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Physiological, biochemical and elemental responses of grafted grapevines under drought stress: insights into tolerance mechanisms

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Abstract

The selection of appropriate grapevine grafts and optimizing irrigation practices for enhancing water use efficiency are critical for viticulture production in the arid regions of UAE, apart from mitigating the effects of changing environmental conditions. Extremely high arid temperatures leading to depleted soil moisture status limit grape production in the country. In order to streamline the production, it is imperative to focus on specific objectives of screening drought-tolerant grafts utilizing several laboratory analytical tools and irrigation management. Five grapevine cultivar-rootstock combinations were evaluated in an open field experiment under induced drought conditions by regulating irrigation at 100%, 75% and 50% field capacity (FC) in an arid region. The net photosynthetic rate increased in Flame Seedless × Ramsey (V1), Thompson Seedless × Ramsey (V2), and Crimson Seedless × R110 (V3) at 50% FC. Stomatal conductance was reduced in V1, V3, Crimson Seedless × Ramsey (V4) and Thompson Seedless x P1103 (V5) at 50% FC. Intercellular CO_2 and transpiration rates were significantly reduced at 50% FC. Water use efficiency, calculated as Pn/gs ratio to relate photosynthesis to stomatal closure, was elevated in all the grafts at 75% FC and 50% FC compared to the control (100% FC). The relative water content (RWC) showed a declining trend in all the grafts with reduced water supply. Nevertheless, the V1 and V4 grafts exhibited the highest RWC at an FC of 50%. The V2 graft produced the highest total dry mass and fresh biomass compared to other grafts. The Chl *a* content decreased, but the Chl *b* content increased at 50% FC in V2. Lutein significantly decreased for V1, while V3 showed an increase at 50% FC. The N, P and K contents in all the grafts, except V3, showed an increasing trend at 50% FC. The scanning electron microscopy observations point to the strong responses of stomatal behaviour upon changes in irrigation, thus facilitating the drought tolerance of the grafts. The findings emphasize the importance of selecting drought-tolerant grapevine grafts, and our study results could serve as guideposts for developing sustainable viticulture in arid regions, providing valuable insights for future research and practical applications in grape production.

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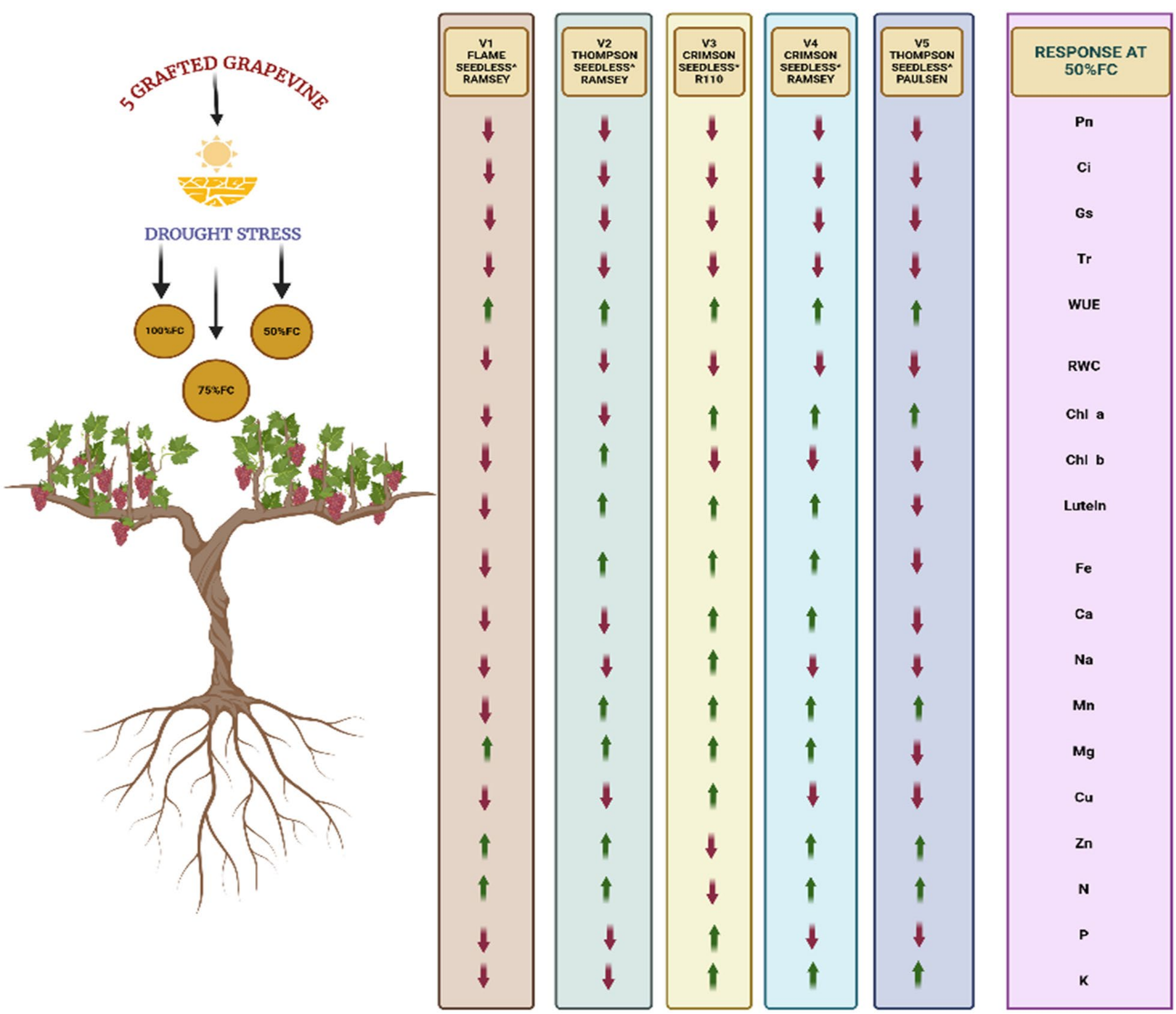
Graphical Abstract



V1 FLAME SEEDLESS^ RAMSEY	V2 THOMPSON SEEDLESS^ RAMSEY	V3 CRIMSON SEEDLESS* R110	V4 CRIMSON SEEDLESS* RAMSEY	V5 THOMPSON SEEDLESS^ PAULSEN	RESPONSE AT 50%FC
↓	↓	↓	↓	↓	Pn
↓	↓	↓	↓	↓	Ci
↓	↓	↓	↓	↓	Gs
↓	↓	↓	↓	↓	Tr
↑	↑	↑	↑	↑	WUE
↓	↓	↓	↓	↓	RWC
↓	↓	↑	↑	↑	Chl a
↓	↑	↓	↓	↓	Chl b
↓	↑	↑	↑	↓	Lutein
↓	↑	↑	↑	↓	Fe
↓	↓	↑	↑	↓	Ca
↓	↓	↑	↓	↓	Na
↓	↑	↑	↑	↑	Mn
↑	↑	↑	↑	↓	Mg
↓	↓	↑	↓	↓	Cu
↑	↑	↓	↑	↑	Zn
↑	↑	↓	↑	↑	N
↓	↓	↑	↓	↓	P
↓	↓	↑	↑	↑	K

Keywords Drought, Irrigation, Elements, Grafted grapevine, Pigments, SEM, Photosynthetic parameters

Introduction

Climate change has greatly impacted viticulture, a topic of growing importance, as changing environmental conditions, especially temperature, can significantly influence grape production in arid and semiarid regions [22]. An increase in temperature exposes grapevines to water deficits and thermal stress, more frequently affecting growth and development [87]. Although grapevines can withstand periods of water deficits (WD), they can still be significantly impacted in terms of quantity and quality of grapes [75]. In this regard, the importance of optimizing irrigation practices and the need for sustainable water management strategies are critical for viticulture production in arid regions to mitigate the effects of changing environmental conditions. Grapevine adaptations to environmental changes have been continuously examined for decades, with particular emphasis on those anticipated in the event of water scarcity [18, 58]. In viticulture, rootstocks have been developed and utilised for production to mitigate the problems caused by drought, salinity, environmental impacts and phylloxera, a root-feeding aphid [14]. Therefore, it is of great significance to identify precisely the role of grapevine rootstocks in mitigating abiotic stresses to establish commercial vineyards in arid regions [47].

Grafting grapevine (*Vitis vinifera* L.) scions onto different rootstocks (Ruggeri 140, Ramsey, and Paulsen 1103), it's possible to alter the structure of the root system to improve water absorption from deeper soil layers and increase root surface contact with the soil, both of which increase resilience to the environment and drought tolerance [23]. Somkuwar et al. [81] emphasised how rootstocks affect plant development and leaf gas exchange both directly and indirectly through variables such as root hydraulic conductivity, vine hormonal status, and root dispersion. By facilitating deeper root penetration and greater contact between root hairs and soil, the grape variety Merlot, when grafted onto both Ramsey and Richter 110, could produce roots that are sharply inclined to the soil surface and have better water absorption capabilities [25]. According to studies, Paulsen 1103 and Ruggeri 140's vertically dispersed root systems make it easier for the grafted vine to obtain nutrients and water from deeper soil layers, increasing its resistance to water shortages [46].

Rootstock scion interactions have been demonstrated to influence soil nutrient uptake, which further facilitated metabolic processes and enzyme activation in plant growth [6]. Each rootstock is unique and exhibits variation in nutrient uptake capacity and regulates the balance of nutrients in tissues [55]; Pulko et al. 2016). The remarkable potassium uptake capability of some rootstocks, including Dog Ridge, Freedom, St. George, and Harmony, could help preserve stomatal function under water stress (Cochrane [16]; Britzke et al. [9]. According to a prior study, petiole potassium contents were noticeably greater in Cabernet Sauvignon grafted onto these rootstocks than in Cabernet Sauvignon grafted onto Paulsen 1103 and 101 – 14 Mgt [30]. When grafted onto Chardonnay and Shiraz, the rootstocks Ramsey and Ruggeri 140 significantly reduced the yield loss brought on by salt in comparison to ungrafted vines, indicating their greater tolerance by preserving osmotic pressure equilibrium [94]. Whole-genome re-sequencing and stress-resistance analysis of grape rootstock genotypes were conducted, which highlighted the significance of rootstocks in safeguarding grapevines from various stresses, including drought [95]. Rootstocks are crucial for enhancing plant resilience to water deficit conditions, potentially affecting mineral uptake and utilization in grafted grapevines. In comparison to SO4, increased *VvHKT1* and *VvHKT2* expression in rootstocks A15 and A17 resulted in lower sodium concentrations in petioles and blades and more sodium retention in the root zone [26]. The cultivar, Kalecik Karasi was grafted to Kober 5BB and demonstrated elevated activities of superoxide dismutase (SOD) and catalase in leaves as the response to boron toxicity. This suggested that grafted grapevines may exhibit a defensive mechanism to shield cells from oxidative stress such as boron toxicity [34]. While producing higher concentrations of specific anthocyanins and carotenoids, Paulsen 1103, 3309 C, and Ruggeri 140 demonstrated good magnesium (Mg) absorption ability, tolerance to low Mg concentrations in the soil, and a rapid response to increased oxidative stress caused by Mg insufficiency [3, 28]. However, by either improving the kinetics or controlling the strength of the high-affinity transport system induction response, rootstocks can alter nitrate absorption [85]. Kulmann et al. [53] studied the expression of genes (*VitviNRT2.4 A* and *VitviNRT3*) that regulated the high-affinity nitrate transporter in root tips and found that it significantly increased in response to 0.5 mM $Ca(NO_3)_2$ supplied to Paulsen 1103 grafted vines after 10 days of nitrogen starvation [14, 70]. The petioles of Flame Seedless, Thompson Seedless, Superior Seedless, and Red Globe grafted to Ramsey typically had high levels of inorganic phosphorus [30]. This could have aided in the formation of nucleic acids, cell membranes, and other energy-supporting substances.

Rootstocks are also shown to significantly impact leaf gas exchange, photosynthesis, CO_2 exchange, and transpiration rate in grafted vines under drought stress. Research has demonstrated that specific rootstocks, such as 110R, 1103P, and 99R, can enhance water use efficiency (WUE) and drought tolerance in grafted vines by improving physiological responses and gaseous exchange under water deficit conditions [29, 57]; Yan 2016). These rootstocks showed an increase in WUE during critical growth stages, leading to improved photosynthesis and stomatal conductance, thereby contributing to preserving essential pigments and overall plant health in grafted vines facing water stress [72]. Moreover, rootstocks with enhanced drought resistance traits helped to maintain optimal leaf gas exchange, photosynthetic activity, and transpiration rate in grafted vines under water deficit conditions, thereby contributing to better plant performance and productivity [104, 105] Investigations by Kodur et al. [51] have explored the accumulation of nutrients and transpiration efficiency (TE) in grapevine rootstocks, highlighting the intricate interplay between root traits, nutrient uptake, and water utilization. The effects of rootstocks on nutrient uptake, transpiration and metabolic pathways can significantly impact grapevine responses to water deficit, underscoring the importance of rootstock selection in sustainable viticulture practices.

Grapes are typically cultivated in temperate and Mediterranean climates. The arid climate of UAE with extremely high temperatures and drought is posing considerable challenges for their commercial production. Several research gaps persist and must be addressed to improve feasibility, sustainability, and commercial viability for grape cultivation. The critical research gaps are the lack of climate-resilient drought-tolerant grafts adapted for extreme heat, high solar radiation, and arid conditions and optimization of water use efficiency. These research gaps could be nullified by utilizing the grafted grapes with extremely drought-tolerant rootstocks where we visualize rootstock scion interaction as has been reported in many other crops to overcome several biotic and abiotic constraints in production. It is also crucial to study drought resistance mechanisms, understanding metabolic adjustments on how different grapevine grafts respond to water scarcity and high evapotranspiration rates. In the above context, it has been reported that many viticultural zones in Mediterranean climate regions may not be suitable for grape production in the near future unless heat-stress-adapted genotypes or stress-tolerant germplasm are developed or identified. Grapevines, like other plants, have developed metabolic strategies to maintain homeostasis and deal with high-temperature stress. These mechanisms include physiological adaptations and activation of signalling pathways and gene regulatory networks governing heat stress response and acquisition of moisture stress tolerance [92]. It is also reported that during abiotic stress, grapevines often encounter heat stress during the growing season that perturbs cell homeostasis, may affect proper development and fruit metabolism and consequently, exert constraints on grape growth, yield and quality. Although the grapevine has a good ability to adapt to various environmental pressures, long-lasting extremely high temperatures or heatwaves may permanently affect yield attributes and vine physiology. Metabolic adjustments such as respiration, photosynthesis and transpiration are very sensitive even in short-term water stress and/or temperature fluctuations. Photosynthesis is the most critical process in plants that is directly or indirectly affected by temperature (Jones et al., 2012). The study hypothesised that the grafted grapevines is the best technique for mitigating the drought and high temperature of the arid region for sustainable grape production.

In the UAE, there is very little information on the behaviour and effects of grafted grapevines subjected to water stress treatment under field conditions. Thus, the present work focuses on the response of five grafted grapevines under field conditions, emphasizing the critical role of rootstocks in improving the physiological performance, nutrient uptake status, pigment levels, and vitality of grafted vines under extreme drought stress, ultimately enhancing WUE and plant resilience in challenging environmental conditions.

Table 1 Drought classification based on SWD1, VC1, and SM in an arid region (101)

Drought Classification	SWD1 Soil wetness deficit Index	VC1 (%) Vegetative condition Index	SM (%) Soil Moisture
No Drought IW/CP (1)	≥ 0	40–100	≥ 40%
Mild Drought IW/CP (0.75)	0 to -2	30–40	≤ 40%
Moderate to severe Drought IW/CP (0.50)	-2 to -5	20–30	≤ 30%

SWD1: Soil Wetness Deficit Index, VC1: Vegetative Condition Index, SM: Soil Moisture

Materials and methods

Grapevine graft materials were procured from South Africa, in collaboration with the ARC Infruitec-Nietvoorbij Institute of the Agricultural Research Council, Stellenbosch. Grafting was done by the cleft graft method and the rootstocks used for grafting purpose were tolerant to drought conditions. The grafting has been done with three table grape varieties (Thomson Seedless, Crimson Seedless and Flame Seedless) and three drought-tolerant rootstocks (Ramsey, 110 Richter and 1103 Paulsen). The five graft combinations used for the experiment were as follows: Flame Seedless × Ramsey (V1); Thompson Seedless × Ramsey (V2); Crimson Seedless × R110 (V3); Crimson Seedless × Ramsey (V4) and Thompson Seedless × P1103 (V5). In grape grafting, it is ideal to use 1-year-old rootstocks (dormant, well-developed root system) with a diameter of about 6–12 mm in size to ensure good compatibility with the scion. In the case of scion, it should also be 1-year old, taken from the previous season's juvenile growth derived from healthy, mature, disease-free canes, and the diameter should match with the rootstock as closely as possible to ensure proper alignment of the cambium cell lines. The selection of graft is based on the versatility of the rootstock to mitigate stress, which is the basic need in arid regions. In this respect, we have chosen the three rootstocks and grafted them with the popular table varieties (Table 1).

Site of the experiment

The study was conducted at the College of Agriculture and Veterinary Medicine, UAE University (UAEU), Al Foah Farms (Latitude: 24.2862° N; Longitude: 55.7216° E. in open field conditions with complete exposure to light conditions. The grafts were maintained in greenhouse conditions before it was planted in the field for five months. After receiving the grafts, they were washed in normal water, drenched in a fungicide solution (Ridomil 1.5 g/L), and potted in polythene bags filled with substrate consisting of sterile sand, dehydrated cow manure, and peat moss, mixed in the ratio of 1:1:1. During bud initiation and acclimation, the grapevines were watered using drip irrigation to maintain optimal soil moisture for survival and growth under simulated conditions of the greenhouse. The greenhouse had a cooling system, supplemental light, and a photoperiod of 16/8 (light/dark; daily PPFD of about 600 μmolms1). Relative humidity (RH) was between 65 and 80%, and temperatures ranged from 23 to 28 °C [7]. After five months in the greenhouse, the field was planted in January 2022. The young vines were planted in trenches 60 × 60 × 60 cm at a spacing of 3 m (row spacing) × 2.5 m (vine spacing) and trained to a flat Trentina trellis system with north-south row orientation. The field soil condition was sandy in nature with very low organic matter content and less than 2% organic carbon. The field nutrient status was assessed before the plating had been undertaken. The planting pits have been conditioned with dehydrated organic manure before plating has been undertaken to improve the planting pits.

Weather data in AL-Ain, Abu dhabi, UAE

The temperature, humidity and wind speed are the primary factors influencing the crop in terms of tolerance to drought. Optimum levels contribute to the maintenance of tissue water content. In an arid region, all these factors enhance the evapotranspiration rate, leading to the complexity of drought effects. The data is presented for three months, covering one month before and one month after drought induction (September to November 2021) (Fig. 1).

Experimental design

A factorial randomized complete block design was employed for the planting experiment. The graft establishment (90%) was successful in about three months. Gap-filling was done with new grafts before irrigation treatment was commenced. The experiment was split into three level irrigation strategies and 9 replicates for each graft combination. In each irrigation treatment, there were 9 grafted plants, each plant is treated as a replicate. Therefore, with three levels of irrigation schedules and five grafted types, the total number of plants established in the experiment was 135.

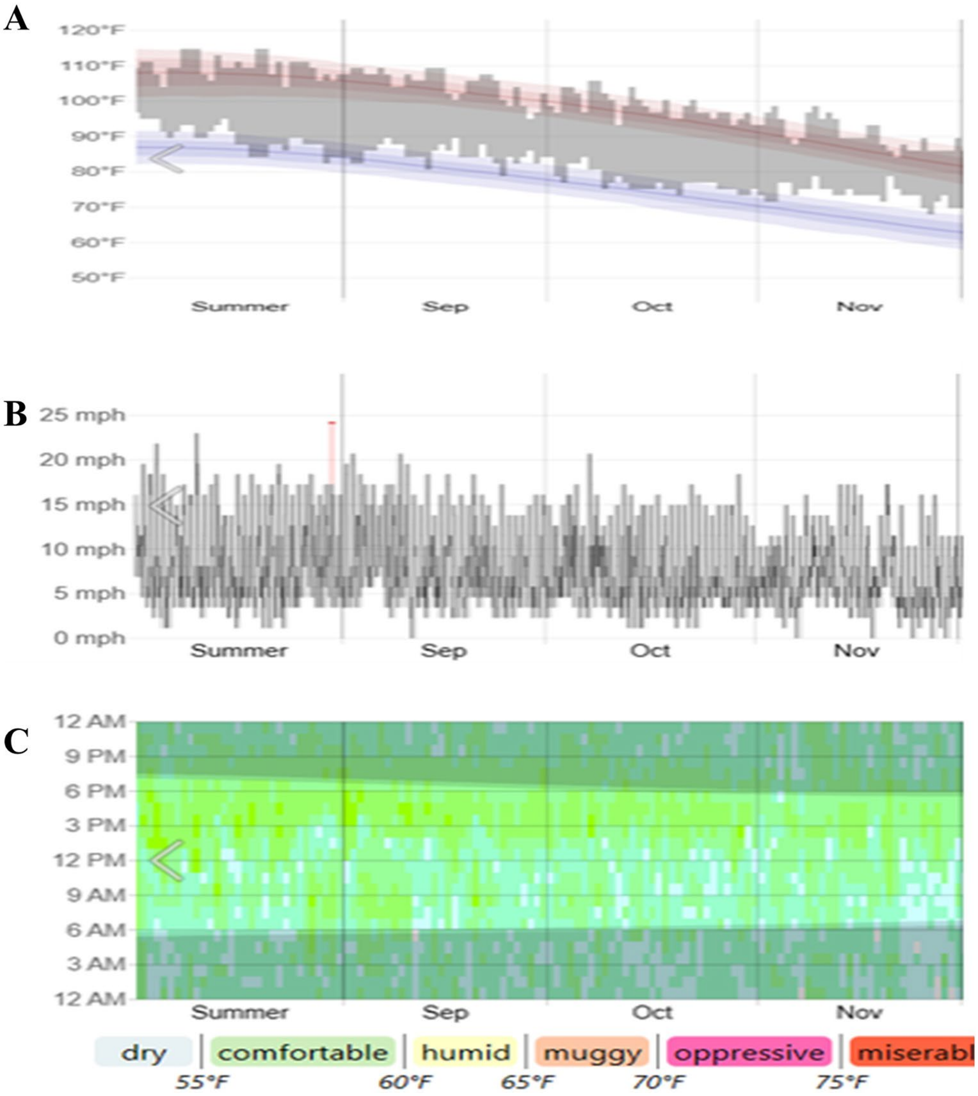


Fig. 1 Temperature (**A**), wind speed (**B**) and humidity data (**C**) (2022) from AL-Ain, Abu Dhabi, UAE. (Courtesy: Data from Abu Dhabi Meteorological Department)

The irrigation levels: a control (WW, 100% of field capacity (FC)); a severe deficit (WS-S; 50% of FC); and an intermediate deficit (WS-I; 75% of FC), applied with controlled drip irrigation. The water deficits were applied for one month, from 1 to 31 October. The grapevine leaves, medium matured with fully expanded lamina, were collected for analysis from the mid part of the vines in the 1st week of November and stored until analysis at − 80 °C. The vines approached the reproductive phase a month after the sampling.

Irrigation treatments

A 200 g soil sample (equivalent to 1 pit) was collected, saturated with water, and placed under pressure for 24 h. The pressure was subsequently released, and soil was collected, weighed, and kept at 65 °C in an oven for 48 h for drying. The weight was noted, and the soil moisture percentage was calculated. Based on IW/PE ratios of 1, 0.75 and 0.5, the calculation for 100% FC, 75% FC, and 50% FC was established. Based on the FC, irrigation at 53 L, 40 L, and 26 L was respectively calculated per pit. Drip irrigation water was supplied both in the morning and evening to meet the quantity of irrigation calculated per pit. The soil moisture was monitored to determine the induction of drought under deficit irrigation. The flow rate was 50%FC 2.1 L/min.; 75% 2.5 L/min.;100%FC 2.2 L/min.

Soil moisture

Soil moisture parameters have been assessed to ascertain the extent of drought under different irrigation regimes [101].

Leaf physiological measurements

Leaf gas exchange (mol H_2O m^{-2} s^{-1}) measurements were performed with a LI-6400 portable photosynthesis system (Li-Cor Inc. Lincoln, NE, USA) [103]. Measurements were made on five plants with five replicates on fully expanded leaves for each treatment (100% FC, 75% FC, 50% FC), for all five combinations between 10:00 AM to 12:00 PM solar time. Leaf gas exchanges were detected as intercellular carbon dioxide (CO_2) concentration (C_i), net photosynthesis (Pn), stomatal conductance (gs) and transpiration rate (Tr) using an infrared gas analyzer (Ciras 1-PP Systems, Amesbury, MA, USA) equipped with a leaf chamber; CO_2 flow was set at 400 ppm, RH to ambient level and saturating light at 1200 µmol m^{-2} s^{-1}. The intrinsic WUE was calculated using Eq. 1.

$$WUE\ (\mu mol\ CO_2\ mmol^{-1}\ H_2O) = \frac{\mathrm{Pn}}{\mathrm{gs}} \tag{1}$$

Shoot biomass

Grape shoots from the five varieties were collected in six biological replicates once the field had been established and completely developed. The shoots were weighed fresh and then dried in an oven at 80 °C until their weight remained constant. Data is presented as mean standard error. Number of shoots and shoot length: After establishing the field layout and planting, the shoot count and the length were measured in six biological replicates. Data is presented with mean standard error.

Measurement of relative water content

Relative water content (RWC) was measured by selecting the leaves of nodes 7–9 from the base of the grapevine as per Jiao et al. [44]. Grapevine leaves subjected to drought treatment and control were taken for the assessment of RWC, and their fresh weight (FW) was recorded. The leaves were submerged in distilled water for 24 h at 4 °C in darkness, after which the turgid weight (TW) was measured. The samples were ultimately dried at 105 °C for 30 min and at 80 °C until a consistent weight was achieved, after which the dry weight (DW) was measured. The RWC was determined using Eq. 2.

$$RWC\ (\%) = \frac{\mathrm{FW}\ -\ \mathrm{DW}}{\mathrm{TW}\ -\ \mathrm{DW}} \times\ 100\% \tag{2}$$

Leaf mineral analysis

The collected leaves were rinsed with deionized water and subsequently chopped into small fragments. The specimens were desiccated in an oven at 60 °C for 48 h and subsequently ground in a grinder. The desiccated plant specimens were subjected to digestion in a microwave oven, as outlined by Kidman et al. [49]. A 0.5 g sample was digested using 10 mL 69% HNO_3 and 2 mL HCl. The containers were sealed and positioned in the microwave digestion apparatus for 15 min at 180 °C. After digestion, it was chilled and diluted with deionised water to a final volume of 100 mL. The amounts of elements (K, Mg, Ca, Na, P, Mn) in the plant digest were quantified using Inductively Coupled Plasma Atomic Emission Spectroscopy (ICP-OES, model 710-ES). Total nitrogen was measured by Vario MACRO cube CHNS, Elementar Co.

Photosynthetic pigments

Pigments were estimated using fully expanded leaves (old and young leaves were randomly pooled) from each treatment. The extraction was carried out using 200 mg of fresh leaf in 25 mL 80% aqueous chilled acetone (v/v). After complete extraction (for incubated for about 24 h with 3–4 times shaking), the mixture was filtered, and chlorophyll a (Chl a) and chlorophyll b (Chl b) were determined by a spectrophotometer at wavelengths of

663 nm and 646 nm, respectively. Pigments were calculated according to the method described by Lichtenthaler [56].

Scanning electron microscopy for leaf micro-structure

Changes in leaf microstructure were studied using scanning electron microscopy (SEM, JEOL JSM–6010LA, SEM, Japan) operating at an accelerating voltage of 20 kV. Leaf samples were cut into small pieces and fixed on aluminium SEM stub with the help of a double-sided adhesive carbon tape, coated with a thin layer of gold using a Cressington 108 Auto Sputter Coater (Ted Pella Inc., Redding, USA). Images were captured at various magnifications.

Statistical analyses

A two-way analysis of variance (ANOVA) was performed using the general linear model (GLM) procedure to calculate the effects of different irrigation treatments and graft varieties on amino acids. Means were compared using Tukey's HSD post hoc comparison test ($P \leq 0.05$) using the Minitab statistical software (Minitab® 21.4.3). Figures were plotted by using Minitab (Minitab® 21.4.3) and Design Expert (V: 13.0.5.0). The supplementary data on the statistical analysis and interpretation (Supplementary Table 1) corresponding to the figures are provided.

Results

Leaf physiological measurements

Net photosynthetic rate (μmol CO_2 $m^{-2}s^{-1}$)

Results showed that deficit irrigation treatments significantly affected the Pn in all the grafted varieties, with V4 (Crimson Seedless × Ramsey) showing significantly lower Pn under all the irrigation regimes (Fig. 2A). At 100% FC (control treatment), Pn was significantly lower in V4 graft, followed by V5, compared with V1 and V2, the latter two of which were on par. The V3 graft had significantly the highest Pn. The Pn values in V4 graft declined significantly by 9.1% and 22.7% at 75% FC and 50% FC, respectively, compared with other grafts. In V1 an increase of 6.5% and a decrease of 3.2% was noticed, in V2, V3, and V5 grafts, the decrease of 6.3% and 9.4%, 4.2% and 12.7%, and 6.5% and 19.4% was observed at 75% and 50% FC respectively. The decrease in Pn observed in grafted grapevines under different deficit irrigation treatments accentuates the impact of water deficits affecting the photosynthetic activity. It is clear from the results that certain grafts responded with higher Pn values at high water deficit, as found for V3, V1 and V2 at 50% FC.

Transpiration rate

The Tr significantly decreased at 75% and 50% FC in comparison to 100% FC. For Tr, the reduction in V1, V2, V3, V4 and V5 was 20%, 25%, 4.3%, 23.9%, and 21.45% at 75% FC, and 30.95% 23.4%, 27.7%, 19%, and 26.2% at 50% FC (Fig. 2B). The Tr decreased significantly at 50%. This served as a protective mechanism to maintain the tissue water to combat the water deficit.

Stomatal conductance

Drought reduced gs by 18.1–45.5%, 19.4–32.3%, 23.5–41.2%, and 40.4–57.1% for V1, V3, V4 and V5 from 75% FC to 50% FC, respectively, in comparison to 100% FC. In V2, the decrease at 75% FC was high (25%), but at 50% FC, a 12.5% decrease was observed (Fig. 2C).

Intercellular CO_2 concentration

The Ci was reduced by 11.9% and 17.3% in V1, 4.8% and 7.1% in V2, 4.6% and 16.6% in V3, 9.8% and 10.9% in V4, and 8.5% and 12.2% in V5, at 75% FC and 50% FC, respectively (Fig. 2D). Overall, the results showed that grafted grapevines with drought-tolerant rootstocks experienced a significant reduction in transpiration rate at water deficits of 75% FC and 50% FC. The Ci and gs were also reduced at lower FC levels, validating the response of tolerant rootstocks when exposed to drought conditions.

Water use efficiency

The intrinsic WUE is used to relate photosynthesis to stomatal closure. This remained higher in the five grafts at 75% FC and 50% FC compared to the control at 100% FC (Fig. 2E). From among the five grafts, V4 showed lower ratios at 75% and 50% FC (Fig. 2E). The drought had significant effects on instantaneous WUE with the increase in the progression of deficit irrigation treatments, expressing drought tolerance. The highest WUE of 34.3% and 31.3% in V1 was recorded at 75% FC and 50% FC, respectively. An accretion of 23.5% and 26.5% in V3, 26.3% and 15.7% in V4 and 17.2% and 10.3% in V5 was observed at 75% FC and 50% FC, respectively. In V2 an increase of 3.7% and 22.2% at 75% FC and 50% FC was noticed compared to the corresponding control treatment. The study found that grapevines grafted onto different rootstocks showed adaptation to water deficit conditions, confirming the rootstocks' ability to maintain plant water status under moisture-stress conditions. The higher intrinsic WUE in the five grafts at 75% FC and 50% FC, compared to 100% FC, is a sign of adaptability under water deficit conditions and bears testimony to the crucial roles of specific rootstocks under challenging conditions. Graft V1 showed a 1% and 6.5% decline at 75% FC and 50% FC, while V2, V3, and V4 showed a 4.3% and 85% decrease at 75% FC and 50% FC, respectively. Graft V5 showed a significant decrease, from 5.4 to 12% at 75% FC to 50% FC, respectively. These results suggested that different grapevine grafts may respond differently to water stress treatment. Overall, the findings highlight the importance of choosing the appropriate

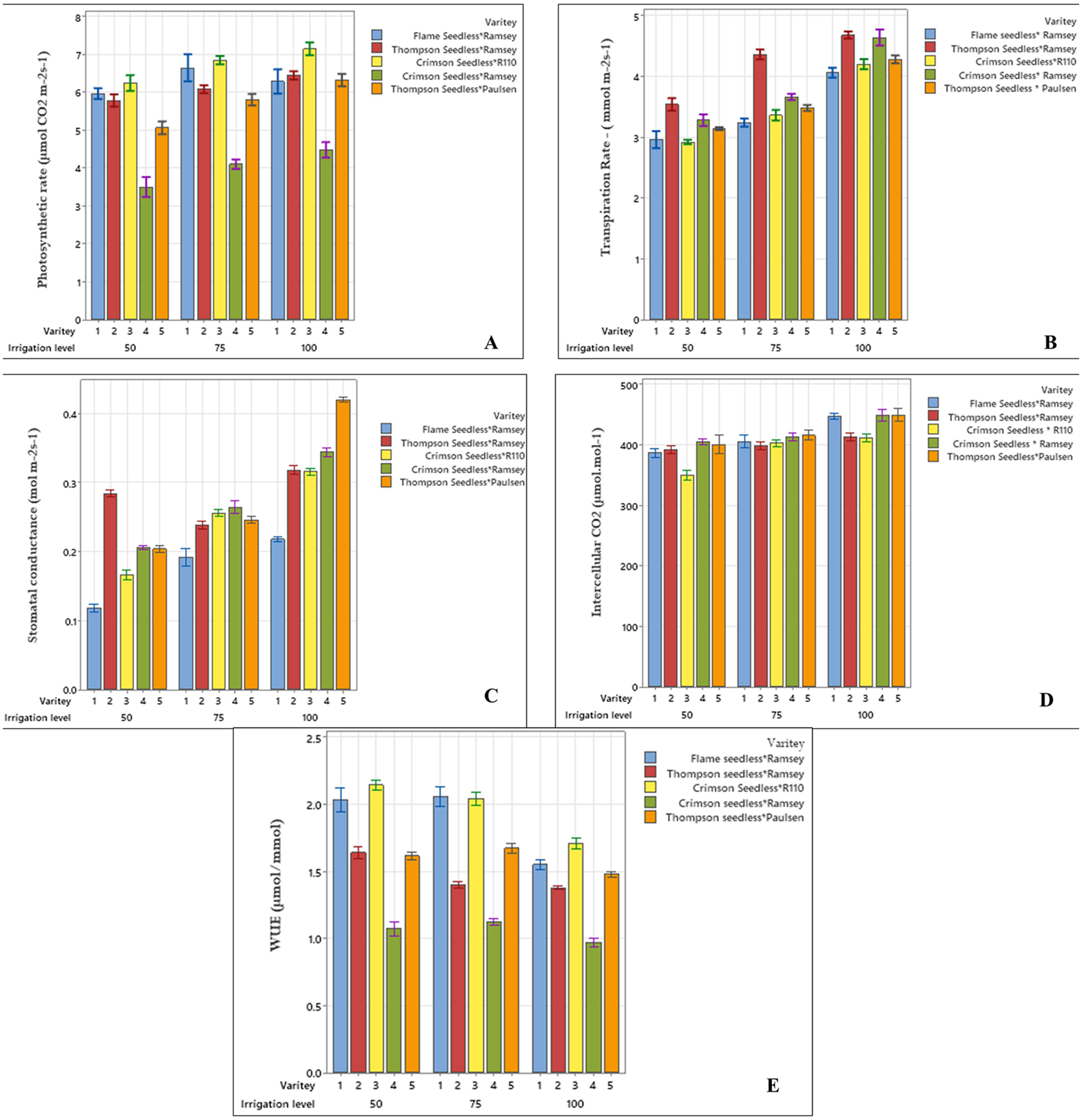


Fig. 2 Comparison of net photosynthetic rate (Pn) (**A**), transpiration rate (Tr) (**B**), stomatal conductance (gs) (**C**), intercellular CO_2 (**D**) and water use efficiency (WUE) (**E**) between five combinations of grafted grapevines (V1, V2, V3, V4, V5) under three regimes of irrigation (100%, 75%, 50% FC; corresponding quantity of water 53 L, 40 L, 26 L, respectively). ($P \leq 0.05$). Vertical bars indicate the standard error. V1: Flame seedless × Ramsey, V2: Thompson seedless × Ramsey, V3: Crimson seedless × R110, V4: Crimson seedless × Ramsey and V5: Thompson seedless × Paulsen

graft combination that can better withstand water stress, ensuring optimal growth and productivity in varying conditions.

Total shoot biomass

Mean values of the total dry matter (TDM) and FW showed a significant reduction at 50% FC when compared with the irrigation at 100% FC (Fig. 3A). Invariably all the grafts reduced the TDM and FW significantly, conversely, graft V4 recorded the lowest dry matter content and corresponding fresh weight. The V2 graft showed the highest FW and TDM compared to the other grafts, followed by V3, thus indicating stress tolerance.

Number of live shoots and length of shoots

Mean values of no. of shoot and shoot length showed varied responses among the varieties (V1, V2, V3, V4 and V5) at 50% FC (Fig. 3B). The high no of shoots is seen in V1 grafts. With only minor variation, the other graft combinations V2, V3, and V5 display a comparatively constant number of shoots in the 2.0–3.0 range. Shoot Length: With an average of roughly 3.5 cm, V2 grafts exhibit the longest shoot length.

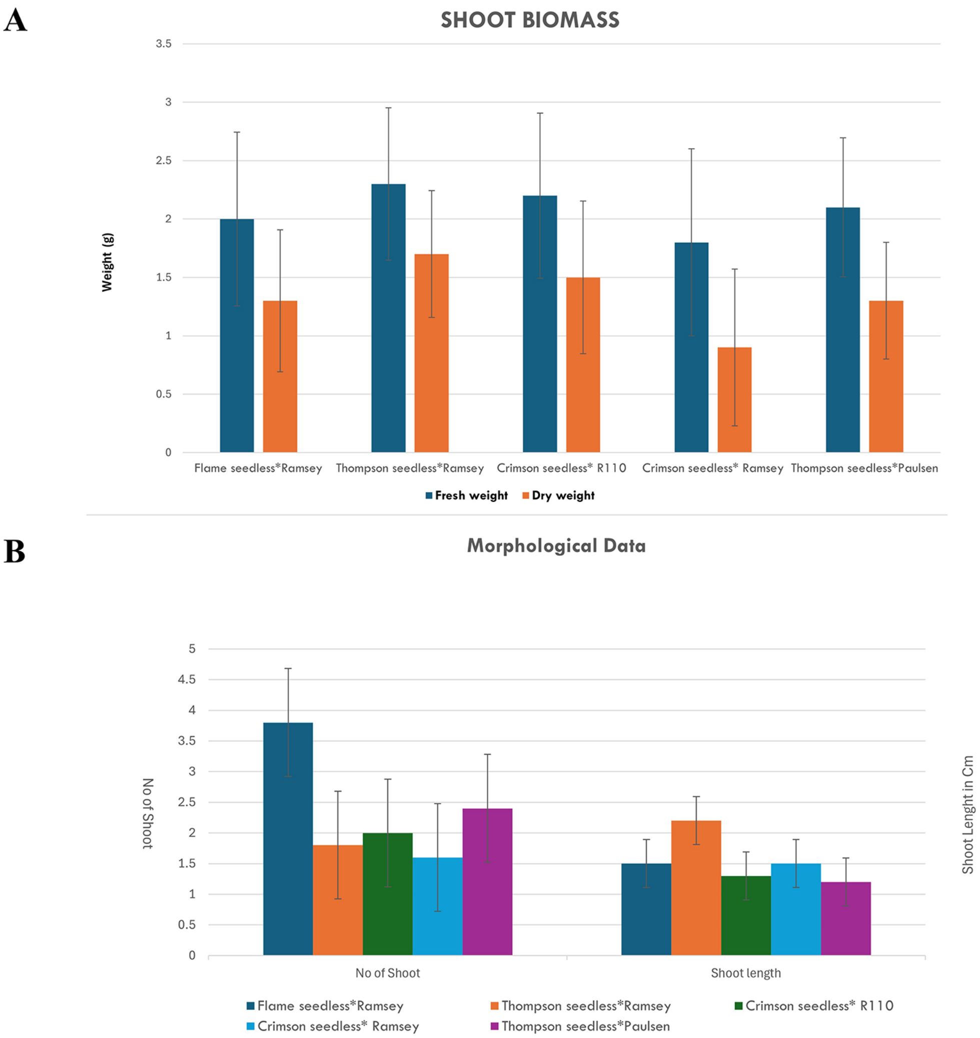


Fig. 3 Mean comparison of shoot biomass (**A**) and morphological data (number of shoots and shoot length in cm) (**B**) between five combinations of grafted grapevines (V1, V2, V3, V4, V5). V1: Flame seedless × Ramsey, V2: Thompson seedless × Ramsey, V3: Crimson seedless × R110, V4: Crimson seedless × Ramsey and V5: Thompson seedless × Paulsen

The remaining graft combinations (V1, V3, V4, and V5) have shoot lengths that are comparable, ranging from 2.0 to 3.0 cm. In terms of shoot count, V1 performed the best, indicating a greater potential for vegetative development under the 50% FC treatment. In comparison to the other combinations, V2 performed better in shoot length, suggesting increased elongation capacity.

Pigments

With a progression of irrigation water from 75% FC to 50% FC, Chl a and b showed varied responses in different graft varieties (Fig. 4A & B). The Chl a and b amounts decreased significantly in the V1 variety by 11.0% and 10.2% at 75% FC, and 14.8% and 9.3% at 50% FC, respectively.

In the V2 graft Chl a content increased by 1.7% at 75% FC and decreased by 4.2% at 50% FC, but Chl b content increased by 19% and 16.7%, respectively, compared with 100% FC. In the V3 graft, Chl a increased by 4.7% and 8.4% and Chl b showed a decline of 14.8% at 50% FC, whereas at 75% FC, the content remained the same as the control. The V4 graft exhibited an increase of 5.1% and 4.6% in Chl a content while Chl b recorded 2% lower than control at 75% FC and 50% FC, respectively. In V5 Chl a and Chl b decreased at 75% FC by 8.2% and 12.9%, while at 50% FC a decrease of 12.9% and 45.2% was noticed, respectively. Overall, the results suggested that different levels of FC had varying effects on the Chl a and b amounts in the V3, V4, and V5 grafts. The response to FC levels was not consistent across all grafts, indicating a complex relationship between water availability and pigment content in grafted grapevines. Results also indicate that rootstocks with drought tolerance mechanisms could affect the scions' response to stress and water use strategy, contributing to maintaining chlorophyll levels under water deficit conditions.

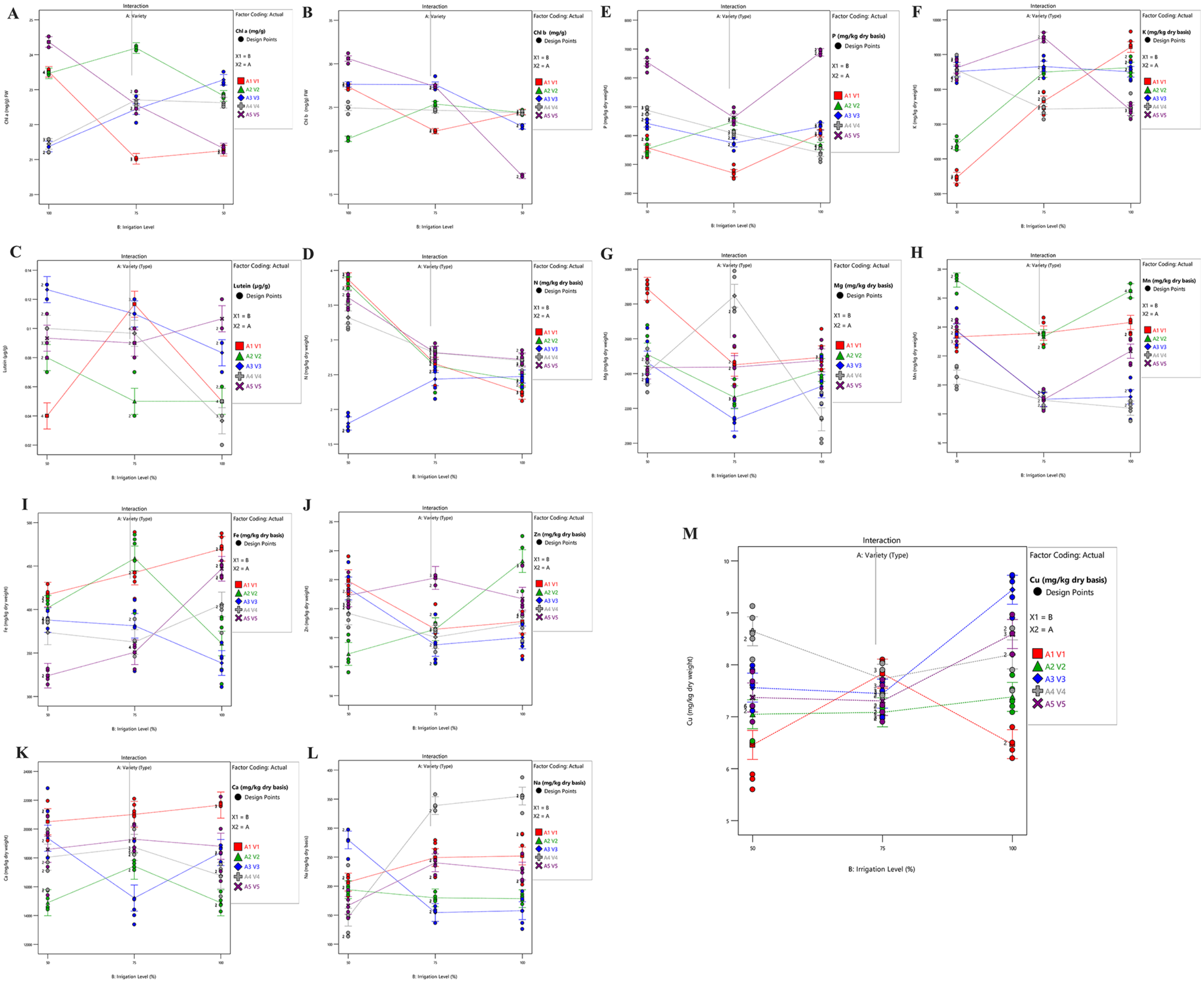


Fig. 4 Comparison of chl a (**A**), chl b (**B**), lutein (**C**), nitrogen (**D**), phosphorus (**E**), potassium (**F**), magnesium (**G**), manganese (**H**), iron (**I**), zinc (**J**), calcium (**K**), sodium (**L**) and copper (**M**) between five combinations of grafted grapevines (V1, V2, V3, V4, V5) under three regimes of irrigation (100%, 75%, 50% FC; 53 L, 40 L, 26 L, respectively). ($P \leq 0.05$). V1: Flame seedless × Ramsey, V2: Thompson seedless × Ramsey, V3: Crimson seedless × R110, V4: Crimson seedless × Ramsey and V5: Thompson seedless × Paulsen

Lutein

The pigment lutein significantly increased by 140% at 75% FC and decreased by 20% at 50% FC in V1, whereas V2 graft exhibited no change at 75% FC when compared to the control, but an increase of 60% was noticed at 50% FC (Fig. 4C). In V3 an increase of 37.5% and 50% occurred at 75% FC and 50% FC respectively, while the V4 graft showed a significant increase of 150% and a 10% decrease. In V5 at 75% FC and 50% FC, a decrease of 22.7% and 18.2% was observed when compared to 100% FC.

The results thus indicated that different graft varieties respond differently to varying levels of irrigation in terms of lutein pigment production. The results also suggest that the rootstocks play a critical role in modulating plant responses to drought stress and preserving pigments in grafted grapevines.

Elements

Grafted grapevines responded differently in terms of mineral content under drought stress. Water deficit levels substantially impacted the levels of nitrogen (N), phosphorus (P), potassium (K), magnesium (Mg), manganese (Mn), iron (Fe), zinc (Zn), calcium (Ca), copper (Cu), and sodium (Na) in the leaves of grafted grapevines. The intricate interactions between rootstocks, water stress, and mineral intake are highlighted by the variations in mineral content seen in several grapevine cultivars under drought stress.

Nitrogen

The N content showed an increasing trend from 75% FC to 50% FC in V1, V2, V4 and V5, changing from 13.04 to 69.3%, 8.3–58.3%, 7.4–22.2%, and 7.4–33.3%, respectively (Fig. 4D). In V3, a significant decrease in N content of 7.7% at 75% FC and 34.6% at 50% FC was seen in comparison to the control treatment. These findings imply that varying degrees of field capacity in distinct treatment groups have an impact on the amount of nitrogen in leaf samples. Reduced soil moisture conditions may influence nutrient availability in sensitive grafts, as seen by the decline in nitrogen concentration at 50% FC in V3.

Phosphorus

The P content decreased in V1, V2, V4 and V5 grafts at 75% FC and 50% FC by 32.5% and 15%, 2.7% and 30.5%, 34.3% and 23.4%, and 54.1% and 40%, respectively (Fig. 4E). The V3 graft exhibited a 7.1% reduction at 75% FC and a 7.7% rise at 50% FC. The decrease in P content in V1, V2, V4, and V5 grafts under water deficit conditions is suggestive of a metabolic derailment with progressive drought.

Potassium

A varied response was noticed in K content of the grafts under stress in comparison to control. It was reduced by 18.5% and 43.5% in V1 and 2.3% and 26.2% in V2 at 75% FC and 50% FC, respectively (Fig. 4F).

In V3 an increment of 1.2% at 75% FC and a decrease of 2.3% at 50% FC was observed. In V4 a 1.4% decline at 75% FC and a significant rise of 13.5% was noticed, whereas in V5 a significant increase of 27% and 16.2% was observed at 75% FC and 50% FC, respectively, when compared to 100% FC. The reduction in K content in V1 and V2 grafts under water deficit conditions suggests a potential impact on plant growth and physiological processes.

Magnesium

The Mg content significantly dropped at 75% FC in graft V1, V2 and in V3 by 2.4%, 5% and 8.7%, respectively, whereas V4 showed an increment of 35.2% at 75% in comparison to 100% FC (Fig. 4G).

Conversely, with the progression of water deficit to 50% FC the grafts V1, V2, V3 and V4 remarkably increased by 16%, 4.1%, 7.8% and 14.3%, respectively, whereas the Mg content in V5 decreased by 0.8% in 75% FC, but at 50% FC was on par with that of the 100% FC treatment.

Manganese

The Mn content decreased at 75% FC in V1, V2, V3 and V5 by 1.7%, 12.2%, 10.5%, and 22.7%, respectively, whereas V4 showed an increment of 4.4% at 75% FC (Fig. 4H). However, at 50% FC in graft V1 the decrease was 4.2%, whereas in V2, V3, V4 and V5 significant increases of 3.1%, 24.2%, 12.1% and 7.3% were noticed respectively in comparison to 100% FC.

Iron

The Fe content significantly decreased at 75% FC and 50% FC in grafts V1, V4 and V5 by 6.4% and 4.3%, 12.2% and 9.8%, and 22.2% and 27.8%, respectively, in comparison to control treatment (100% FC) (Fig. 4I). A significant increase of 27.8% and 11.1% in V2, and 9.3% and 11.8% in V3 at 75% FC and 50% FC was noticed in comparison to 100% FC.

Zinc

The Zn content of grafts V1, V2, V3 and V4 decreased by 2.1%, 18.3%, 3.3% and 5.3% at water deficit treatment of 75% FC, respectively (Fig. 4J). At 50% FC significant increases of 13.5%, 18.7% and 4.2% were observed in V1, V3 and V4, respectively. However, graft V2 experienced a notable decline of 26%, whereas in V5 the Zn content was on par with 100% FC.

Calcium

The Ca content in V1 and V3 decreased by 4.5% and 21.3% at 75% FC, but in V2, V4 and V5 an increase of 21.3%, 11.8% and 2.1%, respectively, occurred in comparison with 100% FC (Fig. 4K). At 50% FC the grafts V1 and V5 showed a decline of 7.2% and 2.1% in Ca content, grafts V3 and V4 increasing with 4.4% and 5.9%, respectively, whereas V2 was on par with 100% FC.

Sodium

The Na content in V1, V3 and V4 decreased by 3.8%, 3.1% and 5.6% and remained unchanged in V2 at 75% FC in comparison to the control treatment (100% FC). The Na content in leaves at 50% FC decreased by 19.2% in V1 and increased by 5.6% in V2, whereas in V3 a highly significant increase of 71.9% was observed (Fig. 4L). In V4 the Na content showed a decreasing trend of 5.7% and 44.4% at 75% FC and 50% FC, respectively. In V5 an increase of 4.2% at 75% FC and a significant decline of 28.9% at 50% FC were observed. These results imply that the amount of salt in the leaves of various grapevine grafts respond to drought stress. Under conditions of water deprivation, some cultivars show large increases or decreases in Na content, while others maintain steady Na levels or show only minor variations. Considering the danger of salinity to plant growth under arid conditions, the physiological reactions of grafted grapevines to drought stress and the function of rootstocks in mediating mineral absorption and ion balances can both be better understood by considering these differences in Na content.

Copper

The Cu content mostly showed a decreasing trend in the grafts. In V1 21.45% increase at 75% FC and 1.5% decrease at 50% FC were noticed. However, in V2, V3 and V5 a decrease of 2.7% and 4.1%, 9.8% and 8.5%, and 23.2% and 23.1% was observed in 75% FC and 50% FC, respectively (Fig. 4M). Conversely, in graft V5 a significant increase of 4.6% at 75% FC was noticed and was on par at 50% FC in comparison with 100% FC. These changes in Cu content that have been observed indicate that various grapevine types react differently regarding copper levels when they are stressed by drought. Numerous mechanisms, including interactions with the rootstock, nutrient uptake, and physiological responses to water scarcity, may have an impact on the variability in Cu content across the grafts. Gaining knowledge of these variations in Cu concentration will help to better understand the dynamics of minerals and grafted grapevines' reactions to stress.

Discussion

Photosynthetic rate

Drought is one of the major abiotic stresses that impede the growth and development of plants. It decreases the photosynthetic rate in sensitive plants, associated with restricted growth and an increase in the incidence of early senescence in plants, as exhibited in grape grafts. As noticed in V4 and V5 grafts, low net photosynthetic activity occurred in the control treatment (100% FC), which further declined significantly in the 75% and 50% FC treatments. This could point to the metabolic inhibition of photosynthesis with slow Rubisco activity along with inhibition of photosynthetic carbon fixation enzymes, disturbing the photosystems and further decreasing ATP regeneration despite the use of a drought-tolerant rootstock, as observed by Pinheiro and Chaves [66]. The protective role of Ramsey, when grafted with Flame seedless and Thomson seedless with respect to net photosynthetic rate, could be elucidated by the reciprocal interaction between scions and rootstocks. This phenomenon is further validated with the response of V5 (Paulsen and Thomson seedless) where the net photosynthetic rate is affected by the progression of drought. This phenomenon was consistent when the Sultana variety was grafted onto 41B, 1103P, and 110R Paranychianakis et al. [65] observed that 41B produced more leaf area and yields, highlighting strong photosynthetic efficiency. Similarly, Nikolaou et al. [64] investigated the impacts of different rootstocks and discovered that when 41B was grafted onto Thompson Seedless, it produced the highest yield and pruning weight.

One of the potential ways to ascertain the tolerance of the grafts could be the ability of sustenance of leaf gaseous exchange during drought and a recovery period after stress alleviation in the light of different agricultural practices, including irrigation impacting stress and recovery cycles. Tolerance to drought is generally characterized by a reduction in *gs*, as noticed in some grafts. The changes that are noticed in terms of stomatal conductance agree with the findings obtained by Gómez-Bellot et al. [32]. A link between *gs* and hydraulic conductance during the diurnal period was reported by Schultz [74]. It is hypothesized that the differences in the water-conducting capacity of stems may be a behavioural protective pattern of the rootstocks, having higher hydraulic conductance and inducing stomatal closure at higher leaf water potentials. In all the grafts, the *gs* is reduced at low FC (50%), pointing to the capability of the rootstocks to combat stress and influence the scions.

Intercellular CO_2 concentration

The *gs* and transpiration rates are linked and can negatively influence photosynthesis efficiency under drought. The C*i* inside the chloroplast is determined by CO_2 diffusion components, which are *gs*, along with mesophyll conductance (gm) [45]. In grape grafts, higher *gs* coincides with higher TE observed under 50% FC in V2 graft. Stomata control the efflux of water out of plant leaves and diffusion of CO_2 into them [91]. In our study with grape grafts, higher C*i* was found at all levels of irrigation without a substantial drop under 50% FC, showing the increased influx of CO_2 as drought protection. This could be countered by the finding of Pinheiro and Chaves [66] that plants often manipulate stomata to stop water loss in situations of water scarcity, which lowers photosynthesis via lowering CO_2 intake. As the inevitable consequence of CO_2 entry through open stomata is concurrent water loss through transpiration, the stomata-related environmental adaptation may also affect plant instantaneous TE. In general, higher *gs* result in a lower TE [33], but in this case, the lower *gs* resulted in a higher TE. The C*i* in response to induced drought in grape grafts showed a characteristic biphasic response in all graft varieties, resulting in a substantial reduction in C*i* as *gs* decreased, which is significant at all levels of field capacity. The observation is consistent with that of Brodribb [10] as reported in bread wheat.

Water use efficiency

WUE is a critical determinant of drought resistance in crops. The intrinsic WUE relates to the events of photosynthesis to stomatal closure and remained higher in five grafts at 75% FC and 50% FC compared to the control at 100% FC (Fig. 2C). Among the five grafts, V4 showed lower ratios at 75% and 50% FC. TE, which indicates WUE at the leaf level under drought, is determined by the complex interaction of transient photosystem activity, CO2 concentration, and the regulation of stomatal activity, resulting in enhanced WUE in grape grafts. Horie et al. [36] reported high plant production in wheat under high stomatal conductance, allowing greater CO_2 fixation under different stress conditions. This translates into maximized soil water use for transpiration; in most instances, elevated Tr and high stomatal conductance during drought stress will result in reduced TE or WUE. This report confirms the stomatal modulation and CO_2 concentration leading to higher WUE in plants under drought stress as observed in grape grafts under 50% FC as severe stress in soil moisture. Amongst genotypes with low WUE, a deep or thick root structure that would facilitate effective soil moisture uptake and WUE are reported by Pinheiro et al. [67]. This is consistent with the scenario of grape grafts, where the rootstocks play a pivotal role in capturing soil water under deficit irrigation, thus trying to enhance water use. The WUE increased significantly, with the highest increase in V1 at 75% FC and 50% FC. This bears testimony to the crucial roles of specific rootstocks under challenging conditions. This could lead to enhanced production of dry matter in drought-resistant grafts and is consistent with the above reports. Consequently, it is unsurprising that the favourable water status in grape grafts under drought stress, as shown by RWC measures, correlates with WUE. Ultimately, crop WUE increased with heightened drought and diminished water availability, as evidenced in grape grafts, corroborating the findings of Myers et al. [62].

Total shoot biomass

Significant differences in total dry biomass among the five grafted grapevines were recorded in the present study. One of the primary mechanisms by which rootstocks influence scion biomass under drought conditions is through the modulation of water uptake and nutrient availability. Rootstocks with robust root systems can enhance the scion's ability to access water and nutrients from deeper soil layers, thereby improving overall water availability during drought. In this study, the higher total shoot biomass was observed in graft V2, followed by V3, V1 and V5. The V4 graft combination exhibited the lowest shoot biomass.

Grafting onto drought-tolerant rootstocks like in V2 and V3 has been shown to improve the WUE of the scion, which is critical for maintaining biomass under stress, in agreement with Prinsi et al. [68]. This was also evident in studies where rootstocks like M4 had been selected for their promising performance under water deficit conditions, leading to increased dry biomass in the scion. The reduction in dry biomass is associated with the impact of drought on photosynthesis. Under water deficit conditions, grapevines often exhibit decreased *gs*, which limits the uptake of CO_2 necessary for photosynthesis [100]. The reduction in CO_2 availability directly impacts the photosynthetic rate and chlorophyll degradation, leading to lower carbohydrate production, as it is necessary for biomass accumulation and growth [35]. In the study, the Chl a and Chl b pigments were not degraded due to the drought-tolerant rootstock, which could have improved the photosynthesis process, further enhancing the plant metabolic functions under drought stress conditions. The root system's hydraulic efficiency was maintained, which is crucial for water uptake and conforms to the results of Gambetta et al. [5, 27] where a less efficient root system showed inadequate water supply to the leaves, exacerbating the stress and leading to further reductions in growth and biomass. It is also evident that the accumulation of reactive oxygen species (ROS) under drought stress causes oxidative damage to cellular structures, impairing metabolic functions and further contributing to reduced biomass. To counteract this, plants may allocate resources to antioxidant defence mechanisms, diverting energy away from growth processes [35]. These findings are consistent with those of Verma et al. [90], who found that Dogridge rootstock increased fresh weight and dry weight, which in turn increased nutritional ion accumulation and the biomass of plant shoots in the V1, V2, V3, and V5 grafts.

Pigments

The status of Chl a and Chl b showed a differential response upon induction of drought. In V1, the Chl b pigment increased at 50% FC, whereas in V3, the Chl a increased at both 75% and 50% FC. In V5, a decrease in both Chl a and Chl b was found. The increase in Chl is a potential drought-protective character evolved by multiple factors, such as the efficiency of the rootstock in maintaining tissue water potential, enhanced CO_2 exchange with the stomatal efficiency maintained under high tissue water potential, and the biosynthesis of proline, which could nullify the activity of chlorophyllase enzyme which is generally activated under stress (Eftekhari et al. 2017; Foroutan et al. [24]. The degradation of Chl b can impair the plant's ability to capture light energy effectively, thereby reducing overall photosynthetic efficiency [77, 79]. The contradiction that is noticed in V1 could be based on differences in the root architecture of the rootstock and the susceptibility of the scion cultivars grafted. It could also be possible that the decrease in chlorophyll under drought stress is primarily due to damage to the chloroplast via the effects of ROS [77, 99]. In V3 graft Chl a increased by 4.7% and 8.4%, and Chl b showed a decline of 14.8% at 50% FC and 75% FC, the content remained like that of the control. The V4 graft exhibited an increase of 5.1% in Chl a content at 75% FC, while Chl b recorded 2% lower than the control at 75% FC and a further 2% lower at 50% FC. Surplus Chl b molecules appear to cause chlorophyllide α oxygenase degradation

[96] when the amount of Chl b available surpasses what is required for the import and stabilisation of light-harvesting proteins. This suppresses Chl b biosynthesis and may raise the Chl a: b ratio [42]. One significant factor contributing to the increase in Chl b in grafted grapevines is the enhanced water retention and improved physiological performance associated with certain rootstocks. Grafting onto rootstocks like 1103P, for example, has been shown to improve photosynthetic efficiency and water content, hence increasing drought resistance [44]. This improved water status can help maintain the stability of chlorophyll pigments, including Chl b, allowing the plant to sustain higher levels of these pigments even under stress conditions. The ability of grafted plants to better manage water stress can lead to a more favorable environment for chlorophyll synthesis and retention, thus promoting the accumulation of Chl b [44]. All these responses point to the fact that the rootstock plays a major role in drought protection of the attached scions for maintaining the chlorophyll content as observed in the study.

Lutein

Lutein and β-carotene function as energy acceptors, thereby quenching excited chlorophyll molecules. The lutein content significantly increased by 140% at 75% FC and decreased by 20% at 50% FC in V1. The V2 graft exhibited no change at 75% FC when compared with the control, but an increase of 60% was noticed at 50% FC. Plants have developed a number of defence mechanisms against ROS-induced cellular component damage, including the production of protective pigments like anthocyanins and carotenoids and the dissipation of excess light energy [40]. The enhanced synthesis of lutein under drought stress can also be linked to the plants' need to optimize light absorption and energy utilization during periods of water deficit. Under drought stress, plants may experience a reduction in chlorophyll content, particularly chlorophyll b, which can impair their ability to capture light energy for photosynthesis [52]. The V3 graft showed an increase of 37.5% and 50% at 75% FC and 50% FC respectively, while the V4 graft showed a significant increase of 150% and a 10% decrease. In V5 at 75% FC and 50% FC, the observed decrease of 22.7% and 18.2% reflected the susceptibility of the graft to drought stress, confirming the above observation that it could not effectively restrict accumulation of ROS which causes oxidative stress, thereby making the graft prone to stress. The results thus indicated that different graft varieties respond differently to varying levels of water deficits in terms of lutein pigment production. Results also suggest that the rootstocks play a critical role in modulating plant responses to drought stress and preserving pigments in grafted grapevines. It smothers chlorophyll triplets and attaches itself to site L1 of all LHC proteins in the thylakoid membrane, which is essential for protein folding [12]. Because of this, lutein has the unique ability to quench dangerous 3Chl*, which stops ROS from forming [20]. The decline in lutein in the V1 graft thus indicated that the threshold level of increase at 75% FC and further decline at 50% FC reflected the role of the pigment in stabilizing the photosystem by preventing formation of free radicals.

Nitrogen

Macronutrients

The N content showed a remarkable increase at 75% FC and 50% FC in V1, V2, V4 and V5, with 13.04–69.3%, 8.3–58.3%, 7.4–22.2%, 7.4–33.3% respectively. In V3 a significant decrease of 7.7% at 75% FC and 34.6% at 50% FC was seen in comparison to control treatment. These findings imply that varying degrees of field water capacity deficits in distinct treatment groups have an impact on the amount of nitrogen in leaf samples. Reduced soil moisture conditions may influence nutrient availability in sensitive grafts as seen by the decline in nitrogen concentration at 50% FC in V3.

Under drought stress, nitrate reductase (NR) activity and NO_3^--content often decreases, while moderate N supply induced by the drought-tolerant rootstocks of grape grafts V1, V2, V4 and V5 might have promoted the NO_3^- accumulation and an increase in the NR activity leading to enhanced absorption and metabolism, in agreement with the observations of Song et al. [82]. It is also possible that there could be an indirect effect on abscisic acid (ABA) content on account of nitrogen concentration under stress. A moderate amount of N improved photosynthetic efficiency and alleviated drought stress. Cotton seedlings treated with moderate to high concentrations of N under drought stress showed notable increases in the activities of SOD, POD and CAT [2]. Based on the observed increase in N content and the sensitivity expressed by the V3 graft, the increased antioxidant enzymatic activities and decrease in MDA content under high N concentration under drought stress found in maize leaves suggest an increase in the redox defence system in response to drought stress as well as soluble proteins [84] based on the observed increase in N content and the sensitivity expressed by V3 graft. The results of the study revealed the ameliorative effects of high N concentration and may be ascribed to the enhancement of N metabolizing enzymes and an increase in the amounts of osmoprotectants (total soluble proteins and free amino acids), as has been reported by Iqbal et al. [41]. However, cytokinin-nitrogen interactions and the bio-communication systems involved in sensing rhizosphere N status and regulating canopy development remain obscure. The decrease in P content in V1, V2, V4, and V5 grafts (at 75% FC and 50% FC by 32.5% and 15%, 2.7% and 30.5%, 34.3% and 23.4%, 54.1% and 40%, respectively) under water deficit conditions is suggestive of a metabolic derailment with progressive drought.

Drought induced a sharp decrease in total P uptake to shoots in all the grafts except V3. It detrimentally affected the nutrient uptake efficiency of roots under moisture stress. Ge et al. [31] reported that in maize, the roots lost the capability to absorb P from the soil, and this was reflected in different organs at different FC. Drought is a significant environmental element that constrains growth and development, and this was reflected in grape grafts despite the presence of tolerant RS, consistent with da Ge et al. [19], where plant productivity was affected because of the restriction in nutrient uptake. During water shortage circumstances of 75% and 50% field capacity, the reduction in water availability for transport-related processes may have induced alterations in the production of several metabolites, therefore disrupting carbohydrate and amino acid metabolism. Low nutrient uptake is the outcome of a reduced transpiration process under soil water deficit conditions leading to leaf senescence and expression of deficiency symptoms, as mentioned by Sun et al. [83]. The nutrient absorption dynamics of tissues are significantly influenced by the intensity and duration of drought stress, as well as the developmental stage. The patterns of P buildup and transport in plant tissues during drought stress can differ significantly, as observed in grape grafts. Furthermore, the impact of dryness may be exacerbated by the limited mobility of nutrients like P, which is significantly diminished in arid soils. Collectively, these findings suggest that the response of grape grafts to drought stress is intricate and contingent upon the severity of the stress, the type of graft, and the developmental stage, including the stage of field establishment during which deficit watering is applied.

Emerging evidence suggests that K is the most important nutrient for plants, contributing significantly to their ability to withstand water stress. It was also shown that K is the cationic solute that drives stomatal movement [71]. The differential responses in the status of K exhibited by the grape grafts (V3 and V4) emphasized the above point and demonstrated tolerant and/or sensitive effects. In the instance of K, similar to P, the reduction of nutrients coincides with diminished nutrient absorption, especially K, due to a low transpiration rate under conditions of soil water deficit, despite K being a highly water-soluble element readily accessible for root hair absorption. Reduced soil K mobility, a lower transpiration rate, and impaired root membrane transporter function are the causes of this drop in absorption [39]. Hu et al. [37] argued consistently that the reduced transpiration rate, as a mode of water conservation, causes impairment of transpirational pull and disability of the root membrane system. To adapt to drought, it is essential to maintain a sufficient K^+ plant nutritional status [11]. This is reflected in V4 and V5 with significant increases of 13.5% and 16.2%, respectively, signifying the combative mechanism exhibited by the rootstock-scion interaction where the role of RS in maintaining adequate K absorption from the soil cannot be overlooked. The mitigation of drought under enhanced absorption as noticed in V4 and V5 could be attributed to multiple factors, like rapid osmotic adjustment and maintenance of turgor pressure in the cells, efficient ROS scavenging, improved WUE and transport across membranes, optimal energy status, leaf photochemistry and intracellular ionic homeostasis and charge balance. This is consistent with the reports of Shabala and Pottosin [76].

Micronutrients

High levels of competing elements, such as K, Ca, and sodium, can inhibit the level of Mg in plants, apart from other potential factors like drought. According to research, plant cells increase Mg transporter activity to make up for low Ca^{2+}, while excessive Ca^{2+} prevents plants from having access to Mg^{2+} [15]. In line with the findings of Zhou et al. [102], the V3 graft significantly reduced the level of magnesium but did not show any decline in photosynthetic activity. This is likely due to the cerium (rare element) ion, which promotes the synthesis of chlorophyll and photosynthetic pigments, increases the activity of magnesium chelatase and chlorophyll synthase in CO_2 assimilation and the antioxidative defence system, and increases Rubisco expression.

The potential role of Mn in reducing moisture stress has been attributed to an increase in stomatal conductance and photosynthesis [48], which may lead to an increase in biomass content, as has been observed in V2 and V3 grafts (Fig. 2E). This is critical from a drought tolerance point of view since it coincides with a high photosynthetic ability to produce more biomass. Significantly higher levels of Mn observed in the V2, V3, V4 and V5 grafts under 50% FC conditions could lead to ureide degradation in leaves, and it was hypothesized that increased leaf Mn would alleviate the accretion of ureide during moisture stress, decrease feedback inhibition, and prolong N fixation. After receiving exogenous ureide treatment, a soybean cultivar that had shown tolerance for N fixation to water deficit had a lower concentration of shoot ureides than a cultivar that was sensitive to water deficit. Ureides delivered through roots also reduced N fixation in well-watered plants [69]. This is consistent with our observations. It is therefore, concluded that leaf Mn concentration promotes ureide breakdown and prolongs N fixation under water deficit. The status of N fixation in grape grafts is consonant with this observation, thus, the role of rootstock scion interaction is elucidated in unequivocal terms.

In drought-stressed grafts, the content of Fe showed varied responses, suggesting tolerance and/or sensitivity. The observation of decreased Fe at 75% FC and 50% FC in grafts V1, V4 and V5 by 6.4% & 4.3%, 12.2% & 9.8%, 22.2% & 27.8%, respectively, could be attributed to drought stress silencing of genes associated with iron transport/homeostasis. Although, in this study, gene expression was not attempted, Araki et al. [1] observed genes associated with iron transport/homeostasis regulating Fe content in the seeds of sorghum. The RNA-sequencing results of leaves demonstrated that drought stress adversely affected the expression of genes associated with photosynthesis, corroborating the observation that drought stress markedly diminished plant biomass. Consistent with the above observation, the grape grafts showed a decrease in biomass production (Fig. 2E) probably associated with the inhibition of gene expression associated with photosynthetic activity.

Dicotyledonous plants often absorb iron directly through iron-regulated transporter 1 (IRT1) [17, 91] using root Fe absorption Strategy I [50, 61]. Protons (H^+) released by the proton pump convert trivalent iron [Fe (III)] to divalent Fe, which is subsequently absorbed from the soil via IRT1 to solubilise Fe from the soil rhizosphere. Additionally, the rhizosphere secretes low molecular weight chemicals (LMC) such as riboflavin and coumarin, which solubilise iron [13]. This has special reference to grapevine grafts. Consistent with dicots and drought-tolerant RS, they should have the ability to release LMC into the soil rhizosphere to solubilize Fe, thus enhancing absorption in V2 and V3 during moisture stress in 50% FC irrigation compared to 100% FC. It could also be visualized that ABA is involved in the regulation of Fe transport as in *Arabidopsis* [54], enhancing the re-utilization and transportation of Fe towards aerial parts during deficit irrigation. This could be the reason for an enhanced Fe content at 50% FC in the grape grafts. ABA responds to drought stress and promotes stomatal closure, thus preventing moisture loss (Van Wallendael et al. 2019), which is consonant with our study. Therefore, the increased Fe accumulation under drought stress might be associated with the response of ABA to environmental stress.

The role of Zn in plant metabolism under drought has been established unequivocally. In addition to being a part of carbonic anhydrase and a stimulator of aldolase, which affects carbon metabolism, zinc is a possible micronutrient that affects crop development [86]. Zinc also plays a crucial part in the metabolism of plant nucleic acids since it is a co-factor of auxins and an essential component of a few biomolecules, including proteins and lipids [59]. In these studies, there was an immediate Zn decrease under deficit irrigation at 75% FC, but it significantly increased again at 50% FC in V1, V3 and V4. The passive absorption of Zn is influenced by variations in soil moisture. Fluctuations in zinc concentrations within the root cell plasma membranes (RCPM) and transporter proteins facilitate the movement of zinc cations. In the context of a significant increase at 50% FC, passive, instead of an active absorption of Zn, is more likely since the RS have the capability of drawing water from the soil, in line with their drought-tolerant characteristics. Graft V1 showed a 1% and 6.5% decline at 75% FC and 50% FC, while V2, V3, and V4 showed a 4.3% and 85% decrease at 75% FC and 50% FC, respectively. Graft V5 showed a significant decrease, from 5.4 to 12% at 75% FC and 50% FC, respectively. The RWC coincides with the amount of Zn in plants where a significantly lower decline in RWC occurred in V1 with 1% and 6.5% at 75% and 50% FC, indicative of the drought-tolerant capacity of the RS while maintaining other vital parameters like antioxidant capacity, photosynthetic efficiency, etc. The $ZnSO_4$ improved RWC in wheat is in consonant with the RWC noticed in grape grafts [73]. Zinc was also found to enhance the proline content in plants, as noticed in grape grafts, resulting in the protection of osmoregulatory enzymes [73]. The reports of Silva et al. [80] agree with the increase in RWC and proline content in plants under drought stress, which is consistent with our results in the osmoregulation process. Antioxidant enzyme systems that improve plant tolerance under stress by increasing SOD, PPO and GPO activity as reported by Sharma et al. [21, 78] could also be a factor in grape grafts, as we noticed the increased activity of antioxidant enzymes (results not shown).

Grapevine grafts utilize Ca effectively under drought, regulating the nutrient status, metabolism and transcription, thereby increasing tolerance to drought. Birgin et al. (2021) reported consistent results in tomato plants subjected to drought. The V2 and V4 grafts showed a significant increase in Ca content at 75% FC but decreased again at 50% FC with V2, the latter of which was on par with the control. This exhibited the significant role of RS in exploiting the available soil water at induction of drought to be absorbed mainly through mass flow through apoplasts to the vascular bundles for upward movement. It showed the tolerance and capability of RS in a graft to derive the ions from the soil. Zhou et al. [102] reported identical results in the mass flow technique of the roots. The structure and function of chloroplasts (including both endosomal systems of mitochondria and chloroplasts) and maintenance of net photosynthetic rate and gas exchange can be stabilised under drought through exogenous application of Ca thus, ensuring the normal operation of PSII. Ca ions stabilized photosynthetic activity and maintained carbohydrate production and feedback inhibition [38].

Except in V3, the Na content declined significantly at 50% FC in V1 (19.2%), V2 (5.5%) and V5 (28.9%). Na at high concentrations (71.9%), as observed in V3, in the cytoplasm could lead to detrimental effects on cellular metabolism (photosynthesis), indicating susceptibility to drought stress. Results agree with those of Nieves-Cordones et al. [63]. Alternatively, Na could be used as an osmoticum by accumulating in the vacuoles, although all the other grafts showed a decrease in Na content. Therefore, it could be concluded that the decline and / or accumulation could be an advantage or disadvantage depending upon the site of accumulation. The observation by Bailey and Scholes [4] is consistent with the findings in this study.

In V1, an increase in Cu of 21.45% at 75% FC and a 1.5% decrease at 50% FC indicated the threshold level at which the graft could tolerate drought. Numerous physiological functions (photosynthesis, respiration, antioxidant system and hormone signal transduction) depend on growth and development [98]. Elevated copper levels in grapevine leaves increased peroxidase and SOD activity and successfully decreased MDA buildup. Cu had an impact on physiological markers such as Tr, root weight, leaf water retention capacity and leaf water content in some common bean cultivars during drought circumstances, protecting the plant from drought [88]. This is consistent with the results found in the leaves of grapevine grafts.

Scanning electron microscope

Thompson paulsen 100% FC– control (At 750X magnification)

The stomatal pores in 100% FC with respect to Thompson × Paulsen at 750X, the stomates were found to be opened with almost 15.2 µm length and width of 5.5 µum. This is an indicator that the plant is not under stress with full FC with normal transpiration and gaseous exchange (Fig. 5).

Thompson paulsen 50% FC– treatment (At 250X and 1200X magnification)

During the manifestation of stress, the plants accumulate calcium ions in the form of calcium oxalates which can sequester calcium into less toxic forms, such as calcium oxalates. These crystals might play a dual role. They not only regulate calcium levels, but also contribute to structural reinforcement of cell walls, which could help maintain cell integrity under osmotic stress. The deposition of these crystals may serve as a defensive measure, physically protecting the leaf tissues from further damage caused by dehydration. The formation of calcium oxalate crystals helps the plant manage this ion excess and avoid potential toxic effects on cells. This mechanism is crucial for maintaining ionic balance within plant tissues under stress conditions.

In 50% FC at 1200X, it could be observed that the aperture of the stomates narrowed, indicating closure to maintain plant water status. It could also be noticed that the guard cells are swollen, and subsidiary cells are enlarged, giving the appearance of sunken stomata (Fig. 5).

Crimson ramsey 50% - treatment (At 1200X, 1300X and 750X magnification)

With the induction of drought, the stomates are partially open with guard cells and subsidiary cells enlarged. Epicuticular wax (ECW) can be noticed as an interface between the leaf surface and the ambient environment as a barrier against water loss. In certain cases, the formation of ECW could increase the reflection of solar radiation. The combination of stomatal regulation and epidermal adaptations (ECW) suggests that Crimson Ramsey is actively responding to drought conditions as a physiological adaptation to survive water-limited environments, and the partial closure of stomata limits photosynthetic activity under drought conditions. Trichomes were noticed. They are hairlike structures that act as an adaptive mechanism to block heat, humidity, and solar radiation (Fig. 5).

Conclusion

Grapes are in great demand in the UAE, but on account of the hostile climate and soil factors, production is almost impossible in this arid region. The present graft technology involving drought-tolerant rootstocks assumes greater significance in this context. The study demonstrated that regulating irrigation at 100%, 75%, and 50% field capacity (FC) significantly influenced key photosynthetic parameters and water use efficiency. The significant reduction in transpiration rates at 50% FC underscores the grafts' adaptive mechanisms to cope with limited water availability. The findings emphasize the importance of selecting drought-tolerant grapevine grafts for sustainable viticulture in arid regions, providing valuable insights for future research and practical applications in grape production. We recommend a combination of Thomson seedless (Scion) × Ramsey (RS) with an irrigation regime of 50% FC (26 L of water) for efficient field establishment and further growth.

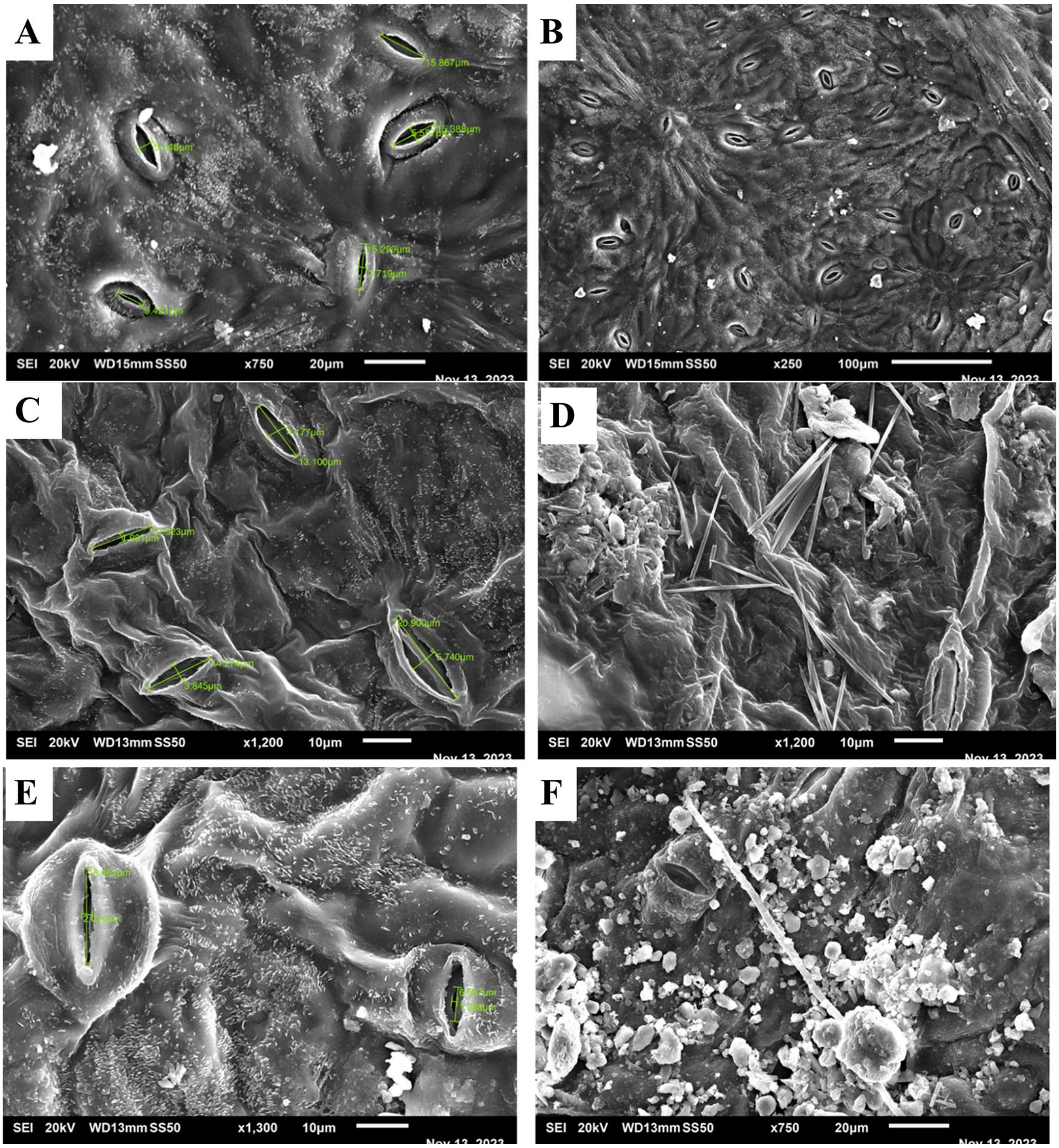


Fig. 5 Scanning electron microscopy (SEM) images of Thompson seedless × Paulsen and Crimson seedless × Ramsey grapevine leaves under control (100%) and irrigation treatment (50%). Thompson seedless × Paulsen (**A**) 100%– control (750X), (**B**) 50%– treatment (250X), (**C**) 50%– treatment (1200X), Crimson seedless × Ramsey (**D**) 50%– treatment (1200X), (**E**) 50%– treatment (1300X) and 50%– treatment (750X)

Supplementary Information

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Supplementary Material 1

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Author contributions

SSK and KA conceived the study and designed the field experiments. SKK supervised the field experiments, collected the field samples, pooled the samples, standardized and analysed the lab experiments, and prepared figures and texts for the manuscript. FA and SKK designed laboratory experiments and standardization. SSK and SKK participated in the discussion and drafted the manuscript. JJH participated as a specialist viticulturist to advise and demonstrate field growing of grapevines and reviewed the manuscript. SS, AR and MSA reviewed the draft before finalizing the manuscript. All authors read and approved the final manuscript.

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Data availability
Data is provided within the manuscript or supplementary information files.

Declarations

Ethics approval
Not applicable.

Consent to participate
Not applicable.

Competing interests
The authors declare no competing interests.

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