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Scientific Article

Grapevine rootstocks under water deficit: biomass, biochemical, and gas exchange attributes

Porta-enxertos de videira sob déficit hídrico: respostas em biomassa, variáveis bioquímicas e trocas gasosas

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ABSTRACT - Water resources used for irrigation should be managed using technologies that improve water use efficiency, mainly in semiarid regions. Using drought-tolerant rootstocks is a strategy to handle this challenge. The objective of this study was to select suitable grapevine rootstocks for cultivation in semiarid regions based on their biomass, biochemical, and gas exchange attributes. The experiment was conducted at the Bebedouro Experimental Field of the Brazilian Agricultural Research Corporation (EMBRAPA Semiarid), in Petrolina, PE, Brazil. Rootstocks from grapevine plants of the cultivars Paulsen 1103, SO4, IAC 313, IAC 572, IAC 766, Ramsey, and 101-14 MgT were subjected to three irrigation water depths (100%, 50%, and 20% ET_0). A randomized block experimental design with four replications was used, in a split-plot arrangement consisting of irrigation water depths in the plots and rootstocks in the subplots. Biochemical, biomass, and gas exchange attributes were assessed for selecting the best rootstocks regarding tolerance to drought using multivariate principal component analysis (PCA) and analysis of variance. The rootstocks IAC 313 and IAC 766 presented the highest root proline synthesis; IAC 766 presented better result for leaf sucrose synthesis; and Paulsen 1103 presented the highest leaf proline synthesis and carotenoid contents, as well as total chlorophyll-to-carotenoid ratio. IAC 313, IAC 766, and Paulsen 1103 presented better performance regarding the studied characteristics and, therefore, are suitable for growing grapevine crops in the Lower Middle São Francisco Valley, mainly under water deficit conditions.

Keywords: *Vitis* sp. Growth. Osmoregulators.

RESUMO - Os recursos hídricos, especialmente em regiões semiáridas, devem ser utilizados com o emprego de tecnologias que permitam aumentar a eficiência e uso da água para irrigação. Uma estratégia para lidar com esse problema é o uso de porta-enxertos tolerantes à seca. Com o objetivo de selecionar porta-enxertos de videira adequados para o cultivo em regiões semiáridas, com base na biomassa, variáveis bioquímicas e nas trocas gasosas, o experimento foi conduzido no Campo Experimental de Bebedouro, pertencente à Embrapa Semiárido, em Petrolina-PE. Foram utilizados os porta-enxertos ‘Paulsen1103’, ‘SO4’, ‘IAC 313’, ‘IAC 572’, ‘IAC 766’, ‘Ramsey’ e ‘101-14 MgT’ submetidos a três lâminas de irrigação (100, 50 e 20% da ETo). O delineamento experimental foi em blocos casualizados com quatro repetições, em parcelas subdivididas, com a parcela principal sendo a lâmina de irrigação e a subparcela os porta-enxertos. Características bioquímicas, de biomassa e relacionadas às trocas gasosas foram utilizadas para seleção dos melhores porta-enxertos quanto à tolerância à seca, por meio de análise multivariada de componentes principais (PCA) e análise de variância. Os porta-enxertos ‘IAC 313’ e ‘IAC 766’ destacaram-se pela maior síntese de prolina radicular, o ‘IAC 766’ apresentou melhor resultado para síntese de sacarose foliar, enquanto ‘Paulsen1103’ se destacou em prolina foliar, carotenoide e razão clorofila total/carotenoide. Pode-se concluir que os porta-enxertos ‘IAC 313’, ‘IAC 766’ e ‘Paulsen 1103’ apresentam melhor desempenho quanto às características estudadas e, portanto, são uma escolha válida para cultivo da videira no Submédio do Vale do São Francisco, especialmente em condições de déficit hídrico.

Palavras-chave: *Vitis* sp. Crescimento. Osmorreguladores.

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INTRODUCTION

Fruit production is the agricultural activity that has grown the most in the last years, providing a high supply to the consumer market and employment opportunities (SILVA, 2019). The production of premium table grapes in Brazil is concentrated in the Lower Middle São Francisco Valley region, encompassing Petrolina in the state of Pernambuco and Juazeiro and Casa Nova in the state of Bahia (LEÃO, 2020). Viticulture is significantly representative in the Brazilian economic context, with a production area of approximately 74,798 ha, including 9,844 ha in the Lower Middle São Francisco Valley region, where 396,676 tons of grapes were produced in 2022 (IBGE, 2022). This region allows two annual harvests due to favorable climate conditions for grape production (LEÃO, 2020).

The use of rootstocks in viticulture is significantly important for preventing biotic and abiotic stresses, such as attack of grape phylloxera and nematodes, as well as water deficit (OLLAT et al., 2016). It has become even more important due to global climate changes, which have increased the demand for new genotypes tolerant to salinity and water deficit (GALBIGNANI et al., 2016; SERRA et al., 2014).

The selection of rootstocks tolerant to water deficit is focused mainly on those that can maintain yield while conserving water resources by reducing the need for irrigation and protecting fruits from damages caused by droughts (ZHANG et al., 2016).

Studies have confirmed the significance of using rootstocks tolerant to water deficit not only for grapevines, but also for coffee and citrus crops; it allows the crop to develop under limiting environmental conditions, maximizing the genetic production potential during water scarcity periods by increasing leaf biomass production, improving root system development, and promoting a rapid plant adaptation to water scarcity conditions (BRINATE et al., 2019; PEIXOTO et al., 2006).

In this context, selecting grapevine rootstocks adapted and tolerant to water deficit promotes higher water use efficiency and conservation of water resources, contributing to the sustainability of the viticulture in the Semiarid region of Brazil.

The objective of this study was to select grapevine rootstocks tolerant to water deficit for cultivation in the Lower Middle São Francisco Valley region, based on their root and shoot biomass production, as well as biochemical and physiological attributes assessed through gas exchange.

MATERIAL AND METHODS

Environmental characterization

The experiment was carried out at the Bebedouro Experimental Field of the Brazilian Agricultural Research Corporation (EMBRAPA Semiarid), in Petrolina, Pernambuco, Brazil (9°08'06"S 40°18'28"W), from August 25 to December 31, 2021. The climate of the region was classified as BSwh', according to the Köppen classification. Climate data collected from a meteorological station installed at the Bebedouro Experimental Field during the experiment are shown in Figure 1.

The experiment was established in 25-liter pots containing a substrate composed of soil from the grapevine growth area. Soil samples from the 0-20 and 20-40 cm layers were collected for chemical analysis to assess soil fertility (Table 1).

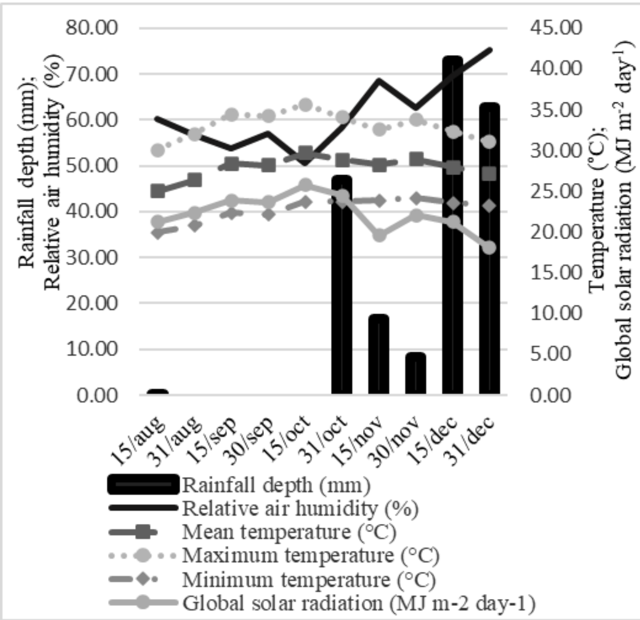

Figure 1. Climate data collected during the experiment, measured with 15-day intervals.

Table 1. Chemical analysis of the 0-20 and 20-40 cm soil layers in the grapevine growth area.

Layer	EC	pH	C	P	K	Na	Ca	Mg	Al	H+Al	SB	CEC	BS
cm	mS cm^{-1}	-------g kg^{-1}------		mg dm^{-3}	------------------------------------cmolc dm^{-3}------------------------------------								%
0-20	0.27	6	0	5.82	0.36	0.07	0.7	0.35	0	0.5	1.4	1.9	74.9
20-40	2.36	5.4	0	2.8	1	0.37	0.6	0.35	0.05	0.7	2.3	3	76.3
	Cu (mg dm^{-3})			Fe (mg dm^{-3})			Mn (mg dm^{-3})				Zn (mg dm^{-3})		
0-20	0.66			8.4			15.6				0.66		
20-40	1.2			12.6			19				0.7		

EC = electrical conductivity; SB = sum of bases; CEC = cation exchange capacity; BS base saturation.

Plant material

Rootstocks from grapevine plants of the cultivars Paulsen 1103, SO4, IAC 313, IAC 572, IAC 766, Ramsey (Salt Creek), and 101-14 MgT were used for presenting medium to high tolerance to drought (LEÃO; SOARES; RODRIGUES, 2009; OLLAT et al., 2016). Seedlings from these rootstocks were transplanted into pots one month after grafting, when they had four expanded leaves. The soil where the rootstocks were grown was fertilized by applying a commercial foliar fertilizer (Ajifol® Gold) 42 days after transplanting, along with monoammonium phosphate (MAP), calcium nitrate, and sulfate magnesium applied through fertigation with weekly intervals.

Characterization of the experiment

A randomized block experimental design with four replications was used, in a split-plot arrangement consisting of irrigation water depths in the plots and rootstocks in the subplots. The experimental unit was composed of two pots containing one plant per pot. The plants were subjected to three irrigation water depths: 100% (control), 50%, and 20% ET_0 (reference evapotranspiration); the water depth was calculated daily (Equations 1, 2, and 3) using climate data from an automatic weather station installed at the Bebedouro Experimental Field.

$$GWD = \left(ETo * \frac{Kc}{Ef}\right) - R \quad (1)$$

where *GWD* is the gross water depth used in the irrigation system; ET_0 is the reference evapotranspiration, *Kc* is the crop coefficient, *Ef* is the irrigation system efficiency, and *P* is the rainfall depth.

$$AWV = GWD * SBE \quad (2)$$

where *AWV* is the applied water volume, and *SBE* is the spacing between emitters.

$$Ti = \frac{AWV}{Ne} * Qe \quad (3)$$

where *Ti* is the irrigation time, *Ne* is the number of emitters per plant, and *Qe* is the emitter flow.

Evaluated variables

The following gas exchange-related variables were evaluated: net photosynthesis (*A*), stomatal conductance (*gs*), transpiration rate (*E*), leaf-to-air vapor pressure deficit, internal-to-external CO_2 concentration ratio in leaf mesophyll, intrinsic water use efficiency (μmol CO_2 mol^{-1} H_2O), net photosynthesis-to-transpiration ratio (instantaneous water use efficiency) (μmol CO_2 $mmol^{-1}$ H_2O), and leaf temperature. The analyses were carried out by readings in a portable infrared gas analyzer (IRGA; Li-6400XT, Li-Color, Lincoln, EUA), applying a photon flow of 1600 μmol m^{-2} s^{-1} and CO_2 concentration of 390 ppm (CHAVES et al., 2016).

Gas exchange analyses were started 15 days after planting (September 14, 21), after following the application of the different irrigation water depths, on the following dates: September 30, October 07, October 19, November 09, December 08, and December 14, 2021. Evaluations were carried out every 15 days, excluding rainy and cloudy days.

Grapevine leaves were collected 93 days after experiment implementation to assess total chlorophyll (*a* and *b*) and carotenoid contents, as well as primary metabolite contents (total soluble carbohydrates, sucrose, and proline). Analyses were carried out at the Plant Anatomy and Biochemistry Laboratory of the Federal Rural University of Pernambuco (UFRPE). Leaf samples were wrapped in aluminum paper foil, frozen in liquid nitrogen, and stored in a freezer at -80 °C.

Plants were uprooted 128 days after planting; roots and shoots were separated for evaluating their fresh weights using a precision digital scale (Ohaus TS4KD, 400 g 4000 g^{-1}). The plant material was then dried in an oven at 70 °C for 48 hours. The roots were crushed and placed in plastic bags for analyses of primary metabolites.

Total chlorophyll (*a* and *b*) and carotenoid contents were determined following the methodology of Bezerra Neto and Barreto (2011); the results were expressed in mmol per kg of fresh weight.

Soluble carbohydrate and sucrose contents were determined using the anthrone method, as described by Yemm and Willis (1954), and proline contents were determined following the method described by Bates, Waldern and Teare (1973). The results were expressed in mg per g of root dry weight or leaf fresh weight.

Statistical analysis

Principal component analysis (PCA) was conducted using the software GENES (CRUZ, 2013) to determine the characteristics that had the most significant contribution to the data variation, focusing on reducing the data structure and investigating the distribution of grapevine rootstocks' data in factorial plots (PC1 versus PC2), which were developed using the software Minitab 20 (MINITAB LLC, 2022). The variables with the highest contribution, as identified by PCA, were subjected to analysis of variance and Scott-Knott mean grouping test using the statistical program Sisvar (FERREIRA, 2022).

RESULTS AND DISCUSSION

The results obtained are shown in the two first principal components, which together accounted for 48.83% of the total data variance (Figure 2). Principal component analysis (PCA) grouped the 23 evaluated variables into eight components, with eigenvalues higher than 1, explaining 94.36% of the total data variance (Table 2). The first component was represented by transpiration rate (*E*) and accounted for 25,99% of the total variance. The second component (total chlorophyll-to-carotenoid ratio) explained 22.84% of the total variance. The third component (root proline contents) explained 12.03% of the total variance. The fourth component (carotenoid contents) explained 10.47% of the total variance. The fifth component (leaf sucrose contents) explained 7.67% of the total variance. The sixth component (shoot fresh weight) explained 6.34% of the total variance. The seventh component (leaf proline contents) explained 5.44% of the total variance. The eighth component (net photosynthesis) explained 3.59% of the total variance.

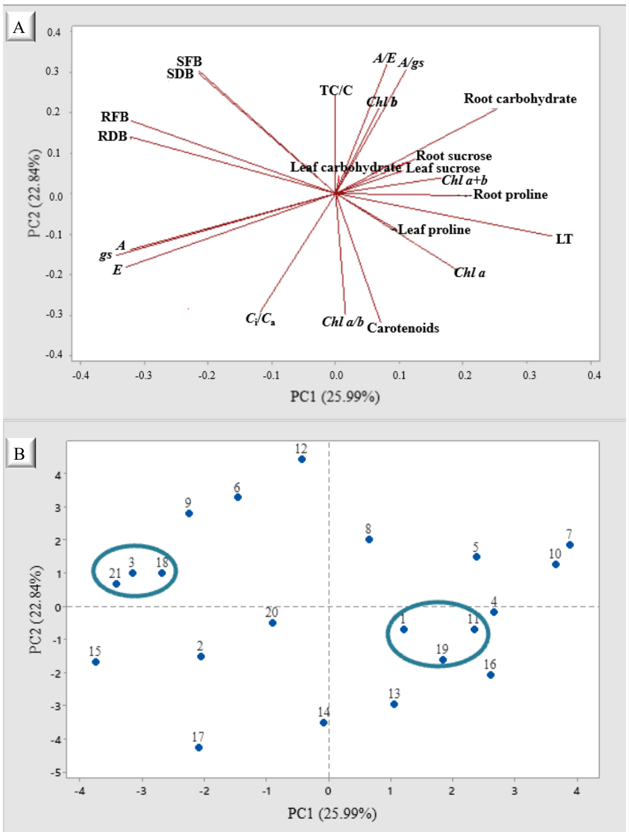

Figure 2. Principal component analysis (PCA) for biochemical, biomass, and gas exchange attributes of grapevine rootstocks. Graph of factorial load of parameters of PC1 and PC2 (A) and distribution of the samples in a score graph (B).

Table 2. First eight components of PCA for 23 biochemical, biomass, and gas exchange attributes assessed in rootstocks of seven grapevine rootstocks cultivars in 2021.

Parameters	Principal components (PC)							
	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
A	-0.322	-0.139	0.223	-0.155	-0.051	-0.068	0.174	-0.024
g_s	-0.345	-0.153	0.195	-0.067	-0.004	-0.099	0.115	-0.038
E	-0.329	-0.182	0.200	-0.073	-0.011	-0.085	0.133	-0.021
LT	0.341	-0.106	-0.204	0.048	-0.028	0.193	-0.018	-0.096
C_i/C_a	-0.120	-0.296	0.019	0.304	0.014	-0.289	-0.195	0.003
A/g_s	0.110	0.305	-0.017	-0.322	-0.059	0.274	0.140	0.044
A/E	0.081	0.322	0.086	-0.203	-0.163	0.020	0.343	-0.066
Leaf carbohydrate	0.005	0.035	0.004	0.041	0.714	-0.100	0.044	-0.117
Leaf sucrose	0.099	0.053	0.371	0.009	-0.056	0.257	-0.359	0.529
Leaf proline	0.097	-0.091	-0.026	-0.130	0.594	0.146	0.297	0.159
Root carbohydrate	0.252	0.208	0.171	-0.096	0.067	-0.182	-0.139	-0.429

A = net photosynthesis; g_s = stomatal conductance; E = transpiration rate; LT = leaf temperature; C_i/Ca = ratio internal-toexternal CO_2 concentration ratio in leaf mesophyll; A/g_s = intrinsic water use efficiency; A/E = net photosynthesis-to-transpiration ratio (instantaneous water use efficiency); Chl *a*/*b* = chlorophyll *a*-to-chlorophyll *b* ratio; Chl *a*+*b* = total chlorophyll; TC/C = total chlorophyll-to-carotenoid ratio; SFB = shoot fresh biomass; SDB = shoot dry biomass; RFB = root fresh biomass; and RDB = root dry biomass.

Table 2. Continuation.

Parameters	Principal components (PC)							
	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Root sucrose	0.124	0.085	0.459	-0.189	-0.007	-0.148	0.107	-0.232
Root proline	0.215	-0.006	0.333	-0.052	0.223	-0.016	-0.405	0.156
Chl *a*/*b*	0.016	-0.303	0.173	-0.374	-0.021	0.074	-0.046	-0.022
Chl *a*+*b*	0.168	0.039	0.283	0.434	-0.063	0.043	0.319	0.054
Chl *a*	0.190	-0.189	0.360	0.090	-0.101	0.110	0.272	0.081
Chl *b*	0.068	0.211	0.082	0.513	-0.001	-0.034	0.205	0.006
Carotenoids	0.070	-0.318	0.172	0.174	0.058	0.338	0.037	-0.279
TC/C	-0.001	0.244	0.049	-0.047	0.068	-0.517	0.139	0.443
SFB	-0.216	0.304	0.174	0.092	0.061	0.042	-0.214	-0.205
SDB	-0.215	0.297	0.157	0.105	0.039	0.072	-0.243	-0.241
RFB	-0.320	0.179	-0.004	0.065	0.097	0.317	0.018	0.074
RDB	-0.325	0.141	0.001	0.068	0.096	0.347	0.059	0.107
Eigenvalue	5.9781	5.2532	2.7671	2.4071	1.7633	1.4577	1.2501	0.8268
Variance (%)	25.99	22.84	12.03	10.47	7.67	6.34	5.44	3.59
Cumulative variance	25.99	48.83	60.86	71.33	78.99	85.33	90.77	94.36

A = net photosynthesis; g_s = stomatal conductance; E = transpiration rate; LT = leaf temperature; C_i/Ca = ratio internal-toexternal CO_2 concentration ratio in leaf mesophyll; A/g_s = intrinsic water use efficiency; A/E = net photosynthesis-to-transpiration ratio (instantaneous water use efficiency); Chl *a*/*b* = chlorophyll *a*-to-chlorophyll *b* ratio; Chl *a*+*b* = total chlorophyll; TC/C = total chlorophyll-to-carotenoid ratio; SFB = shoot fresh biomass; SDB = shoot dry biomass; RFB = root fresh biomass; and RDB = root dry biomass.

The distribution of the variables and their dynamics in the PCA are shown in Figure 2A. Shoot fresh and dry biomasses increased as the leaf proline content decreased. Similarly, internal and external CO_2 concentrations increased as the leaf carbohydrate content decreased. Decreases in leaf and root sucrose contents may be connected to increases in A, g_s, and E (Figure 2A).

The genotypes were grouped according to their phenotypic similarity (Figure 2B); for example, 1, 11, and 19 (rootstocks 101-14 MgT X 20% ET0, IAC 766 X 50% ET0 and SO4 X 20% ET0, respectively) presented similar leaf carbohydrate and proline contents, as well as root fresh biomass, and were plotted in the lower right of the graph. Genotypes 3, 18, and 21 (rootstocks 101-14 MgT X 100% ET0, Ramsey X 100% ET0 and SO4 X 100% ET0, respectively) presented similar A, E, g_s, leaf temperature, and root proline contents and were plotted in the upper left of the graph (Figure 2B). These results denote a high positive correlation among leaf and root carbohydrate and proline contents, A, E, g_s, leaf temperature, and root fresh biomass, resulting in higher factorial loads in the PCA.

PCA is a useful technique for reducing data and identifying variables that contribute the most to explaining the total variance of a dataset (JOLLIFFE, 2002). Mehmood et al. (2014) applied this technique to a dataset and found that eight principal components were needed for each evaluated crop season to explain approximately 80% of the total variance. These components were selected based on eigenvalues and factorial loads of the evaluated characteristics that contributed the most to the standard deviations.

The eight variables that most contributed to the data variance were subjected to analysis of variance and Scott-Knott mean grouping test. The results for primary metabolites and shoot biomass are shown in Tables 3 and 4. The means of the rootstocks were analyzed within the irrigation water depths when there was significance between rootstocks and irrigation water depths.

Leaf sucrose contents were stable in the rootstock IAC 766 (Table 3), regardless of the irrigation water depth. However, when considering the rootstocks within irrigation water depths (Table 4), the rootstocks 101-14 MgT, IAC 313, SO4, and IAC 766 presented no significant difference to each other under irrigation water depths of 20% and 100% ET_0, but differed from the rootstock IAC 766 under irrigation depth of 50% ET_0, which presented higher sucrose contents than the other rootstocks under the three evaluated irrigation water depths. The rootstocks IAC 572, Paulsen 1103, and Ramsey presented different leaf sucrose contents to the other rootstocks under irrigation of 100% ET_0 (Table 4). Thus, sucrose contents presented significant increase under irrigation of 100% ET_0 compared to the other evaluated conditions, as reported by Santos, Moreira, and Rodrigues (2013), who found that water limitations do not affect leaf sugar contents.

Metabolic changes in enzyme activity and contents of amino acids or carbohydrates are expected responses when plants are subjected to water stress, as they need to maintain their metabolic activities and growth by reallocating surplus photoassimilates, often as sucrose, to be hydrolyzed and utilized as an osmotic regulator (XU et al., 2018). Additionally, water deficit can be used to increase leaf sugar contents, fruit production, and other quality attributes of grapevines (SANTOS; MOREIRA; RODRIGUES, 2013).

Table 3. Biochemical and biometric attributes of grapevine rootstocks.

Rootstocks	Leaf sucrose (mg g^{-1} of fresh biomass)	Leaf proline (mg g^{-1} of fresh biomass)	Root proline (mg g^{-1} of dry biomass)
101-14 MgT	2.10 ± 0.30 c	3.43 ± 0.78 b	0.05 ± 0.00 d
IAC 313	2.32 ± 0.32 b	3.52 ± 0.64 b	0.16 ± 0.07 a
IAC 572	1.99 ± 0.22 c	3.36 ± 0.72 b	0.10 ± 0.05 b
IAC 766	2.70 ± 0.72 a	3.51 ± 0.37 b	0.16 ± 0.06 a
Paulsen 1103	1.90 ± 0.09 c	4.55 ± 0.99 a	0.11 ± 0.04 b
Ramsey	2.10 ± 0.19 c	2.90 ± 0.44 c	0.08 ± 0.02 c
SO4	2.30 ± 0.19 b	3.03 ± 0.24 c	0.08 ± 0.02 c
Mean	2.20	3.47	0.10
Irrigation water depths			
20% ET_0	4.11 a	3.69 a	0.10 b
50% ET_0	3.85 a	3.39 b	0.14 a
100% ET_0	4.42 a	3.33 b	0.07 c
Rootstocks	Shoot fresh biomass (g $plant^{-1}$)	Carotenoids (mmol kg^{-1} of fresh biomass)	Total chlorophyll-to-carotenoid ratio (mmol kg^{-1} of fresh biomass)
101-14 MgT	115.42 ± 60.10 b	0.16 ± 0.04 b	9.42 ± 2.59 b
IAC 313	209.94 ± 104.54 a	0.19 ± 0.08 b	7.34 ± 1.84 b
IAC 572	205.48 ± 145.85 a	0.13 ± 0.05 b	9.98 ± 3.17 b
IAC 766	192.47 ± 103.45 a	0.19 ± 0.15 b	16.36 ± 14.91 a
Paulsen 1103	107.03 ± 67.99 b	0.31 ± 0.09 a	4.40 ± 0.77 c
Ramsey	143.84 ± 91.15 b	0.32 ± 0.08 a	4.89 ± 0.90 c
SO4	136.24 ± 82.39 b	0.18 ± 0.11 b	8.57 ± 7.06 b
Mean	165.83	0.21	8.71
Irrigation water depths			
20% ET_0	69.41 c	0.25 a	6.75 a
50% ET_0	140.66 b	0.21 b	9.04 a
100% ET_0	265.82 a	0.17 c	10.33 a

Means ± standard deviations followed by the same letter in the columns are not significantly different from each other by the Scott-Knott test ($p < 0.05$).

Leaf proline contents (Table 3) were higher in the rootstock Paulsen 1103, even when subjected to water deficit (Table 4), denoting its higher adaptation ability to limited water conditions.

Ferreira-Silva et al. (2009) reported that the accumulation of free amino acids, such as proline, may be connected to abiotic stresses, denoting a correlation with plant osmoprotection. Therefore, the higher leaf proline contents in the rootstock Paulsen 1103 denotes a protection strategy, highlighting its higher tolerance to water deficit conditions and confirming results reported in several studies (FAYEK; RASHEDY; ALI, 2022; LO'AY; EL-EZZ, 2021; SOUZA; SOARES; REGINA, 2001).

The interaction between rootstocks and irrigation water depths was significant for root proline contents. The rootstocks IAC 313 and IAC 766 were significantly different from the others (Table 3), but they presented different results to each other as a function of irrigation water depths. IAC 313 stood out with the highest root proline contents under water deficit (20% ET_0) and along with IAC 766 under the irrigation water depth of 50% ET_0 (Table 4). Higher root proline contents were found under the irrigation water depth of 50% ET_0 for most rootstocks; however, 101-14 MgT and SO4 presented similar root proline contents under the three irrigation water depths.

Many plants adopt a strategy of reallocating sucrose and other solutes to storage and growth organs, such as roots, mainly in response to drought, to search for more water (XU et al., 2018). This process decreases photosynthesis because plants require osmotic adjustment. Additionally, plants accumulate amino acids, such as proline, to mitigate the harmful effects of water deficit (LO'AY; EL-EZZ, 2021). In the present work, this translocation of solutes to the roots occurred; however, it was not sufficient to contribute to the osmotic adjustment of the plants; however, under high water stress (20% and 50% ET_0), there was a tendency to increase proline content in the roots (Tables 3 and 4).

Table 4. Means and standard deviations for biochemical and biometric attributes of grapevine rootstocks grown under different irrigation water depths.

Rootstocks	Leaf sucrose (mg g^{-1} of fresh biomass)		
	20% ET_0	50% ET_0	100% ET_0
101-14 MgT	2.07 ± 0.13 a A	1.97 ± 0.10 d A	2.33 ± 0.44 a A
IAC 313	2.14 ± 0.22 a B	2.58 ± 0.07 b A	2.25 ± 0.42 a B
IAC 572	1.80 ± 0.13 b B	2.25 ± 0.08 c A	1.93 ± 0.04 b B
IAC 766	2.30 ± 0.07 a B	3.52 ± 0.70 a A	2.28 ± 0.29 a B
Paulsen 1103	1.91 ± 0.07 b A	1.92 ± 0.14 d A	1.88 ± 0.04 b A
Ramsey	2.27 ± 0.19 a A	2.11 ± 0.10 d A	1.92 ± 0.04 b A
SO4	2.19 ± 0.15 a A	2.28 ± 0.25 c A	2.43 ± 0.04 a A
Mean	2.09 B	2.37A	2.15 B
	Leaf proline (mg g^{-1} of dry biomass)		
101-14 MgT	3.36 ± 0.39 b B	2.92 ± 0.37 b B	4.01 ± 1.05 a A
IAC 313	3.49 ± 0.65 b A	3.83 ± 0.56 a A	3.22 ± 0.72 b A
IAC 572	3.87 ± 0.52 b A	3.64 ± 0.37 a A	2.56 ± 0.43 b B
IAC 766	3.29 ± 0.36 b A	3.57 ± 0.41 a A	3.65 ± 0.34 a A
Paulsen 1103	5.27 ± 0.34 a A	3.93 ± 1.32 a B	4.45 ± 0.71 a B
Ramsey	3.37 ± 0.33 b A	2.85 ± 0.26 b A	2.48 ± 0.10 b A
SO4	3.18 ± 0.34 b A	3.01 ± 0.19 b A	2.91 ± 0.04 b A
Mean	3.69 a	3.39 B	3.33 B
	Root proline (mg g^{-1} of dry biomass)		
101-14 MgT	0.05 ± 0.01 c A	0.05 ± 0.00 d A	0.05 ± 0.00 b A
IAC 313	0.18 ± 0.02 a B	0.22 ± 0.04 a A	0.06 ± 0.03 b C
IAC 572	0.08 ± 0.04 c B	0.14 ± 0.04 b A	0.07 ± 0.04 b B
IAC 766	0.11 ± 0.03 b B	0.24 ± 0.01 a A	0.13 ± 0.04 a B
Paulsen 1103	0.09 ± 0.01 b B	0.15 ± 0.02 b A	0.07 ± 0.01 b B
Ramsey	0.09 ± 0.02 b A	0.10 ± 0.01 c A	0.06 ± 0.03 b B
SO4	0.08 ± 0.01 c A	0.09 ± 0.01 c A	0.06 ± 0.01 b A
Mean	0.10 B	0.14 a	0.07 C
	Shoot fresh biomass (g plant^{-1})		
101-14 MgT	52.06 ± 21.18 a B	110.05 ± 28.68 a B	184.16 ± 16.84 b A
IAC 313	96.39 ± 19.46 a C	216.24 ± 52.54 a B	317.2 ± 65.94 a A
IAC 572	74.17 ± 42.12 a C	163.2 ± 87.05 a B	379.05 ± 55.78 a A
IAC 766	95.05 ± 49.17 a C	170.88 ± 56.69 a B	311.47 ± 38.11 a A
Paulsen 1103	44.64 ± 24.24 a B	96.45 ± 19.15 a B	180.01 ± 59.61 b A
Ramsey	63.45 ± 17.09 a B	118.49 ± 53.43 a B	249.59 ± 54.13 b A
SO4	60.13 ± 28.93 a B	109.31 ± 21.92 a B	239.28 ± 26.98 b A
Mean	69.41C	140.66B	265.82 a
	Carotenoids (mmol kg^{-1} of fresh biomass)		
101-14 MgT	0.15 ± 0.02 c A	0.12 ± 0.04 c A	0.19 ± 0.01 a A
IAC 313	0.22 ± 0.09 b A	0.19 ± 0.09 b A	0.16 ± 0.05 a A
IAC 572	0.15 ± 0.05 c A	0.09 ± 0.06 c A	0.16 ± 0.02 a A
IAC 766	0.21 ± 0.15 b B	0.32 ± 0.06 a A	0.04 ± 0.03 b C
Paulsen 1103	0.35 ± 0.05 a A	0.35 ± 0.11 a A	0.22 ± 0.02 a B
Ramsey	0.39 ± 0.01 a A	0.35 ± 0.03 a A	0.22 ± 0.07 a B
SO4	0.26 ± 0.09 b A	0.06 ± 0.04 c B	0.20 ± 0.08 a A
Mean	0.25 a	0.21B	0.17C
	Total chlorophyll-to-carotenoid ratio (mmol kg^{-1} of fresh biomass)		
101-14 MgT	8.44 ± 0.22 a B	12.48 ± 2.20 a A	7.34 ± 0.29 b B
IAC 313	6.55 ± 2.25 a A	7.82 ± 2.39 b A	7.66 ± 0.59 b A
IAC 572	9.48 ± 0.80 a A	12.85 ± 3.65 a A	7.60 ± 1.98 b A
IAC 766	9.25 ± 4.47 a B	4.92 ± 1.06 b B	34.90 ± 9.71 a A
Paulsen 1103	3.56 ± 0.53 a A	5.01 ± 0.19 b A	4.60 ± 0.62 b A
Ramsey	5.11 ± 0.34 a A	3.91 ± 0.50 b A	5.64 ± 0.70 b A
SO4	4.86 ± 1.13 a B	16.28 ± 7.86 a A	4.55 ± 0.72 b B
Mean	6.75 a	9.04 a	10.33 a

Means ± standard deviation followed by the same lowercase letter in the columns comparing rootstocks, or uppercase letter in the rows comparing water depths, are not significantly different from each other by the Scott-Knott test ($p < 0.05$).

The rootstocks under limiting water conditions (20% ET_0) presented significant decreases in shoot fresh biomass compared to those under irrigation water depth of 100% ET_0. The rootstocks in the IAC group, in general, are different from the others (Table 3); they presented higher shoot biomass under irrigation of 100% ET_0, mainly IAC 572, whose shoot fresh biomass was higher than those found for Paulsen 1103, SO4, 101-14 MgT, and Ramsey (Table 4). These results are consistent with those found by Tecchio et al. (2011) for IAC 572, which presented higher shoot dry biomass than rootstocks of the other cultivars.

Leaf carotenoid contents were affected by the water availability, with higher values found for the rootstocks Paulsen 1103 and Ramsey under low water availability compared to those found for 101-14 MgT, IAC 313, IAC 572, and IAC 766. Considering the irrigation water depth 50% ET_0, the rootstocks Ramsey, Paulsen 1103, and IAC 766 showed the highest carotenoid contents, significantly differing from the other rootstocks (Table 4).

Carotenoids are light-collecting pigments, moderators in protein assembly, and protect chlorophylls from harmful photo-destructive reactions that occur in the presence of oxygen (COGDELL, 1985). No decreases in carotenoid contents were found in the present study for any of the rootstock cultivars when comparing the irrigation water depth of 100% ET_0 with low water availability conditions (20% and 50% ET_0). The maintenance of carotenoid contents in grapevine rootstocks during water deficit indicates that the photosystem II is preserved, as carotenoids are associated with this photosystem (NASCIMENTO; NASCIMENTO; GONÇALVES, 2019; SILVA et al., 2014).

The interaction between rootstock and irrigation water depth was significant for total chlorophyll-to-carotenoid ratio (TC/C) (Table 4). However, most rootstocks presented no significant differences for this variable when comparing the three evaluated irrigation water depths. TC/C decreased as the water availability was decreased only in the rootstock IAC 766. The rootstock SO4 presented lower TC/C under the irrigation water depths of 20% and 100% ET_0, indicating poor pigment recovery when plants are irrigated after water stress.

Lo'ay and EL-Ezz (2021) found higher pigment contents, mainly carotenoids, in grape leaves of Flame Seedless scions grafted onto Paulsen 1103 in all phenological stages (flowering, fruit set, filling, and harvest), denoting a positive performance of this rootstock in the synthesizing these pigments, mainly under water deficit conditions, as also found in the present work. According to these authors, a low chlorophyll-to-carotenoid ratio confirms an increase in plant carotenoid production and the consequent improvement of the leaf protection system and protection to water deficit. In the present study, the rootstock IAC 766 presented lower total chlorophyll-to-carotenoid ratio under low water availability conditions (20% and 50% ET_0).

The interaction between rootstock and irrigation water depth was significant for net photosynthesis (*A*) (Table 5), with no significant difference for the different evaluation periods. The mean *A* decreased throughout the experiment, mainly in the last evaluations when the effects of the water deficit intensified, as expected. Water deficit in the 20% ET_0 irrigation resulted in a significant decrease in *A* on September 30, October 07, December 08, and December 14 (Table 5). This result was not found on the other evaluation dates, which may be attributed to the high air temperatures and solar radiation on the evaluation day. According to Gobbo-Neto and Lopes (2007), annual, monthly, and daily temperature variations are among the factors that most affect plant development, explaining low production even under favorable edaphic conditions. On November 09 and December 14, the results found for *A* under irrigation water depth of 100% ET_0 were lower than those found under low water availability conditions (20% and 50% ET_0), denoting that temperature and solar radiation have a higher effect on photosynthesis than water stress.

The physiological difference of plants under high and low water availability conditions is also a significant factor to consider. According to Zhang et al. (2016), grapevine plants rapidly adapt to water availability conditions, climate, and daily variations in temperature and evapotranspiration, presenting distinct characteristics such as increased leaf area and root and shoot fresh biomasses. In the present work, physiological changes were more noticeable in plants under irrigation water depth of 100% ET_0, combined with the occurrence of significant changes in daily temperature, solar radiation, insolation, or evapotranspiration.

Decreases in net photosynthesis (*A*) are common in plants under stress, especially water stress. Souza, Soares, and Regina (2001) reported that one of the first plant's responses to water deficit is the stomatal closure, leading to a decrease in CO_2 diffusion to the leaf mesophyll, resulting in decreased photosynthesis. These authors evaluated Niagara Rosada grapevine scions grafted onto Paulsen 1103 and 101-14 MgT and found that the rootstock Paulsen 1103 presented higher net photosynthesis-to-transpiration ratio (*A/E*) than 101-14 MgT 12 days after suspending irrigation. However, in the present study, these two rootstocks presented high *A* throughout the experiment period, mainly in the last evaluation dates (Table 5).

The interaction between rootstock and irrigation water depth was significant for transpiration rate (*E*), which presented a decreasing trend throughout the experiment on three evaluation dates (September 30, October 07, and December 14) (Table 7). This interaction was not significant on four evaluation dates (September 14, October 19, November 09, and December 08), indicating isolated effects of rootstocks and irrigation water depths (Table 6). *E* decreased under water deficit (20% ET_0) on four evaluation dates (September 30, October 07, October 19, and December 08) (Table 6). however, the other three readings (on September 14, November 09, and December 14) presented similar *E* among the irrigation water depth treatments, or even higher *E* under low water availability conditions when compared to the highest water availability.

Variations in *E* among rootstocks in response to different irrigation water depths and evaluation dates did not allow for the identification of trends for a specific rootstock or a group of rootstocks under lower water availability conditions (20% and 50% ET_0) (Table 7), which indicates an adaptative strategy. According to Zhang et al. (2016), plants with higher vegetative growth expend more energy and, depending on the environment, tend to reduce their metabolic activities at some times of the day to control energy expenditure. Souza, Soares, and Regina (2001) evaluated Niagara Rosada grapevine scions grafted onto Paulsen 1103 and 101-14 MgT by fully suspending and partially suspending irrigation to evaluate the effects of water deficit over time; they reported that *E* tends to decrease over time in non-irrigated plants, whereas irrigated plants tend to maintain a constant *E* over time.

Table 5. Means and standard deviations for leaf net photosynthesis (*A*) in grapevine rootstocks at seven evaluation dates.

Rootstocks	A (µmol CO_2 m^{-2} s^{-1})			
	September 14	September 30	October 07	October 19
101-14 MgT	19.38 ± 1.96 a	17.46 ± 3.77 b	12.18 ± 6.91b	13.05 ± 2.61 a
IAC 313	17.26 ± 2.70 a	15.59 ± 4.38 b	10.38 ± 5.4 b	10.09 ± 2.12 b
IAC 572	14.04 ± 3.31 b	16.50 ± 4.94 b	11.68 ± 6.23 b	9.79 ± 1.4 b
IAC 766	15.76 ± 1.61 b	16.27 ± 2.88 b	9.79 ± 5.68 b	10.62 ± 2.31 b
Paulsen 1103	16.6 ± 2.19 b	17.36 ± 3.93 b	13.87 ± 5.74 a	12.00 ± 2.84 a
Ramsey	17.98 ± 3.21 a	22.25 ± 3.91 a	14.76 ± 6.44 a	14.46 ± 2.05 a
SO4	16.65 ± 3.88 b	18.25 ± 3.67 b	10.86 ± 6.89 b	9.59 ± 2.88 b
Mean	16.81	17.67	11.93	11.37
Irrigation water depths				
20% ET_0	17.08 a	14.02 c	4.50 c	10.80 a
50% ET_0	16.67 a	17.96 b	14.45 b	11.21 a
100% ET_0	16.68 a	21.03 a	16.84 a	12.10 a

	November 09	December 08	December 14
101-14 MgT	19.72 ± 3.76 a	12.77 ± 6.56 a	8.17 ± 6.12 a
IAC 313	11.58 ± 4.19 d	12.15 ± 5.31 a	5.04 ± 3.63 a
IAC 572	11.22 ± 2.93 d	11.34 ± 4.87 a	4.10 ± 4.22 a
IAC 766	16.95 ± 3.54 b	11.16 ± 5.61 a	4.68 ± 2.69 a
Paulsen 1103	19.62 ± 3.30 a	13.67 ± 6.23 a	6.68 ± 4.71 a
Ramsey	20.51 ± 3.76 a	12.59 ± 6.26 a	5.73 ± 6.02 a
SO4	15.47 ± 2.16 c	8.23 ± 4.80 b	8.23 ± 4.86 a
Mean	16.44	11.78	6.09
Irrigation water depths			
20% ET_0	18.34 a	6.99 b	4.20 b
50% ET_0	16.75 a	13.00 a	8.93 a
100% ET_0	14.23 b	15.12 a	3.88 b

Means ± standard deviations followed by the same letter in the columns are not significantly different from each other by the Scott-Knott test ($p < 0.05$).

Table 6. Means and standard deviations for transpiration (*E*) in grapevine rootstocks at seven evaluation dates.

Rootstock	*E* (mmol H_2O m^{-2} s^{-1})			
	September 14	September 30	October 07	October 19
101-14 MgT	5.44 ± 0.75 a	4.02 ± 1.46 c	3.34 ± 1.95 b	4.39 ± 0.9 b
IAC 313	5.02 ± 0.66 a	3.52 ± 1.58 c	2.74 ± 1.26 b	3.35 ± 0.89 c
IAC 572	4.55 ± 1 a	4.00 ± 1.71 c	3.01 ± 1.47 b	3.11 ± 0.97 c
IAC 766	4.86 ± 0.61 a	3.81 ± 1.04 c	2.62 ± 1.52 b	3.44 ± 0.98 c
Paulsen 1103	5.01 ± 0.83 a	4.26 ± 1.45 b	3.78 ± 1.83 a	4.09 ± 1.13 b
Ramsey	5.35 ± 1.27 a	5.21 ± 1.44 a	4.12 ± 1.85 a	5.06 ± 0.6 a
SO4	5.23 ± 1.13 a	4.53 ± 1.44 c	3.12 ± 2.20 b	3.50 ± 1.15 c
Mean	5.07	4.19	3.25	3.85
Irrigation water depths				
20% ET_0	5.18 a	2.91 c	1.22 c	3.72 a
50% ET_0	4.96 a	4.25 b	3.83 b	3.76 a
100% ET_0	5.06 a	5.43 a	4.70 a	4.06 a

	November 09	December 08	December 14
101-14 MgT	4.63 ± 1.03 a	3.79 ± 1.99 a	2.55 ± 1.96 a
IAC 313	2.38 ± 0.89 c	3.42 ± 1.42 a	1.43 ± 1.04 b
IAC 572	2.31 ± 0.66 c	3.04 ± 1.42 b	1.13 ± 1.07 b
IAC 766	3.72 ± 0.96 b	3.00 ± 1.72 b	1.30 ± 0.81 b
Paulsen 1103	4.83 ± 1.10 a	3.95 ± 1.78 a	2.10 ± 1.48 a
Ramsey	4.41 ± 0.76 a	3.38 ± 1.66 a	1.61 ± 1.71 b
SO4	3.68 ± 0.83 b	2.25 ± 1.09 b	1.62 ± 1.50 b
Mean	3.71	3.28	1.68
Irrigation water depths			
20% ET_0	4.25 a	1.82 b	1.37 b
50% ET_0	3.81 a	3.57 a	2.70 a
100% ET_0	3.07 b	4.40 a	0.97 b

Means ± standard deviations followed by the same letter in the columns are not significantly different from each other by the Scott-Knott test ($p < 0.05$).

Table 7. Means and standard deviations for leaf transpiration (*E*) in grapevine rootstocks at three evaluation dates within three irrigation water depths.

Rootstocks	*E* (mmol H_2O m^{-2} s^{-1}) (September 30)		
	20% ET_0	50% ET_0	100% ET_0
101-14 MgT	2.36 ± 0.48 a C	4.25 ± 0.57 a B	5.46 ± 0.82 a A
IAC 313	2.18 ± 0.88 a C	3.21 ± 1.15 a B	5.18 ± 0.92 a A
IAC 572	2.10 ± 0.89 a C	4.42 ± 0.48 a B	5.49 ± 1.29 a A
IAC 766	2.96 ± 0.96 a B	4.11 ± 0.63 a A	4.37 ± 1.07 a A
Paulsen 1103	3.62 ± 0.88 a B	3.51 ± 0.77 a B	5.65 ± 1.56 a A
Ramsey	3.88 ± 0.99 a B	5.74 ± 1.16 a A	6.04 ± 1.28 a A
SO4	3.28 ± 0.47 a C	4.53 ± 1.57 a B	5.78 ± 0.86 a A
Mean	2.91C	4.25B	5.42A

Means ± standard deviation followed by the same lowercase letter in the columns comparing rootstocks, or uppercase letter in the rows comparing water depths, are not significantly different from each other by the Scott-Knott test ($p < 0.05$).

Table 7. Continuation.

Rootstocks	*E* (mmol H_2O m^{-2} s^{-1})		
	20% ET_0	50% ET_0	100% ET_0
	(October 07)		
101-14 MgT	0.88 ± 0.49 a C	3.94 ± 0.65 b B	5.19 ± 0.42 a A
IAC 313	1.25 ± 0.27 a B	3.24 ± 0.47 b A	3.73 ± 0.96 b A
IAC 572	1.10 ± 0.23 a B	3.71 ± 0.47 b A	4.21 ± 0.45 b A
IAC 766	0.96 ± 0.26 a B	3.12 ± 0.82 b A	3.79 ± 1.38 b A
Paulsen 1103	1.78 ± 0.54 a C	3.73 ± 0.55 b B	5.82 ± 0.90 a A
Ramsey	1.77 ± 0.33 a B	5.65 ± 0.84 a A	4.96 ± 0.58 a A
SO4	0.80 ± 0.68 a C	3.40 ± 0.69 b B	5.16 ± 2.01 a A
Mean	1.22C	3.83B	4.70A
	(December 14)		
101-14 MgT	1.63 ± 0.78 a B	5.04 ± 0.86 a A	0.97 ± 0.21 a B
IAC 313	1.43 ± 1.01 a A	2.20 ± 1.13 a A	0.67 ± 0.33 a A
IAC 572	1.47 ± 1.05 a A	1.36 ± 1.14 a A	0.56 ± 0.55 a A
IAC 766	1.65 ± 1.19 a A	1.36 ± 0.73 a A	0.89 ± 0.18 a A
Paulsen 1103	1.47 ± 0.69 a A	3.03 ± 1.78 a A	1.82 ± 1.45 a A
Ramsey	1.22 ± 1.36 a B	2.93 ± 1.22 a A	0.69 ± 0.41 a B
SO4	0.70 ± 0.37 a B	2.96 ± 1.95 a A	1.20 ± 0.70 a B
Mean	1.37B	2.70A	0.97B

Means ± standard deviation followed by the same lowercase letter in the columns comparing rootstocks, or uppercase letter in the rows comparing water depths, are not significantly different from each other by the Scott-Knott test ($p < 0.05$).

CONCLUSIONS

Grapevine rootstocks IAC 313, IAC 766, and Paulsen 1103 presented better performance regarding primary metabolites, shoot biomass, pigments, and gas exchanges, composing important adaptation strategies to water deficit. The results provide important contribution for the choice and use of grapevine rootstocks in the Lower Middle São Francisco Valley region, Brazil, mainly under water deficit conditions.

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