



Gene expression and physiological responses in grapevine under water stress conditions

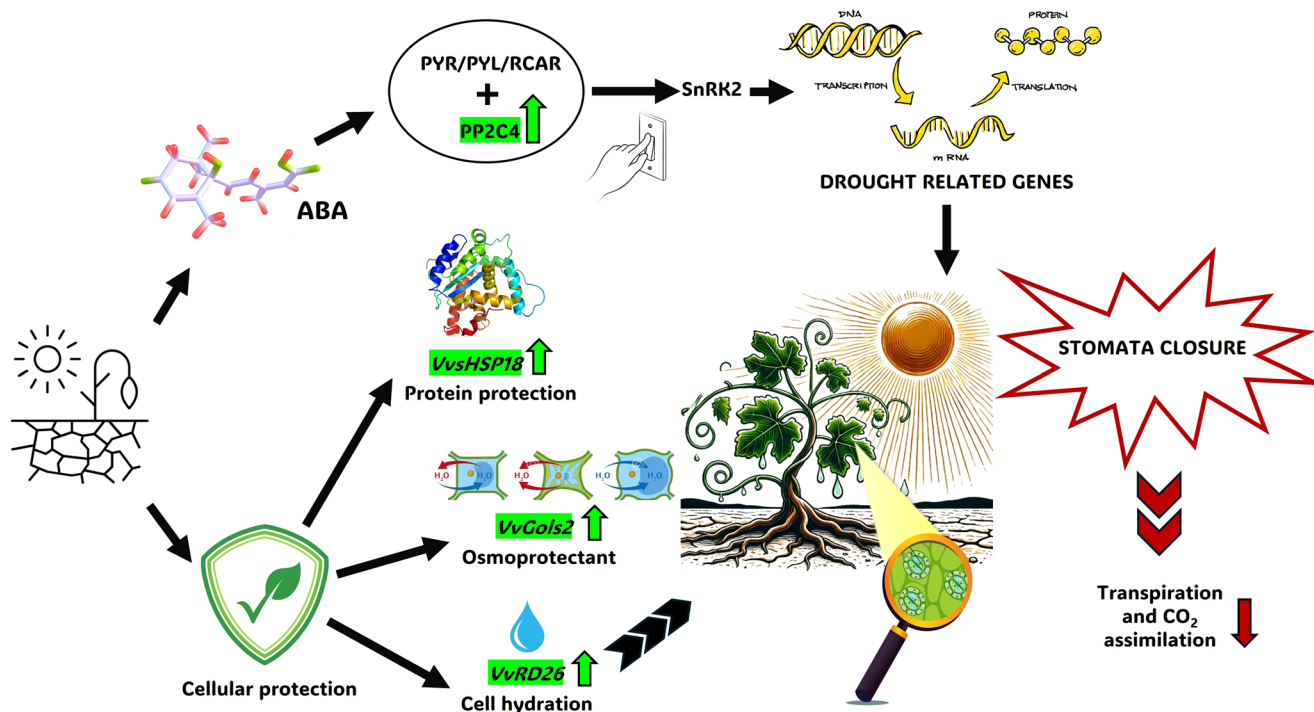
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Abstract

Grapevine (*Vitis vinifera* L.) productivity is highly sensitive to water deficit, a condition of increasing concern in Mediterranean viticulture. The cultivar ‘Italia’, one of the most economically important table grapes in southern Italy, was selected to investigate physiological and molecular responses to drought. Six candidate genes previously identified in transcriptomic analyses (*VvPP2C4*, *VvPP2C8*, *VvGolS1*, *VvGolS2*, *VvHSP18*, and *VvRD26*) were analyzed using quantitative real-time PCR under controlled water stress conditions. The results revealed significant changes in expression, with four genes showing marked differential regulation, particularly those related to ABA signaling and osmoprotection. These findings provide the first targeted validation of candidate drought-responsive genes in ‘Italia’, highlighting their functional role and offering valuable information for breeding strategies aimed at improving grapevine resilience and sustainability under climate change.

Graphical Abstract



Keywords Grapevine · Abiotic stress · Drought stress · Physiological response · Gene expression

Communicated by Jin Hoe Huh

1 Introduction

The grapevine (*Vitis vinifera* L.) has a significant economic, cultural, and nutritional value worldwide, with table grapes representing a key segment. According to the latest OIV statistics, Italy the main global exporter, with 452,000 tons exported in 2021 after Chile and Peru (OIV, 2024), reflecting its significant role in the international market. Due to their recognized quality, Italian table grape varieties are in high demand throughout Europe and beyond (ISMEA, 2023). Puglia, in southern Italy, is the leading region with about 24,000 hectares and annual production of 386.250 tonnes, corresponding to 51% of national values (ISMEA, 2023). Among the table grape varieties, ‘Italia’ (a hybrid of ‘Bicane’ × ‘Muscat of Hamburg’) has a considerable economic importance thanks to its large golden berries, crisp texture, muscat flavour and good shelf life, supporting its commercial success (Ferrara et al. 2014, 2018; Piarulli et al. 2024). The variety contributes close to one million tonnes and several hundred million euros to the Italian table grape sector (ISTAT 2023).

Climate change, in particular the increasing incidence of water stress in Mediterranean regions, has raised interest in genetic strategies to improve drought tolerance in grapevines. Water stress negatively affects photosynthesis, transpiration, berry growth and sugar accumulation, reducing the overall quality and market value of table grapes (Gambetta et al. 2020). Growers are adopting innovative water management strategies, but these require economic cost and changes to conventional practices, raising concerns over long-term sustainability (Nikolaou et al. 2020).

Plants tolerate water stress through physiological, biochemical, and molecular mechanisms. Key processes include stomatal regulation to minimize water loss, osmotic adjustment using proline and sugars, and scavenging of reactive oxygen species (ROS) to prevent cell damage (Patakas et al. 2002; Buckley et al. 2019; Gupta et al. 2020). Photosynthetic efficiency is reduced during prolonged drought, mainly stomatal closure, although grapevine maintains activity until conductance drops below a critical threshold (Chaves et al. 2010; Hochberg et al. 2013; Dayer et al. 2020).

At the molecular level, drought response is finely regulated by a complex network of genes. Critical is the Absciscic acid (ABA) signalling pathway, which controls stomatal closure and induces genes for osmoprotectants, antioxidant enzymes, and aquaporins (di Rienzo et al. 2014; He et al. 2018a; Kuromori et al. 2018). Protein phosphatases 2Cs (PP2Cs) act as negative regulators. In grapevine nine *VvPP2C* genes have been identified at first, with *VvPP2C4* shown to play a crucial role (Boneh et al. 2012a, b; He et al. 2018b). Other families involved in drought response include *VvRD* (Responsive to Dehydration) genes, such

as dehydrins, which contribute to the maintenance of cell hydration (Wang et al. 2012; Matus et al. 2014), and the heat shock protein (*HSPs*) genes, which protect protein integrity (Liu et al. 2020; Rocheta et al. 2014; Ji et al. 2019). Galactinol synthase (*GolS*) genes produce raffinose-family oligosaccharides that stabilize cells during dehydration. To date, 12–15 *VvGolS* genes have been reported, some regulated by transcription factors such as *VvDof17d* (Pillet et al. 2012; Wang et al. 2021; Shirazi et al. 2024). In addition, antioxidant enzymes like superoxide dismutase (SOD) and catalase (CAT) also mitigate ROS damage, while various transcription factors regulate drought-related expression patterns (Salazar-Parra et al. 2012; Wang et al. 2008; Tu et al. 2016; Haider et al. 2017a).

Based on recent transcriptomic data several genes had previously been identified as differentially expressed in grapevine; however, they had never been individually validated. In this work, we provide the first targeted qRT-PCR validation of six candidate genes in the variety ‘Italia’ subjected to water stress and parameterizing the physiological measurements of evapotranspiration and assimilation. These genes include ABA-related genes *VvPP2C4* and *VvPP2C8*, osmoprotectants genes *VvGolS1* and *VvGolS2*, as well as *VvHSP18* and *VvRD26* encoding structural proteins for stress tolerance.

The results will provide insights into drought-related pathways and will be useful in breeding plans for more resilient grapevine varieties.

2 Material and methods

2.1 Trial design

The experiment was conducted from September to October 2013 in a greenhouse at the University of Bari (Bari, Southern Italy) using self-rooted plants of *V. vinifera* L. cv Italia cultivated in 4 L pots (di Rienzo et al. 2014). A randomized complete block design was adopted, and plants were randomly shifted every four days to avoid spatial effects. The greenhouse temperature was kept at $+30 \pm 2.5$ °C, assuring a relative humidity (RU) of 40–70%. Twelve plants were irrigated at soil field capacity, allowing water drainage; then, irrigation was stopped for six plants (labelled as no irrigated plants, NI). On the contrary, six plants were irrigated daily to field capacity, allowing water to drain (labelled as control plants, C). The soil water potential (ψ_s) was monitored using a Watermark Meter apparatus every three days.

2.2 Physiological parameters

During the experiment (37 days), eco-physiological measurements were carried out every three days between 11:00 a.m. and 1:00 p.m. at an average PAR of 600 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. For each plant, healthy, well-exposed mature leaves from the middle part of the shoot were monitored according to the protocol of Camposeo and Vivaldi (2011). Transpiration rate (E ; $\text{mmol H}_2\text{O m}^{-2} \cdot \text{s}^{-1}$), net assimilation rate (A ; $\mu\text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$) and leaf gas exchange in terms of stomatal conductance (g_s ; $\text{mM H}_2\text{O m}^{-2} \text{s}^{-1}$) were monitored using a portable open-system gas analyzer (model LCA-4, ADC Ltd.-UK) and a leaf chamber (PLC4-B). In addition, leaf water potential (ψ ; MPa) was measured with a chilled mirror psychrometer (model WP-4T, Decagon Devices, Inc.-USA) on leaves enclosed in a plastic bag before excision and pressurized within 20 s.

2.3 RNA extraction and qPCR

For RNA extraction, grapevine leaves were collected at four different time points, namely T0 (starting point), T14 (14 days), T30 (30 days), and T37 (37 days). The tissue (100 mg) was ground in liquid nitrogen, and RNA extraction was performed using the Spectrum Plant Total RNA Kit (Sigma-Aldrich, St. Louis, MO) according to the manufacturers protocol. The extracted RNA was further purified using lithium chloride (LiCl) to remove contaminants. Total RNA was mixed with LiCl (Sigma-Aldrich, St. Louis, MO) to a final concentration of 3 M, and the resulting solution was incubated overnight at 4 °C. After centrifugation at 13,000 g, the RNA pellet was washed with 70% ethanol and dissolved in water. RNA quality and quantity were assessed through a Nanodrop 2000 spectrophotometer (Thermo Scientific, Wilmington, DE) and the resulting products were visualized by agarose gel electrophoresis.

The PN40024 *V. vinifera* genome 12X V2 prediction, available on the CRIBI Biotech website (<http://genomes.cribi.unipd.it/>) was used to obtain the gene sequences (*VvPP2C4*: VIT_211s0016g03180, *VvPP2C8*: VIT_213s0019g02200, *VvGolS1*: VIT_207s0005g01980, *VvGolS2*: VIT_214s0060g00790, *VvHSP18*: VIT_213s0019g02850, *VvRD26*: VIT_219s0014g03290). Gene-specific primer pairs were designed with Primer3Plus (<https://www.primer3plus.com/index.html>), avoiding regions of cross-homology for each gene. The sequence of the primers is provided in Table 1. The synthesis of the first strand cDNA for subsequent quantitative real-time PCR was performed with the iScript™ Select cDNA synthesis kit (Bio-Rad) following the methodology indicated by the manufacturer, using 500 ng of RNA in 20 μl reaction volume.

The mixture for the quantitative real-time polymerase chain reaction (qRT-PCR) consisted of 10 μl SsoAdvanced Universal SYBR® Green Supermix (Bio-Rad Hercules, CA, USA), 500 nM of each primer, 1 μl cDNA (100 ng/ μl) and RNase-free water up to 20 μl . The CFX96 Touch Real-Time PCR Detection System (Bio-Rad Hercules, CA, USA) was used to perform the reaction. Thermal cycling began with denaturation at 95 °C for 30 s, followed by 39 cycles of 10 s at 95 °C and 30 s at 54 °C. A melting curve analysis was performed to verify the specificity of each primer pair, with the temperature increasing by 0.5 °C every 5 s from 65 °C to 95 °C. Each qRT-PCR assay was performed in triplicate with three biological replicates. Gene expression levels were normalized using β -actin (di Rienzo et al. 2014) as the endogenous reference gene. Then, the comparative Ct method ($2^{-\Delta\Delta C_t}$) was employed to analyze the expression levels of the target genes. The significance of the expression levels of the NI samples was compared with the control using the t-test method ($P < 0.05$) for the independent sample.

Table 1 List of primers used for RT-qPCR analysis of grapevine cv. ‘Italia’ samples

Primer name	Primer sequence 5’-3’	Function	PN40024 12X V2*
<i>PP2C4_F</i>	AGGAGAGGGAGGGAAAGTCA	Protein phosphatase 2c	VIT_211s0016g03180
<i>PP2C4_R</i>	ACAGGGCAAACCTATGGCTC		
<i>PP2C8_F</i>	CAGACAGAAGGTGGGTGGG		VIT_213s0019g02200
<i>PP2C8_R</i>	AATTCTGTGGGTGCCCTCTT		
<i>GOLS1_F</i>	AGCATACGTGGCCTTCTTG	Galactinol synthase	VIT_207s0005g01980
<i>GOLS1_R</i>	TTCTCGGGTGGGTAAACCG		
<i>GOLS2_F</i>	TACAAGCCCATTCACCCAC		VIT_214s0060g00790
<i>GOLS2_R</i>	TAAGCCGGTCTAGGGATGTG		
<i>HSP18_F</i>	CACGTCTTCAAGGCCGATCT	Heat shock proteins	VIT_213s0019g02850
<i>HSP18_R</i>	ATGGCAGCCTTCACCTCATC		
<i>RD26_F</i>	CCAGCTGCTTCCACCTTA	Responsive to desiccation	VIT_219s0014g03290
<i>RD26_R</i>	CACAAGGTACAAACCGTGGAA		
<i>actin_F</i>	GCACCCTTCGCACGATATGA	β -actin	di Rienzo et al. 2014
<i>actin_R</i>	TGACGCAAGGCAAGGACTGA		

*V2 annotations obtained from CRIBI (<http://genomes.cribi.unipd.it/grape/>) by a BLAST search of the gene sequence provided by NCBI (<http://www.ncbi.nlm.nih.gov>)

2.4 Statistical analysis

To determine the statistical differences and the significance between the irrigation treatments, the Analysis of Variance test (ANOVA) and the t-test were carried out with a significance level of 0.05. The correlation between the physiological parameters (stomatal conductance, net assimilation rate and transpiration rate) and the expression levels of the six analyzed genes was evaluated using Pearson's correlation coefficients.

3 Results

3.1 Physiological parameters

During the experiment, the soil water potential (ψ_s) in the control plants was maintained at an average of -14 kPa, corresponding to the field capacity (Supplementary Fig. 1). In contrast, the value at T37 dropped to -200 kPa in the no-irrigated (NI) plants. The leaf water potential also shows a significant decrease in the NI plants, starting from time point T30 (Table 2).

The transpiration rate (E) and the net assimilation rate (A) varied in the control (C) plants with values ranging from 0.49 to 1.31 mmol H₂O m⁻²·s⁻¹ (average 0.96 mmol H₂O m⁻²·s⁻¹) and 2.97 and 0.83 mmol H₂O m⁻²·s⁻¹ (average 5.01 mmol H₂O m⁻²·s⁻¹), respectively. At the end of the experiment, E was reduced from 0.27 to 0.07 mmol H₂O m⁻²·s⁻¹, and A from 1.37 to 0.16 μ mol CO₂ m⁻²·s⁻¹, in NI plants, which corresponds to ψ_s values of -200 kPa (Fig. 1A and B). Significant differences between C and NI plants were observed starting from T14 for A and from T30 for E. The stomatal conductance showed values ranging from 0.013 to 0.037 mM H₂O m⁻² s⁻¹ in the C plants. In contrast, the values decreased drastically from 0.010 to 0 mM H₂O m⁻² s⁻¹ for NI plants, revealing significant variation from T30 (Fig. 1C).

Table 2 Soil water potential (ψ_s Kpa) and leaf water potential (ψ_l MPa) evaluated in Control (C) plants and no-irrigated plants (NI) at four different time points. *indicates significant ($P < 0.05$) differences from the control, as assessed by t-test

Sampling times	ψ_s (kPa)		ψ_l (MPa)	
	C	NI	C	NI
T0	-12.67	-15.33	-1.47	-1.34
T14	-13.00	-13.43	-2.02	-2.00
T30	-15.33	-137.57*	-1.93	-2.59*
T37	-15.00	-200.00*	-2.34	-2.87*

3.2 Gene expression analysis

The expression analysis focused on six genes: the genes *VvPP2C4* and *VvPP2C8*, related to the ABA and MAPK signalling pathways; the genes *VvGolS1* and *VvGolS2*, involved in osmoprotection; and the genes *VvHSP18* and *VvRD26*, involved in cellular protection.

The expression levels of the selected genes were estimated at the beginning of the experiment (T0) and after 14 (T14), 30 (T30) and 37 days (T37). Throughout the experiment, the *VvPP2C8* gene showed no significant changes in expression in the NI plants compared to the control, while the expression of the *VvPP2C4* gene significantly increased in the NI plants after 37 days without irrigation (Fig. 2a and b).

As for *VvGolS* genes, the expression of the *VvGolS1* gene did not show significant variation at any of the time points analyzed. At the time point 37, a significant increase in the expression of the *VvGolS2* gene was observed in NI plants compared to the control (Fig. 2c and d).

Looking at *VvHSP18* and *VvRD26* genes, a significant increase in the expression levels was detected for the *VvHSP18* gene in NI plants compared to the controls only at T37, while the *VvRD26* gene showed a significant over-expression starting from T14 and 80-fold at T37 in the NI samples compared to the control (Fig. 2e and f).

3.3 Correlation analysis

The correlation analysis confirmed the correlation between the expression of the analyzed genes and the variations in physiological parameters observed throughout the experiment. Among the genes, *VvHSP18* showed a moderate positive correlation with the *VvGolS1* gene ($r = 0.67$) and a weaker positive correlation with A ($r = 0.37$). Conversely, *VvRD26* stands out with strong negative correlations with A ($r = -0.62$), E ($r = -0.61$), and *gs* ($r = -0.52$). Additionally, *VvPP2C4* correlates negatively with A ($r = -0.59$) and E ($r = -0.53$) (Fig. 3).

4 Discussion

The grapevine displays a coordinated physiological and molecular response to mitigate water stress and ensure survival. Water stress activates a variety of stress-responsive genes that regulate protective pathways and stabilise cellular structures. These genes also maintain osmotic balance and mitigate oxidative damage (Thalmann and Santelia 2017; Clément et al. 2011; Yang et al. 2012; Yu et al. 2018). Among them, several members of transcription factors such as *VvNAC17*, *VvWRKY48*, *VvbZIP45* and *VvERF* are known

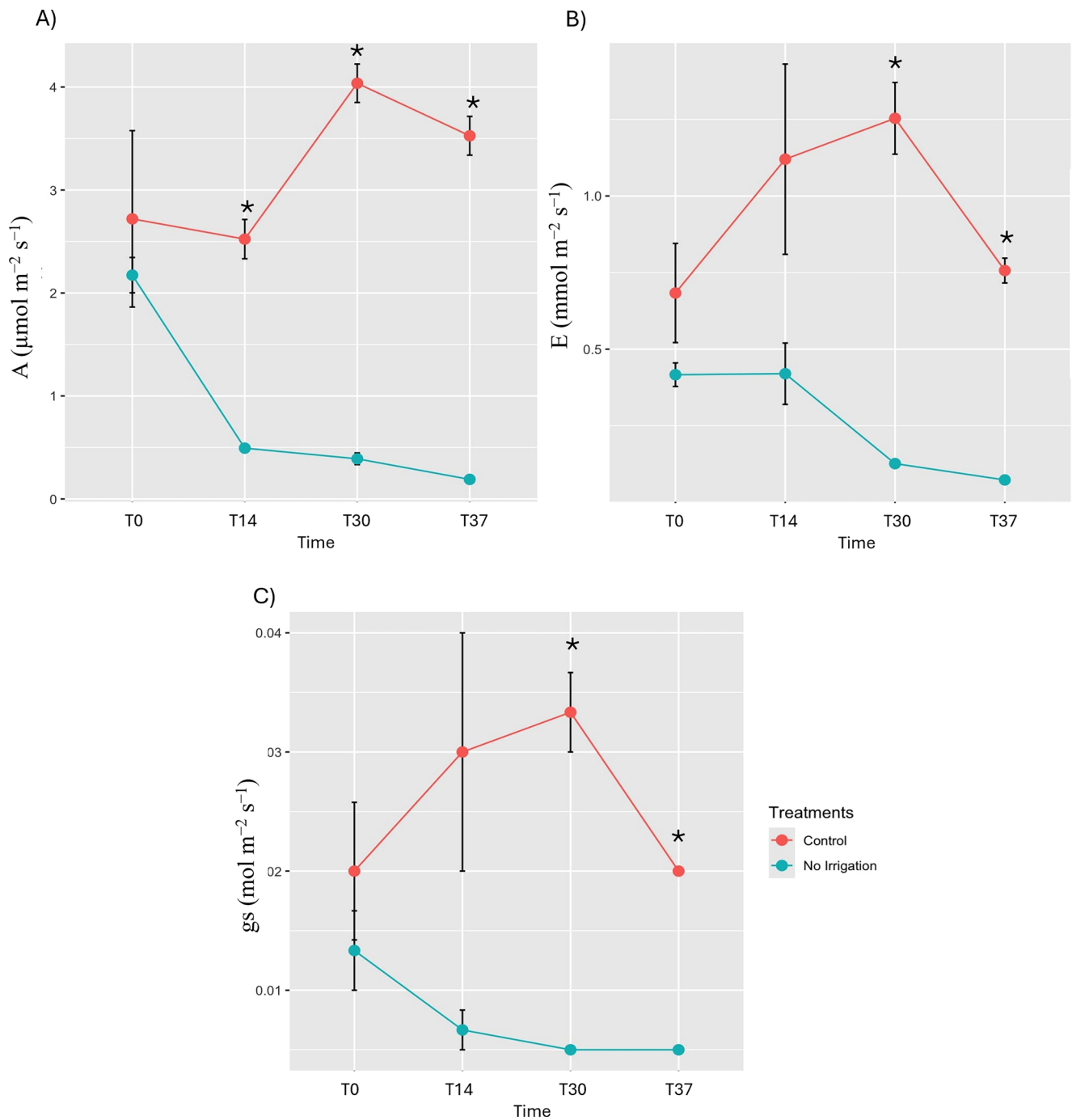


Fig. 1 (A) Net assimilation rate (A , $\mu\text{mol m}^{-2} \text{s}^{-1}$), (B) transpiration rate (E , $\text{mmol m}^{-2} \text{s}^{-1}$) and (C) stomatal conductance (g_s , $\text{mol m}^{-2} \text{s}^{-1}$) in grapevine cv. 'Italia' well-irrigated (Control) and no irrigated plants.

Asterisks indicate significant differences between control and no-irrigated plants using the independent-sample t-test method (* $P < 0.05$)

to regulate downstream responses (Jin et al. 2025; Zhao et al. 2018; Niu et al. 2023; Hopper et al. 2016). These genes activate genes encoding protective molecules, including dehydrins (*VvDHN1*) and enzymes enabling osmolyte accumulation, such as *VvP5CSI* (Pyrroline-5-carboxylate synthetase 1) (Li et al. 2024; İbrahim et al. 2019). In addition, aquaporins such as Plasma Membrane Intrinsic Proteins

(PIPs), including *VvPIP2;1* and *VvPIP2;2*, play a critical role in adjusting water content (Yang et al. 2021a). Genes related to photosynthesis and cell growth, such as expansins (*VvEXPI*), also play a role in conserving energy and limiting water loss (Dal Santo et al. 2016). High-throughput sequencing has identified numerous DEGs under drought, including hormone-responsive genes, osmotic regulators

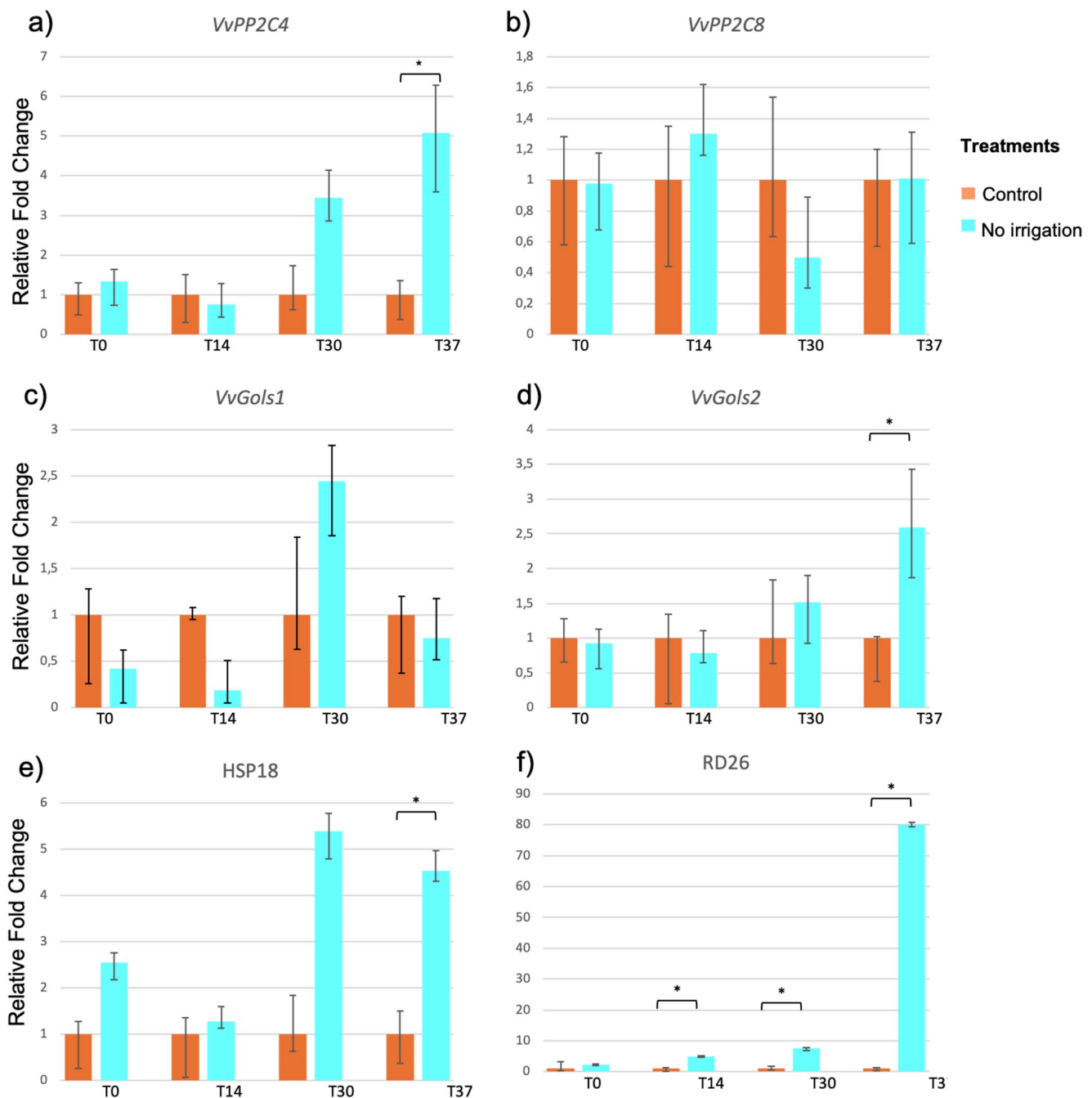


Fig. 2 Relative Expression levels fold change of the *VvPP2C4* (a), *VvPP2C8* (b), *VvGolS1* (c), *VvGolS2* (d), *VvHsp18* (e) and *VvRD26* (f) genes. Error bars represent standard deviations obtained by the means

of three biological replicates. Asterisks indicate significant differences compared with the expression level of the control using the independent-sample t-test method (* $P < 0.05$; ** $P < 0.01$)

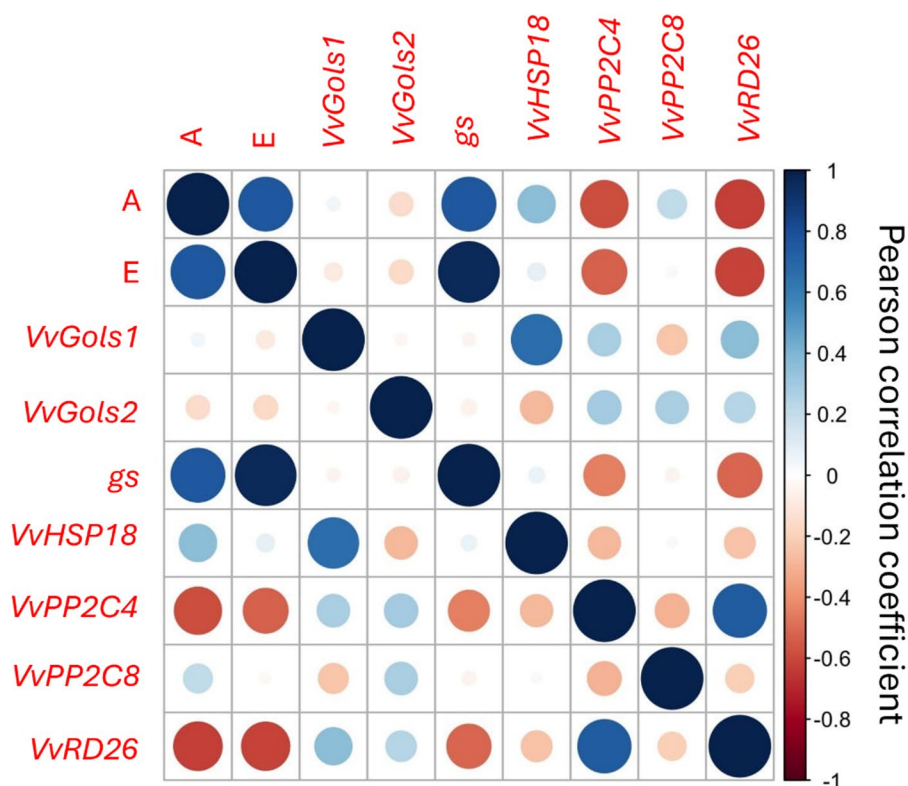
(*RD22*, *RD26*, *XERICO*, *DRS1*), ABA-regulated transcription factors (*DREB1A*, *MYB102*), and ROS-scavenging enzymes (catalases, ascorbate peroxidases) (Cochetel et al. 2020; Catacchio et al. 2019; Tan et al. 2023).

However, a significant knowledge gap exists, as only a small subset of these has sustained experimental validation of their expression dynamics using the quantitative real-time PCR (RT-qPCR). To fill this gap, we monitored the

variations in the expression levels of six candidate genes involved in the ‘Italia’ table grape cultivar subjected to 37 days of drought.

Vines under drought treatment substantially reduced A, E and gs compared to control, confirming the critical role of water availability in the maintenance of grapevine physiological function and regulation of photosynthetic and transpiration processes (Yang et al. 2021b; Gambetta et al.

Fig. 3 Correlation matrix between physiological parameters (transpiration rate-E, net assimilation rate-A and stomatal conductance-gs) and the expression levels of the six selected genes (*VvGols1*, *VvGols2*, *VvHSP18*, *VvPP2C4*, *VvPP2C8*, and *VvRD26*). The Pearson correlation coefficients are represented by the circles' size and color: blue tones indicate positive correlations, while red tones indicate negative correlations. Stronger correlations are depicted by larger circles with deeper color intensities



2020). Well-irrigated vines consistently exhibited higher A, E and gs till later time points, reflecting a progressive drought-induced adjustment that ultimately leads to stomatal closure, reduced CO₂ assimilation and decreased water loss (Hockberg et al., 2013; Gambetta et al. 2020).

Key parameters such as leaf water potential, stomatal conductance, and photosynthetic efficiency are tightly linked to drought-responsive gene regulation. Under drought, salinity, or cold stress, plants regulate the stomatal closure to conserve water while regulating genes to promote osmotic adjustment in leaves through ABA accumulation (Zhao et al. 2017; Niu et al. 2018). ABA orchestrates the recruitment of diverse molecular components to generate and propagate endogenous signals essential for cellular processes (Mane et al. 2007; Yoshida et al. 2010). The process is regulated by protein kinases and protein phosphatases (PP2C), which act as negative regulators to modulate plant responses to abiotic stress and play complementary roles in modulating signal transmission, catalysing phosphorylation and dephosphorylation events (Dalal et al. 2015; Haider et al. 2017a; Szostkiewicz et al. 2010; Dupeux et al. 2011). In the absence of ABA, PP2Cs inhibit Sucrose non-fermenting-related kinase 2 (SnRK2s) through dephosphorylation, thereby preventing the activation of ABA-responsive genes. However, when ABA binds to the protein receptor complex PYR/

PYL/RCAR, the activity of PP2Cs is inhibited, allowing SnRK2 autophosphorylation and the activation of downstream transcription factors, ultimately inducing stress-responsive gene expression (Hirayama et al. 2007; Yang et al. 2017). Recently, many authors reported a wider number of *VvPP2C* family members, indicating the complexity of the grapevine genome (He et al. 2018b; Zhang et al. 2021; Guo et al. 2023). To address this complexity, we focused on the expression of *VvPP2C4* and *VvPP2C8*, which have been suggested to play a role in ABA- and drought-related responses.

In this study, *VvPP2C4* was significantly overexpressed after 37 days of drought, whereas *VvPP2C8* showed no change. This observation aligns with previous reports on the involvement of *VvPP2C* family genes in drought response, and with transcriptome and microarray studies showing overexpression of these genes under ABA treatment and drought stress (Boneh et al. 2012b; Rattanakon et al. 2016; Rossdeutsch et al. 2016; Zhang et al. 2021; Cochetel et al. 2020). The interaction of *VvPP2C4* with several *VvRCAR*-ABA receptors, but not *VvPP2C8*, is consistent with *Arabidopsis* studies and highlights genotype-specific ABA regulatory mechanisms (Raghavendra et al. 2010; Lumba et al. 2014; Batool et al. 2018). The delayed induction of *VvPP2C4* suggests its involvement in long-term drought

adaptation, likely acting as a negative regulator in the ABA signaling pathway to modulate stomatal closure and limit water loss. Its negative correlation with net assimilation and transpiration further supports this role (Gambetta et al. 2020; Catacchio et al. 2019). Concerning the *VvGolS* genes, which catalyze the first step in raffinose family oligosaccharide (RFO) biosynthesis, *VvGolS2*, but not *VvGolS1*, was upregulated under drought. This pattern is consistent with cultivar-dependent regulation observed in previous studies and suggests that protective galactinol accumulation may occur via an ABA-independent pathway (Zuther et al. 2004; Sengupta et al. 2015; Cochetel et al. 2020; Tan et al. 2023; Gu et al. 2018; Dai et al. 2020; dos Santos et al. 2020). Functional evidence from *Arabidopsis* and *Nicotiana* supports the role of RFOs in osmoprotection and stress tolerance (Taji et al. 2002; Zhuo et al. 2013).

VvHSP18, a small heat shock protein, exhibited a threefold increase in transcript abundance, confirming its involvement in protein stabilization and oxidative stress management. This is consistent with previous transcriptomic analyses in multiple grapevine cultivars under abiotic stress (Haider et al. 2017b; Catacchio et al. 2019; Cochetel et al. 2020; Venios et al. 2020; Tan et al. 2023).

Finally, the NAC transcription factor *VvRD26* exhibited an 80-fold induction, highlighting its central role in orchestrating downstream stress-responsive genes and in restricting stomatal opening, thereby influencing photosynthetic efficiency. This substantial induction is among the most pronounced observed in our study, underscoring its pivotal role in the drought response. The activity of *VvRD26* likely reflects crosstalk between ABA and jasmonic acid (JA) signalling pathways during drought adaptation (Fujita et al. 2004; Tran et al. 2004; Jiao et al. 2023; Fang et al. 2024). Notably, in *Arabidopsis*, RD26 has been shown to regulate stomatal closure and photosynthetic efficiency under drought stress, suggesting a conserved mechanism across species (Fujita et al. 2004).

Together, these coordinated molecular responses, combined with physiological adjustments, illustrate a multifaceted strategy to cope with water deficits. The observed variability among grapevine cultivars underscores the complex interplay of genetic and environmental factors in drought resilience (Schultz 2003; Dal Santo et al. 2016).

5 Conclusions

This study provides new insight into the molecular mechanisms enabling the ‘Italia’ grapevine cultivar to respond to drought stress. Physiological adjustments, primarily through stomatal regulation, ensured water conservation but at the cost of reduced photosynthesis.

The significant up-regulation of *VvPP2C4* and *VvRD26*, along with a high correlation with the observed physiological parameters, underlines their critical role in ABA-mediated drought tolerance pathways. Similarly, the enhanced expression of *VvGolS2* and *VvHSP18* highlights their contributions to osmoprotection and cellular homeostasis under water deficit conditions. Conversely, the lack of significant changes in *VvPP2C8* and *VvGolS1* suggests genotype-specific responses and regulatory variations.

Our work, exploring the genetic and physiological basis of drought tolerance in the cv. ‘Italia’ table grape, emphasizes the potential of leveraging our findings to develop resilient grapevine varieties. Future research should explore the crosstalk among these molecular pathways in cultivars with different water stress tolerance and validate their utility in field conditions to enhance the adaptability and sustainability of viticulture in water-limited environments.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s13580-026-00802-6>.

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Author contributions Conceptualization: CM, MMM and SC; Formal analysis: IM, MAS, SP and GAV; Funding acquisition: CM; Investigation: IM, MAS, SP, VF, GAV and DN; Methodology: IM, VF, GAV, MMM and CDG; Writing – original draft: IM, MMM, and GAV; Writing – review and editing: IM, MAS, SP, DN, CDG, GAV, VF, MMM, SC and CM.

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Data availability All data generated or analysed during this study are included in this published article.

Declarations

Competing interests There is no declaration of interest statement.

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