Photosynthetic activity in avocado leaf ontogeny as a result of compatibility rootstock/scion in three locations in Colombia

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ABSTRACT

In Colombia, the evidence of rootstock/scion incompatibility in avocado cv. Hass graft union has been increasing, generating concern among farmers. The objective was to evaluate the photosynthetic response of the avocado trees due to rootstock/scion compatibility in three locations. A split plots design with a blocking factor per locality was used. The main plot corresponded to the type of graft union (compatible and incompatible) and the subplots to leaf age during the 2020 and 2021 seasons. Climatic (water balance) and gas exchange variables (photosynthesis, transpiration, stomatal conductance, leaf temperature, and efficiency in instantaneous water use) were measured. The results indicate that the photosynthetic performance was not affected when the water balance was negative. Compatibility did not significantly affect gas exchange variables (*A, gs, E, Tl, and WUEi*) during the main and secondary harvest period. The leaf age/harvest period interaction shows that during the first months of leaf development, *A*, g_s, *E*, and *Tl* are greater and are detrimental over time. It is concluded that the rootstock/scion compatibility does not significantly modify the capacity to assimilate CO_2. At the same time, the variation in avocado photosynthetic activity depends on the age of the leaves and the harvest season.

Keywords: gas exchange; grafting; leaf age; climate conditions; harvest seasons.

INTRODUCTION

The importance of grafting woody plants is related to the fact that through the rootstock/scion union, desirable characteristics can be transmitted between both tissues. Such as greater water absorption, tolerance to water stress, and greater efficiency in using nutrients, in addition to the earliness to start production (Lazare *et al*., 2019). It is reported that this practice increases fruit production, improves fruit quality, and extends tolerance to low and high temperatures, increasing the positive response to salinity and heavy metal stress (Oster & Arpaia, 2007; Nawaz *et al*., 2016).

The compatibility and incompatibility generated from the rootstock/scion union are defined by the degree of affinity between the two tissues in contact (Goldschmidt, 2014). Such affinity is derived from a successful and lasting connection, as long as this union lasts over time with an adequate plant performance (rootstock + scion). On the contrary, incompatibility is considered as the inability to achieve a successful connection between different tissues (Goldschmidt, 2014). According to the above, there are different ways to measure compatibility related to morphological, metabolic, and physiological attributes. For example, low compatibility is associated with asymmetric growth between the rootstock and the scion, which is

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visibly marked. This symptom of incompatibility has been reported in peach plants due to weak connections that do not last over time, causing little lignification of the cellular tissue, which can even lead to the death of the grafted tree (Álvarez, 2019).

Homografts (autografts) and heterografts (rootstock and scion belonging to different species of the same genus) are the most widely used for the propagation of fruit trees, especially avocado cv. Hass, and it has been established that taxonomic closeness is recognized as an affinity (compatibility) requirement for the survival of this union (Mudge *et al.*, 2009). Regarding incompatibility, in heterografts, a low connection between vascular tissues has been found, a fact that hinders the transport of assimilates, nutrients, and water between them, leading to reductions in plant yield (Kawaguchi *et al.*, 2008).

In apple plants grafted on different rootstocks, it was shown that when the connections established between the xylem and the phloem were successful, the calluses formation between the rootstock and scion decreased, equalizing the diameter of the rootstock and the scion. When there were separations in the connections, this condition could even cause the death of the grafted plants (Rasool *et al.*, 2020). In the case of peach, the rootstocks that provided greater vigor produced an incompatibility that generated the loss of plants, even years after planting (Najt *et al.*, 2011).

The rootstock/scion relationship must be symbiotic or cooperative since the first tissue supplies nutrients and water from the soil through the roots. The second one is the part that performs photosynthesis. Recent studies have shown that this set exchanges nutrients and water, hormones, proteins, and genetic macromolecules (Wang *et al.*, 2017). Additionally, successful connections between tissues also favor gas exchange parameters such as stomatal conductance, internal CO_2 concentration, and photosynthesis (Roy & Basu, 2009). Hu *et al.* (2006a) suggest that plants grafted onto some rootstocks improve nutrient uptake and that this results in an increase in the photosynthetic rate. In cucumbers, for example, high photosynthetic rates and an increase in fruit development are reported when graft compatibility is present (Rouphael *et al.*, 2010).

In general, the maximum rates of photosynthesis, transpiration, and stomatal conductance under saturated light conditions appear shortly before full leaf expansion and then decline with leaf age (Xu *et al.*, 1997). A study in avocados indicates that leaves can operate at their optimum physiological right after leaf expansion until at least 70-98 days after sprouting. Such information may be helpful in canopy management to maximize photosynthetic efficiency (Schaffer *et al.*, 1991).

Therefore, more information on the physiological aspects of grafted plants of avocado cultivars is necessary. In Hass avocado trees, where morphological alterations between tissues (rootstock and scion) are evident in the grafted plants used in commercial orchards in Colombia, this study aims to evaluate the photosynthetic response as a result of the compatibility between the rootstock and the scion in three locations in Colombia.

MATERIALS AND METHODS

Location

The study was carried out in three commercial orchards registered to export avocado cv. Hass located in Anserma (Caldas) at an altitude of 2,000 masl, Rionegro (Antioquia) at 2,175 masl, and El Peñol (Antioquia) at 2,198 masl. The trees were grafted on Creole rootstock originating from seed. The orchards were planted in 2013 (8 years).

Experimental design

A split-plot design with a blocking factor by location was used. Three factors were evaluated - the main one corresponded to the type of graft (Tg), the second was the leaf age development (La), and the third corresponded to the season harvest (Hp). The Tg factor was defined by two treatments (compatible and incompatible) derived from the ratio between the diameter of the rootstock stem (RD) and the diameter of the scion stem (SD), measured at 5 cm below and above the graft union. A compatible tree was considered when RD/SD was equal to 1 ± 0.05, and an incompatible tree when RD/SD was less than 0.95. The leaf age factor (subplot) corresponded to six stages of leaf ontogeny development (9 months) in two season harvests; the main one in the year 2020 (2020P) from April to December, and the secondary in 2021 from September to June (2021T).

Experimental unit

In each locality, nine compatible trees and nine incompatible trees were selected. Indeterminate reproductive structures (inflorescences) emitted after flowering in February 2020 (flowering of the first and main harvest 2020) and September 2020 (flowering of the second harvest 2021), which were in a state of indeterminate growth (517/110) according to the BBCH scale proposed by Alcaraz *et al.* (2013) were marked on each tree. Monthly, on a leaflet arranged in the fifth position from the meristem, at each cardinal point (north, south, east, and west), and from the beginning of leaf expansion (one month after marking) until the harvesting of the fruits of this growth flow (month nine) gas exchange measurements were made. An LCpro open-mode infrared gas analyzer (IRGA) (ADC BioScientific Ltd., UK) was used for this. Measurements were made between 9 am and 3 pm during each day.

Evaluated variables

Using a photosynthetic photon flux density of 1,100 µmol photons m^{-2} s^{-1}, measurements of photosynthetic rate (*A*) in µmol CO_2 m^{-2} s^{-1}, transpiration rate (*E*) in mmol H_2O m^{-2} s^{-1}, stomatal conductance (g_s) in mmol H_2O m^{-2} s^{-1} and leaf temperature (*Tl*) in °C were made. Through the *A*/*E* ratio, the estimation of the instantaneous efficiency water use (*WUEi*) was made. Additionally, using a WachtdogTM 2000 weather station, during the development of the study, the climatic variables were recorded: minimum, average, and maximum temperature (°C), relative humidity (%), and daily rainfall (mm) for the consolidation of monthly averages in each locality between February 2020 and June 2021. Evapotranspiration was estimated with the FAO ETo Calculator version 3.1 software from the mean values of temperature, humidity, and rainfall of each locality (Allen *et al.*, 2006). The water balance was calculated from rainfall and daily evapotranspiration in each study area.

Statistical analysis

The statistical analysis consisted of a mixed linear model for the variables, performing a significant multiple difference test using the adjustment for multiplicity by family through Holm's correction. Through this model two analyses of variance blocking by location (Anserma, Peñol, and Rionegro) was realized. The first consisted of analyzing the main plot corresponded to the type of graft factor (Tg), and the subplots to the leaf age development (La). In the second analysis, the main plot consists of La, and the subplot by the harvest period (Hp) (2020P and 2021T). In both analyses, a comparison test of means according to the test of least significant difference through Holm's correction was realized.

Statistical analyzes were performed using the packages "ggplot2 (Wickham, 2016), "lme4" (Bates *et al.*, 2015), "lmerTest" (Kuznetsova *et al.,* 2017), "agricolae" (De Mendiburu, 2021) included in the statistical environment of the R project. The R software (R Core Team, 2021) was used.

RESULTS AND DISCUSSION

Climatic conditions in the localities under evaluation

Regarding the climatic conditions during the 18 months of evaluation in the three locations, the maximum temperature records in Anserma were reached during February 2020, with an average of 22.6 °C and relative humidity of 77%, while the minimum temperature (14 °C) was achieved during the March 2021 season (Figure 1A). In February 2020, a negative water balance (-3.5mm) was recorded, derived from evapotranspiration that reached 97.4 mm and only 93.9 mm of rainfall (Figure 1B). El Peñol locality's maximum temperature was consistently above 23.7 °C, with an average relative humidity of 79% (Figure 1C). The lowest rainfall was recorded in January (21 mm) and April (59.6 mm) of 2020, a fact that negatively influenced the water balance, obtaining -86.3 mm and -52.5 mm, respectively (Figure 1D). In the Rionegro location was reported an average temperature of 17.2 °C and a relative humidity of 72.5% (Figure 1E). The periods of low rainfall occurred in January (67.2 mm), February (59.4 mm), and May (84.5 mm) of 2020, as well as in January (89.9 mm) and April (68 mm) of 2021, which added higher evapotranspiration during these months was the cause of negative water balances (Figure 1F). Having said the above and, as reported by Minvivienda (2020), the municipalities of Anserma (Caldas), El Peñol, and Rionegro (Antioquia) are characterized by temperate climates, with predominantly cold conditions.

In this regard, the means for all localities for temperature (18 °C), relative humidity (77.9%), rainfall (1,674 mm), and altitude (2,141 masl) are adjusted to the favorable conditions for the avocado crop. Since, as Garrido (2013) affirmed the avocado cv. Hass presents an optimum temperature between 18 and 25 °C, where maximum temperatures do not exceed 35 °C and minimum temperatures are not below 13 °C, a condition similar to that recorded during the evaluation period. Also, the altitude of the localities remained within the recommended since Bernal & Díaz (2020) reported the highest yield in orchards located between 1,800 and 2,200 masl for avocado cv. Hass in the

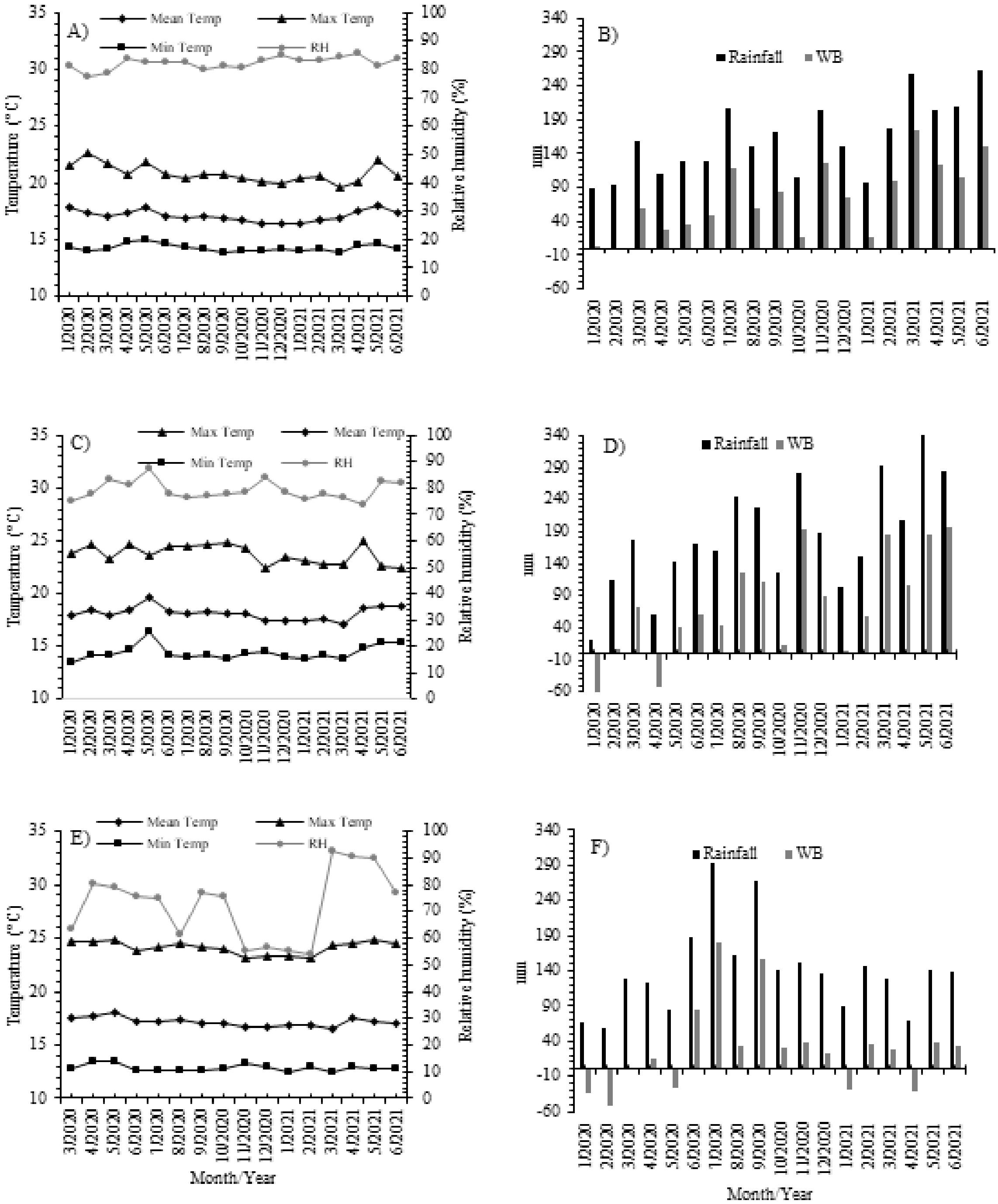

Figure 1: Mean (Temp), maximum (Max Temp), and minimum (Min Temp) temperature. Relative humidity (RH), rainfall (P), and water balance (WB) in Anserma (A, B), Peñol (C, D), and Rionegro (E, F) during the evaluation period.

department of Antioquia - Colombia, altitude similar to that of the properties evaluated (2,050, 2,175, and 2,198 masl). Finally, Alfonso (2008) recommends that rainfall be between 1,200 and 1,800 mm year^{-1}, which was met during the study period, with values between 1,674 mm year^{-1} (Rionegro) and 2,214 mm year^{-1} (Peñol), a fact that shows favorable conditions during the evaluation.

Gas exchange
Graft union compatibility

In general, the scion stem diameter is slightly larger than the rootstock stem diameter due to the lignification of the graft union region. When the scion stem diameter is much greater than that of the rootstock stem in the graft union region, it may be indicative of anatomical incom-

Table 1: Gas exchange variables at different ages of leaf development in compatibles and incompatibles avocado cv. Hass graft during the main harvest period in 2020

Factor	*Tl*	*E*	g_s	*A*	*WUEi*
Type of graft (Tg)			***p* value**		
	0.552	0.923	0.327	0.475	0.609
			Mean		
Compatible	28.99	4.16	0.13	6.46	1.65
Incompatible	29.42	4.13	0.13	6.09	1.55
Leaf age – La (Months)			***p* value**		
	4.77E-04	0.464	0.256	0.004	0.043
			Mean		
2	29.61 ab	4.1	0.13	8.14 a	2.04 a
4	30.15 a	4.09	0.12	7.54 a	1.92 ab
5	29.88 ab	4.5	0.13	4.90 b	1.08 c
6	29.08 ab	3.9	0.13	5.14 b	1.68 abc
9	26.30 b	3.97	0.14	4.78 b	1.16 bc
Tg * La			***p* value**		
	0.821	0.991	0.736	0.766	0.888

Leaf temperature (*Tl*), transpiration rate (*E*), stomatal conductance (g_s), net photosynthesis (*A*), and instantaneous water use efficiency (*WUEi*). Means followed by the same letter in the same column are not significantly different according to adjustment for multiplicity by family through Holm's

patibility between the two components. This anatomical graft incompatibility is caused by different cell division rates of the rootstock and the scion cambium, leading to a discontinuity in the xylem and phloem vessels between the rootstock and scion (Rodrigues *et al*., 2004). However, according to the results obtained in this study, for a location as a blocking factor, the main plot of the type of graft (Tg), and the subplot of the leaf age (La) for the main harvest 2020 and secondary harvest 2021, the analysis of variance for the gas exchange variables did not show significant differences ($p > 0.05$) for the interaction Tg*La nor the main factor Tg. A similar result was reported by Fallahi *et al.* (2001) in apple scions grafted on three rootstocks. Scion grafted on "Ottawa 3" rootstock presented a statistically similar net foliar photosynthesis compared to the "M.7 EMLA" rootstock.

An opposite result was indicated by Corelli *et al.* (2001), who reported that pear trees (*Pyrus communis*) decrease *A* when there is an incompatibility between the rootstock and the scion. In addition, Ferree (1992) also showed that the rootstock influenced the apple gas exchange since the values increased when the trees were grafted compared to non-grafted trees. Hu *et al.* (2006b) reported a reduction in stomatal conductance in citrus and, consequently, in CO_2 assimilation during noon, mainly due to the high vapor pressure deficit. This phenomenon is enhanced to a greater extent on scions grafted on dwarf rootstocks since their compatibility was poor (Martínez *et al.*, 2013). Contrary to what was reported in this study due to the absence of significant differences in these variables. In addition to the above, other authors reported that the net CO_2 assimilation rate and stomatal conductance increase after grafting a vigorous scion on some tomato rootstocks (Yang *et al.*, 2015; Penella *et al.*, 2016).

For leaf age, there were significant differences for the variable's *Tl* (p = 4.77 E-04), *A* (p = 0.004), and *WUEi* (p = 0.043) during the 2020 harvest (Table 1), and for *E* (p = 1.38E-04), g_s (p = 0.003) and *WUEi* (0.010) for the 2021 season. In this way, during the year 2020, the A presented a significant reduction between the fourth and the fifth month (150 days of development), continuing with slight modifications until 300 days of leaf development. The *WUEi* was unstable during the different measurement times and changed significantly according to the age of the leaf. The increase in *A* between the second and fourth month favored efficiency since, during the measurements, *E* was not significantly different (Table 1).

For the 2021 season, *E* presented the highest values in the second and fourth month of leaf development, a period in which the transition from young to adult leaf took place, characterized by a high transpiration rate, which subsequently decreased until reaching senescence. The values of

Table 2: Gas exchange variables at different ages of leaf development in compatibles and incompatibles avocado cv. Hass graft during the secondary harvest period in 2020

Factor	*Tl*	*E*	g_s	*A*	*WUEi*
Type of graft (Tg)			***p* value**		
	0.444	0.433	0.667	0.948	0.718
			Mean		
Compatible	26.2	2.56	0.13	0.15	5.92
Incompatible	26.7	2.86	0.14	5.85	3.07
Leaf age – La (Months)			***p* value**		
	0.053	1.38E-04	0.003	0.131	0.010
			Mean		
2	28.39	4.82 b	0.19 a	5.82	1.43 b
4	26.55	4.49 b	0.17 ab	4.81	1.06 b
5	24.77	1.37 a	0.11 c	6.19	4.55 a
6	26.26	1.70 a	0.11 c	7.4	4.37 a
9	26.3	1.17 a	0.14 bc	5.22	4.47 a
Tg * La			***p* value**		
	0.976	0.667	0.910	0.628	0.748

Leaf temperature (*Tl*), transpiration rate (*E*), stomatal conductance (g_s), net photosynthesis (*A*), and instantaneous water use efficiency (*WUEi*). Means followed by the same letter in the same column are not significantly different according to adjustment for multiplicity by family through Holm's

E during the second (4.82 mmol H_2O m^{-2} s^{-1}) and fourth (4.49 mmol H_2O m^{-2} s^{-1}) months were higher, thus decreasing the *WUEi* during these months, coupled with differences in the rate of *A*, being significantly higher in months five (6.19 µmol CO_2 m^{-2} s^{-1}) and six (7.4 µmol CO_2 m^{-2} s^{-1}) (Table 2).

Leaf ontogeny

On the other hand, regarding the split-plot analysis by location as blocking factor, leaf age as the main plot, and subplot the harvest period (Hp), during the 2020 and 2021 seasons, the interaction La*Hp presented significant differences ($p < 0.05$) for the gas exchange variables *Tl* (p = 2.89E-04), E (p = 3.91E-10), g_s (2.73E-06), *A* (p = 1.44E -06) and *WUEi* (p = 1.28E-14).

During the main harvest of 2020, *A* was higher between February and April, with values above 7.54 µmol CO_2 m^{-2} s^{-1}, then decreased from May to September below 5.14 µmol CO_2 m^{-2} s^{-1}. This decrease can be attributed to the thermal effect. Mandemaker (2008) consider optimum temperatures for avocado between 20 and 24 °C ± 5 °C and decreases below this range can induce avocado leaves losses of up to 20% in the photosynthetic capacity. In this sense, no substantial changes in *Tl* were observed during the main harvest (2020). However, for the 2021 season, the average leaf temperature was higher at the beginning of leaf development (2 months) than in later stages, where a decrease to 26 °C was observed (Figure 2C), mainly influenced by the environmental conditions that occurred at the end of 2020 and until June 2021 (Figure 1). In the case of the 2021 secondary harvest, the *A* presented a considerable increase during June, reaching 7.40 µmol CO_2 m^{-2} s^{-1}, while in the other months, the values fluctuated between 4.81 and 6.19 µmol m^{-2} s^{-1} (Figure 2A).

Bielczynski *et al.* (2017) states that younger leaves present higher rates of *A* reducing as development progresses since, structurally, by increasing the thickness of the mesophyll, the space of the chloroplast on the cell surface required for gas exchange increases. Increases in *A* at early leaf ages precede a decrease during maturity and senescence attributed to changes in the photosynthetic apparatus, as indicated by Jiang *et al.* (1993) in soybean (*Glycine max*); Jiang & Rodermel (1995); Miller *et al.* (1997; 2000) in tobacco (*Nicotiana tabacum*) and Makino *et al.* (1983) in rice (*Oryza sativa*). Similar to what was observed for *A* in the 2020 season after the fifth month of avocado leaf development. Similarly, in Arabidopsis plants, it was shown that photosynthesis decreases over time due to reductions in leaf biomass (Stessman *et al.*, 2002). On the other hand, Dillen *et al.* (2012) and Sun *et al.* (2015) reported that the rate of photosynthesis reaches the maximum value after the end of leaf expansion and finally declines during senescence.

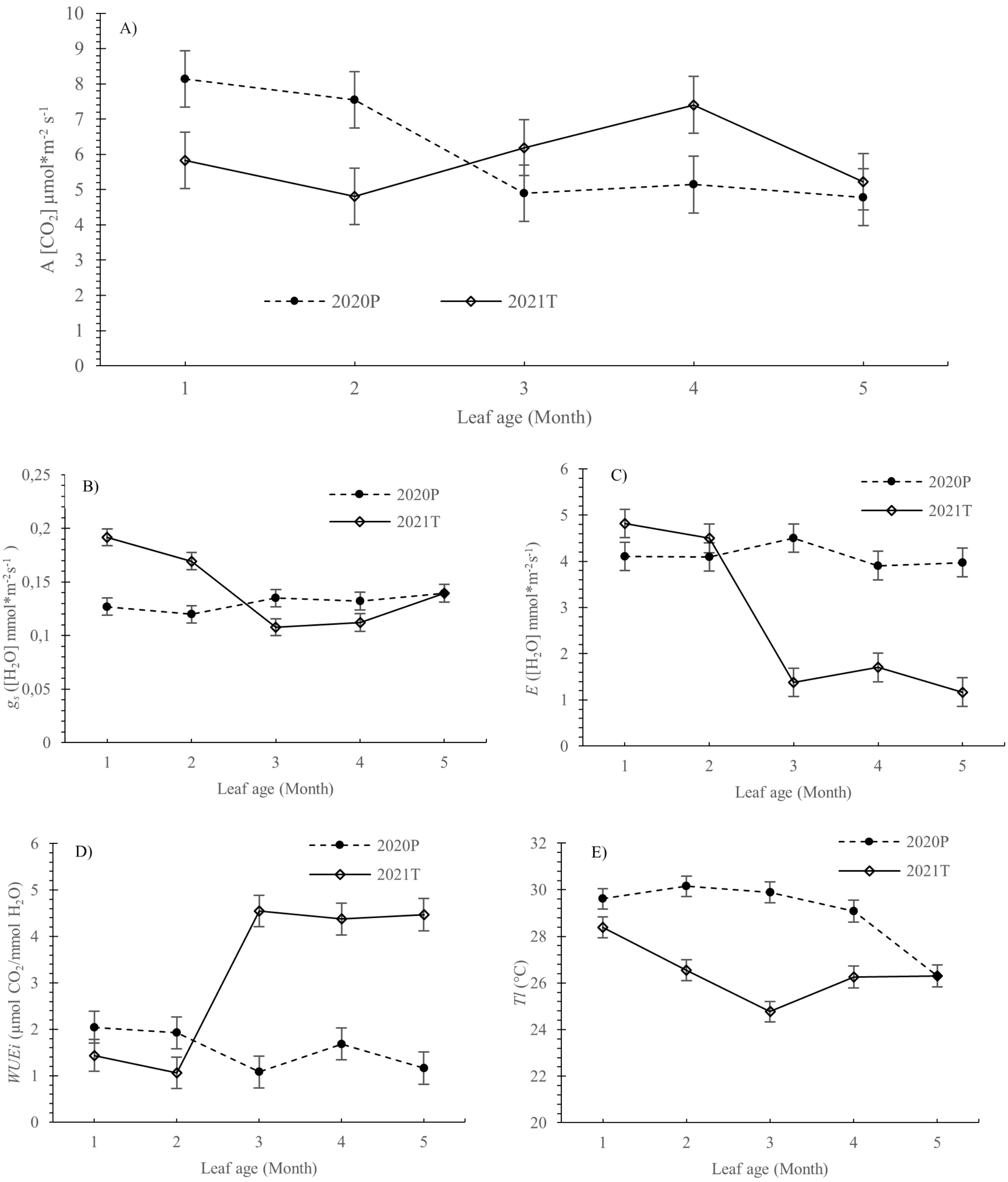

Figure 2: Gas exchange variables: A) leaf temperature (Tl); B): transpiration rate (E); C): stomatal conductance (gs); D) net photosynthesis (A); E) instantaneous water efficiency use (WUEi) during main (2020) and secondary (2021) harvest for the leaf age and harvest period interaction.

The stomatal conductance was stable during the 2020 season since the records only showed variations between 0.12- and 0.14-mm H_2O m^{-2} s^{-1}. In the case of the 2021 season, and specifically, during the first months of the year, g_s was significantly higher between February and April compared to May to September, where it only reached a value of 0.140 mm H_2O m^{-2} s^{-1} (Figure 2B). In a water stress study in avocado leaves, Chartzoulakis *et al.* (2002) report a linear relationship between g_s and photosynthesis, finding a significant reduction in gas diffusion (conductance) associated with a high density of spongy mesophyll cells, an event contrary to what was reported in this study.

The *E* presented significant differences for the 2020 and 2021 harvest, exhibiting a similar behavior for the two periods during the first months of leaf development. However, during the 2021 season, there was a decrease in transpiration during May, June, and September when senescence occurred (Figure 2D). According to Lyu *et al.* (2022), transpiration is reduced with increasing temperature and water availability. In this sense, lower temperatures were recorded during the main harvest period (2020), contrary to the secondary harvest, where temperatures were higher, and the reduction in *E* for the secondary harvest would be associated with a regulatory thermal effect on avocado leaves.

Like g_s, the *WUEi* presented a stable behavior during the 2020 season, with a slight variation in its values between 1.08 to 2.04 µmol CO_2/mmol H_2O, while in 2021, *WUEi* expressed a change greater, from 1.06 to 4.55 µmol CO_2/ mmol H_2O. In addition, in 2021, from May to November, the values increased considerably, reaching 4.46 µmol CO_2/mmol H_2O at the leaf development end. This phenomenon was influenced by the decrease in *E* during the period (Figure 2E). Compared with the above, in a study that aimed to identify the most promising rootstock for the development of mango seedlings (*Mangifera indica* L.) carried out in Espirito Santo, Brazil, it was found that the *E* of the plants increased when the rootstock "Oleo" was used, because this material conferred an increase in g_s to the canopies, added to a higher *A*, which was enough to obtain a higher *WUEi* (*A*/*E*) (Faria *et al.*, 2020).

CONCLUSIONS

The morphological disparity between the rootstock/scion size of the stem did not significantly affect the avocado plants' photosynthetic performance. The interaction between the age of the leaf and the harvest season influences the photosynthetic variables. It is notorious that the avocado maximizes its capacity to assimilate CO_2 during the earlier leaf development, with a significant decrease after two months of leaf age.

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CONFLICT OF INTERESTS

This study has significant contributions from all the authors, who agree with its publication and state that there are no conflicts of interest.

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