ROOTSTOCK AND SCION INTERACTIONS UNDER CONDITIONS OF SOIL WATER DEFICIT IN AVOCADO †

[INTERACCIÓN DE PORTAINJERTO E INJERTO EN CONDICIONES DE DÉFICIT HÍDRICO EN EL SUELO EN AGUACATE]

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SUMMARY

Background. Drought is the main factor that reduces crop yield, and grafting is used to confer resistance traits. **Objective.** The effect of water deficit on water relations, gas exchange, and proline content was determined in two avocado cultivars, 'Colín V-33' and 'Hass', grafted onto three clonal rootstocks ('Colin V-33' (C), 'Fuerte' (F), and 'Hass' (H)). **Methodology.** Two-year-old avocado plants of 'Colín V-33' and 'Hass' were grafted onto three rootstocks: 'Colin V-33', 'Fuerte', and 'Hass'. The plants were grown in a greenhouse for 1.4 years. From that point, half of the grafted plants remained without irrigation, while the other half was watered every other day. Stomatal conductance and CO_2 assimilation were measured daily, and on day 13, soil and leaf samples were taken for water relations and leaf samples for proline content. **Results.** The cultivar 'Colin V-33' and its combinations showed a conductance of 132 mmol m^{-2} s^{-1}, while 'Hass' reached 150 mmol m^{-2} s^{-1}. Both decreased after 7 days without irrigation, with variations in their combinations. CO_2 assimilation followed a similar pattern. In well-watered plants, there were no differences in water potential (Ψ_{ω}), but in non-irrigated plants, 'Colin V-33' showed a greater decrease in leaf Ψω, whereas in 'Hass', this occurred in the H/H and H/F combinations. The osmotic potential (Ψ_{π}) was lower in non-irrigated plants with 'Hass', especially in C/H and H/H (-1.80 and -1.81 MPa respectively). Turgor potential (Ψ_{ρ}) was unaffected. Proline concentration was higher in all combinations, particularly in H/H and H/F. **Implications.** Grafting is useful for identifying cultivars sensitive or resistant to water deficit. **Conclusion.** The combinations with 'Colin V-33' show the best water use efficiency and greater resistance to water deficit. The scion/rootstock interaction significantly affects gas exchange, water relations, and proline concentration under water deficit. Low proline concentrations in this species appear linked to water deficit resistance.
Key words: *Persea americana* Mill.; soil water deficit; gas exchange; plant water relations; proline.

RESUMEN

Antecedentes. La sequía es el factor principal que reduce el rendimiento de los cultivos y los injertos se usan para conferir características de resistencia. **Objetivo**. Se determinó el efecto de déficit hídrico en relaciones hídricas, intercambio de gases y prolina en dos cultivares de aguacate, 'Colín V-33' y 'Hass' injertados en tres porta injertos clonales ('Colin V33'(C), 'Fuerte' (F) y 'Hass' (H)). **Metodología**. Plantas de aguacate de dos años de edad de 'Colín V-33' y 'Hass' fueron injertadas en tres porta injertos 'Colin V-33', 'Fuerte', y 'Hass'. Las plantas se desarrollaron en invernadero durante 1.4 años. A partir de ese momento la mitad de las plantas injertadas permanecieron sin regar y la otra mitad se regó cada tercer día. Se midió diariamente la conductancia estomática y asimilación de CO_2 y en el día 13 se tomaron muestras de suelo y hojas para relaciones hídricas y muestras de hojas para contenido de prolina.

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Resultados. El cultivar ‘Colin V-33’ y sus combinaciones mostraron una conductancia de 132 mmol m^{-2} s^{-1}, mientras que ‘Hass’ alcanzó 150 mmol m^{-2} s^{-1}. Ambas disminuyeron tras 7 días sin riego, con variaciones en sus combinaciones. La asimilación de CO_2 siguió un patrón similar. En plantas bien regadas no hubo diferencias en el potencial de agua (Ψ_ω), pero en las plantas sin riego, ‘Colin V-33’ mostró una disminución mayor de Ψ_ω en la hoja, mientras que en ‘Hass’ ocurrió en las combinaciones H/H y H/F. El potencial osmótico (Ψ_π) fue más bajo en plantas sin riego con ‘Hass’, especialmente en C/H y H/H (-1.80 y -1.81 MPa respectivamente). El potencial de turgencia (Ψ_ρ) no se vio afectado. La concentración de prolina fue mayor en todas las combinaciones, destacando H/H y H/F. **Implicaciones**. Injertar es útil para identificar cultivares sensibles o resistentes al déficit hídrico. **Conclusión.** Las combinaciones con 'Colin V-33' mostraron la mejor eficiencia en el uso del agua y una mayor resistencia al déficit hídrico. La interacción entre el injerto y el portainjerto afecta significativamente el intercambio de gases, las relaciones hídricas y la concentración de prolina en condiciones de déficit hídrico. Las concentraciones bajas de prolina en esta especie parecen estar relacionadas con la resistencia al déficit hídrico.

Palabras clave: *Persea americana* Mill.; déficit hídrico en el suelo; intercambio de gases; relaciones hídricas en plantas; prolina.

INTRODUCTION

Grafting is an ancient and common practice in fruit and vegetable crops to induce resistance characteristics to biotic and abiotic stress like drought, salinity, pest, and diseases and also to improve yield and fruit properties (Melnyk and Meyerowitz, 2015). After grafting the new plant characteristics is the result of a strong interaction between rootstock and scion carrying up and down stream different physiological and genetic information (Caruso *et al*., 2022; da Saúde *et al*., 2022). Ions, proteins, and plant growth regulators substances are the main components to convey such information (Else *et al*., 2018). Xylem tissue is the main pathway to transporting up and down this components, and the difference in diameter or length of its vessels between root stock and scion must affect the transfer of information. For instance, differences in xylem features in avocado (vessels diameter) have been reported and it is suggested that this could affect water transport (Reyes-Santamaría *et al*., 2002). Questions arise like how will the sap flow be when two water transport conducts of different diameter are joined together?, will the water resistance transport increase or decrease?, how will the concentrations of chemicals (nutrients or plant growth substances for instance) to which rootstock and scion were not used to are now sensed and read?, how growth and gas exchange will be affected?. An understanding of long-distance communication is essential to predict the effect of environmental and developmental cues on plant response and to design practices to improve plant performance.

There are few studies in avocado where the effects of water deficit in the soil have been pursued. These studies have shown that under conditions of water deficit, CO_2 assimilation and transpiration are reduced as a result of stomatal closure (Chartzoulakis *et al*., 2002; Lahive *et al*., 2018, Ribeiro *et al*., 2022; Santos *et al*., 2022; Lee *et al*., 2022). Therefore, the aim of this study was to determine the effect of soil water deficit on water relations, gas exchange and proline accumulation in two avocado cultivars ‘Colin V33’ and ‘Hass’ grafted in three clonal rootstocks (‘Colin V33’, ‘Fuerte’ and ‘Hass’).

MATERIALS AND METHODS

Plant material and growth conditions

Two year old plants of avocado cultivars ‘Colin V-33’ and ‘Hass’ were grafted on three clonal avocado rootstocks ‘Colin V-33’, ‘Fuerte’, and ‘Hass’, (Table 1). Plants were grown under greenhouse conditions in black plastic pots (15 x 25 cm) with a silty clay loam texture soil, pH 5.5, and an electric conductivity of 0.49 dS m^{-1}. After one year plants were transplanted into large pots 40 cm diameter and 70 cm length with the same kind of soil. Once the plants were transplanted they were maintained under greenhouse conditions for five months before the experiment started. During this time plants were watered every other day maintaining soil water content higher than 70% of field capacity.

Table 1. Avocado graft combinations of three rootstocks and two scions.

Scion	Rootstock		
	‘Colin V-33’ (C)	‘Fuerte’ (F)	‘Hass’ (H)
‘Colin V-33’ (C)	C/C	C/F	C/H
‘Hass’ (H)	H/C	H/F	H/H

Irrigation treatments

After five months, the pots received a last watering to field capacity. From this moment on, half of the grafted plants (combinations) remained unwatered and the other half was watered every other day. Over the following 13 d, measurements of stomatal conductance and CO_2 assimilation were performed and at day 13 leaf and soil samples were taken for water relation evaluations and leaf samples to quantify proline content.

Stomatal conductance and CO_2 assimilation

Stomatal conductance (g_s) and CO_2 assimilation rate (*A*) were determined *in situ* every day at noon (maximum irradiance) in the youngest full expanded leaf. An open and portable infrared gas analysis system was used (CIRAS-1, PPSystems) and measurements were recorded after a steady state condition was reached into the cuvette.

Water relations

Total leaf water potential (Ψ_ω) was determined in the previous leaf to which gas exchange was measured at the time when g_s was statistically different between well-watered plants and those where water was withheld. The leaf was cut at the base of the petiole and rapidly inserted into a Scholander type pressure chamber (Soil moisture equipment, Corp Santa Barbara, CA) with part of the petiole protruding outside the chamber. Then the pressure inside the chamber was raised slowly until a balance pressure was reached (xylem water potential). Thereafter pressure was released and the leaf was wrapped in aluminium foil and stored in liquid nitrogen to determine the osmotic potential later.

Leaf osmotic potential (Ψ_π) measurements were made on half of the leaf removed from the pressure chamber. Tissue was allowed to thaw and then placed inside of a hypodermic syringe to extract the sap. 10 µL of sap were placed in a disc of filter paper and the osmotic potential was measured in a vapour pressure osmometer (Model 5520, Wescor, Inc., Utha, USA). Turgor pressure Ψ_ρ was calculated as the difference between Ψ_ω and Ψ_π.

Soil water potential was evaluated by placing a soil sample into a commercial Wescor psychrometer (C-52, Wescor, Inc., Utah, USA) and incubated for 4 h for thermal and water vapour equilibrium at 20 °C. The Ψ_ω of the sample was determined by connecting the chamber to a dew-point micro voltimeter (HR-33T, Wescor, Inc., Utah, USA) and operated in the dew-point mode.

Leaf proline content

This amino acid was evaluated in half of the leaf used to determine osmotic potential. Tissue was freeze dried for 48 h and then, proline content was quantified using the colorimetric method reported by Bates *et al.* (1973).

Statistical analysis

The experiment was arranged in a complete randomised design with a factorial treatment arrangement 2 x 2 x 3, where the principal factors were soil water content (well-watered and withhold water), scions (‘Colin V-33’ and ‘Hass’) and rootstocks (‘Colin V-33’, ‘Fuerte’ and ‘Hass’). A variance analysis and means multiple comparisons (Tukey, $P \leq 0.05$) were performed, using the Statistic Analysis System (SAS, 1989).

RESULTS

Stomatal conductance and CO_2 assimilation

Stomatal conductance (g_s) and CO_2 assimilation for both ‘Colin V-33’ and ‘Hass’ and all their combinations (C/C, C/F and C/H) and (H/C, H/F and H/H) were steady with no differences among treatments for the first six days after withholding water. In general, ‘Colin V-33’ scion and its combinations had the lower stomatal conductance (average 132 mmol m^{-2} s^{-1}) while ‘Hass’ scion and its three combinations had the highest stomatal conductance (average of 150 mmol m^{-2} s^{-1}). Withholding water had a differential effect in gas exchange in ‘Colin V-33’ and ‘Hass’ and on their three combinations. A reduction in stomatal conductance in ‘Colin-V33’ started after day 7 ($P< 0.0001$) in the combination C/F, while the combinations C/C and C/H started to be significantly reduced after day 12 ($P<0.0001$). This reduction in stomatal conductance increased gradually with time and by day 13 the lowest value in this variable was obtained. Stomatal conductance was also reduced significantly in ‘Hass’ by day 7 ($P<0.0001$) when ‘Fuerte’ was used as rootstock while for H/H and H/C combinations the stomatal conductance was significantly reduced ($P<0.0001$) after day 8 and 9 respectively after withholding water. The lowest values in this variable were also obtained at day 13 (Figure 1 and 2).

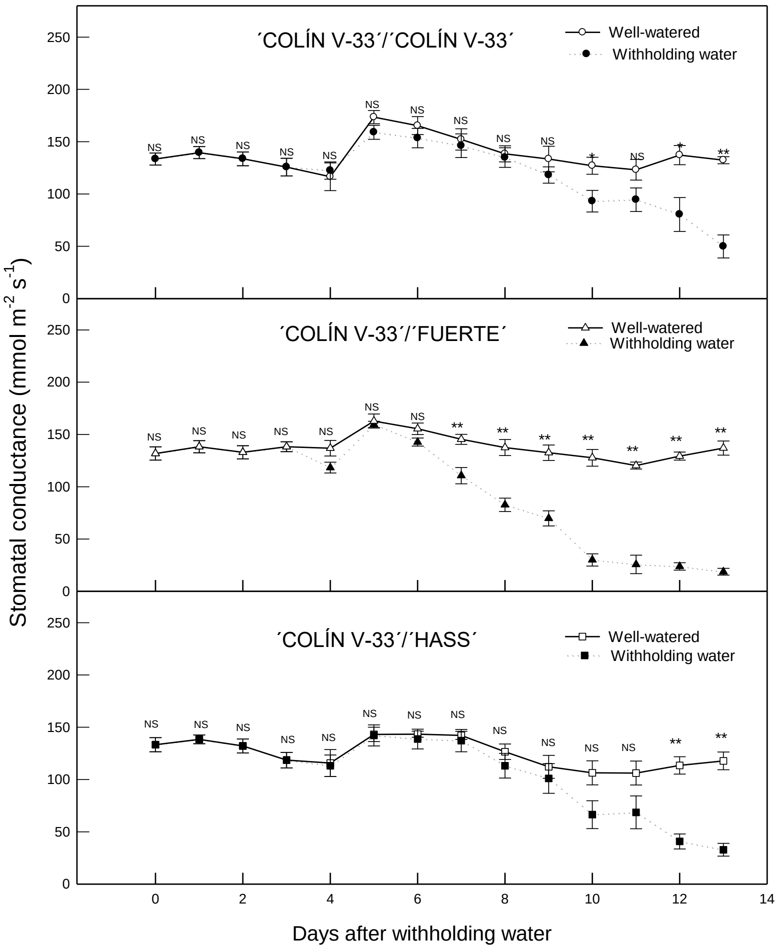

Figure 1. Effect of withholding water in stomatal conductance of the scion ‘Colin V-33’ on three clonal rootstocks. Each point represents the average of five replicates ± SE. NS, * and **, non-significant and significant to *P*≤ 0.05 and 0.01, respectively, according to Student-t test.

CO_2 assimilation had a similar behaviour to stomatal conductance. The combination C/C had significant differences (P<0.0001) after day 8 and 9 of withholding water but afterwards it recovered for the next three days but then it was reduced drastically by day 13. C/F combination started to reduce its CO_2 fixation after day 9 of withholding water and this reduction was increased with time. In the C/H combination CO_2 assimilation was significantly reduced (P<0.0001) after day 12.

CO_2 assimilation for all the ‘Hass’ combinations had similar behaviour to stomatal conductance. It was observed that the combination H/C started to reduce significantly CO_2 fixation after day 9, the combination H/F after day 7 while in the combination H/H this variable was reduced significantly up to day 13 of withholding water (Figure 3 and 4).

When the data of stomatal conductance and CO_2 assimilation were analysed as factors it was found that the cultivar ‘Colin V-33’ was statistically different to ‘Hass’ when both were used as scions. When the rootstock factor was analysed it was found again that the cultivar ‘Colin V-33’ was statistically different (P<0.0001) to ‘Hass’ and ‘Fuerte’, while these cultivars were similar between them. Soil water content was statistically different after day 7 for both variables (stomatal conductance and CO_2 assimilation rate).

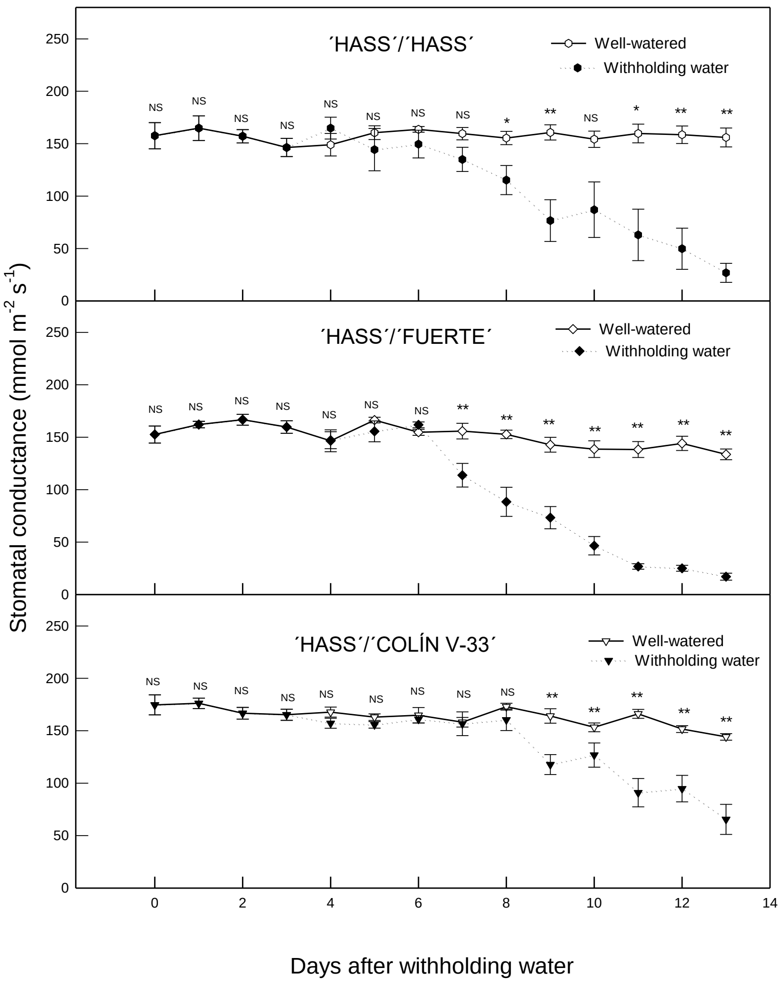

Figure 2. Effect of withholding water in stomatal conductance of the scion 'Hass' on three clonal rootstocks. Each point represents the average of five replicates ± SE. NS, * and **, non-significant and significant to $P \leq 0.05$ and 0.01, respectively, according to Student-t test.

Water relations

Total leaf water potential at the end of the experiment (day 13) was statistically different in well-watered compared to droughted plants (P<0.0001). Under well-watered conditions there were no differences in leaf water potential in any of the combinations. Under drought conditions it was found that 'Colin V-33' used as scion was less susceptible to water potential reduction under conditions of soil water limitation. When 'Hass' was used as scion the water potential was reduced significantly when H/H and H/F combinations were under withholding water conditions while in the same conditions 'Colin V-33' used as scion the values of leaf water potential were similar under both conditions (Figure 5). Similarly, all the combinations scion/rootstock under drought condition showed the lower values of osmotic potential and C/H and H/H had the lowest values (-1.80 and -1.81 MPa, respectively) (Figure 6), however they were not statistically different to those combinations under well-watered conditions. Leaf turgor pressure (Figure 7) was not affected by withholding water for 13 days however, again the combinations H/H and H/F had the lowest values (0.28 and 0.26 MPa, respectively). Soil water potential was not affected significantly in most of the combinations except for H/H and H/F when water was withheld (Figure 8).

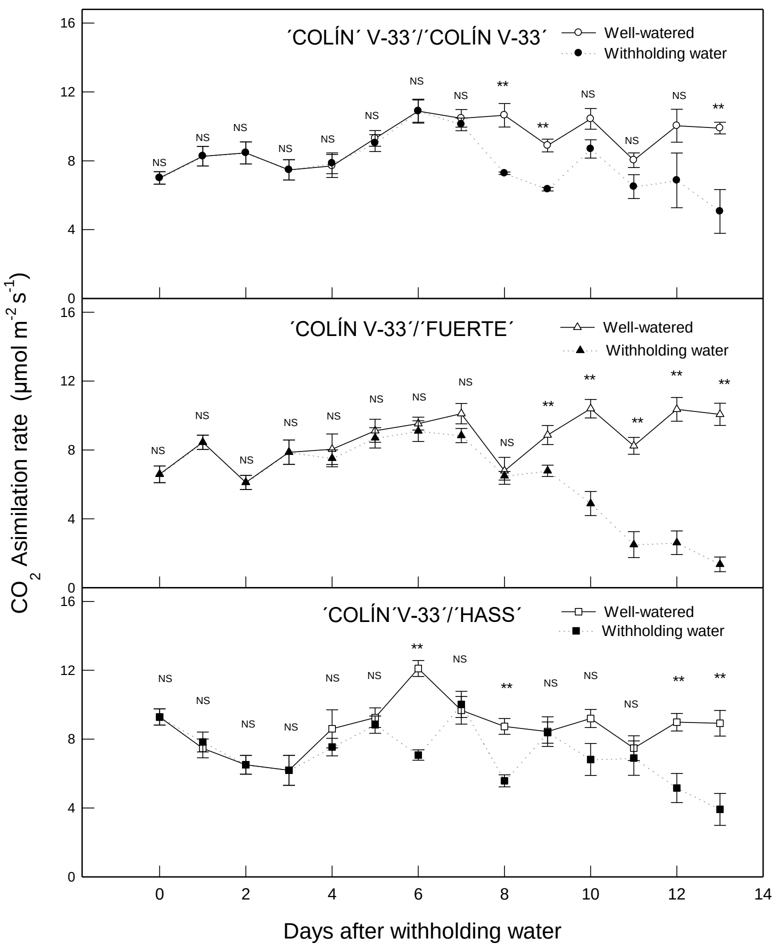

Figure 3. Effect of withholding water in CO_2 assimilation of the scion 'Colin V-33' on three clonal rootstocks. Each point represents the average of five replicates ± SE. NS, * and **, non-significant and significant to $P \leq 0.05$ and 0.01, respectively, according to Student-t test.

Proline content

Under water deficit proline content was increased in all the combinations in comparison to well-watered plants. The combinations H/H and H/F had the highest concentration with values of 8.21 and 6.46 µmol g^{-1} of dry weight, respectively (Figure 9).

DISCUSSION

Withholding water had a marked effect in all the variables measured, it was also clear a differential effect of this condition in dependency of the scion/rootstock combination used. When 'Colin V-33' was used as scion, stomatal conductance was lowest in all cases, on the contrary when 'Hass' was used as scion all the combinations had the highest values in stomatal conductance. A Similar behaviour was also found for CO_2 assimilation. A possible explanation to these results may be due to the water conducting system that 'Colin V-33' has, in average lower vessel diameter than 'Hass' which may confer some advantage to be less prone to cavitation under stress conditions although 'Colin V-33' had the highest xylem area in proportion to the total. These results suggest that the water conducting system of 'Colin V-33' may support more leaf area even under water stress conditions (Reyes-Santamaría *et al*., 2002). Another possible explanation to the results found in this study may be related to stomatal size in these cultivars. It was found that 'Colin V-33' has small stomata (15.1 µm) in comparison with 'Hass' (19.4 µm); even though 'Colin V-33' showed a higher stomatal frequency (646 stomata per mm^2) compared to 'Hass' (360 stomata per mm^2) (data not published). This may indicate that 'Colin V-33' might have a genetically fixed stomatal system able to control gas exchange under stress conditions. It would be useful to evaluate stomata size, and frequency in some other avocado material. It was clear that when 'Fuerte' was used as rootstock independently of the scion, these combinations started to reduce stomatal conductance and CO_2 assimilation before any other combination. It is not easy to explain this response but it is likely to be related to the anatomical characteristics of the water conduction system of 'Fuerte' as well as the intrinsic properties of the radical system since the concentration of growth regulator substances (mainly inhibitors) produced in this organ under stress conditions might be regulating the behaviour of the aerial part (Davies *et al*., 1994). Differences in the root system have been observed in clonal plants of 'Colin V-33' and 'Fuerte' where 'Fuerte' shows a major branching of its root system which is thinner and suberized and with a higher number of radical apices in comparison to 'Colin V-33' (Barrientos-Priego *et al*., 1986). Borys (1986) has mentioned that the structure of fine roots represents a limitation in water absorption, on the other hand it has also been found that water enters more easily through the root tips where the endodermis is not suberized (Gambetta *et al*., 2013). This may explain the major water absorption when 'Fuerte' is used as rootstock under water deficit conditions and a fast response in terms of stomatal inhibition as a result of an inhibitory signal generated in the root. Although it has been observed that adventitious roots of 'Colin V-33' seem to be less suberized and they do not absorb more water than 'Fuerte'.

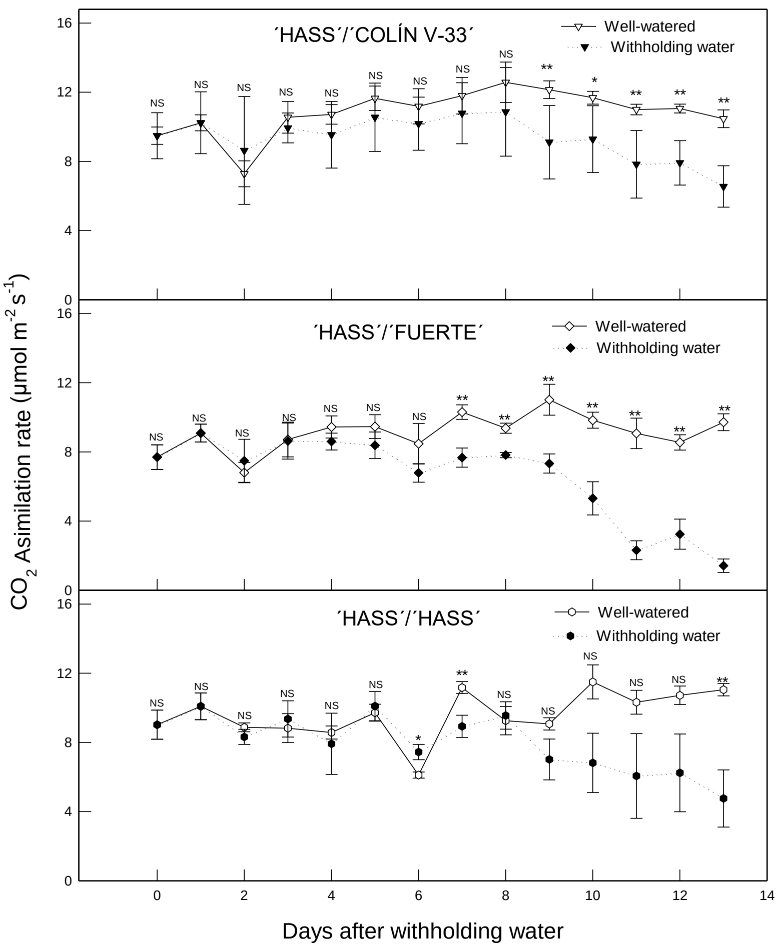

Figure 4. Effect of withholding water in CO_2 assimilation rate of the scion 'Hass' on three clonal rootstocks. Each point represents the average of five replicates ± SE. NS, * and **, non-significant and significant to $P \leq 0.05$ and 0.01, respectively, according to Student-t test.

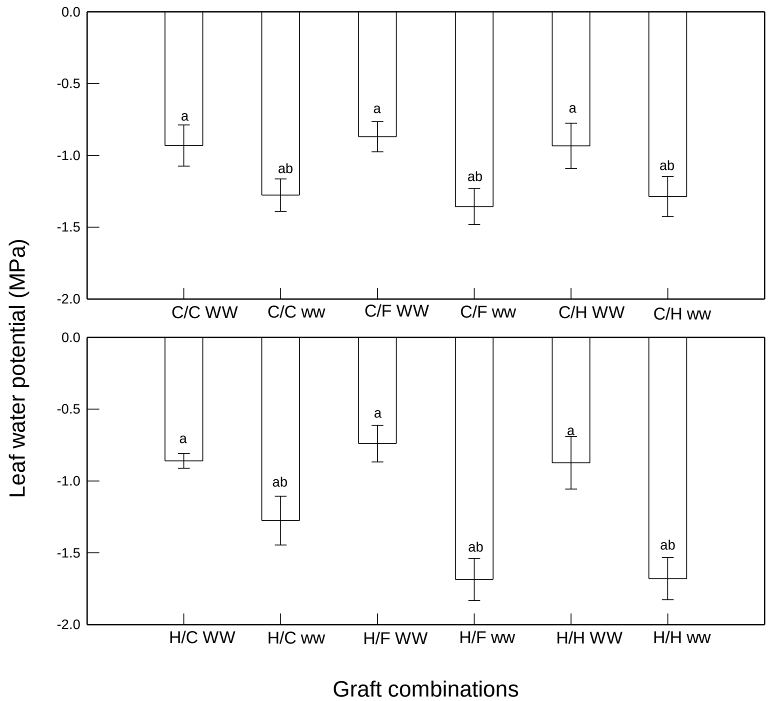

Figure 5. Leaf water potential for scion/rootstock combinations of avocado plants. Each bar represents the average of five replicates ± SE. A similar letter means a non-statistical difference according to Tukey's test ($P \leq 0.05$). H: 'Hass', C: 'Colín V-33', F: 'Fuerte', WW: well-watered and ww: withholding water.

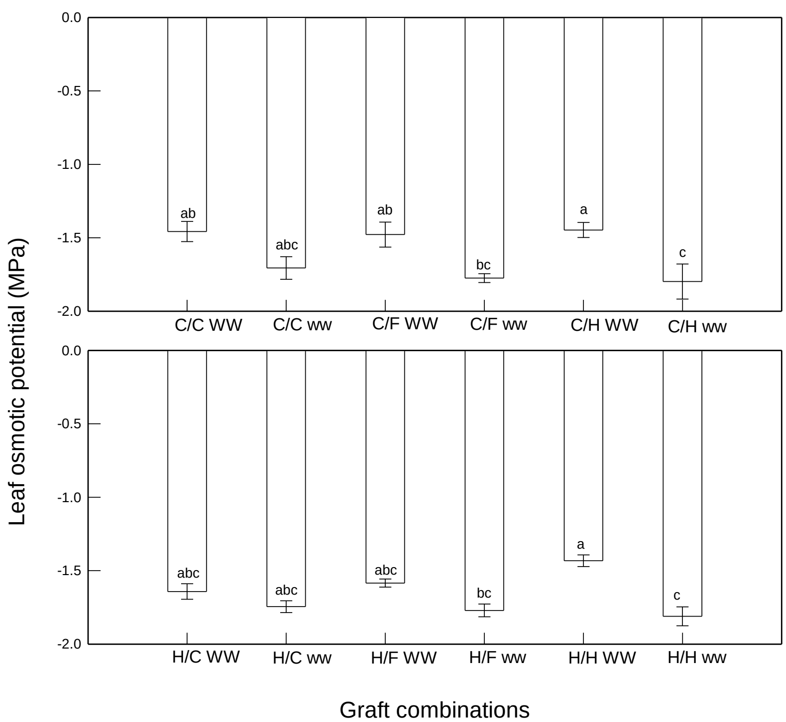

Figure 6. Leaf osmotic potential for scion/rootstocks combination of avocado plants. Each bar represents the average of five replicates ± SE. A similar letter means a non-statistical difference according to Tukey's test ($P \leq 0.05$). H: 'Hass', C: 'Colín V-33', F: 'Fuerte', WW: well-watered and ww: withholding water.

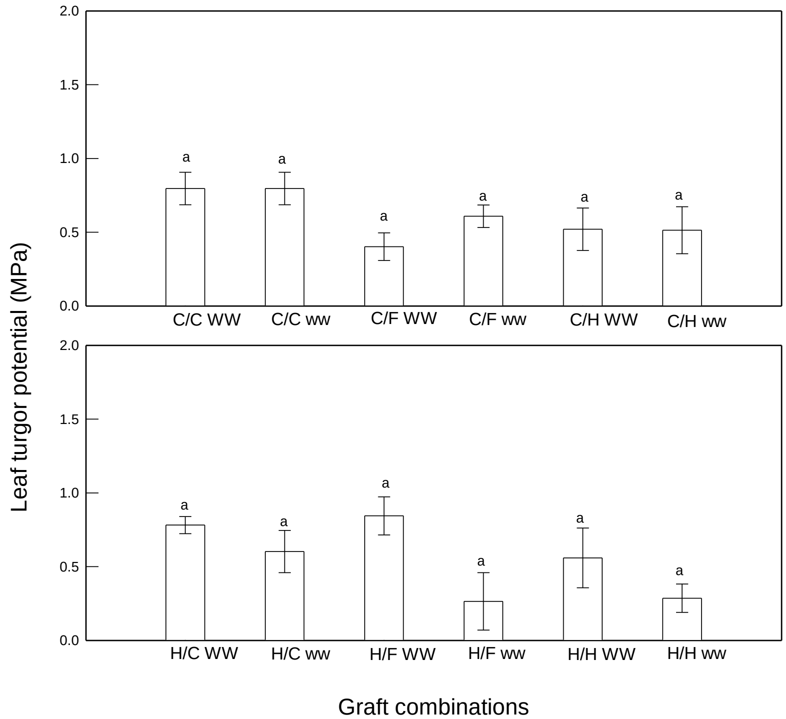

Figure 7. Leaf turgor potential for scion/rootstock combinations of avocado plants. Each bar represents the average of five replicates ± SE. A similar letter means a non-statistical difference according to Tukey's test ($P \leq 0.05$). H: 'Hass', C: 'Colín V-33', F: 'Fuerte', WW: well-watered and ww: withholding water.

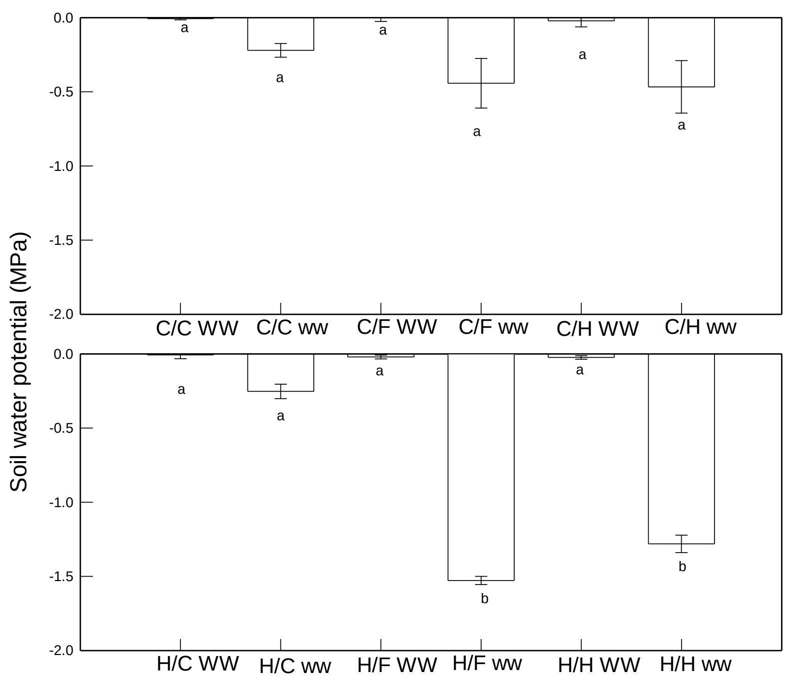

Figure 8. Soil water potential for scion/rootstock combinations of avocado plants. Each bar represents the average of five replicates ± SE. A similar letter means a non-statistical difference according to Tukey's test ($P \leq 0.05$). H: 'Hass', C: 'Colín V-33', F: 'Fuerte', WW: well-watered and ww: withholding water.

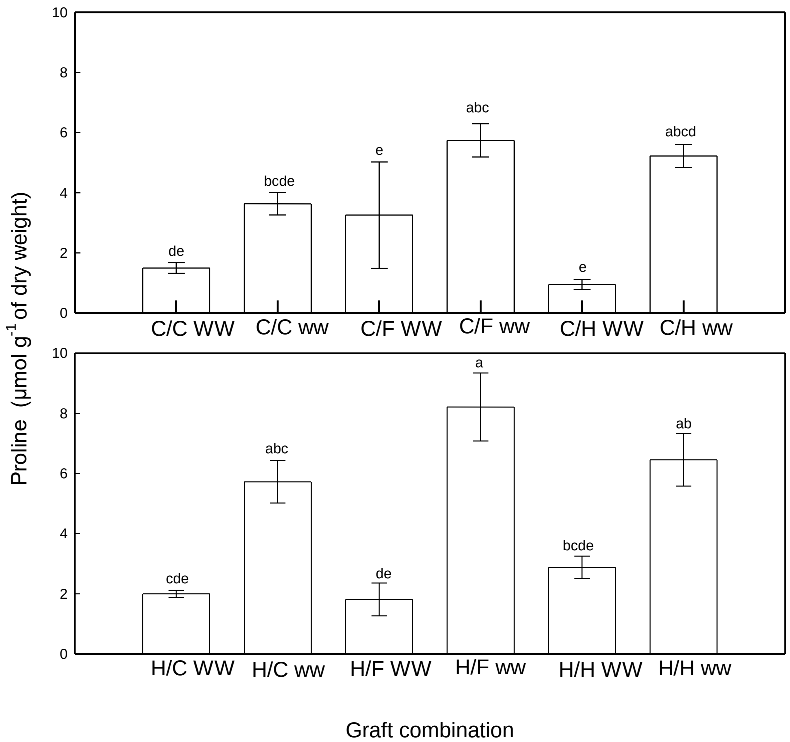

Figure 9. Leaf proline concentration for scion/rootstock combinations of avocado plants. Each bar represents the average of five replicates ± SE. A similar letter means non-statistical difference according to Tukey's test ($P\leq 0.05$). H: 'Hass', C: 'Colín V-33', F: 'Fuerte', WW: well-watered and ww: withholding water.

There is much information about root-shoot communication and the regulation of growth and gas exchange under water deficit conditions (Davies and Zhang, 1991; Davies *et al*., 1994) all these results are a likely explanation of why traditionally in fruit culture is very common to use scions or rootstocks which may have a better performance under a special environmental condition.

The response found in gas exchange in all the combinations studied had a marked influence in water relations. Leaf total water potential in most of the combinations was not affected even though stomatal conductance was affected, however, once again leaf water potential of H/F and H/H was significantly lower than the other combinations in comparison with well-watered plants. A similar behaviour was observed in soil water potential since significantly differences were found between well-watered and drought plants in H/F and H/H combinations. Leaf osmotic potential was also affected during withholding water when 'Hass' was used as rootstock.

Under conditions of water deficit an increase in the concentration of the amino acid proline has been found in different species (Aspinall and Paleg, 1981) including avocado (Barrientos-Priego and Rodríguez-Ontiveros, 1994). Similar results were found in all the combinations experiencing water deficit. It is also worth noticing that when 'Fuerte' and 'Hass' were used as rootstocks they were the combinations with the higher concentration in this amino acid and apparently they were the most sensitive to reduce stomatal conductance and CO_2 assimilation when water deficit was imposed. It has been thought that the endogenous increase in this amino acid may confer some kind of resistance to stress conditions however it has also been found that species which are resistant to water deficit are the ones with small concentration of this compound under water deficit conditions (Andrade *et al*., 1995).

CONCLUSION

The combinations with 'Colin V-33' show the best water use efficiency and greater resistance to water deficit. The scion/rootstock interaction significantly affects gas exchange, water relations, and proline concentration under water deficit. Low proline concentrations in this species appear linked to water deficit resistance.

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Conflict of interest: There is not any conflict of interest

Compliance with ethical standards: Does not apply

Data availability: Data available with Carlos Trejo (catre@colpos.mx), all data is contained in this document.

Author contribution statement (CRediT). M.I. Reyes-Santamaría, Investigation, Formal analysis, Writing - original draft., **C. Trejo** –Conceptualization, Funding acquisition, Methodology, Writing - review & editing., **A.F. Barrientos-Pliego** - Methodology, Supervision, Writing-review & editing., **T. Terrazas** - Supervision, Writing–review & editing.

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