envolvimento de outros possíveis fatores no crescimento e na produtividade.

**Palavras-chave:** *Coffea arábica*; Fotossíntese; Produtividade; Adaptabilidade; Irrigação.

## Abstract

Coffee growing has been expanding in the Brazilian Cerrado. To identify genotypes adapted to the conditions, in 2015, an experiment was implanted with 35 genotypes of *Coffea arabica*, irrigated, in Ceres, Goiás, Brazil, latitude 15°21'00.67", longitude: 49°35'56.98", Altitude approximately 570 m. The coffee trees showed differences in growth and, in the first harvest, were grouped into low, medium and high productivity. Seeking to understand the divergences in growth and productivity between coffee trees, gas exchange between 9:00 - 10:00 h was evaluated; 12:00 - 13:00 h and 15:00 - 16:00 h, in five phenological phases of the second harvest (fruit formation, fruit filling, maturation, after harvest and vegetative phase), of three coffee trees (Sarchimor MG 8840, Catucaí Amarelo 2SL and IBC - Palma 2) with high, medium and low productivity, respectively, in the first harvest. The genotypes showed the same pattern of productivity in the first and second crop. Gas exchange in coffee trees, with

different productive potential, grown in the Cerrado, under irrigation, varied between genotypes and phenological phases. The best results prevailed in the formation and filling phases of the fruits. Variation of the genotypes was observed between the phenological phases. Despite the differences found, gas exchange does not explain the divergences in the growth and production responses of the studied genotypes, indicating the involvement of other factors in the growth and productivity of coffee trees cultivated in the Cerrado.

**Keywords:** *Coffea arabica*; Photosynthesis; Productivity; Adaptability; Irrigation.

## Resumen

El cultivo del café se ha expandido en el Cerrado brasileño. Para identificar genotipos adaptados a las condiciones, en 2015, se implementó un experimento con 35 genotipos de *Coffea arabica*, regados, en Ceres, Goiás, Brasil, latitud 15°21'00.67", longitud: 49°35'56.98", altitud de aproximadamente 570 m. Los cafetos mostraron diferencias de crecimiento, y en la primera cosecha, se agruparon en productividad baja, media y alta. Tratando de comprender las divergencias en el crecimiento y la productividad entre los cafetos, se evaluó el intercambio de gases entre las 9:00 - 10:00 h, 12:00 - 13:00 h y 15:00 - 16:00 h, en cinco fases fenológicas de la segunda cosecha (formación del fruto, llenado del fruto, maduración, después de la cosecha y fase vegetativa), de tres cafetos (Sarchimor MG 8840, Catucaí Amarelo 2SL e IBC - Palma 2) con alta, media y baja productividad, respectivamente, en la primera cosecha. Los genotipos mostraron el mismo patrón de productividad en la primera y segunda cosecha. El intercambio de gases en cafetales, con diferente potencial productivo, cultivados en el cerrado, bajo riego, varió entre genotipos y fases fenológicas. Los mejores resultados prevalecieron en las etapas de formación y llenado de los frutos. Se observó variación de los genotipos entre las fases fenológicas. A pesar de las diferencias encontradas, el intercambio de gases no explica las divergencias en las respuestas de crecimiento y producción de los genotipos estudiados, lo que indica la participación de otros posibles factores en el crecimiento y la productividad.

**Palabras clave:** *Coffea arábica*; Fotosíntesis; Productividad; Adaptabilidad; Riego.

## 1. Introduction

Coffee is one of the most commercialized agricultural products in the world, being considered a culture with great social and economic impacts in about 80 countries. In Brazil, there are more than 130 cultivars registered with the Ministry of Agriculture, with different

responses of growth, production and resistance to diseases, allowing to indicate specific genetic materials for the different regions of the country.

With predictions global climate change, plants need to adapt to different environments cultivation (Charbonnier et al., 2017). The coffee tree has great adaptability, presenting physiological, biochemical, anatomical or morphological changes, according to the edaphoclimatic characteristics (Ferreira et al., 2013). However, increases in temperature and CO<sub>2</sub> emissions, which currently reach 400 ppm (parts per million), can compromise the coffee tree (Rodrigues et al., 2018), causing economic and social impacts. Thus, seek to select genotypes with yield, quality and resistance to pests and diseases for the different growing regions (Ovalle-Rivera et al., 2015).

Aimind to select coffee plants adapted to the Cerrado edaphoclimatic conditions, in 2015, an experiment with 35 genotypes of *Coffea arabica* was installed at the Instituto Federal Goiano - Campus Ceres - GO, in order to select those with the best growth and production performance. In the first harvest, the genotypes showed divergences in growth (Sousa et al., 2019), and were grouped into low, medium and high productivity, probably due to their interaction with edaphoclimatic conditions, causing biochemical, physiological, anatomical and morphological changes.

The analysis of gas exchange is an important tool to determine the adaptation of plants to different environments, which can vary both due to factors intrinsic to the genotype and the phenological phase as well as to environmental factors (Souza et al., 2016). During the phenological phases of the coffee tree, there is variation in the source-drain relationship (Mendonça et al., 2011). As in the coffee tree the reproductive phase of the current year and the vegetative phase of the following year are simultaneous, and the growing fruits are preferred drains, the plant tends to increase the production of photoassimilates to supply the demands of the fruits in formation, as well as the formation of vegetative buds (Mendonça et al., 2011).

The variation in the assimilation of carbon between the phenological phases and the alterations in the assimilation of carbon in different coffee genotypes occur, mainly, due to stomatal limitations in the growth phase and non-stomatal ones in the resting period (Silva et al., 2004). Araújo et al., (2008) did not observe differences in the photosynthetic capacity between coffee leaves in the sun and in the shade and attributed the low rate of carbon assimilation to the diffusive limitations, and not to biochemical or photochemical restrictions. DaMatta et al., (1997), evaluating gas exchange in *Coffea arabica* cv Red Catuaí and C.

*canephora* cv Kouillou, verified great reductions in photosynthetic rates in both cultivars from summer to winter, with greater intensity for *Coffea arabica* cv Red Catuaí.

Given the variations in carbon assimilation in coffee trees, and still with the intention of understanding the relationship between gas exchange and growth and productivity, it becomes opportune to know the behavior of gas exchange, in different phenological phases and moments of the day, of coffee trees with different productive responses. Thus, the objective of the work was to evaluate gas exchange at different times of the day and phenological phases of coffee trees with divergence in growth and productivity.

## 2. Material and Methods

We did a field experiment as oriented by Pereira et al. (2018). The experiment was installed at the Instituto Federal Goiano - Campus Ceres - GO, in the São Patrício Valley, Centro Goiano, in the city of Ceres - GO, in April 2015. However, gas exchange analyzes were carried out in the stages of fruit formation, filling and maturation, after the harvest and vegetative of the second harvest, between January and August 2018.

Experimental area has South latitude 15°21'00.67", West longitude 49°35'56.98", altitude of approximately 570 m. The soil is characterized as Red Latosol (Santos et al., 2013). According to the Köppen classification, the local climate is Aw, hot and semi-humid with a well-defined season, from May to September. The average annual temperature is 27.7°C, with minimum and maximum averages of 19.0 and 36.4°C, respectively, and annual precipitation of approximately 1,601 mm.

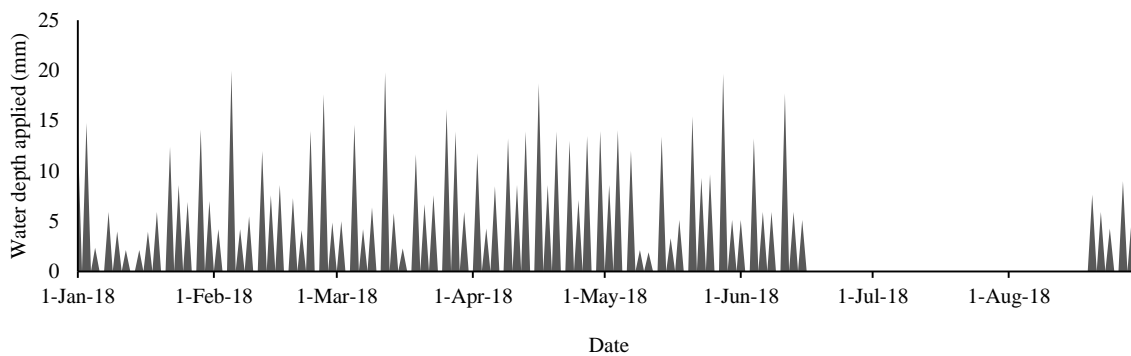
The chemical and physical properties of the soil in the experimental area when planting coffee seedlings were: 37.7% sand, 8.3% silt and 54.0% clay; pH (in water) = 5.80; M.O = 20.30 gdm<sup>-3</sup> (colorimetric); P = 12.8 mg dm<sup>-3</sup>; K = 0.2 cmolc dm<sup>-3</sup>; Ca = 3.0 cmolc dm<sup>-3</sup>; Mg = 1.80 cmolc dm<sup>-3</sup>; H + Al = 2.70 cmolc dm<sup>-3</sup> (SMP buffer at pH 7.5); and V = 65.7%.

Maintenance fertilization was carried out according to the recommendation of the 5th approach of the Minas Gerais State Soil Fertility Commission (Guimarães et al., 1999), with 150 kg of P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup>, and 130 kg of N ha<sup>-1</sup> and 100 kg of K<sub>2</sub>O ha<sup>-1</sup>, divided into three plots.

The control of pests and diseases was through constant monitoring, according to the need of the culture. Between the coffee plantation was planted brachiaria (*Urochloa decumbens*), with mowing according to the growth of the brachiaria (Rocha et al., 2016). The weeds were controlled along the planting line, also with periodic mowing.

The drip irrigation type was made up of simple 16 mm polyethylene lateral lines and self-compensating emitters, with a flow of  $2.2 \text{ L h}^{-1}$ , spaced 0.5 m apart. The coffee plantation was irrigated three times a week (Mondays, Wednesdays and Fridays). The reference evapotranspiration (ET<sub>o</sub>) was estimated using the Class A Tank, according to the Penman-Monteith model (Allen et al., 1998). The water depth was calculated using a crop coefficient (K<sub>c</sub>) equal to 1 [new crop (1 to 3 years) and spacing 2 - 3.6 x 0.5 - 1.0] (Oliveira et al., 2007) and applied as shown in Figure 1. A period of water stress was adopted between 06/18/2018 to 08/20/2018 (63 days), to standardize flowering, as recommended by Guerra et al. (2005) and Ronchi et al. (2015).

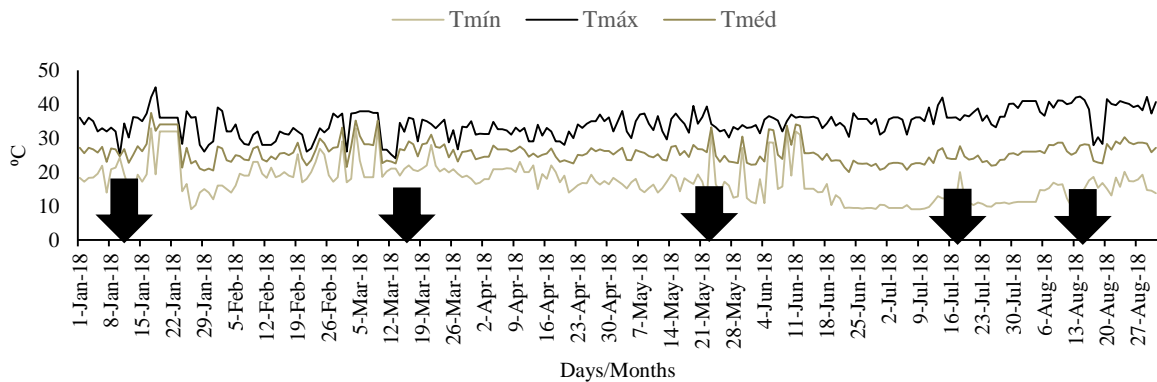
**Figure 1.** Water depth applied in the experiment from January to August 2018.



Source: Authors.

The values of maximum, average and minimum temperatures during the period of the experiment are shown in Figure 2, as well as the dates of the readings of gas exchange in the phenological phases.

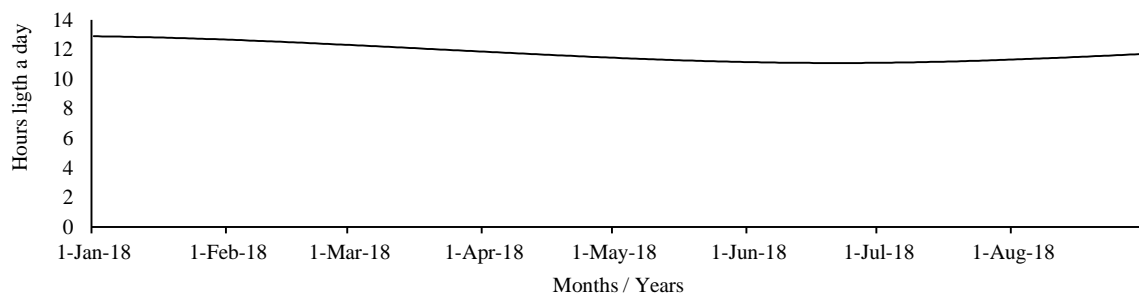
**Figure 2.** Maximum, average and minimum temperature in the municipality of Ceres - GO, from January 1st to August 31st, 2018.



Source: Authors.

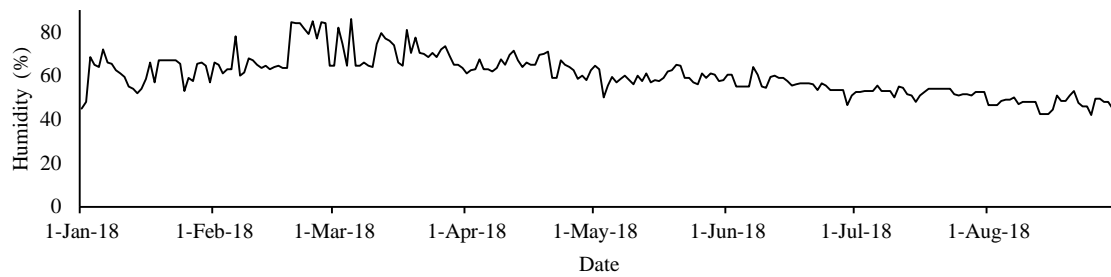
Figures 3, 4, 5 and 6 show the values of the photoperiod, relative air humidity, pluviometric precipitation and evapotranspiration of the Class A Tank at the IF Goiano - Campus Ceres, respectively, during the experimental period.

**Figure 3.** Photoperiod recorded during the conduct of the experiments, from January to August 2018.



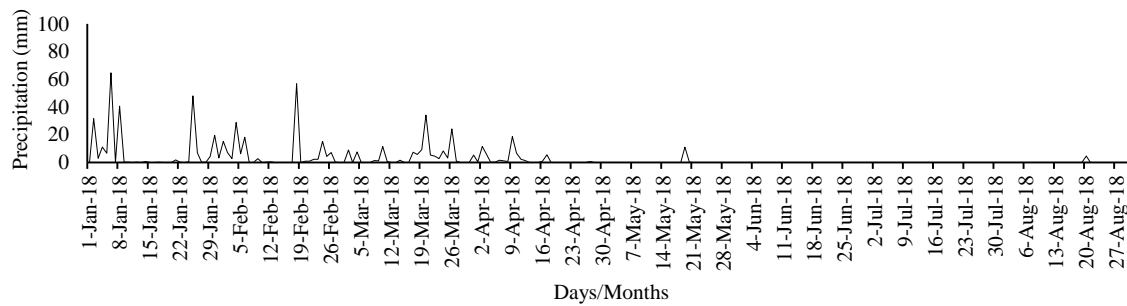
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**Figure 4.** Relative air humidity recorded from January to August 2018.



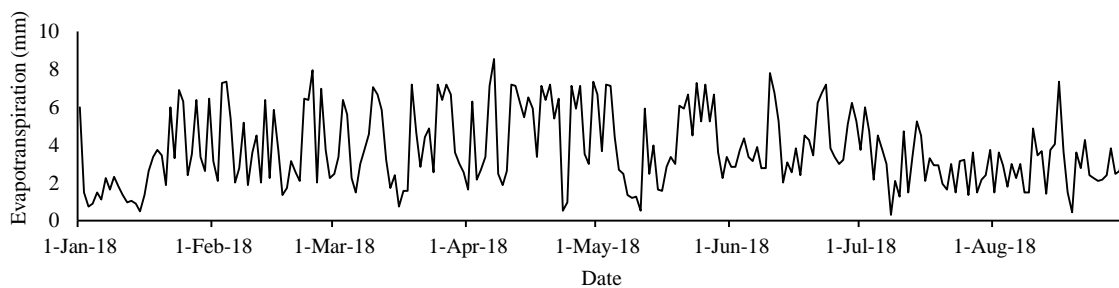
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**Figure 5.** Pluviometric precipitation recorded from January to August 2018.



Source: Authors.

**Figure 6.** Evapotranspiration monitored by the Class A tank from January 1 to August 31, 2018.



Source: Authors.



The experiment was carried out in subdivided plots, in randomized blocks, three plants as repetitions, and three readings on each leaf. The five phenological phases (fruit formation, fruit filling, maturation, after harvest and vegetative) were the plots, and the three genotypes (Sarchimor MG 8840, Catucaí Amarelo 2SL and IBC - Palma 2) the subplots. Among the 35 genotypes of *Coffea arabica* grown at the IF Goiano - Campus Ceres, since 2015, chose himself a genotype was with high (Sarchimor MG 8840), medium (Catucaí Amarelo 2SL) and low (IBC - Palma 2) productivity in the first crop.

Gas exchange readings were taken between 9:00 - 10:00 h; 12:00 - 13:00 h; and between 15:00 - 16:00 h, on 10/Jan/2018 (fruit formation), 16/Mar/2018 (fruit filling), 26/May/2018 (maturation), 19/Jul/2018 (after the harvest) and 18/Aug/2018 (vegetative phase), days with clear sky, without clouds, on the last fully expanded leaf, exposed to the sun, with a plagiotropic branch on the north side of the plant, from the middle third of the plant, using a gas analyzer infrared, IRGA, portable, model CI - 340, manufactured by CID, Inc., USA.

Air and leaf temperature ( $^{\circ}\text{C}$ ), photosynthetically active radiation ( $\mu\text{mol.m}^{-2}.\text{s}^{-1}$ ), liquid photosynthesis ( $\mu\text{mol.m}^{-2}.\text{s}^{-1}$ ), stomatal conductance ( $\text{mmol.m}^{-2}$ ) were evaluated  $.\text{s}^{-1}$ ), transpiration ( $\text{mmol.m}^{-2}.\text{s}^{-1}$ ) and vapor pressure deficit (kPa). The data obtained in the evaluations were submitted to analysis of variance, F test and the means compared by the Tukey test at 5% probability of error, using the SISVAR program.

### 3. Results and Discussion

#### *Gas exchange in coffee trees between 9 and 10am*

The average temperature of the air, the photosynthetically active radiation and the relative humidity of the air, during the readings in the phenological phases were, respectively: formation of the fruit ( $40.33^{\circ}\text{C}$ ,  $2,038.42 \mu\text{mol.m}^{-2}.\text{s}^{-1}$  and 59, 22%), fruit filling ( $35.28^{\circ}\text{C}$ ,  $1.580.74 \mu\text{mol.m}^{-2}.\text{s}^{-1}$  and 69.5%), maturation ( $21.86^{\circ}\text{C}$ ,  $51.88 \mu\text{mol.m}^{-2}.\text{s}^{-1}$  and 62.47%), after harvest ( $21.09^{\circ}\text{C}$ ,  $37.15 \mu\text{mol.m}^{-2}.\text{s}^{-1}$  and 54.42%) and vegetative phase ( $29.29^{\circ}\text{C}$ ,  $523.85 \mu\text{mol.m}^{-2}.\text{s}^{-1}$  and 47.31%).

Photosynthesis varied between the phenological phases and it was not observed difference between the genotypes in each phenological phase. The highest photosynthesis values were obtained when filling the fruit, ranging from 9.79 to  $11.94 \mu\text{mol.m}^{-2}.\text{s}^{-1}$  (Figure 7). Probably the leaf temperature elevated and high vapor pressure deficit (Table 1) were

factors limiting liquid photosynthesis in fruit formation. The greatest liquid photosynthesis was observed in the fruit filling phase (Figure 7), when compared to the fruit formation phase, although both comprise the fruiting period. The high demand for photoassimilates may be the result of limitations imposed by the environment, since in the fruit formation phase there was a difference in leaf temperature greater than 9°C in relation to fruit filling (Table 1).

In addition to the high leaf temperature, observed an increment of photosynthetically active radiation greater than 20% in relation to the fruit filling phase. These factors can act in inhibit liquid photosynthesis. High leaf temperature (which reached 47.37°C in the fruit formation phase) can trigger damage to photosynthesis, especially the activity of key enzymes during the carboxylative step, such as Rubisco (DaMatta et al., 2016) and photosynthetically active radiation, which was well above the light saturation point for coffee trees, can trigger processes that lead to plant oxidative stress (DaMatta et al., 2004).

Photosynthetically active radiation above 800  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and average air temperature higher 35°C, associated with the reduction of relative air humidity, result in stomatal closure and greater vapor pressure deficit (DaMatta et al., 2008). Even in the cultivation of irrigated coffee trees, with water stress to standardize flowering, the highest values of vapor pressure deficit, for the three genotypes, occurred in the fruit formation phase, the period with the highest leaf temperature (Table 1).

Stomatal conductance varied between the phenological phases, obtaining the highest values in the phases of fruit filling and ripening. Regarding the genotypes, only in the phase fruit filling, a difference was observed between the genotypes, Catucaí Amarelo 2 SL presented greater stomatal conductance than the IBC - Palma 2 (Figure 8).

The difference in stomatal conductance between the genotypes, in the phase fruit filling, did not cause a difference in photosynthesis. Even with the divergence in growth and productivity, coffee plants showed the same response to liquid photosynthesis. The fruit filling phase occurred in the period with summer characteristics, with high radiation, temperature and humidity, corroborating with DaMatta et al. (1997).

Photosynthesis can also be limited by stomatal conductance (Miner et al., 2017). When analyzing figures 7 and 8 (photosynthesis and conductance), the fruit filling and maturation phases were those with the highest stomatal conductance, just as the fruit filling phase was the one with the highest photosynthetic rate. However, as is already known (Farquhar & Sharkey, 1982), this is not necessarily a direct relationship, since high rates of photosynthesis were not observed in the maturation phase, with photosynthesis in this phase being limited by some other factor, which is probably the low rate of PAR radiation, which

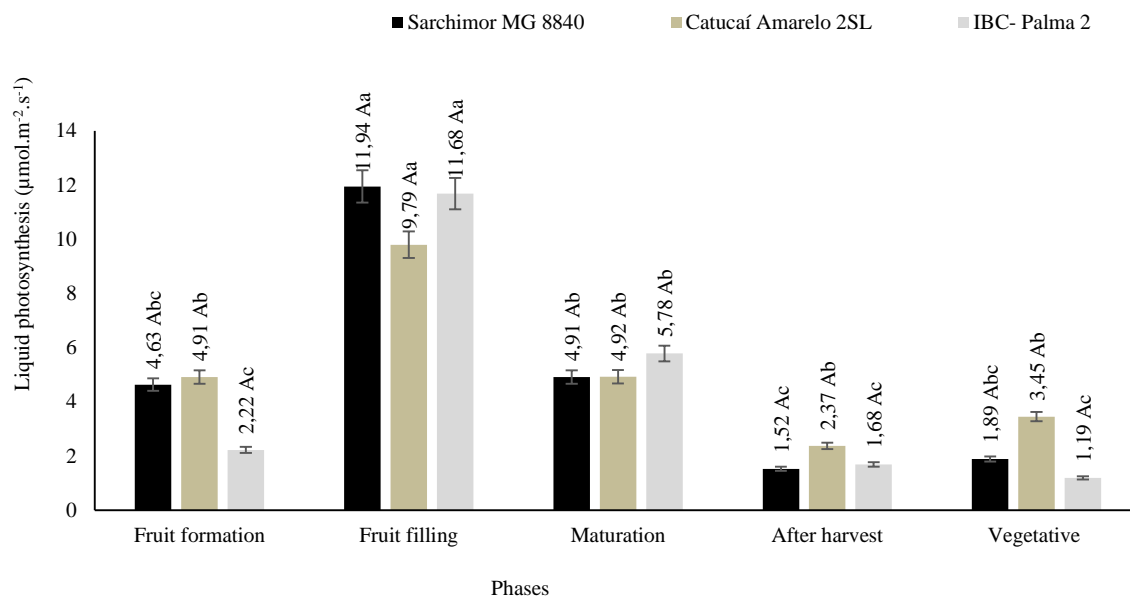
may have limited the availability of products from the photochemical step of photosynthesis. This same limitation may also have been the cause of the low photosynthetic rates during the post-harvest phase.

During the vegetative phase, although conditions such as leaf temperature and photosynthetically active radiation were within ranges considered non-limiting for good photosynthetic performance (DaMatta et al., 2004), it is deduced that the most limiting factor at the reduced photosynthetic rate has been the low stomatal conductance, compared to the other phases. The vegetative phase occurred in the period with the lowest relative humidity and still with the suspension of irrigation to synchronize the flowering of the subsequent harvest.

In addition to the interference of environmental factors in photosynthetic rates, there is an intrinsic influence on the phenological phase, prevailing higher production of photoassimilates in the fruit filling (Mendonça et al., 2011). In function on the demand for photoassimilates in the different phenological phases, there may be a change in the photosynthetic rate of plants. Corroborating the data observed in this work, Laviola et al., (2007) stand out that in the filling of the fruits there are peaks in the production of photoassimilates. Morais et al. (2003) report that in the flowering and fruiting phases, the plants increase their photosynthetic capacity, however, after removing the fruits, this capacity decreases, the same was observed in this work. This plasticity behavior is inherent to the genotype and can lead to different productions, due to the differentiated ability of partitioning of photoassimilates (source-drain relationship).

Although the study was carried out with irrigated coffee, the transpiration factor deserves attention, since the irrigation suspension is part of the crop management, in addition to being carried out in an environment with prolonged drought period. Like photosynthetic rates, transpiration rates can also be limited by stomatal conductance, however, once again this relationship is not always direct and can be influenced by environmental factors (Farquhar & Sharkey, 1982). In the case of this work, it can be seen that the lowest transpiratory rates occurred precisely in the phases of lower vapor pressure (Table 1 and Figure 9), even though there were high rates of stomatal conductance in the maturation phase.

**Figure 7.** Liquid photosynthesis in phenological phases of coffee trees (*Coffea arabica*), between 9:00 and 10:00 am, with different growth and productivity responses. Capital letters compare the genotypes within each phase, and lower case letters compare the phases within each genotype. Bar indicates standard error.



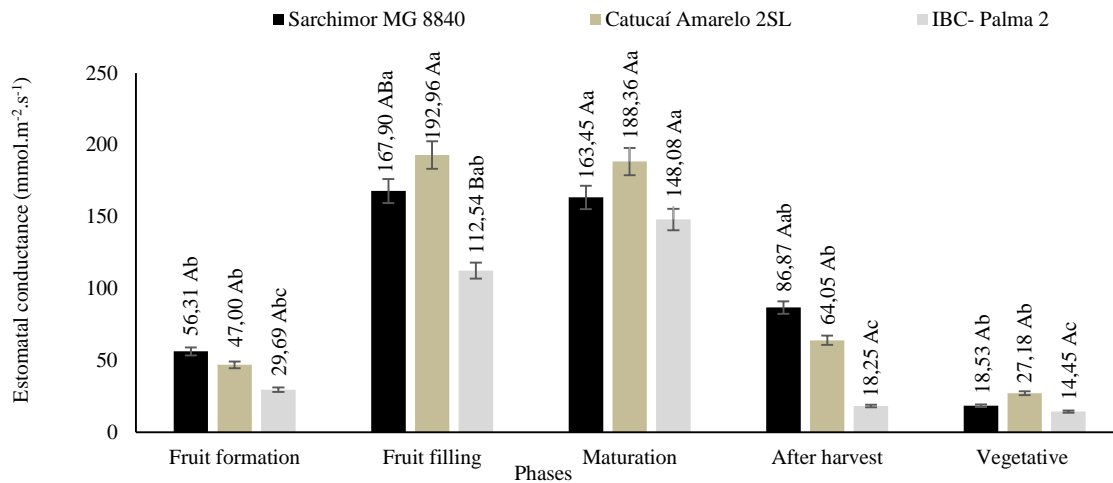
Source: Authors.

**Table 1.** Leaf temperature and vapor pressure deficit (DPV) in different phenological phases of coffee trees (*Coffea arabica*), between 9:00 am and 10:00 am, with different growth and productivity responses.

Phases	Temperature (°C)			DPV (kPa)		
	Genotypes			Genotypes		
	Sarchimor MG 8840	Catucaí Amarelo 2SL	IBC – Palma 2	Sarchimor MG 8840	Catucaí Amarelo 2SL	IBC – Palma 2
Fruit formation	44,10 Ba*	45,32 Aba	47,37 Aa	5,73 Ba	6,42 Ba	7,49 Aa
Fruit filling	38,73 Ab	37,50 Ab	38,24 Ab	3,11 Ab	2,97 Ab	3,59 Ab
Maturation	22,36 Ad	22,09 Ad	22,09 Ad	0,48 Ac	0,42 Ac	0,45 Ac
After harvest	20,56 Ad	21,52 Ad	22,26 Ad	0,74 Ac	0,86 Ac	0,95 Ac
Vegetative phase	30,04 Bc	33,69 Ac	32,21 Abc	2,53 Bb	3,5 Ab	2,86 Ab
CV(%)	7,08			26,41		

\* Capital letters compare the genotypes within each phase and lowercase letters compare the phases within each genotype. Source: Authors.

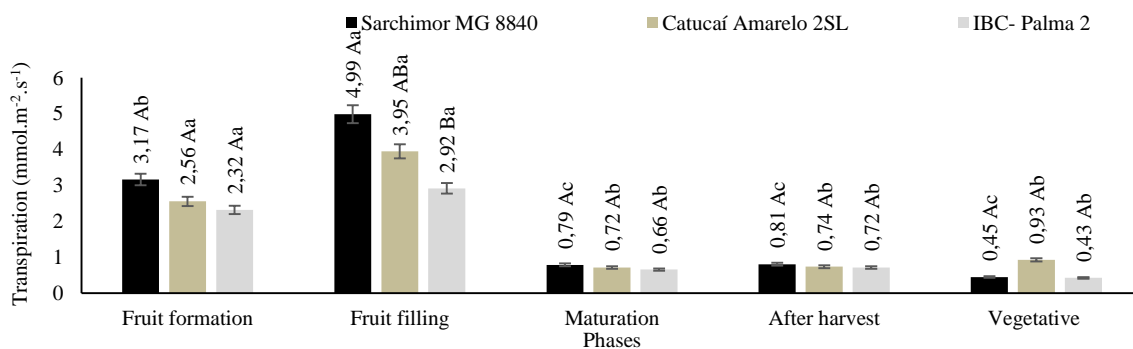
**Figure 8.** Stomatal conductance in phenological phases of coffee trees (*Coffea arabica*), between 9:00 am and 10:00 am, with different growth and productivity responses. Capital letters compare the genotypes within each phase, and lower case letters compare the phases within each genotype. Bar indicates standard error.



Source: Authors.

The highest values of transpiration were observed in the phases of formation and fruits filling, Sarchimor MG 8840 being superior to the IBC - Palma 2 in the phase of fruits filling (Figure 9). The low values of transpiration during the phases of the maturation, after harvest and vegetative can be related to the relative humidity of the air, suspension of irrigation, causing stomata closure and, consequently, reduction in transpiration, as well as in photosynthesis (Figure 7).

**Figure 9.** Transpiration in phenological phases of coffee trees (*Coffea arabica*), between 9:00 and 10:00 am, with different responses of growth and productivity. Capital letters compare the genotypes within each phase, and lower case letters compare the phases within each genotype. Bar indicates standard error.



Source: Authors.

Morais et al. (2003) point out that high photosynthetically active radiation and high temperature increase the difference in vapor pressure between the air and the leaf, and, consequently, increase perspiration, which acts as a thermoregulator.

Considering that the objective of this investigation was to verify possible elements in gas exchanges from 9:00 am to 10:00 am that could provide a basis for the differences in growth and production that occurred in the previous year among the studied genotypes it was observed that although the plants in the different phenological phases had significant differences in liquid photosynthesis, either due to factors intrinsic to the plants or the environment, between the different genotypes, within each phase, there was no significant difference in this parameter, which is the most important for production purposes. This leads to the belief that other factors, inherent to the genotype, are determinant for the differences in production.

Even with the divergence in stomatal conductance and transpiration between the genotypes in the phase fruit filling, there was no difference in net photosynthesis between 9:00 and 10:00 between the genotypes of coffee plants with productivity different.

#### ***Gas exchanges in coffee trees between 12 and 13h***

The average air temperature, the photosynthetically active radiation and relative air humidity average in the phenological phases were, respectively: fruit formation (44.57°C, 2,018.16  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$  and 59.22 %), fruit filling (43.16°C, 2,121,57  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$  and 69.52%), maturation (29.34°C, 62.20  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$  and 62.47%), after harvest (30.71°C, 40.67  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$  and 54.42%) and vegetative phase (38.51°C, 1,191.25  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$  and 47.31%).

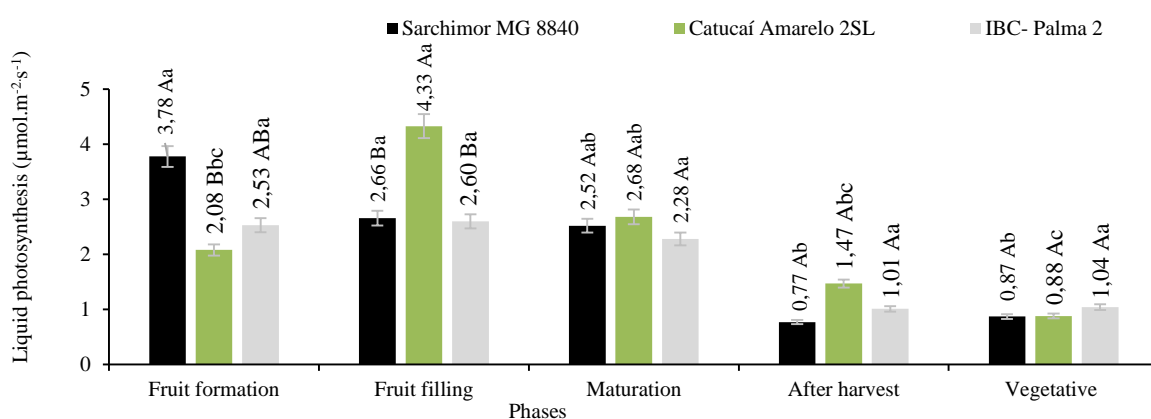
The interaction of the phenological phases with the genotypes influenced photosynthesis (Figure 10). In the fruit formation phase, Sarchimor MG 8840 showed greater photosynthesis than Catucaí Amarelo 2SL. In the phase fruit filling, Catucaí Amarelo 2SL showed greater photosynthesis compared to the other genotypes. In the maturation phases, after harvest and vegetative, there was no significant difference between the genotypes (Figure 10).

Regarding genotypes, Sarchimor MG 8840 showed the highest values of photosynthesis, in the phases of formation, fruit filling and maturation. Catucaí Amarelo 2SL obtained the highest values in fruit filling and maturation, while IBC - Palma 2 did not show any significant difference between the phases (Figure 10).

Although there was a difference in the photosynthetic rate between the genotypes, it must be considered that the net photosynthesis in Sarchimor MG 8840, between 9:00 and 10:00, reached  $11.94 \mu\text{mol.m}^{-2}.\text{s}^{-1}$  (Figure 7), without differentiating it from the other genotypes, whereas between 12:00 and 13:00 it was only  $2.66 \mu\text{mol.m}^{-2}.\text{s}^{-1}$  (Figure 10). High values of temperature and radiation can cause photosynthesis photoinhibition, however some cultivars can adapt, being tolerant to stress conditions (DaMatta, 2004). The divergence between the genotypes may be associated with the mechanisms of tolerance to stress conditions, especially at high temperatures and solar radiation, because in the phases in which a difference was observed between the genotypes, the temperature was above  $43^{\circ}\text{C}$  and the radiation above  $2000 \mu\text{mol. m}^{-2}.\text{s}^{-1}$ , probably causing photoinhibition.

Silva et al. (2004) observed that coffee tree growth predominates in the hot and rainy season, a period in which the rate of net carbon assimilation was higher. Despite evidence of variation in growth and photosynthesis in coffee plants in different seasons, it was observed a great variation in liquid photosynthesis throughout the day, mainly in the stages of fruit formation and filling (Figures 7 and 10), possibly due to the photoinhibition and changes in photorespiration.

**Figure 10.** Liquid photosynthesis in phenological phases of coffee trees (*Coffea arabica*), between 12:00 and 13:00, with different responses of growth and productivity. Capital letters compare the genotypes within each phase and lower case letters compare the phases within each genotype. Bar indicates standard error.



Source: Authors.

Stomatal conductance varied between genotypes and phenological phases (Figure 11). In fruit formation and maturation, Sarchimor MG 8840 showed greater conductance than IBC - Palma 2. In the other phases, it was not observed difference between the genotypes. The highest values of conductance were obtained in fruit formation and fruit filling (Figure 11), moments with higher leaf temperature and vapor pressure deficit (Table 2). According to

Shimazaki et al. (2007), the decrease in stomatal conductance occurs so that there is also a decrease in transpiration. Under high temperatures, with stomatal closure, there is also an increase in leaf temperature (Table 2), caused by the limitation of latent heat dissipation, due to the reduction in transpiration (Rodrigues et al., 2018).

Once again it is clear that that sweating is linked to DPV, since the lowest rates coincided with the lowest DPV. Stands out, however, that during the vegetative phase, although the DPV was at a level equivalent to the phases of fruit formation and filling, the transpiratory rates were very low, which in this case is presumed to be limited by the low stomatal conductance.

The low stomatal conductance in Catucaí Amarelo 2SL and IBC - Palma 2 during the maturation phase was not reflected in a difference in the photosynthesis rate, which remained at the Sarchimor MG 8840 level. However, both in the after harvest and vegetative phase, low photosynthetic rates were observed at the same time as low rates of stomatal conductance, suggesting limitation of photosynthesis by stomatal conductance.

Although there were low photosynthetic rates in the vegetative phase, the radiation conditions of the environment, unlike the maturation and after harvest phases, do not seem to be a limiting factor in the low rates of photosynthesis and stomatal conductance, but rather the suspension of irrigation imposed for flowering uniformity.

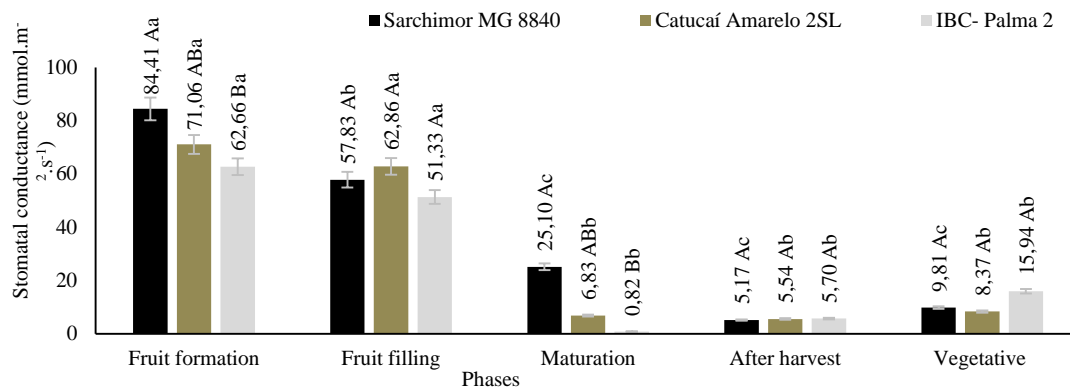
**Table 2.** Leaf temperature and vapor pressure deficit (DPV), between 12:00 and 13:00, in different phenological phases of coffee trees (*Coffea arabica*) with different growth and productivity responses.

Phases	Temperature (°C)			DPV (kPa)		
	Genotypes			Genotypes		
	Sarchimor MG 8840	Catucaí Amarelo 2SL	IBC – Palma 2	Sarchimor MG 8840	Catucaí Amarelo 2SL	IBC – Palma 2
Fruit formation	47,17 Aa*	47,23 Aa	47,56 Aab	6,58 Aa	6,78 Aa	7,09 Aa
Fruit filling	47,01 Aa	44,31 Ba	49,32 Aa	7,01 Aa	5,58 Bab	8,07 Aa
Maturation	29,52 Ab	29,37 Ac	30,42 Ac	1,44 Ac	1,06 Ad	1,47 Ac
After harvest	31,47 Ab	30,58 Ac	31,39 Ac	3,02 Ab	2,76 Ac	2,99 Ab
Vegetative phase	44,21 Aa	37,82 Bb	44,50 Ab	7,8 Aa	4,67 Bb	7,4 Aa
CV(%)	5,98			23,01		

\* Capital letters compare the genotypes within each phase and lowercase letters compare the phases within each genotype. Source: Authors.



**Figure 11.** Stomatal conductance in phenological phases of coffee trees (*Coffea arabica*), between 12:00 and 13:00, with different responses of growth and productivity. Capital letters compare the genotypes within each phase, and lower case letters compare the phases within each genotype. Bar indicates standard error.

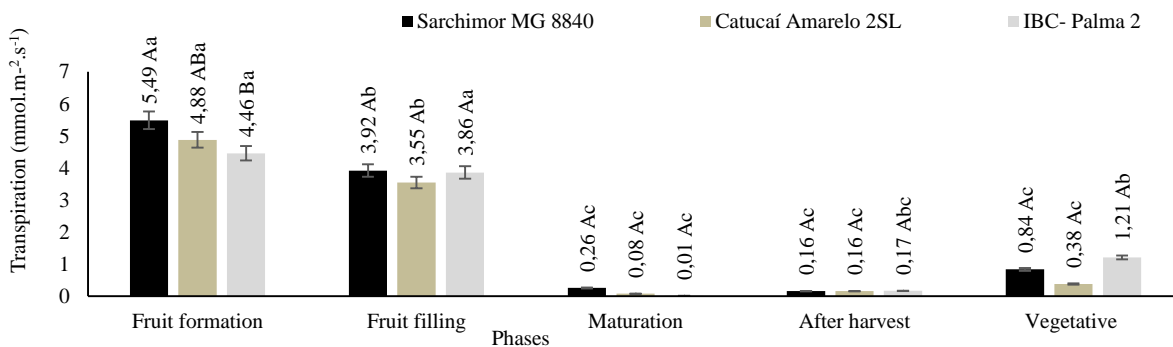


Source: Authors.

Transpiration was greater in fruit formation and filling (Figure 12), as well as stomatal conductance and vapor pressure deficit, indicating the close relationship between vapor pressure deficit, stomatal conductance and transpiration. In fruit formation, Sarchimor MG 8840 showed greater transpiration than IBC - Palma 2, and in fruit filling there was no difference between genotypes. In the maturation phases, after harvesting and vegetative, transpiration reduced dramatically (Figure 12), coinciding with the lowest values of stomatal conductance (Figure 11).

High transpiration rates can lead to the plant becoming dehydrated, due to excess water loss into the atmosphere (DaMatta et al., 2016). However, for the irrigated condition of the experiment, transpiration may be beneficial to production, as the plant's water demand may be satisfactorily met. Peloso et al. (2017) state that the reduction in conductance stomatal and transpiration can lead to less CO<sub>2</sub> influx into the chloroplasts, compromising the accumulation of biomass by the plant.

**Figure 12.** Transpiration in phenological phases of coffee trees (*Coffea arabica*), between 12:00 and 13:00, with different responses of growth and productivity. Capital letters compare the genotypes within each phase, and lower case letters compare the phases within each genotype. Bar indicates standard error.



Source: Authors.

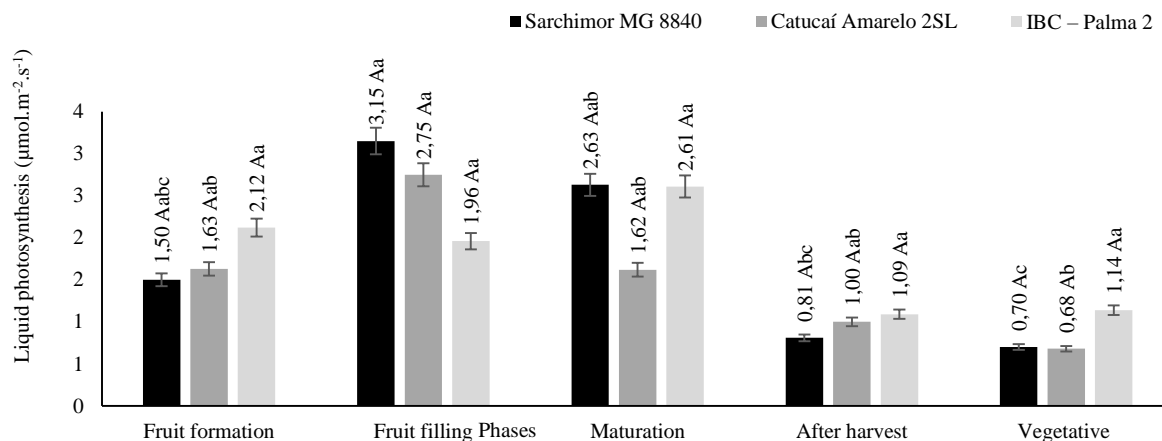
According to Rodrigues et al. (2018), the average annual temperature for the cultivation of arabica coffee varies between 18<sup>0</sup>C and 23<sup>0</sup>C. However, during this experiment, the average air temperature was above 40<sup>0</sup>C in some phases. Lemos et al. (2012) state that these conditions can increase the value of the vapor pressure deficit and stomatal closure, and consequently, the reduction in sweating.

### ***Gas exchanges in coffee trees between 15 and 16h***

The average temperature of the air, the photosynthetically active radiation and the average of the relative humidity of the air, during the readings in the phenological phases were, respectively: formation of the fruit (40.96<sup>0</sup>C, 1.390.15  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$  and 59.22%), fruit filling (39.81<sup>0</sup>C, 1,279.23  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$  and 69.52%), maturation (29.58<sup>0</sup>C, 62.84  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$  and 62.47%), after harvest (31.36<sup>0</sup>C, 33.24  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$  and 54.42%) and vegetative (34.52<sup>0</sup>C, 82.38  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$  and 47.31%).

It was observed The same liquid photosynthesis response between the genotypes in the phenological phases. However, there was variation in the behavior of the genotypes between the phenological phases. The net photosynthesis of Sarchimor MG 8840 in the phase fruit filling was superior to that obtained in the after harvest and in the vegetative phase. In the Catucaí Amarelo 2SL, the liquid photosynthesis in the phase fruit filling was greater than that found in the vegetative phase, while it was observed no difference in the net photosynthesis between the phases in the IBC - Palma 2 (Figure 13).

**Figure 13.** Liquid photosynthesis in phenological phases of coffee trees (*Coffea arabica*), between 15:00 and 16:00, with different growth and productivity responses. Capital letters compare the genotypes within each phase, and lower case letters compare the phases within each genotype. Bar indicates standard error.



Source: Authors.

The highest values of liquid photosynthesis were not associated with leaf temperature and vapor pressure deficit. In the maturation phase, it was observed the same photosynthesis values, despite the divergence of leaf temperature and vapor pressure deficit with the phases of fruit formation and filling (Table 3).

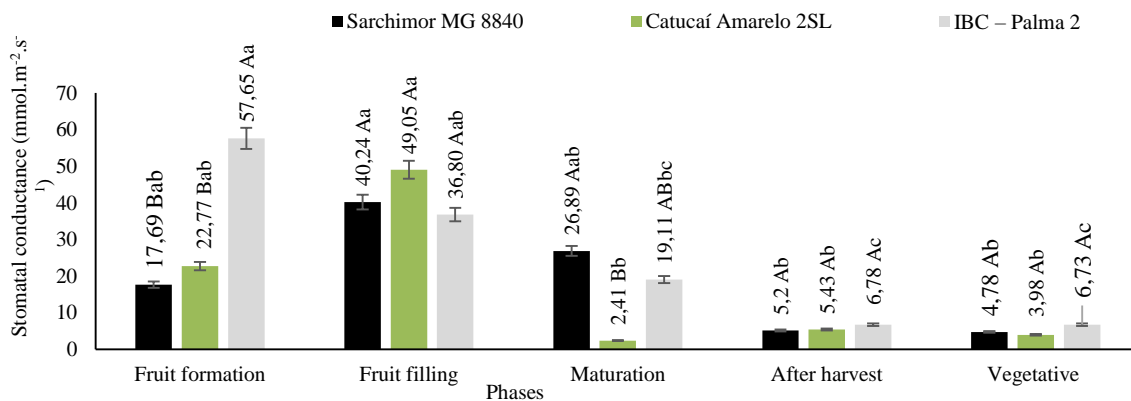
**Table 3.** Leaf temperature and vapor pressure deficit (DPV), between 15:00 and 16:00, in different phenological phases of coffee trees (*Coffea arabica*) with different growth and productivity responses.

Phases	Temperature (°C)			DPV (kPa)		
	Genotypes			Genotypes		
	Sarchimor MG 8840	Catucaí Amarelo 2SL	IBC – Palma 2	Sarchimor MG 8840	Catucaí Amarelo 2SL	IBC – Palma 2
Fruit formation	44,22 Ba	42,10 Ca	46,61 Aa	7,01 Aa	5,71 Ba	7,00 Aa
Fruit filling	43,59 Ba	39,18 Cb	46,09 Aa	5,91 Aa	4,16 Bb	6,86 Aa
Maturation	30,00 Ac	29,88 Ad	30,24 Ac	1,29 Ac	1,34 Ac	1,34 Ad
After harvest	31,93 Ac	31,23 Ad	31,94 Ac	3,28 Ab	3,10 Ab	3,27 Ac
Vegetative phase	34,59 Ab	35,00 Ac	35,78 Ab	3,80 Ab	3,91Ab	4,12 Ab
CV(%)	4,94			22,3		

\* Capital letters compare the genotypes within each phase and lowercase letters compare the phases within each genotype. Source: Authors.

The stomatal conductance in the fruit formation and maturation phases differentiated between the genotypes. In fruit formation, IBC - Palma 2 showed greater conductance than the other genotypes. In the maturation phase, Sarchimor was superior to Catucaí Amarelo 2SL (Figure 14).

**Figure 14.** Stomatal conductance in phenological phases of coffee trees (*Coffea arabica*), between 15:00 and 16:00, with different responses of growth and productivity. Capital letters compare the genotypes within each phase, and lower case letters compare the phases within each genotype. Bar indicates standard error.

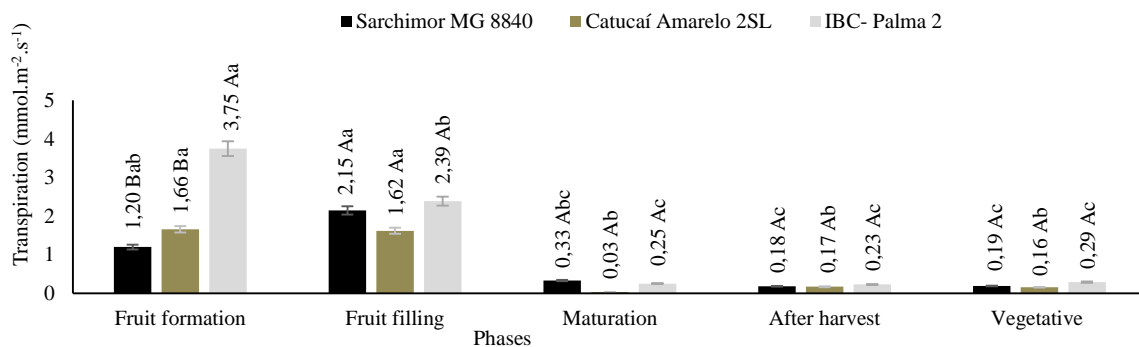


Source: Authors.

It is emphasized that despite the IBC - Palma 2 showing greater stomatal conductance in the fruit formation phase, it did not favor liquid photosynthesis. On the other hand, even with a lower rate of stomatal conductance in the maturation phase, Catucaí Amarelo 2SL maintained the same rate of photosynthesis as the other genotypes. Such responses indicate photosynthetic limitations due to other factors that could be affected by the highest leaf temperature among the genotypes.

Sweating in IBC - Palma 2 in fruit formation was superior to other genotypes. In the other phases, there were no differences between the genotypes (Figure 15). Sweating was not related to leaf temperature and vapor pressure deficit (Table 3).

**Figure 15.** Transpiration in phenological phases of coffee trees (*Coffea arabica*), between 15:00 and 16:00, with different responses of growth and productivity. Capital letters compare the genotypes within each phase, and lower case letters compare the phases within each genotype. Bar indicates standard error.



Source: Authors.

The increase in sweating can be related to climatic factors, however, it can also be related to factors of the plant itself (Rezende et al., 2011). In the phases of fruit formation and filling, there was also greater stomatal conductance, so the opening of the stoma favors the absorption of CO<sub>2</sub> and, in this process, there is also the water leaving the plant through transpiration (Santos, 2017).

According to Rodrigues et al. (2018), the thermal range considered favorable to the cultivation of arabica coffee, is between 18<sup>o</sup>C and 23<sup>o</sup>C, of average annual temperature. However, the average air temperature above 40<sup>o</sup>C, during the experiment, remained well above the range considered as optimal for the growth of coffee plants. Situations like these can increase the value of the vapor pressure deficit and cause stomatal closure, to reduce excess sweating (Lemos et al., 2012).

It was observed liquid photosynthesis oscillation between the reading schedules. The highest values of liquid photosynthesis were obtained in between 9:00 and 10:00 am in the phase fruit filling. While Sarchimor reached 11.94  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$  between 9 am and 10 am, it dropped to 2.66  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$  between 12 pm and 1 pm and was 3.15  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$  between 15:00-16:00h. Catucaí Amarelo 2SL arrived at 9.79  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$  between 9 am and 10 am, reduced to 4.33  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$  between 12 pm and 1 pm and 2.75  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$  between 3 pm and 4 pm. The IBC - Palma 2 reached 11.68  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$  between 9:00 and 10:00, reduced to 2.60  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$  between 12:00 and 13:00h and 1.96  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$  between 15:00 and 16:00h (Figures 07, 10, 13). This divergence of liquid photosynthesis between genotypes under stress conditions, mainly temperature, radiation and air humidity can provide different

responses in productivity due to differences in tolerance mechanisms, especially in photoinhibition, as well as photorespiration.

Between 15:00 and 16:00 the plants are still under stress conditions due to high temperature and high vapor pressure deficit, indicating the plant's permanence in stress conditions for a long period during the day, which can compromise the production of photoassimilated and consequently meet the demands of the drains, growth and productivity.

Despite the suspension of irrigation standardize flowering, it limits stomatal conductance, making it difficult to produce photoassimilates in the vegetative phase right after fruiting.

The proposal to identify gas exchange characteristics to explain the difference in genotype productivity it was not clear. It was expected that the genotype with the highest growth and or highest productivity would have the greatest net photosynthesis, however, it did not occur, demonstrating the involvement of other factors. The genotypes showed the same productivity response in the first and second crop. While the Sarchimor MG 8840 produced 32.0 sc ha<sup>-1</sup>, the yellow Catucaí 2SL produced 25.4 sc ha<sup>-1</sup>, and the IBC - Palma 2, only 3.6 sc ha<sup>-1</sup> in the second harvest (Ávila et al., 2020). On the other hand, he observed the variation in gas exchange between the times of the day and the seasons (phenological phases). Thus, the genotypes with higher productivity probably have other mechanisms, different from gas exchange, to overcome the difficulties imposed by the environment.

#### **4. Conclusion**

Coffee trees altered gas exchange between times of the day and between phenological phases. However, these changes do not explain the differences in the growth and productivity of irrigated coffee trees in the Cerrado.

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