

## Graft compatibility effects on cv. Hass avocado fruit growth

### Compatibilidade do enxerto e seu efeito no crescimento da fruta de abacate cv. Hass

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#### ABSTRACT

The rootstock/scion morphological alterations are one of the limitations in the use of grafting, which has been defined as an incompatibility between these two tissues. However the effect of rootstock-scion interactions on reproductive potential, fruit set, yield efficiency, and avocado fruit quality characteristics are complex and poorly understood. This research aimed to evaluate the fruit growth of avocado cv. Hass in trees with incompatibilities between the rootstock and the graft in the main producing regions in Colombia. The split-plot design with a locality-blocking factor was used. The main plot corresponded to the compatibility and harvest factor, and the subplots to the age of fruit development. The statistical analysis consisted of a mixed linear model for the variables of respiratory rate and morphological growth of the fruit, performing a significant multiple difference test using the adjustment for multiplicity by family through Holm's correction. The compatibility treatment and the harvest season did not affect the fruit respiratory rate nor the variables of growth and development of cv. Hass. However, the age of development significantly affected both the respiratory rate and the variables of fruit growth.

**Index terms:** Respiratory rate; *Persea americana*; grafting; main and secondary harvest.

#### RESUMO

As alterações morfológicas no porta-enxerto/copa são uma das limitações no uso da enxertia, em frutíferas, sendo definida como uma incompatibilidade entre esses dois tecidos. No entanto os efeitos das interações porta-enxerto/copa no potencial reprodutivo, frutificação, eficiência de produção e características de qualidade do abacate são complexos e pouco compreendidos. Sendo o presente trabalho teve como objetivo avaliar o crescimento do fruto do abacateiro cv. Hass em árvores com incompatibilidades entre o porta-enxerto e o enxerto nas principais regiões produtoras da Colômbia. Foi utilizado um delineamento de parcelas subdivididas com fator de bloqueio de localidade. A parcela principal correspondeu à compatibilidade e fator de colheita e as sub parcelas à idade de desenvolvimento dos frutos. A análise estatística consistiu um modelo linear misto para as variáveis frequência respiratória e crescimento morfológico do fruto, realizando-se um teste de diferenças múltiplas significativas utilizando o ajuste para multiplicidade por família através da correção de Holm. O tratamento de compatibilidade e a época de colheita não afetaram a taxa respiratória dos frutos nem as variáveis de crescimento e desenvolvimento da cv. Hass. No entanto, a idade de desenvolvimento do fruto afetou significativamente tanto a taxa respiratória quanto as variáveis de crescimento dos frutos.

**Termos para indexação:** Frequência respiratória; *Persea americana*; enxertia; safra e safrinha.

#### INTRODUCTION

Grafting has been used in agriculture for several years as an effective method for fruit and vegetable production (Baron et al., 2019). This practice consists of the union of two tissues, a rootstock that provides an efficient root system and a scion or aerial system with desirable, productive characteristics (Silit et al., 2020). This union favors tolerance to biotic and abiotic factors that affect crop production. Therefore, in recent years, the importance of the role played by rootstocks in avocado (*Persea americana* Mill.) cultivation has been recognized (Silit et al., 2020), since avocado cv. Hass (a hybrid between the Guatemalan-37% and Mexican-63% races) plantations

are currently experiencing rampant growth in tropical and subtropical areas, where grafting heavily relies on non-Hass open pollination seedling rootstocks (Reyes-Herrera et al., 2020). The inheritance of the effects of the rootstock on the "Hass" avocado cultivar encompasses a wide range of genetically complex characteristics related to economically relevant attributes (Reyes-Herrera et al., 2020). According to Wang et al. (2017), this is related to the predominant role of the rootstock-scion interaction instead of the independent additive effects of each genotype, with combined effects mainly on the transport of water and nutrients and the large-scale movement of hormones, proteins, and messenger RNAs.

During the production of superior materials, efforts have been focused on the search for rootstocks that not only favor increased yield; if not also, they confer physiological and biological attributes to the scion, mediated by good compatibility derived from the scion-rootstock affinity (Silit et al., 2020).

Among the limitations in the use of grafting in fruit trees, it has been identified that the affinity between the rootstock and the graft (scion) is one factor that ensures successful compatibility between these two tissues. Graft compatibility generally is defined as a sufficiently close genetic (taxonomic) relationship between the cultivar (scion) and rootstock to allow the formation of a successful graft union (Loupit; Cookson, 2020). There is rootstock/scion compatibility when a given combination can form a solid and durable graft union resulting in the development of a successful graft. (Gainza et al., 2015). In contrast, incompatibility is graft union failure caused by metabolic, developmental, and anatomical differences between the scion and rootstock (Pina; Errea, 2005). The incompatibility leads to unhealthy trees, breakage at the graft union, premature death or failure of the graft combination, and incapacity to form a solid and lasting functional scion/rootstock union (Zarrouk et al., 2006).

It has been reported that good connections between the scion and the rootstock improve some agronomic characteristics, especially by conferring tolerance to abiotic stress (Díaz; Bernal; Tamayo, 2020; Mudge et al., 2009). In avocados, little has been studied about this compatibility, and this relationship is unknown. Sometimes, the compatibility symptoms associated with the difference in tissues between the rootstocks and the scion are evident long after planting the tree in the field, which affects the yield and fruit quality in the advanced years of the crop (Pina; Errea, 2005). Regarding avocado fruit growth and development, the rootstock provides the tree through the root system with nutrients, water, and other molecules such as hormones and proteins necessary for proper fruit development. While the scion provides the necessary photo assimilates through photosynthesis, according to Lazare et al. (2020), an adequate rootstock-scion association must guarantee high yields and good fruit quality. Abiotic factors, such as light intensity, water stress, temperature, and soil fertility; biotic factors, such as pests and diseases; and genetic factors, such as the rootstock, modify yields and fruit quality (Mickelbart, 2012; Silit et al., 2020). These factors can be favored by an excellent rooting system that tolerates unfavorable conditions and that guarantees the early growth of the fruit, reducing its permanence over the tree (Lira et al., 2020; Ozdemir; Topuz, 2004; Peña et al.,

2008; Schaffer; Wolstenholme; Whiley, 2013; Van Den Berg et al., 2021). These characteristics have determined the fruit time growth and its dynamics for some producing areas (Albacete et al., 2015; Márquez-Santos; Hernández-Lauzardo; Castrejón-Gómez, 2020).

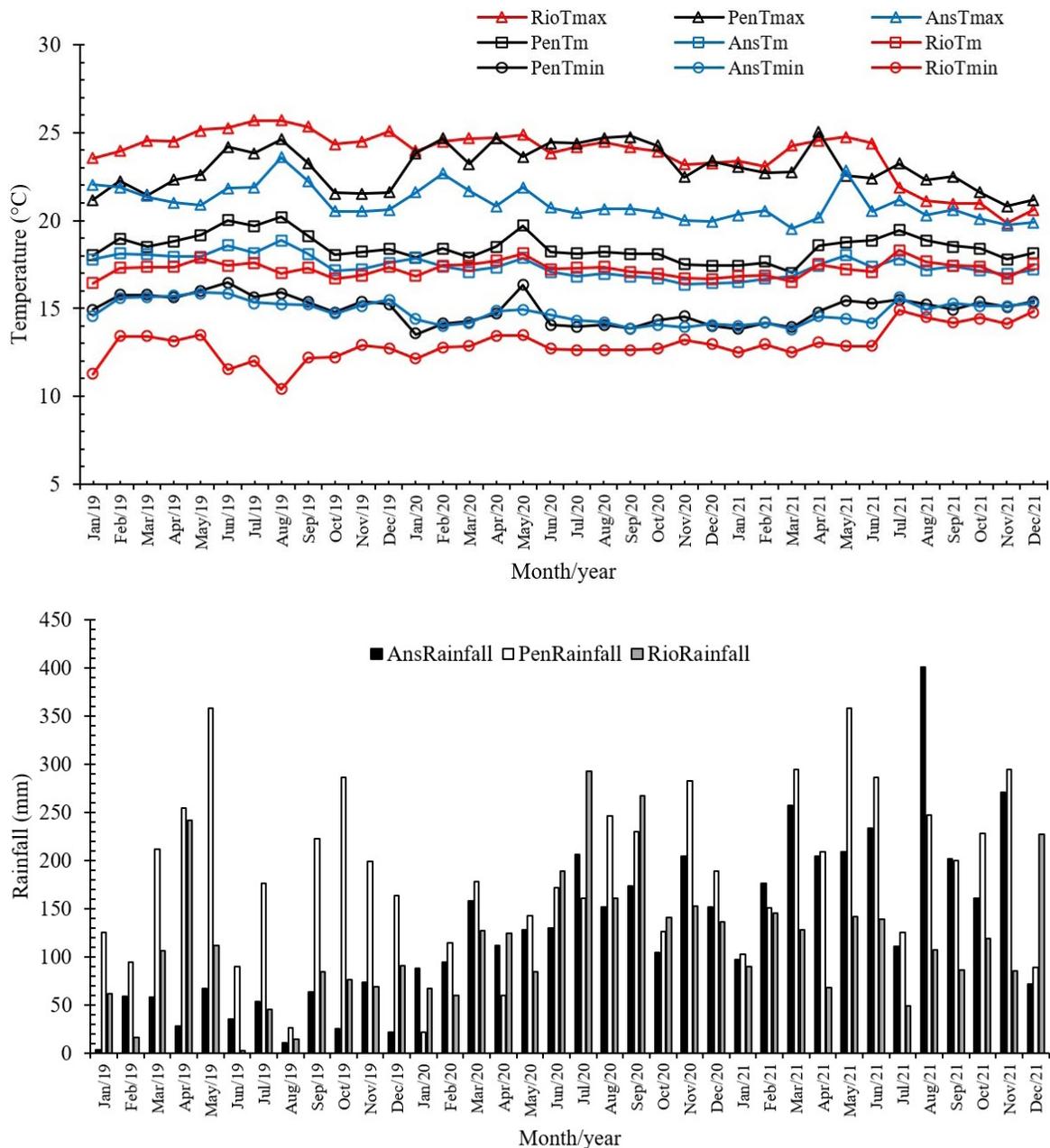
Compared to other fruit trees, such as apple trees, avocado fruit has an accelerated respiratory rate, a product of the use of fixed carbon and the energy performance achieved in the mitochondria. Besides, an excellent rooting system allows an adequate supply of water and nutrients and favors photosynthetic activity (Blanke et al., 1991; Scherrer et al., 2011); essential for fruit development due to the dry matter is the main parameter for determining the fruit harvest maturity (Carvalho et al., 2014; Liu et al., 1999). Since it has been proven that the rootstock favors the absorption of nutrients and a good connection between the rootstock and the scion is vital for the movement of solutes through the vascular system, there must be no interruptions between them at their point of connection (graft scar) (Silit et al., 2020). In fruit trees such as citrus, it has been reported that a symptom of non-affinity in grafted trees is due to unequal growth between the diameter of the rootstock and the graft in peaches the lower development of the pattern affects yield and generates foliar senescence (Najt et al., 2011). In vegetables of the Solanaceae family, the lack of affinity between the rootstock and the graft causes poor vascular connections. It affects the movement of photoassimilates, minerals, and water (Kawaguchi et al., 2008), which suggests that the rootstock/scion ratio is vital for plant performance.

In this sense, in commercial orchards of avocado cv. Hass in Colombia, morphological alterations have been evidenced by differences in the rootstock and scion diameter, which has generated an alteration of the tree stem, defined as an incompatibility between these two tissues; since the difference in the diameters in the grafting-union region may be related to anatomical graft incompatibility (Darikova et al., 2011). Likewise, the effect of rootstock-scion interactions on reproductive potential, fruit set, yield efficiency, and avocado fruit quality characteristics are complex and poorly understood. A healthier understanding of rootstock scion interactions would aid in the future's more effective selection and use of rootstocks. Thus, we present working hypotheses that when in the grafting union, the cultivar's trunk diameter is much larger than that of the rootstock, the avocado Hass fruit growth and development are affected. Therefore, to fill this research gap, the present study aims to evaluate the fruit avocado cv Hass growth and development in trees with and without morphological alterations, defined as incompatibilities and compatibles between the rootstock and the scion in the main producing regions in Colombia.

## MATERIAL AND METHODS

**Location:** The research was carried out in 3 commercial orchards registered to export avocado cv. Hass. The trees were grafted on Creole rootstock originating from seed. The orchards were planted in 2013 (8 years). The first orchard is in Anserma (Caldas) at an

altitude of 2,000 m a.s.l.; the second orchard is in the municipality of Rionegro (Antioquia) at 2,175 m a.s.l., and the third orchard in El Peñol (Antioquia) at 2,198 m a.s.l. The climatic variables were recorded through a portable weather station, “Watchdog™ 2000” and are shown in Figure 1.



**Figure 1:** A) Monthly maximum (Tmax), minimum (Tmin), and mean (Tm) temperatures, and B) monthly rainfall (mm) in Anserma (Ans), Peñol (Pen), and Rionegro (Rio) from 01/2020 to 06/2021.

**Experimental design:** A split-plot design with a blocking factor by location was used. The main plot corresponded to the compatibility factor (C), and the subplots to the age of fruit development (A). The compatibility 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 scar. A compatible tree was considered when RD/SD was equal to  $1 \pm 0.05$ , and an incompatible tree when RD/SD was less than 0.95 (Figure 2). The fruit age factor (subplot) corresponded to six stages of fruit ontogeny development (9 months) in two season harvests; the main one in the year 2020 (2020P) and the secondary in 2021 (2021T).

**Experimental unit:** In each locality, nine compatible trees and nine incompatible trees were selected. On each tree, 100 fruits issued after flowering in February 2020 (flowering of the main harvest in 2020) and September 2020 (flowering of the secondary harvest in 2021) were marked. The selected fruits were in a development stage of 711, according to the BBCH scale proposed by Alcaraz; Thorp and Hormaza (2013).

**Fruit respiratory rate:** For each fruit and at each evaluation age, the respiratory rate (ppm CO<sub>2</sub>) was determined for two hours, with a frequency of four seconds between readings, for a total of 1800 readings per fruit in

each sampling. LabQuest2 CO<sub>2</sub> sensors (Vernier) inside the respiration chamber were used. To differentiate the total CO<sub>2</sub> (TCO<sub>2</sub>) emitted by the fruits from that found inside the respiration chamber, the value recorded in each reading (Ti) was subtracted from the initial value captured by the sensors (T0).

The specific CO<sub>2</sub> rate was calculated as the relation of TCO<sub>2</sub> recorded at the end of each evaluation in ppm (Tf) and the whole fruit dry biomass reached (TFB).

**Fruit growth and development:** Length (L; cm), diameter (D; cm), and fresh weight (FW; g) were determined for all the sampled harvested fruits. Each fruit was dissected into its tissues for the determination of fresh (FPM; g) and dry pericarp matter (DPM; g), as well as the fresh (FSM; g) and dry seed matter (DSM; g). The total fruit biomass (TFB; g) and the length-diameter relationship (RLD) were also evaluated. For the dry matter, the fruit tissues were placed separately in a Memmert UL 80<sup>®</sup> oven (Memmert GmbH + Co. KG, Büchenbach, Germany) at 60 °C until a constant weight was reached, and later, using an analytical balance, determine the dry weight of each tissue.

**Statistical analysis:** The statistical analysis consisted of a mixed linear model for the variables of respiratory rate and morphological growth of the fruit, performing a significant multiple difference test using the adjustment for multiplicity by family through Holm's correction.



(A)



(B)

**Figure 2:** Rootstock/scion compatibility (A) and incompatibility (B).

This model performed two variance-blocking analyses by location (random effects) (Anserma, Peñol, and Rionegro). The first consisted of analyzing the compatibility treatment (C) as the main plot (fixed effects) and the fruit age (A) as a subplot (fixed effects). In the second analysis, the main plot (fixed effects) consists of the harvest season (H) (2020P and 2021T) and the fruit age (A) as a subplot (fixed effects). In both analyses, a comparison test of means according to the test of least significant difference through Holm's correction was realized, the medians of fruit respiratory rate and the means for L, D, FFW, FPM, DPM, FSM, DSM, and TFB variables by the fruit age growth in each treatment were used for the analysis of variance.

Statistical analyzes were performed using the packages "ggplot2" (Wickham, 2016), "lme4" (Bates et al., 2015), "lmerTest" (Kuznetsova; Brockhoff; Christensen, 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

### Fruit respiratory rate - Compatibility treatment (C) as the main plot and the fruit age (A) as a subplot

Main harvest season 2020P: Next, the results of the fruit respiration rate (FRR) for the analysis of splits plots, main plot compatibility (C), and subplot age of fruit development (A) during the main harvest (2020P) are presented. For this harvest period, the compatibility factor ( $p=0.253170$ ) and the Compatibility by Harvest season interaction ( $p=0.985633$ ) did not significantly affect the respiratory rate of the avocado fruit. In contrast, the fruit age factor (A) presented significant differences ( $p=0.002232$ ) in  $\text{CO}_2$  concentration measured at each age of fruit development during this harvest period. On average, the fruits harvested from compatible and non-compatible trees presented a respiratory rate reaching maximum values of 1,790.45 ppm of  $\text{CO}_2$  during the evaluation period (Table 1).

On the other hand, during the main harvest (2020P), the  $\text{CO}_2$  concentration increased with the age of fruit development; with a monthly increase of 16.7% (383.9 ppm  $\text{CO}_2$ ) during the nine months of development; showing the greatest increase of 72.87% between the fifth and sixth month of growth, going from 887.4 to 1,560.4 ppm  $\text{CO}_2$  (Table 1).

Secondary harvest season 2021T: Regarding the analysis of variance blocking by location and main plot compatibility (C) and subplot fruit age development (A) for 2021T, as in 2020P, neither the compatibility factor

( $p=0.885837$ ) nor the C\*A interaction ( $p=0.911309$ ) affected FRR in 2021T. FRR was only significantly affected ( $p=0.001211$ ) by the age of fruit development, as in 2020P.

Table 2 shows the results of the comparison of means of FRR of avocado fruits cv. Hass for 2021T, where the fruit age of development presented a significant increase in the concentration of  $\text{CO}_2$  emission between ages 4 and 9 months of fruit development. From the fourth month of growth, there were constant increases, which led to an enhancement of 37,830.6% (3,787.7 ppm  $\text{CO}_2$ ) in FRR by the ninth month of fruit growth (harvest time), with the greatest FRR increase between the fifth (1,008.1 ppm  $\text{CO}_2$ ) and ninth month (3,787.7 ppm  $\text{CO}_2$ ).

**Table 1:** The comparison test of fruit respiratory rate of avocado cv. Hass for the compatibility and fruit age treatment during the main harvest season (2020P).

Treatment	$\text{CO}_2$ (ppm)	Fruit age (month)	$\text{CO}_2$ (ppm)
Compatible	1,427.85 a*	4	698.4 c
Incompatible	1,646.22 a	5	887.4 bc
Mean	1,537.03	6	1,560.4 b
		9	3,002.2 a

\* Mean values with similar lowercase letters in each column do not differ significantly at 5%, according to the least significant difference test through Holm's correction.

**Table 2:** The comparison test of fruit respiratory rate of avocado cv. Hass for the compatibility and fruit age treatment during the secondary harvest season (2021T).

Treatment	$\text{CO}_2$ (ppm)	Fruit age (month)	$\text{CO}_2$ (ppm)
Compatible	1,630.5 a*	4	434.5 bc
Incompatible	1,862.5 a	5	1,008.1 b
Mean	1,745.5	6	1,400.2 b
		9	3,785.7 a

\* Mean values with similar lowercase letters in each column do not differ significantly at 5%, according to the least significant difference test through Holm's correction.

### Fruit respiratory rate - Harvest season factor (H) as the main plot and the fruit age (A) as a subplot

From the second analysis, considering the harvest factor (H) as the main plot and the fruit development age (A) as a subplot, it was observed, as in the previous analysis, that age development was the only factor that presented

significant differences for FRR of avocado fruits. However, this variable does not differ for the harvest (2021T and 2020P;  $p=0.42$ ) and the interaction H \* A ( $p=0.42$ ).

Such the compatibility factor analysis, the fruits' FRR was independent of the harvest season (2021T and 2021P). The avocado fruits presented the same respiratory pattern and, on average, reached maximum CO<sub>2</sub> emission values of 1,553.6 ppm (Table 3). On the other hand, the fruit age and its stage of development significantly affected the maximum values of CO<sub>2</sub> emitted from its respiratory activity, with an average monthly increase of 423.6 ppm, with a rise of 57% (534 ppm) between 4 and 9 months; and 463.9% (2,541.4 ppm CO<sub>2</sub>) between the fourth and ninth month of development (Table 3).

**Table 3:** The comparison test of fruit respiratory rate of avocado cv. Hass for the harvest season and age factors.

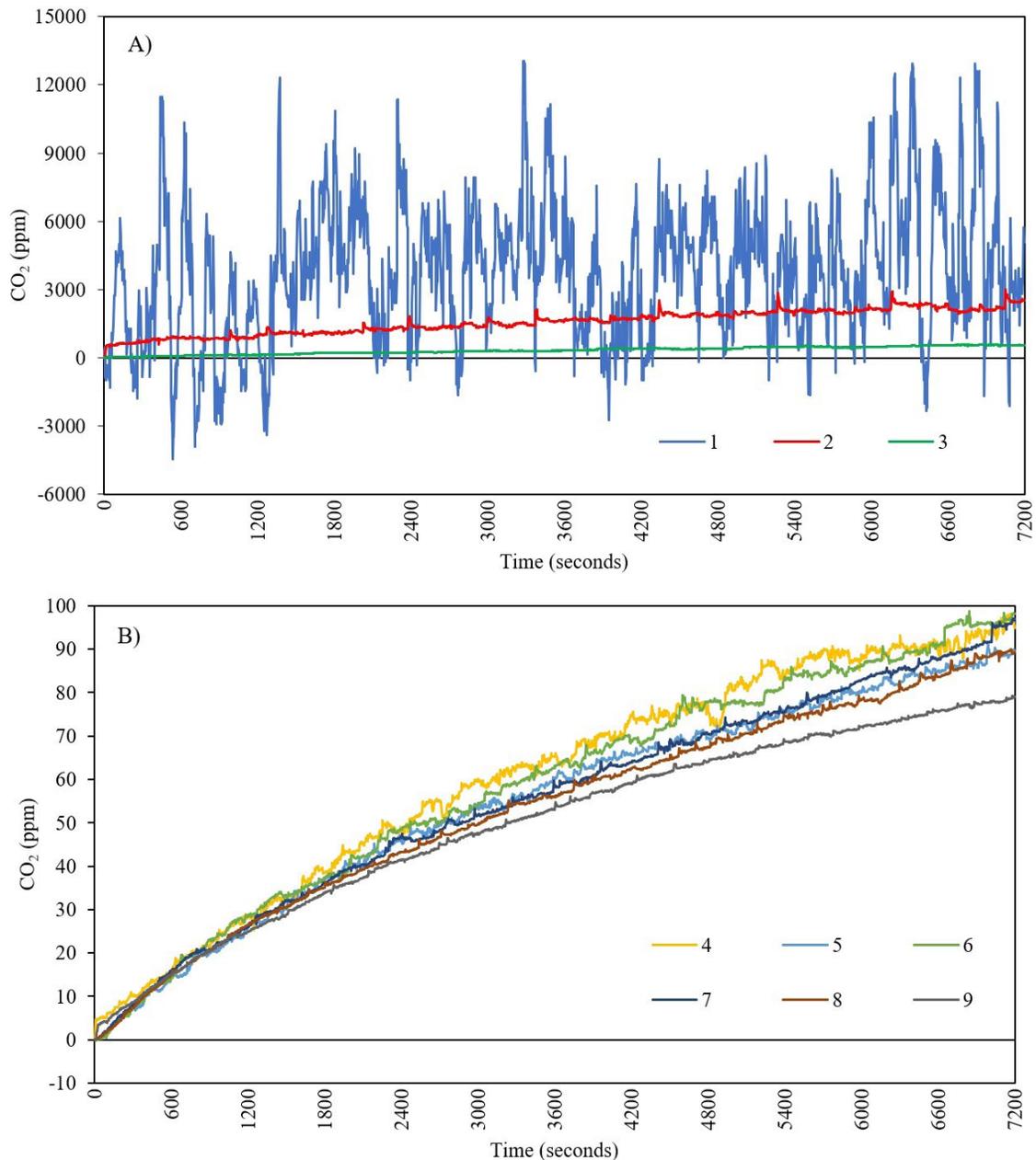
Treatment	CO <sub>2</sub> (ppm)	Fruit age (month)	CO <sub>2</sub> (ppm)
Compatible	1,537.0 a*	4	698.4 c*
Incompatible	1,570.3 a	5	935.7 bc
Mean	1,553.6	6	1,469.7 b
		9	3,239.8 a

\* Mean values with similar lowercase letters in each column do not differ significantly at 5%, according to the least significant difference test through Holm's correction. P: main season harvest. T: Secondary or Travesia harvest season.

The specific and total CO<sub>2</sub> rate: Figure 3 shows the respiratory curves of avocado fruits cv. Hass in the different stages of development, where four respiratory patterns are observed. The first is given for the fruits of a month's age, which present a high and variable respiration rate (-4,450 and 13,053 ppm g<sup>-1</sup> biomass) which fluctuates over time and is characterized by production and consumption peaks of CO<sub>2</sub>. The second pattern is evident for the fruits of two months' age, which is variable but less fluctuating than the first respiratory pattern, accentuating positive values (0 and 3005 ppm g<sup>-1</sup> biomass). The third pattern for fruits three months' age presents a slightly fluctuating respiration. Still, it does not explain a stable behavior in their average values, giving a slight reduction in the proportion of CO<sub>2</sub> but remaining different from the fruit of more than four months of age (Figure 3A). Finally, the fourth respiratory pattern (fourth to the ninth month age) was characterized by being stable until harvest with continuous CO<sub>2</sub> concentration values (0 and 98 ppm g<sup>-1</sup> biomass), where the fruit remains stable until the end of harvest (Figure 3B).

On the other hand, about the specific respiratory rate, Figure 4 shows the behavior of the absolute respiratory rate of the fruit, which was constructed with the set of measurements made during the 2020P and 2021T harvest seasons without discriminating the compatibility treatment in the fruits of avocado cv. Hass. The total CO<sub>2</sub> respiration rate shows an increasing behavior over time as fruit development increases, observing a double sigmoid curve, even though from month 7 of development, the total CO<sub>2</sub> rate tends to stabilize. A reduction was evidenced in the specific respiration, which was calculated from the amount of CO<sub>2</sub> released per gram of biomass of the fruit. In contrast, as the fruit increases its biomass, the CO<sub>2</sub> released falls abruptly during months one to three. The fourth month ahead of development presents a similar trend in the respiratory rate of CO<sub>2</sub> per gram of biomass.

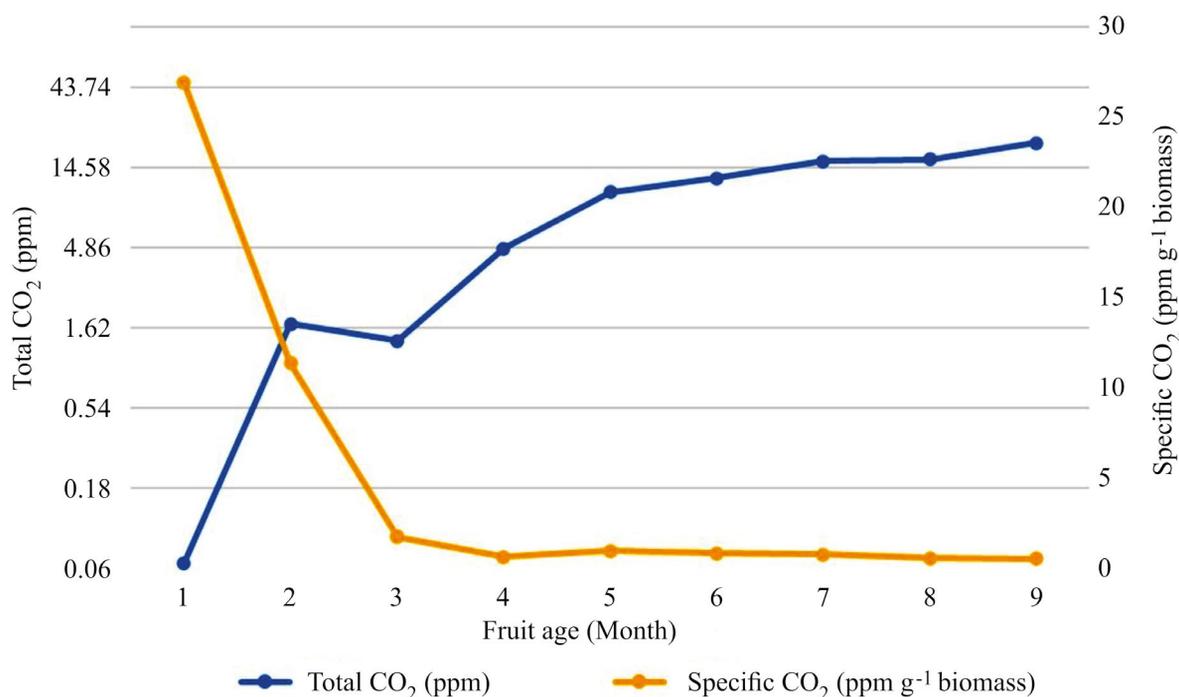
The fruit respiratory rate was not affected by the compatibility and harvest factors. The fruits in the first trimester presented a slow growth, accompanied by a low total CO<sub>2</sub> respiratory rate but a very high CO<sub>2</sub> biomass<sup>-1</sup> ratio, which is characteristic of this type of fruit. Simkin et al. (2020) indicate that the high rate of cell differentiation present during the first third of fruit development increases respiratory rates. This is preceded by a highly demanding period of energy (ATP) obtained through cell respiration. Consequently, Simkin et al. (2020) reported that avocado fruit contributes between 10 and 15% of the total fixed carbon, which can be synthesized by the CO<sub>2</sub> produced in the respiratory phase. Blanke (1992) found that in the avocado fruit, the enzyme phosphoenolpyruvate carboxylase (PEPC) is responsible for recapturing part of the respiratory CO<sub>2</sub> accumulated inside the fruits. The activity of PEPC was found at a concentration of 106 μmol CO<sub>2</sub> when external meters reported fruit respiration between 40 to 60 μmol CO<sub>2</sub>. The respiratory rate decreases as the fruit grows, and rates are less fluctuating since the fruit is in the process of cell elongation and the beginning of seed formation (Cowan et al., 2001). This is consistent with what was found in the present study, where respiratory patterns were reduced during this period (Figure 1). In the final fruit growth stage, the fruits reached their physiological maturity with a percentage of 22% DPM (Figure 4) in the ninth month of development. Rodríguez and Henao (2016) considered dry fruit matter content between 22 and 30% as the optimal index for harvest. Analogous results were reported by Rodríguez and Henao (2016) for avocado cv. Hass in 8 localities between 1800 and 2200 m a.s.l., for DPM with means between 22 and 24.9%, optimal for fruit commercialization.



**Figure 3:** Respiration curve of avocado fruit cv. Hass through the ontogeny of the fruit about the total CO<sub>2</sub> emitted (ppm). A) Fruit age between the first and third month of development. B) Fruit age between the fourth and ninth month of development.

Regarding the above, at harvest time, the fruit respiratory rate was very homogeneous and low (0 - 0.98 ppm CO<sub>2</sub>), possibly attributable to the fact that the fruits in this phase are in accumulation of sugars, according to Liu et al. (1999). The fruit respiration rate decreases with their biomass because the fruit loses

fixation capacity, which is attributed to the reduction in stomatal density during the ontogeny of the fruit. Blanke (1992) reported that after anthesis, the maximum stomatal frequency in avocado fruits was 50 to 75 stomata mm<sup>-2</sup>, which decreased with surface expansion during fruit development.



**Figure 4:** The CO<sub>2</sub> concentration released at each fruit stage development and fruit-specific respiratory rate per gram of biomass produced.

#### Fruit growth and development – Compatibility treatment (C) as the main plot and the fruit age (A) as a subplot

Main harvest season 2020P: During 2020P, as for the respiratory rate variables, both the Compatibility factor ( $p > 0.05$ ) and the interaction C \* A ( $p > 0.05$ ) did not significantly affect the different fruit growth and development variables. In contrast, the harvest age factor (A) did significantly affect fruit length ( $p = 9.656e-08$ ), fruit diameter ( $p = 7.194e-09$ ), fresh fruit weight ( $p = 3.195e-08$ ), the fresh ( $p = 5.417e-08$ ) and pericarp dry matter ( $p = 4.277e-06$ ), the fresh ( $p = 2.065e-06$ ) and seed dry matter ( $p = 3.837e-09$ ) and the total fruit biomass ( $p = 2.006e-11$ ) during main harvest season. The only variable that was not affected by either of the two factors and the interaction was the length-diameter ratio of the fruit ( $p > 0.05$ ).

Table 4 shows the means comparisons for the fruit's growth and development variables during 2020P. D presented a constant linear increase where D increased by 2 cm (32.01%) between the fourth and ninth age month in this variable; on the other hand, L presented an increase of 2.5 cm (30.81%). FFW showed a constant growth concerning the fruit development age

between the fourth and the ninth month; it was possible to reach an average weight of 107.95 g, ending the growth cycle (harvest times) at 136.5 g average. PDM was characterized during 2020P by slowly increasing between the fourth and seventh month (13.9 to 15.9%), accelerating in the last two months of fruit formation. The eighth month had a percentage increase of 17%. It ended in the ninth month of development (at harvest), where it reached 22.8%, considered an optimal fruit dry matter for marketing to international markets. SDM and PDM presented an increasing rate in their percentage of biomass, where the highest values were reached in the eighth and ninth months (6.21 and 7.47g). The increase in SDM during fruit development was marked, beginning the fourth month of growth with 12% dry matter and increasing through growth seasons at 14.3, 18.6, 22.3, and 30.4%, to end with 37% dry matter in the seed at harvest. FTB, as well as PDM, presented a constant growth in the percentage of dry matter from the fourth month (13.6%) to the eighth month (18.6%) age, which in the ninth month of development (at harvest) presents an exponential increase reaching 23.7% of dry matter. The length-diameter ratio (RLD) showed an average ratio of 1.26 throughout the fruit development cycle.

**Table 4:** Comparison test of means for the fruit morphological variables of growth for avocado cv. Hass during the main harvest season (2020P).

Treatment	Variable*								
	D (cm)	L(cm)	FFW (g)	FPM (g)	DPM (g)***	FSM (g)	DSM (g)***	FTB (g)***	LDR
Compatible	5.3 a	6.7 a	101.0 a	89.6 a	15.7 a (17.5%)	10.4 a	2.8 a (26.9%)	18.4 a (18.2%)	1.3 a
Incompatible	5.2 a	6.7 a	98.4 a	84.5 a	15.6 a (18.5%)	10.8 a	3.0 a (27.8%)	18.6 a (18.9%)	1.3 a
Fruit age									
4	4.3 d	5.5 d	54.0 d	49.4 d	6.9 c (13.9%)	4.2 c	0.50 d (12.0%)	7.4 c (13.6%)	1.3 a
5	4.8 c	6.2 c	73.3 c	65.9 c	9.1 c (13.7%)	6.9 bc	0.98 c (14.3%)	10.3 c (13.7%)	1.3 a
6	5.3 b	6.9 b	97.4 b	87.2 b	13.1 b (15.1%)	9.5 b	1.9 b (18.6%)	14.9 b (15.3%)	1.3 a
9	6.3 a	8.0 a	162.0 a	135.9 a	30.9 a (22.8%)	20.1 a	7.5 a (37.1%)	38.4 a (23.7%)	1.3 a

\* L: Fruit length, D: Fruit Diameter, FFW: Fresh fruit weight, FPM: Fresh Pericarp weight, DPM: Dry pericarp weight, FSM: Fresh seed weight, DSM: Dry seed weight, FTB: Fruit total dry biomass, LDR: Length/Diameter ratio. \*\* According to the least significant difference test through Holm's correction, treatments with a common letter do not differ significantly at the 5% level. \*\*\* The percentage values correspond to the dry matter reached in each season of fruit development.

Secondary harvest season 2021T: As in 2020P, neither the compatibility factor ( $p>0.05$ ) nor the C\*A interaction ( $p>0.05$ ) affected the avocado fruit growth variables in 2021T. Only the fruit age factor significantly affected the variables L ( $p=0.0001089$ ), D ( $p=5.009e-09$ ), FFW ( $p=0.000455$ ), FPM ( $p=0.0004934$ ), DPM ( $p=4.172e-05$ ), FSM ( $p=0.00972$ ), DSM ( $p=0.003096$ ) and FTB ( $p=1.45e-05$ ). The L/D ratio was not affected by the harvest season factor ( $p=0.1010$ ), like those observed with the compatibility factor. Table 5 shows the means comparisons for the morphological variables of fruit development during the 2021T harvest season, with behaviors suchlike those observed in the main harvest (2020P). The fruit diameter presented a constant growth from the first month to the ninth month of growth, with an increase of 4 cm. It should be noted that 88% of the growth occurred in the first six months of fruit development, while in the last third of growth (months 7 to 9), the increase was only 12% (0.74 cm). An intermediate growth phase characterized L during the first third of fruit growth, where a 2.6 cm length was reached. The second third was the most important stage of development, in which the increase was 38.23% (4.2 cm), and finally, in the last third of growth, L increased by 0.74 cm, completing the fruit growth by 15.8%. FFW increased from the fourth month of development, where the increase was constant, reaching a total weight of 158.8 g at the end of the cycle. DPM presented a continuous contribution between the fourth and sixth month of growth, where DPM represented between 14.1 and 15.1% of the total fruit dry weight; however, in the ninth month, a greater increase was observed, representing 21% of total dry matter for the end of

the cycle. Like FFW, the dry seed matter presented the same growth tendency characterized by a constant increase in dry matter accumulation in the first two-thirds of development (13.3 to 17.7%). DSM doubled in the last third of growth, reaching a contribution of 40.6% of FTB. FTB grew to 23.6% at harvest time, similar to 2020P (23.7%). The behavior of this variable increased over time, characterized by a growth of 58.9% (18g) during the last third of fruit development.

#### Fruit growth and development – Harvest season (H) as the main plot and the fruit age (A)

As a – subplot: In this analysis, which considered the harvest season as the main plot, a large part of the fruit growth variables was significantly affected by the harvest season – H (main plot), the fruit age (A), and the H \* A interaction. In this sense, H \* A significantly affected L ( $p=9.72e-09$ ), D ( $p=2.04e-10$ ), FPM ( $p=1.14e-05$ ), DPM ( $p<2.20e-16$ ), FSM ( $p=2.24e-4$ ), DSM ( $p=0.012$ ), TFB ( $p<2.2e-16$ ). Such other results, the factor H ( $p=0.864$ ), A ( $p=0.326$ ), and H \* A ( $p=0.070$ ) did not significantly affect the L/D ratio of the fruit.

Table 6 shows the means comparison tests for the fruit growth variables. It is evident that the main harvest 2020P was significantly higher ( $p<0.05$ ) for L, D, FFW, FPM, DPM, FSM, and DSM, than 2021T. D and L presented 13% (0.6 cm) and 13.6% (0.8 cm) more growth, respectively, compared to the 2021T. FFW, FPM, and DPM showed higher increases during 2020P, which reached 14.2g (16.6%), 12.5g (16.8%), and 2.4 (8.8%), respectively. Although the net value DPM was significantly higher for the main crop, the percentage contribution of this tissue to TFB was similar between 2020P and 2021T.

DSM presented higher values for 2021T, equivalent to an increase of 6.9% compared to the main harvest P2020. The fruit age factor for the 4, 5, 6, and 9-month evaluations presented an increase of 100% for D, equivalent to 3.1 cm from 4 to 9 months of growth (harvest time). Similarly, L showed a rise of 4.1 cm, equal to 102.4%. FFW, FPM, DPM, FSM, and TFB increased progressively through the fruit ages growth, where they presented a behavior as reported that was evaluated individually in the 2020P and 2021T harvest seasons. During the first two-thirds of fruit growth, these variables increase slowly, while during the third, the increase is around 50% on average.

Figure 5 shows the H\*A interactions for the fruit growth variables during the different ages in the main (2020P) and secondary (2021T) harvest seasons. In the fourth age month, D (Figure 5aA), L (Figure 5B), FFW (Figure 5C), FPM (Figure 5D), DPM (Figure 5E), FSM (Figure 5F), DSM (Figure 5G), and TFB (Figure 5H) the value of these variables was lower during 2021T than 2020P. The fruit presented, on average, a lower growth associated with 2021T, as observed during the first stages of growth (first trimester). The fruit growth during 2021T was slow, increasing during the second and third trimesters of development, which is why this difference could have been influenced (Table 6).

**Table 5:** Comparison test of means for the fruit morphological variables of growth for avocado cv. Hass during the secondary harvest season (2021T).

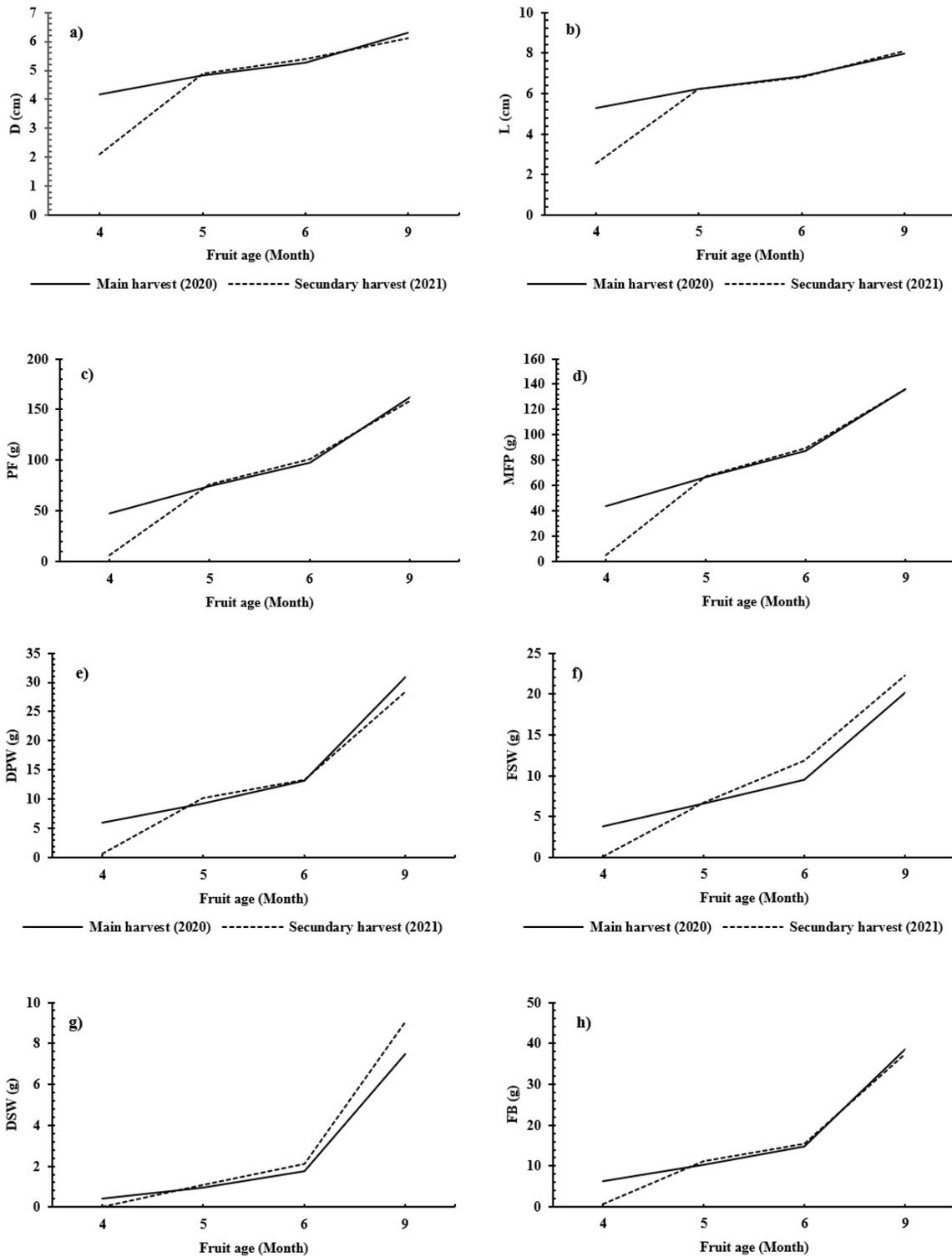
Treatment*	Variable*								
	D (cm)	L(cm)	FFW (g)	FPM (g)	DPM (g)***	FSM (g)	DSM (g)***	FTB (g)***	LDR
Compatible	4.7 a	5.9 a	88.8 a	77.0 a	13.4 a (17.4%)	10.4 a	3.2 a (30.8%)	16.6 a (18.7%)	1.3 a
Incompatible	4.6 a	5.9 a	82.3 a	72.2 a	12.9 a (17.9%)	10.0 a	2.9 a (29.0%)	15.9 a (19.3%)	1.3 a
Fruit age									
4	2.1 d	2.6 c	6.3 c	5.4 c	0.80 d (14.1%)	0.20 c	0.0 b (13.3%)	0.80 d (12.2%)	1.2 a
5	4.9 c	6.2 b	75.9 b	67.5 b	10.2 c (15.1%)	6.7 c	1.1 b (16.4%)	11.3 c (14.9%)	1.3 a
6	5.4 b	6.8 b	101.1 b	89.4 b	13.3 b (15.1%)	11.9 b	2.1 b (17.7%)	15.4 b (15.2%)	1.3 a
9	6.1 a	8.1 a	158.8 c	136.1 a	28.4 a (21.0%)	22.2 a	9.0 a (40.6%)	37.4 a (23.6%)	1.3 a

\* L: Fruit length, D: Fruit Diameter, FFW: Fresh fruit weight, FPM: Fresh Pericarp weight, DPM: Dry pericarp weight, FSM: Fresh seed weight, DSM: Dry seed weight, FTB: Fruit total dry biomass, LDR: Length/Diameter ratio. \*\* According to the least significant difference test through Holm's correction, treatments with a common letter do not differ significantly at the 5% level. \*\*\* The percentage values correspond to the dry matter reached in each season of fruit development.

**Table 6:** Comparison test of means for the fruit morphological variables of growth for avocado cv. Hass for the harvest season and age factors.

Harvest season	Variable*								
	D(cm)	L(cm)	FFW (g)	FPM (g)	DPM(g)***	FSM (g)	DSM (g)***	FTB (g)***	LDR
2020P	5.2 a	6.7 a	99.7 a	87.1 a	15.6 a (17.9%)	10.6 a	2.9 b (27.4%)	18.5 a (18.6%)	1.3 a
2021T	4.6 b	5.9 b	85.5 b	74.6 b	13.2 b (17.6%)	10.2 a	3.1 a (30.4%)	16.2 a (18.9%)	1.3 a
Fruit age									
4	3.1 d	3.9 d	27.1 c	24.7 c	3.3 c (13.4%)	2.0 d	0.20 b (10%)	3.6 d (14.6%)	1.2 a
5	4.9 c	6.2 c	74.9 c	67.0 b	9.7 b (14.5%)	6.6 c	1.0 b (15.2%)	10.7 c (16%)	1.3 a
6	5.3 b	6.8 b	98.9 b	88.1 a	13.2 b (15%)	10.4 b	1.9 b (18.3%)	15.1 b (17.1%)	1.3 a
9	6.2 a	8.0 a	160.7 a	136.0 a	29.9 a (22%)	21.0 a	8.1 a (38.6%)	38.0 a (27.9%)	1.3 a

\* L: Fruit length, D: Fruit Diameter, FFW: Fresh fruit weight, FPM: Fresh Pericarp weight, DPM: Dry pericarp weight, FSM: Fresh seed weight, DSM: Dry seed weight, FTB: Fruit total dry biomass, LDR: Length/Diameter ratio. P: main season harvest. T: Secondary or Traviesa harvest season. \*\* According to the least significant difference test through Holm's correction, treatments with a common letter do not differ significantly at the 5% level. \*\*\* The percentage values correspond to the dry matter reached in each season of fruit development.



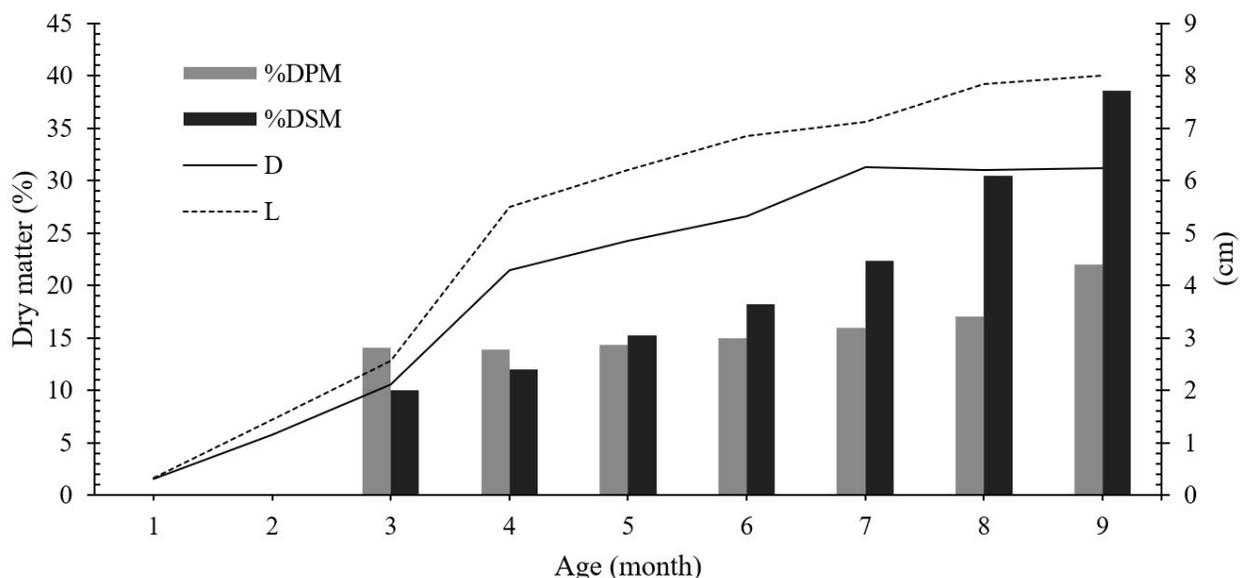
**Figure 5:** H\*A interaction for fruit diameter (a), fruit length (b), fresh fruit weight (c), fresh pericarp weight (d), dry pericarp weight (e), fresh seed weight (f), dry seed weight (g), and total fruit biomass (h) through the different fruit growth of avocado cv. Hass during the main 2020P and secondary 2021T harvest seasons.

Finally, Figure 6 summarizes the growth dynamics of the avocado fruit cv. Hass during an entire period of development (months 1 to 9), taking the average data from the main (2020P) and secondary (2021T) harvest seasons independent of the compatibility treatment for the variables D, L, DPM, and DSM for each month of growth. D and L of the fruit have increasing characteristics, where they are characterized by presenting an accelerated rate until the fourth month. At this point, the fruit has reached 68.7% of L, 78.7% of D, 63.1% of DPM, and 31.2% of the total percentage of DSM. This means that the growth rate for avocado fruits in terms of development is more accentuated for D, L, and DPM during the first four months. After the fourth month, growth is observed to be slower for the D, L, and DPM. The DSM presents an increase in biomass in the last third of development, where the gain is exponential, achieving a rise of 52.8% concerning this tissue's total percentage of biomass.

Graft incompatibility is broadly categorized as “translocated” and “localized” (Zarrouk et al., 2006; Darikova et al., 2011). In the case of “translocated” incompatibility, symptoms (scion and root growth stop, reduced carbohydrate translocation at the union, wilting of leaves, leaf chlorosis, and early leaf drop) are observed at the early stages of plant development. The “Localized” incompatibility leads to graft union malformation due to physiological and morphological changes (disruption of vascular cambium, lower rate of tissue differentiation, lack

of lignification, and vascular disruption continuity), which impaired grafting union formation (Errea, 1998; Zarrouk et al., 2006). These changes might cause the graft union to rupture (Pina et al., 2017). In this sense, the difference in the scion/rootstock ratio of trunk circumference above/below the graft union (anatomical grafting incompatibility) is useful in assessing potential rootstock-scion incompatibility and can be considered a located incompatibility (Mickelbart et al., 2007). According to Rodrigues (2004) is caused by different rates of rootstock and cultivar cambium cellular division, leading to a discontinuity in the xylem vessels. The formation of new cambium derived from the tissue callus appears to be delayed in heterografts and interspecific grafts compared to homografts and intraspecific grafts (Pina et al., 2012).

The interactions between several parameters related to the grafted plant physiology and morphology (water and minerals translocation, leaf gas exchange, tree size, flowering, fruit set, and fruit quality) are essential. They provide a source for choosing the most compatible graft combination for specific environments and good fruit quality since the rootstock/scion combination affects fruit yield and biochemical and physiological parameters. Selecting a suitable combination is fundamental for increased production of trees; therefore, the rootstock/scion combination is a key factor to be well thought-out in orchards before taking up the planting procedure (Rasool et al., 2020).



**Figure 6:** Growth curve of avocado fruits cv. Hass as a function of diameter (D), length (L), dry pericarp matter (DPM) percentage, and dry seed matter (DSM) percentage during a production cycle.

The fruit growth did not present significant differences in the compatibility factor. The main harvest show fruit greater than those produced during 2021T. Díaz, Bernal, and Tamayo (2020) reported higher yield in the main harvest season, which is characterized by larger volumes of production associated with a greater extraction of nutrients for this cycle, increasing the morphological variables of the fruit and its biomass. Oliveros et al. (2010) reported similar results in the cultivation of coffee (*Coffea arabica*) var. Caturra, where the productive period of the main harvest presented better productive characteristics generating larger fruits than the secondary harvest season.

Similarly, the present study found that the variables of D, L, PF, FPM, DPM, and FSM, presented significant differences during 2019P, presenting fruits of greater weight, length, and diameter, a desirable characteristic for an international market (Table 4). Ge et al. (2019) evaluated the morphological growth of avocado fruits var. Guikenda finds a dynamic like that presented by cv. Hass, where the fruits showed a constant change in D and L throughout their cycle, drastically increasing these two variables from 65 to 105 days of development (2–3.5 months), a period in which avocado cv. Hass begins its exponential growth similarly (figure 2), showing a growing linear trend throughout its development. This is analogous to that reported by Alcaraz and Hormaza (2014), who determined the fruit growth of avocado cv. During a complete production cycle, Hass reached values for a length of 8.7 cm and a diameter of 5.8 cm, similar to what was found in this evaluation (Figure 4). Soule and Harding (1955) stated that the environmental characteristics present during the fruit growing seasons could determine the quality, presenting superior fruits than when the environmental conditions are not favorable. In this order of ideas, the fruit development of the main crop occurs between February and December, which presents the warmest seasons (17.5°C) and regular periods of rainfall (170 mm month<sup>-1</sup>).

On the other hand, the secondary harvest seasons began in September to June and reached cold months (16.4°C) and dry months associated with January - February (102.5 mm month<sup>-1</sup>), which could influence fruit growth and therefore produce uneven development (Figure 1 and 2). LDR behaved stably throughout the evaluation, presenting a ratio of 1.28, which gives the fruit a geometric shape that resembles that of an ellipsoid, which is such that reported by Bayram and Seyla (2019) who, during ten harvest cycles evaluated fruits of avocado

cv. Fuerte, Bacon, and Zutano found this same pattern in the geometric shape of the fruit during its growth. DPM at the end of the growth cycle (the ninth month of fruit development) remained during the two harvest periods at an average of 22% (Tables 5 and 6), which is similar to that reported by Rodríguez and Henao (2016) and Rodríguez et al. (2018), who affirmed that the optimal point of maturity for the commercialization of avocado cv. Hass is between 22 and 30%. In this sense, the localities of Rionegro, El Peñol, and El Retiro between 2,000 and 2,200 meters above sea level presented dry pericarp matter means between 22, 96, and 24.9%, which affirms that the fruits evaluated in the three studies locations showed optimal values for their growth, development, and maturity for the fruit harvest.

The grafting method is widespread in fruits and vegetables, where the compatibility between the rootstock and the graft plays an essential role in the development of the tree (Feucht; Treutter, 1991; Long; Kaiser, 2010;). The present study evaluated the compatibility effect between the rootstock and the graft. The compatibility treatment did not present significant differences in the fruit's respiratory variables, growth, and development. This result is suchlike that reported in other fruit species, where Martins et al. (2021) found in cherry (*Prunus avium* L.) that the compatibility between the rootstock and the graft does not affect the quality of the fruit, having a similar diameter, length, and weight in plants evaluated with these morphological differences. Fredes et al. (2016) assessed the effect of the rootstock in the cultivation of watermelon (*Citrullus lanatus*), and no significant differences were found in the growth and development of the fruits compared to incompatible graft treatments. Contrary to what was mentioned, Fallik and Ziv (2020) reported higher fruit growths and total solids in watermelon crops (*Citrullus amarus* Schrad) where grafted on interspecific and compatible hybrids of *Cucurbita maxima* Duchesne and *C. moschata* Duchesne. Aslam et al. (2020) evaluated cucumber (*Cucumis sativus* L.) grafted on pumpkin hybrids (*Cucurbita moschata* L.), presenting higher fresh weight and dry matter accumulation in the fruits when the rootstock was compatible with the graft compared to the treatment without grafting.

Goldschmidt (2014) states that there is no precise definition of graft compatibility. Generally, this means establishing a successful graft union and extended survival and proper functioning of the composite grafted plant. For this, taxonomic affinity is a prerequisite for graft compatibility. It is generally considered that graft incompatibility increases with the taxonomic distance

but predicting compatibility is not always easy (Gautier et al., 2019). Homografts (=autografts) are presumably always compatible, and heterografts are nearly always compatible (interspecific grafts). Most Colombian commercial avocado cv. Hass plantations currently rely on open-pollinated half-sib interracial seedling rootstocks derived from selected “criollo” “plus trees” (Bernal et al., 2020; Cañas-Gutiérrez et al., 2015). The selection of a suitable rootstock is rarely based on the scion’s genotype and the environment or agro-climatic zone in which the grafted tree will be cultivated. In other words, due to a triple rootstock/scion/environment interaction, rootstock selection from “criollo” seedling genotypes is challenging (Cañas-Gutiérrez et al., 2022). The genetic origin of the creole materials used in Colombia as rootstocks is unclear. Hence, it is unknown if what has been defined as anatomical compatibility and incompatibility (differences between the cultivar and rootstock trunk diameter) is related to the taxonomic affinity between the cv. Hass (45% Guatemalan and 55% Mexican) and the Creole rootstocks. Despite Colombia’s research has focused on studying their avocado creole genetic diversity, it is necessary to know the genetic relationship of commonly used creole rootstocks with the different ecological races or botanical varieties widely distributed (Mexican – *P. americana* var. *drymifolia*; Guatemalan - *P. americana* var. *guatemalensis* L.O. Williams, and West Indian - *P. americana* var. *americana* Mill).

Little is known about the mechanisms that cause graft compatibility/incompatibility in the avocado cv. Hass. In general, many studies have been carried out to understand the graft incompatibility genetic basis, the transcript/metabolite, or enzyme activity markers. However, it should be deepened by specifying the analysis of different tissues to differentiate the grafting incompatibility responses of the scion, rootstock, interface, and callus tissues.

## CONCLUSIONS

The incompatibility of rootstock/scion did not affect the fruit growth neither modified the respiratory rate of fruits of cv. Hass. The fruit growth was affected by season harvest, while the main harvest presented fruits with better characteristics in size and weight than the secondary harvest season. The fruit growth was characterized by showing linear growth, followed by a linear flat phase with the ontogeny of the fruit.

## AUTHORS CONTRIBUTION

Conceptual idea: Cano Gallego, L. E.; Bernal Estrada, J. A.; Cordoba Gaona, O. J.; Methodology desing: Cano Gallego, L. E.; Cordoba Gaona, O. J.; Data collection: Cano Gallego, L. E.; Data analysis and interpretation: Cano Gallego, L. E.; Bernal Estrada, J. A.; Hernandez Arredondo, J. D.; Correa Londoño, G. A.; Cordoba Gaona, O. J., and Writing and editing: Cano Gallego, L. E.; Bernal Estrada, J. A.; Hernandez Arredondo, J. D.; Correa Londoño, G. A.; Cordoba Gaona, O. J.

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