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Conventional and newly bred rootstock effects on the ecophysiological response of *Vitis vinifera* L. cv. Tempranillo

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ABSTRACT

Achieving more environmentally sustainable vineyards, particularly regarding efficient water use, is paramount in semi-arid grape-growing regions. Rootstocks may be a possible strategy to address these challenges, but require a comprehensive evaluation of their effect on the scion, including ecophysiological traits. The objectives of this study were 1) to characterize the physiological response of Tempranillo cultivar grafted onto five commercial (1103 P, 110 R, 140Ru, 420 A, and SO4), and seven recently bred (RG2, RG3, RG4, RG6, RG7, RG8 and RG9) rootstocks and 2) to elucidate the relationships between agronomic and physiological traits conferred by grapevine rootstocks. This was carried out over three seasons (2018–2020) in a typical Mediterranean vineyard by determining water relations, leaf gas exchange, carbon isotope ratios and vegetative development and yield components. The results highlighted the different behaviour of 'Tempranillo' vines due to the rootstock effects on vine water status, photosynthetic performance, hydraulic conductance, vegetative growth and yield parameters. Overall, rootstocks inducing vigour and yield in the scion, such as 140Ru and RG8, showed higher leaf gas exchange rates and hydraulic conductance at the whole-plant level due to less negative water potentials, suggesting a higher water uptake and transport capacity than RG2, RG7 and RG9. The RG rootstocks showed a very wide range of ecophysiological responses, but only RG8 outperformed compared to the most widely used commercial rootstocks. Moreover, this response was modulated by the season and the block soil type, suggesting the importance of rootstock selection according to the edaphoclimatic conditions. Therefore, this study highlights the high potential of rootstocks to adapt to water scarcity by improving crop water productivity in vineyards and provides physiological insights for future studies and breeding programmes.

1. Introduction

Grapevine (*Vitis vinifera* L.) is widespread throughout the world, particularly in semiarid areas such as the Mediterranean basin. It is a crop traditionally grown under rainfed and deficit irrigation conditions. Therefore, in the context of climate change, viticulture is particularly vulnerable to the predicted increase in the frequency and intensity of droughts and heat waves, mainly because of their implications on vine performance and grape quality (Fraga et al., 2016; Guiot and Cramer, 2016; Sadras et al., 2017; van Leeuwen and Destrac-Irvine, 2017). These effects can be summarized as yield reduction and increased berry sugar concentrations, reduced must acidity and secondary metabolite concentrations, which may affect wine alcohol content, pH, colour and aroma (Medrano et al., 2003; Mira de Orduña λ, 2010; Rienth et al., 2021).

To address with these challenges, vineyard irrigation has been steadily increasing as a way to overcome severe drought and heat stress and to ensure more regular and predictable yields and adequate grape ripening (van Leeuwen et al., 2009; Flexas et al., 2010). However, the availability of water resources in semi-arid environments hinders the

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sustainability of this practice, even if it is deficit irrigation (Fereres and Soriano, 2007; Romero et al., 2022). In this sense, there are field practices that allow increasing the efficiency of water use in the vineyard in a sustainable way, such as the use of drought-adapted plant material, appropriate canopy and soil management practices, etc. (Medrano et al., 2015a; Costa et al., 2016; Buesa et al., 2022a; Ramírez-Cuesta et al., 2023). Sustainable agronomic practices aim to improve the ratio between the biomass obtained and the total amount of water transpired by the plant, defined as water use efficiency (WUE) (Flexas et al., 2010). This can lead to higher crop water productivity (WP_c), defined as marketable yield per total amount of water used (Rodrigues and Pereira, 2009). In this regard, the large genetic diversity within *Vitis vinifera* has been shown to be an important tool for adaptation to climate change by means of improving WUE (Bota et al., 2001, 2016; Lavoie-Lamoureux et al., 2017; Romero et al., 2018). Furthermore, this large variability in WUE and WP_c has recently been found within cultivars (Tortosa et al., 2016; Buesa et al., 2021).

Rootstocks have the ability to influence the performance of the scion, mainly by modifying vine vigour, crop load and grape ripening, but also by influencing its tolerance to environmental conditions, especially soil moisture (Marguerit et al., 2012; Tramontini et al., 2013; Rossdeutsch et al., 2016; Edwards et al., 2022; Marín et al., 2019, 2022a; Vilanova et al., 2021). In European viticulture, grafting is almost mandatory due to phylloxera (*Daktulosphaira vitifoliae*), an insect that feeds on the roots of *Vitis vinifera* cultivars and causes the vines to die. European cultivars must therefore be grafted onto American *Vitis* species or American interspecific hybrids of *Vitis* species that confer resistance or tolerance to phylloxera infection (May, 1994). Most conventional rootstocks are hybrids of three species: *V. riparia, V. rupestris* and *V. berlandieri* (Keller et al., 2010). In this regard, Riaz et al. (2019) showed that existing grape rootstocks are closely related to each other and have a narrow genetic background (Wang et al., 2023). Despite this narrow genetic diversity, there seems to be room for improvement in their breeding, as the effects of current rootstocks produce a highly variable range of scion responses (McCarthy et al., 1997; Keller et al., 2012; Romero et al., 2018; Marín et al., 2020; Peiró et al., 2020). Rootstocks determine rooting ability, water and nutrient uptake capacity, and thus the tolerance to abiotic factors such as temperature, pH, drought, flooding and salinity, etc. (Medrano et al., 2015).

Therefore, in a context of climate change more prone to water deficit, a possible strategy to achieve sustainable vineyards could be the breeding of new rootstocks with greater water use efficiency and balanced grape ripening (Merli et al., 2016; Marín et al., 2022a; Villalobos-Soublett et al., 2022; Rahmani et al., 2023). However, rootstock breeding programmes are very time consuming. Most of the rootstocks used today were bred a century ago, focusing on resistance to pests and viruses rather than in the adaptation to abiotic stresses (Ollat et al., 2016; Marín et al., 2021). Currently, many public and private efforts are underway to provide the market with a sufficient range of rootstocks adapted to different environmental conditions and production objectives. This is the case of the rootstock breeding programmes developed in recent decades by the INRA in France (Fercal, Gravesac, Nemadex AB), the Univertisty of Geisenheim in Germany (SO4, 5C, 5BB, 125AA and Börner), the University of Milan in Italy (M and G series), the University of Pannonia in Hungary (Georgikon series), the CSIRO in Australia (Merbein series) and the USDA in the USA (Kingfisher, Matador, Minotaur). More recently, the RG series has been developed by the “Vitis Navarra” nursery in Spain by crossing two of the most successful rootstocks for Mediterranean climates and soils: Richer 110, which has good drought tolerance, and 41B, which performs very well in calcareous soils. These hybrids have recently been agronomically evaluated by Marín et al. (2022a) in comparison with their parents when grafted with Tempranillo and Syrah cultivars. It is worth noting that the RG rootstocks showed a very wide range of performance compared to their parents in terms of yield, pruning mass and grape composition, with the RG8 being outstanding for inducing high vigour and yield and a good balance between acidity and sugars.

The choice of the most appropriate rootstock is a key decision for the vineyard adaptation to the challenges of climate change. To this end, a comprehensive knowledge of the physiological traits that rootstocks confer on the scion, leading to an increase in WUE and WP_c, is required (Alsina et al., 2011; Ollat et al., 2016; Labarga et al., 2023). Particular attention should be paid to the mechanisms involved in the regulation of vine water status, as this is the primary parameter affected by water deficit (Simonneau et al., 2017). Achieving improvements in resource use depends, among other factors, on root extraction capacity. This in turn depends on the volume of soil explored by the roots and/or on the adjustment of the hydraulic conductivity of the root system by increasing the root surface area (de Herralde et al., 2006; Alsina et al., 2011; Gambetta et al., 2012, 2020). It should be noted that vine responses cannot be fully explained in terms of soil water and nutrient availability alone. It is also necessary to consider the plant’s ability to uptake and transport them, which can be improved by using an appropriate rootstock (Zhang et al., 2016; Verslype et al., 2023). A more vigorous root system could provide greater access to water and nutrients. However, it is also important to consider the root response to soil water deficit, as this will ultimately determine the ability to withstand periods of resource scarcity (Marguerit et al., 2012; Pérez-Álvarez et al., 2023). In this sense, the ability to regulate transpiration is strongly determined by the rootstock, which influences stomatal conductance through hydraulic and chemical mechanisms (Tombesi et al., 2015; Lavoie-Lamoureux et al., 2017). It is recognized that the rootstock genotype can have a greater influence on stomatal conductance and vigour than the grapevine cultivar itself (Koundouras et al., 2008; Lavoie-Lamoureux et al., 2017; Merli et al., 2016). Thus, rootstocks that confer an anisohydric behaviour, explained by the high stomatal conductance rates and reduced water potential, may be of interest as long as there is the possibility to apply emergency irrigation if the soil water deficit is too severe (Pou et al., 2012). Otherwise, a more isohydric behaviour may be more appropriate, as a tighter stomatal regulation would lead to lower vigour and therefore improve the vineyard’s resilience to climate change (Alsina et al., 2007; Pou et al., 2008; Romero et al., 2018; Edwards et al., 2022). We hypothesized that iso- and anisohydric behaviour could be regulated by rootstock capacity for water uptake and transport (hydraulic conductance).

This work aimed to characterize the ecophysiological response of Tempranillo cultivar grafted onto twelve rootstocks, five conventional and seven recently bred, over three seasons and under a wide range of water status. Specifically, we studied 1) the effect of grapevine rootstocks on water relations, leaf gas exchange parameters, hydraulic conductance, nutritional status and crop water productivity, and 2) analysed the relationship between these ecophysiological traits and the agronomic performance of the scion. To our knowledge, this is the first field trial to assess the drought tolerance mechanisms conferred by so many grapevine rootstocks, integrating stomatal and hydraulic regulation, thus allowing discussion of the range of iso/anisohydric behaviours they induce in the scion.

2. Material and methods

2.1. Location and vineyard management

The experiment was carried out during three consecutive seasons (2018–2020) in an experimental vineyard located in Miranda de Arga (42°27’50.6"N 1°48’10.6"W, altitude 308 m, Navarra, Spain). The vineyard was planted in 2011 with *Vitis vinifera* L. cv. Tempranillo grafted onto 12 rootstocks.

The vines were pruned to 5 two-shoot spurs per vine on a unilateral ‘cordon de Royat’ and trained on a vertical north-south trellis system. Plant spacing was 3 m between rows and 1 m between plants (3333 vines·ha^{-1}), and the field was drip irrigated by two 4 L·h^{-1} pressure compensated emitters (AZUD PRO, AZUD, Spain) placed 0.5 m along a single drip line suspended under the vines. Canopy management consisted of manual shoot thinning before bloom and no shoot trimming. Soil management consisted of maintaining and mowing a permanent spontaneous cover in the inter-row, while the crop-line was kept free of vegetation with herbicide over a 1 m width. 'Tempranillo' budburst in this area usually occurs at the end of March, bloom in June, veraison in mid-August and harvest at the end of September.

2.2. *Environmental conditions and vineyard management*

Before planting, soil samples were taken with an auger from the surface soil (0–20 cm) at three points in the vineyard area. The soil samples were combined together, homogenized and sent to Agrolab facilities (Mutilva Baja, Navarra, Spain) for analysis. The soil at the site was classified as a Quaternary sedimentary soil with a sandy loam texture with the presence of pebbles, highly calcareous ($CaCO_3$ = 40.7%), with 8% of active lime and a pH-H_2O (1:2.5) of 8.6. The organic matter content was about 2%. The soil had a low salinity (0.4 $dS{\cdot}m^{-1}$) and a medium cation exchange capacity (12.35 $cmol(+){\cdot}kg^{-1}$). The assimilable potassium and magnesium contents were 3.72 and 2.54 $cmol(+){\cdot}kg^{-1}$ (30.1% and 20.6% of CEC), respectively. This may lead to deficiencies in Mg uptake due to antagonism with the high K content in the soil (Stockdale et al., 2013). The plot has a slope of 1.8%, with a gradient of surface stoniness decreasing from top to bottom.

The climate of the area is Continental-Mediterranean, with an average rainfall of 400–500 mm per year. During the experimental seasons, total precipitation was 545, 414 and 475 mm in 2018, 2019 and 2020, respectively. The seasonal reference evapotranspiration (ET_o) was 1115, 1255 and 1040 mm, respectively. Climatic data were obtained from the Agroclimatic Information Service of Navarre (SIAR, Spain), located in Miranda de Arga (Supplementary Figure 1). Fertigation was applied from July to September, four times in 2018 and five times in 2019 and 2020, accounting for approximately 36 and 48 mm, respectively. All rootstocks were equally irrigated and fertigated with approximately 30, 20, and 60 $kg{\cdot}ha^{-1}$ of N, P_2O_5, and K_2O, respectively. Pest control and disease control was carried out by 'Vitis Navarra'. These included preventive treatments with copper- and sulphur-based compounds.

2.3. *Experimental design and treatments*

The experimental design of the plot followed a completely randomized experimental design with two blocks. Block 1 was placed at the bottom and block 2 at the top of the plot. Within each block, each treatment consisted of 10 vines grafted on the same rootstock located in a single row. Only the 8 vines in the middle were monitored, as the plants at either end of the row were considered as buffers.

Five commercial rootstocks and seven recently bred rootstocks were evaluated: Paulsen 1103 (1103P), Richter 110 (110R), Ruggeri 140 (140Ru), 420A Millardet et de Grasset (420A), Sélection Oppenheim 4 (SO4), and newly bred hybrids, which are referred to as the RG series (RG2, RG3, RG4, RG6, RG7, RG8 and RG9). The breeding programme of the RG series was fully described in Marín et al. (2022a) and a brief description of the pedigree and breeding information of the 12 rootstocks is provided in Table 1. The genetic background of the rootstocks was confirmed through 25 SSR markers as detailed in Marín et al. (2022a).

2.4. *Field measurements*

The ecophysiological evaluation was carried out in Block 1 during the 2018–2020 seasons. In addition, in the 2020 season (third season), vines from the Block 2 were used for an additional analysis of the soil effect on rootstock-scion performance. This was because of the differences observed in vine vigour between the blocks. For vine performance determinations, the yield components and pruning mass of the 8 experimental vines of each block were weighted together. For the physiological determinations, only 6 of the vines were selected for uniformity of development among the 8 middle vines. These 6 vines were considered as individual replicates and were identified with tape on the trunk and measured throughout the experiment. To compensate for the effect of the time of day on genotype responses, the determinations were made in two measurement cycles. In addition, the order of measurements was varied on the different dates. Determinations of water relations, gas exchange and hydraulic conductance were performed on day of the year (DOY) 255 in 2018; 199 and 240 in 2019; and in 205 and 240 in 2020. Between late August and early September of each season, vine nutritional status, vegetative growth and yield components, as well as grape carbon isotope ratios were assessed.

Table 1
Full name, abbreviation and genetic background of the rootstocks (Riaz et al. 2019) used in the present study with Tempranillo in the 2018, 2019, and 2020 seasons in Miranda de Arga, Navarra, Spain.

Rootstock	Abbreviation	Genetic background
Paulsen 1103	1103P	*V. berlandieri cv. Rességuier 2* × *V. rupestris cv. du Lot*
Richter 110	110R	*V. berlandieri cv. Boutin B* × *V. rupestris cv. du Lot*
Ruggeri 140	140Ru	*V. berlandieri cv. Boutin B* × *V. rupestris cv. du Lot*
420A Millardet et de Grasset	420A	*V. berlandieri* × *V. riparia*
Selection Oppenheim n°4	SO4	*V. berlandieri cv. Rességuier 2* × *V. riparia G. de M.*
RG2, RG3, RG4, RG6, RG7, RG8, RG9	RG series	41 B MGt (*V. vinifera* × *V. berlandieri*, clone V14D) × 110R (*V. rupestris* × *V. berlandieri*, clone 1D)

2.4.1. *Water relations*

Vine water potential was determined using a pressure chamber (model 600, PMS Instruments Company, Albany, OR, USA). Stem water potential (Ψ_{stem}) was measured on one healthy leaf per replicate (Supplementary Table 1) that had been placed 1 h before the measurement in zip-lock bags covered with a metallized high-density polyethylene reflective film (SonocoRF, Sonoco Products Co., Hartsville, South Carolina, USA) at mid-morning (9:30–11:00 solar time). In addition, leaf water potential at pre-dawn (3:00–5:00 solar time) was measured in leaves (Ψ_{PD}) also on one healthy leaf per replicate (Supplementary Table 1).

2.4.2. *Leaf gas exchange*

Leaf gas exchange rates (A_N, net photosynthesis, g_s, stomatal conductance and E, transpiration) were measured in 1 fully sun-exposed (PAR > 1500 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$) mature leaf per replicate (Supplementary Table 1) using an infrared open gas exchange analyser system (Li-6400xt, Li-cor Inc., Lincoln, Nebraska, USA). The CO_2 concentration inside the 6 cm^2 chamber was 400 $\mu mol\ CO_2{\cdot}mol^{-1}$ air, and the air flow was 500 $\mu mol\ (air){\cdot}min^{-1}$. All measurements were made between 8:30 and 11:30 solar time, the same date as for Ψ_{stem}. Intrinsic water use efficiency (WUE_i) was calculated as the ratio of A_N to g_s (Bota et al., 2001).

2.4.3. *Hydraulic conductance*

In 2020, the hydraulic conductance from root to stem ($K_{root\text{-}stem}$) was estimated using the equation proposed by Tsuda and Tyree (2000) and adapted by Romero et al. (2010), which is based on a hydraulic analogue of Ohm's law. Briefly, it consists in calculating the hydraulic conductance between the root and the stem as the quotient of the maximum leaf transpiration rate and the difference in water potential between the soil and the stem (Ψ_{stem}). The soil water potential was assumed to be in equilibrium with the Ψ_{PD}. In addition, the hydraulic conductance was scaled to the whole-plant level (K_{plant}) by extrapolating leaf transpiration (E) to the total leaf area of the vine (Nardini and Salleo, 2000; Lovisolo et al., 2002):

$$\mathrm{Kplant} = \frac{\mathrm{Eplant}}{(\Psi\mathrm{pd} - \Psi\mathrm{stem})}$$

Whole-plant transpiration (E_{plant}) was calculated by extrapolating the E to the total leaf area of the vine, which was estimated using allometric relationships (see Section 2.4.5).

2.4.4. Vine nutritional status

The nutritional status of the vines was determined by analysing the petiole tissue in each experimental season (2018, 2019 and 2020). Three leaves were taken from each replicate and mixed and grinded to make a single sample per genotype and block combination (Supplementary Table 1). All samples were washed with distilled water, dried in an oven at 65 °C for 48 h and ground. Cations were analysed in an inductively coupled plasma spectrometer (iCAP series 6500, Thermo Fisher Scientific, Franklin, MA, USA) after digestion with HNO_3-$HClO_4$ (2:1). Anions were analysed by ion chromatography (850 professional IC, Metrohm, Herisau, Switzerland). Total N concentration was determined using an elemental analyser (LECO TruSpec Micro Series, St. Joseph, MI, USA).

2.4.5. Vegetative growth and yield components

Vegetative parameters and yield components were determined for each experimental vine and season. At the end of the season, the trunk perimeter was measured with a tape measure and the trunk section was then calculated. During ripening, the number of shoots per vine were counted and the diameter of each shoot was measured. The total shoot cross-sectional area per replicate was then calculated. The total leaf area per vine (LA) was estimated using the allometric relationship between shoot basal diameter and shoot leaf area reported by Santesteban et al. (2010). In winter, the pruning mass was recorded in the field using a manual weighing scale.

At harvest, grape yield was determined by weighing all the clusters produced in all the experimental vines in each block (Supplementary Table 1). Cluster mass was calculated as the quotient of grape yield and number of clusters. Berry mass was determined in a 200-berry sample per genotype and block combination. In addition, the LA-to-yield ratio was estimated. Crop water productivity (WP_c) was estimated as the ratio between grape yield (fresh weight) and the amount of total amount of water received through rainfall and irrigation during the growing season (from 1st April to 31st August).

2.4.6. Carbon isotope ratios

Carbon isotope ratios ($\delta^{13}C$) were determined from samples of 50 berries per genotype, randomly collected at harvest in the 2018 and 2019 seasons (Supplementary Table 1). Determinations of $\delta^{13}C$ were performed in centrifuged must using an elemental analyser (NC2500, Carlo Erba Reagents, Rodano, Italy) coupled to an isotopic mass spectrometer (Thermoquest Delta Plus, ThermoFinnigan, Bremen, Germany). The carbon isotope ratio was expressed as $\delta^{13}C = [(Rs - Rb)/Rb] \times 1000$, where Rs is the $^{13}C/^{12}C$ ratio of the sample and Rb is the $^{13}C/^{12}C$ of the PDB (Pee Dee Belemnite) standard (0.0112372).

2.5. Statistical analysis

First, the data were checked for normality ($p < 0.05$) and if the data set was not normal, a logarithmic transformation of the original data was used. Second, the combined effect of rootstock (R), date and year (Y) was analysed by generalised linear mixed model (GLMM) using restricted maximum likelihood (REML), considering selected vines as a random factor in addition to the fixed factors (R, Y and R × Y). Thirdly, analysis of variance (ANOVA; $p < 0.05$) was used to evaluate the effects of rootstock (R) and block (B) and their interaction on all variables. When a significant interaction between the main factors was detected, one-way ANOVAs were performed. Fourthly, the g_s–Ψ_{stem} regressions obtained specifically for each genotype were compared by a two-way analysis of covariance (ANCOVA; $p < 0.05$) (Tortosa et al., 2019). GLMM, ANOVA, ANCOVA and post hoc tests (Duncan) were performed using the Statgraphics Centurion XVI package (version 16.0.07) (Statgraphics Technologies, The Plains, VA, USA), and regressions were obtained using SigmaPlot (version 11.0) (Systat Software, San Jose, CA, USA). Finally, a Principal Component Analysis (PCA) including physiological and agronomic variables was performed to investigate the relationship between the rootstock responses to water availability using a multivariate approach. Hierarchical clustering on principal components (HCPC) was performed to establish clusters of rootstocks with similar behaviour (HCPC from FactoMineR (Lê et al., 2008)). The data were standardized within each parameter and year prior to PCA and the HCPC. PCA and HCPC were performed with version 3.6.1 (R Studio: Integrated Development for R., Boston, MA, USA) for Windows.

3. Results and discussion

3.1. Environmental conditions and vineyard management

The meteorological conditions at the experimental site from January to September are shown in Supplementary Figure 1. Rainfall was 438, 243 and 363 mm in 2018, 2019 and 2020, respectively (Supplementary Figure 1A). These amounts of rainwater, compared to the 38–48 mm applied by irrigation, highlight the importance of soil water holding capacity in making it potentially available to the crop (Buesa et al., 2022a). The reference evapotranspiration (ET_o) from January to September was 982, 1129 and 938 mm, respectively (Supplementary Figure 1B). The highest ET_o was recorded in June and July of 2019, resulting in higher ET_o values in that year. The mean temperature over the years ranged from 13.4° to 13.6°C. The 2020 season was warmer than the previous two, with mean temperature in February and May of 2020 being more than 4 °C higher than the same months in 2018 (Supplementary Figure 1A). On the other hand, soil temperatures mainly differed between years mainly in summer, when the soil temperature for 2018 was about 2 °C higher than the mean summer soil temperature recorded for 2019 and 2020 (Supplementary Figure 1B).

3.2. Rootstock and year interactions on vine physiology

The water status and gas exchange parameters recorded in 'Tempranillo' grapevines grafted onto 12 different rootstocks are presented as seasonal averages, since there was no significant interaction between rootstock and date within each year for these parameters (Table 2). Nevertheless, rootstock genotype and year showed a significant interaction for most of the parameters measured in Block 1, suggesting that the response of rootstock genotype was modulated by environmental conditions. Nevertheless, the effect of the genotype explained 13% of the variance in these traits (Table 2), while year explained 5% and the interaction of both factors 7%. Likewise, Migicovsky et al. (2021), in a similar scion-rootstock experiment, also found an interactive effect of rootstock genotype and season on the growth-related phenotypic traits of 'Cabernet Sauvignon' and 'Chardonnay' over five years of study, which they explained it by the rainfall in the dormant season. This could also explain the differences in our study, where vine water status and gas exchange parameters were enhanced in 2018, when rainfall was higher in the dormant season (Supplementary Figure 1A).

3.2.1. Vine water relations

The lowest seasonal stem water potential (Ψ_{stem}) values (more negative) were reported for some of the RG rootstocks (Table 2). For instance, RG6 showed the lowest average values in 2018 and 2019 (−1.11 and −1.02 MPa, respectively) and intermediate values in 2020 (−0.75 MPa). On the contrary, 140Ru and RG8 were the rootstocks that more consistently showed the highest Ψ_{stem} (less negative values) over the seasons, followed by 110R and 420A. It should be noted that the

Table 2
Seasonal values of stem water potential (Ψstem), stomatal conductance (gs), net photosynthesis (AN) and intrinsic water use efficiency (WUEi) of 'Tempranillo' grapevines grafted onto 12 rootstocks measured early-mid morning in block 1 across three seasons and in block 2 in 2020 in Miranda de Arga, Navarra, Spain.

Block	Year	Rootstock	Ψ_{stem} (Mpa)				g_s (mol $CO_2 \cdot m^{-2} \cdot s^{-1}$)				A_N (µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$)				WUE_i (µmol $CO_2 \cdot mol\ H_2O$)			
Block 1	**2018**	**1103P**	-0.87	±	0.04	b	0.201	±	0.021	ab	12.1	±	0.6	bc	73.9	±	4.0	efg
		110R	-0.70	±	0.04	c	0.262	±	0.021	bcd	14.7	±	0.6	d	66.8	±	4.0	def
		140Ru	-0.56	±	0.04	d	0.316	±	0.019	de	17.4	±	0.6	e	40.0	±	3.7	a
		420A	-0.72	±	0.04	c	0.290	±	0.018	cde	15.0	±	0.5	d	63.9	±	3.4	cde
		RG2	-0.92	±	0.04	b	0.183	±	0.018	a	11.0	±	0.5	ab	80.6	±	3.4	g
		RG3	-0.93	±	0.04	b	0.249	±	0.021	bc	14.8	±	0.6	d	55.0	±	4.0	bc
		RG4	-1.06	±	0.04	a	0.227	±	0.019	abc	14.8	±	0.6	d	57.7	±	3.7	cd
		RG6	-1.11	±	0.04	a	0.207	±	0.021	ab	14.5	±	0.6	d	71.6	±	4.0	efg
		RG7	-0.69	±	0.03	c	0.272	±	0.016	cde	10.2	±	0.5	a	76.5	±	3.0	fg
		RG8	-0.86	±	0.04	b	0.327	±	0.021	e	17.3	±	0.6	e	45.1	±	4.0	ab
		RG9	-0.76	±	0.04	c	0.277	±	0.021	cde	10.9	±	0.6	ab	79.3	±	4.0	g
		SO4	-0.88	±	0.04	b	0.262	±	0.019	bcd	13.3	±	0.6	cd	69.3	±	3.7	defg
		CV	19%				18%				17%				20%			
	2019	**1103P**	-0.86	±	0.04	bc	0.232	±	0.015	ab	15.6	±	0.5	abc	68.7	±	2.6	de
		110R	-0.70	±	0.06	de	0.314	±	0.015	de	18.2	±	0.5	de	58.8	±	2.6	abc
		140Ru	-0.55	±	0.05	e	0.354	±	0.017	ef	19.3	±	0.6	e	55.4	±	2.9	ab
		420A	-0.67	±	0.05	e	0.317	±	0.017	de	19.3	±	0.6	e	62.4	±	2.9	bcd
		RG2	-0.83	±	0.05	cd	0.203	±	0.017	a	14.3	±	0.6	a	73.1	±	2.9	ef
		RG3	-1.00	±	0.05	ab	0.259	±	0.017	bc	17.4	±	0.6	cd	68.5	±	2.9	de
		RG4	-0.97	±	0.05	abc	0.244	±	0.016	abc	16.2	±	0.6	bc	67.2	±	2.8	cde
		RG6	-1.02	±	0.05	a	0.218	±	0.017	ab	16.7	±	0.6	bcd	79.2	±	2.9	f
		RG7	-0.87	±	0.05	bc	0.258	±	0.017	bc	15.2	±	0.6	ab	60.7	±	2.9	bcd
		RG8	-0.62	±	0.05	e	0.394	±	0.017	f	20.1	±	0.6	e	51.3	±	2.9	a
		RG9	-0.87	±	0.05	bc	0.255	±	0.016	bc	15.2	±	0.6	ab	61.3	±	2.7	bcd
		SO4	-0.87	±	0.05	bc	0.286	±	0.017	cd	19.3	±	0.6	e	69.1	±	2.9	de
		CV	19%				21%				11%				12%			
	2020	**1103P**	-0.79	±	0.03	bc	0.288	±	0.018	bc	18.4	±	0.7	bc	66.9	±	2.5	cd
		110R	-0.68	±	0.03	de	0.384	±	0.021	d	18.8	±	0.8	bc	50.3	±	2.9	a
		140Ru	-0.59	±	0.03	e	0.344	±	0.021	cd	20.3	±	0.8	c	59.5	±	2.9	bc
		420A	-0.71	±	0.03	cd	0.337	±	0.021	cd	17.5	±	0.8	b	56.3	±	2.9	ab
		RG2	-0.92	±	0.03	a	0.225	±	0.021	a	12.4	±	0.8	a	56.4	±	2.9	ab
		RG3	-0.84	±	0.03	ab	0.321	±	0.021	cd	17.3	±	0.8	b	55.8	±	2.9	ab
		RG4	-0.79	±	0.03	bc	0.326	±	0.018	cd	17.3	±	0.7	b	53.5	±	2.5	ab
		RG6	-0.75	±	0.03	bcd	0.361	±	0.021	d	18.4	±	0.8	bc	52.0	±	2.9	ab
		RG7	-0.77	±	0.03	bcd	0.215	±	0.021	a	12.6	±	0.8	a	60.5	±	2.9	bcd
		RG8	-0.61	±	0.03	e	0.352	±	0.021	d	18.6	±	0.8	bc	54.0	±	2.9	ab
		RG9	-0.78	±	0.03	bcd	0.238	±	0.021	ab	13.9	±	0.8	a	60.4	±	2.9	bcd
		SO4	-0.77	±	0.03	bcd	0.285	±	0.021	bc	18.8	±	0.8	bc	68.6	±	2.9	d
		CV	13%				18%				15%				10%			
Significance of effects		**R**	*** (17%)				*** (15%)				*** (9%)				*** (9%)			
		Year	* (1%)				*** (5%)				*** (12%)				ns (1%)			
		R*Y	** (8%)				** (9%)				ns (3%)				* (9%)			
Block 2	**2020**	**1103P**	-1.00	±	0.03	bcd	0.160	±	0.012	ef	10.1	±	0.8	bcd	81.2	±	3.6	b
		110R	-0.89	±	0.03	fg	0.130	±	0.012	bcde	10.1	±	0.8	bcd	96.4	±	3.4	c
		140Ru	-1.05	±	0.03	bc	0.115	±	0.012	abcd	7.9	±	0.8	ab	79.9	±	3.6	b
		420A	-0.91	±	0.03	efg	0.154	±	0.013	def	11.1	±	0.8	d	76.1	±	3.6	ab
		RG2	-0.96	±	0.03	cdeg	0.113	±	0.012	abc	8.3	±	0.8	abc	87.1	±	3.6	bc
		RG3	-1.08	±	0.03	b	0.098	±	0.012	ab	7.7	±	0.8	ab	83.3	±	3.4	b
		RG4	-1.17	±	0.03	a	0.144	±	0.012	cdef	10.7	±	0.8	cd	84.3	±	3.6	b
		RG6	-1.01	±	0.03	bcd	0.160	±	0.012	ef	10.5	±	0.8	cd	77.5	±	3.4	b
		RG7	-0.84	±	0.03	g	0.137	±	0.012	bcde	10.0	±	0.8	bcd	84.9	±	3.4	b
		RG8	-1.01	±	0.03	bcd	0.140	±	0.012	cde	9.7	±	0.8	bcd	82.7	±	3.4	b
		RG9	-0.99	±	0.03	bcde	0.090	±	0.012	a	6.9	±	0.8	a	80.1	±	3.4	b
		SO4	-0.95	±	0.03	def	0.182	±	0.012	f	11.2	±	0.8	d	66.9	±	3.4	a
		CV	9%				20%				15%				9%			
Significance of effects		**R**	* (8%)				*** (7%)				*** (7%)				ns (2%)			
		Block	*** (25%)				*** (47%)				*** (40%)				*** (34%)			
		R*B	* (6%)				** (5%)				* (4%)				** (8%)			

Data are averages and standard errors of six vines at one date in 2018 and at two dates in 2019 and 2020. Within each column, season and block, different letters indicate significant differences (Duncan test; $p>0.05$) and CV the coefficient of variation. *, **, *** and ns indicate significant differences at the 0.05, 0.01, 0.001 levels of probability and non-significant, respectively. Within each factor, the percentage of explained variance is indicated between brackets.

coefficient of variation (CV) of Ψ_{stem} found among the rootstocks ranged from 13% to 19% over the years and that, in general, the RG rootstocks showed on average 0.13 MPa more negative Ψ_{stem} values than the commercial ones (Table 2).

3.2.2. *Leaf gas exchange parameters*

Stomatal conductance (g_s) in Block 1 showed significant differences among the rootstocks, with CV ranging from 18% to 21% over the seasons (Table 2). Overall, the RG2, RG3, RG4 and RG6 showed lower g_s compared to that of 140Ru, but also compared to RG8 rootstock, with some exceptions found in 2020. RG2 stood out for having the lowest g_s values, ranging from 0.183 to 0.225 mol $CO_2 \cdot m^{-2} \cdot s^{-1}$ over the seasons. On the contrary, the g_s for 140Ru and RG8 ranged between 0.316 and 0.354 mol $CO_2 \cdot m^{-2} \cdot s^{-1}$ and 0.327 and 0.394 mol $CO_2 \cdot m^{-2} \cdot s^{-1}$, respectively. These values referred to a mild or absence of water stress, which was defined for a range of g_s from 0.150 to 0.400 mol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (Flexas et al., 2002; Cifre et al., 2005). This was the threshold around which most rootstocks ranged on average over the seasons (Table 2), with a few exceptions in the RG genotypes. However, this does not detract from the fact that the range of g_s at some point in the season reflected moderate-to-severe stress, with g_s values between 0.05 and 0.15 and < 0.05 mol $CO_2 \cdot m^{-2} \cdot s^{-1}$, respectively (Fig. 1A).

Plant water status is closely related to carbon assimilation rates and WUE_i, as previously reported (Chaves et al., 2010; Pou et al., 2008; Zúñiga et al., 2018; Villalobos-González et al., 2019). Thus, our results showed that the rootstocks inducing higher g_s in the scion had the highest values of A_N (i.e., 140Ru, RG8, 110R, and SO4) (Table 2). Conversely, the lowest values of A_N were recorded on the RG2, RG7 and RG9 rootstocks. According to previous studies, the limited photosynthetic performance could be triggered by passive (hydraulic signals) or active (upregulation of abscisic acid) signals (Pou et al., 2008; Tombesi et al., 2015). Accordingly, the review conducted by Marín et al. (2020) showed that traditional rootstocks can significantly affect scion g_s and leaf A_N under water deficit conditions. Moreover, new rootstocks such as M4 have been reported to perform better under moderate-to-severe water deficit compared to rootstocks with low tolerance to water deficit (i.e. SO4 or 101–14 Millardet et De Grasset) (Meggio et al., 2014; Merli et al., 2016) and with the drought tolerant rootstock 1103P (Frioni et al., 2020).

The WUE_i values tended to be higher in the RG rootstocks, with the exception of RG8 and, in some seasons RG3, RG4 and RG6 (Table 2). It is well known that vines with lower water availability (i.e. less irrigation) exhibit higher WUE_i values (Bota et al., 2001; Torres et al., 2021). Therefore, our results suggest that some RG rootstocks increased WUE_i by impairing both vine water status and gas exchange rates.

3.2.3. Stomatal conductance response to stem water potential

The wide range of water stress experienced by all rootstocks allowed studying stomatal responses by using the relationship between stomatal conductance g_s and Ψ_{stem} (Bota et al., 2016). As expected, the relationship between Ψ_{stem} and g_s was highly significant across seasons (Fig. 1A), as well as within each rootstock (Fig. 1B), with the sole exception of RG7. It is well known that low values of Ψ_{stem} are associated with reduced g_s, because vines subjected to mild to moderate water deficit close their stomata as an early response to water deficit in order to reduce water loss and consequently carbon assimilation (Chaves et al., 2003; Medrano et al., 2003). However, as indicated by the low value of the Pearson's coefficient of this regression (Fig. 1A), water potential regulation was not tightly linked to stomatal control. This leaves room to discuss the effect of the rootstock in modulating stomatal behaviour (see following section) (Lovisolo et al., 2010; Tramontini et al., 2013).

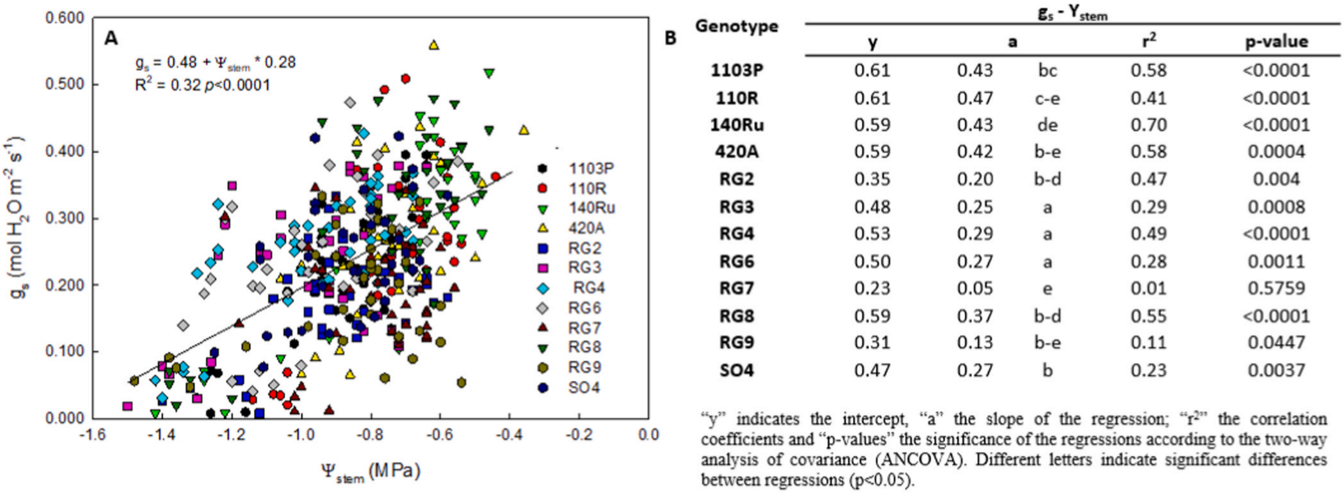
3.3. Rootstock and Block interactions on vine physiology

3.3.1. Vine water relations and leaf gas exchange parameters

Differences in vine vigour were observed between the field blocks (Supplementary Table 2). This was related to the water holding capacity of the soil between the blocks, as evidenced by the large differences in Ψ_{PD} (in DOY 205 in 2020, Block 1 showed on average −0.23 ± 0.01 MPa while Block 2 showed −0.46 ± 0.01 MPa), a proxy for the matric potential of the soil. Therefore, during the 2020 season, an additional study of the block was carried out on the water relations and the gas exchange parameters of the 'Tempranillo' vines grafted onto the 12 rootstocks (Tables 2 and 3). The results showed a significant interaction between block and rootstock genotype for most of the parameters measured, except for the Ψ_{PD}. Overall, all the rootstocks showed lower Ψ_{PD}, Ψ_{stem} and leaf gas exchange rates in the Block 2 than in the Block 1 (Tables 2 and 3). This indicates that the vines in Block 2 suffered higher water deficit (moderate water stress) than those in Block 1 (mild water stress). Block explained 22% of the variance in Ψ_{PD}, while genotype explained only 2% (Table 2). This was likely due to the lower water holding capacity of the soil in Block 2 compared to Block 1 (i.e. greater presence of pebbles and shallower soil). Within each block, the CV of Ψ_{stem}, $\Psi_{PD,}$ g_s, and A_N were fairly similar, with some RG rootstocks showing the lowest values, but some differences were recorded between blocks (Tables 2 and 3). On the other hand, the 140Ru, 110R and RG8 rootstocks performed better in the Block 1, whereas, in the Block 2, the best photosynthetic performance was recorded for 420A and SO4 rootstocks. This interactive effect was also observed in the WUE_i, where 110R showed the highest and lowest values in the Block 2 and Block 1, respectively, while the opposite behaviour was recorded for SO4 (Table 2).

It is well known that the structure and development of grapevine root system depends on both environmental and genetic factors (Marín et al., 2020). In this regard, Renouf et al. (2010) showed that the potential quality of a soil can be improved by the correct choice of rootstock, but in soils with lower potential quality, the rootstock genotype cannot compensate for the loss of grapevine performance, since root distribution is mainly determined by soil properties, while the rootstock modifies root density and root activity (Smart et al., 2006; Keller, 2010; Alsina et al., 2011).

The gradient between Ψ_{stem} and Ψ_{PD} showed that the highest difference was recorded in RG2, while 140Ru and RG8 had the lowest difference (Table 3). These results, together with the higher slopes of the relationship between g_s and Ψ_{stem} for 140Ru and RG8 (Fig. 1B), suggested a better stomatal regulation compared to RG2.



Genotype	g_s - Ψ_{stem}				
	y	a		r^2	p-value
1103P	0.61	0.43	bc	0.58	<0.0001
110R	0.61	0.47	c-e	0.41	<0.0001
140Ru	0.59	0.43	de	0.70	<0.0001
420A	0.59	0.42	b-e	0.58	0.0004
RG2	0.35	0.20	b-d	0.47	0.004
RG3	0.48	0.25	a	0.29	0.0008
RG4	0.53	0.29	a	0.49	<0.0001
RG6	0.50	0.27	a	0.28	0.0011
RG7	0.23	0.05	e	0.01	0.5759
RG8	0.59	0.37	b-d	0.55	<0.0001
RG9	0.31	0.13	b-e	0.11	0.0447
SO4	0.47	0.27	b	0.23	0.0037

"y" indicates the intercept, "a" the slope of the regression; "r^2" the correlation coefficients and "p-values" the significance of the regressions according to the two-way analysis of covariance (ANCOVA). Different letters indicate significant differences between regressions (p<0.05).

Fig. 1. General relationship between stomatal conductance (g_s) and stem water potential (Ψ_{stem}) in 'Tempranillo' grapevines grafted onto 12 rootstocks across the 2018–2020 seasons (A) and the individual linear regression equation for each rootstock (B).

Table 3
Predawn water potential (Ψ_{PD}), gradient between Ψ_{stem} and Ψ_{PD}, root-to-shoot hydraulic conductance ($K_{root\text{-}stem}$) and whole plant hydraulic conductance (K_{plant}) of 'Tempranillo' grapevines grafted onto 12 rootstocks per block, and their interaction across 2020 season in Miranda de Arga, Navarra, Spain.

Block	Rootstock	Ψ_{PD} (Mpa)		$\Delta\Psi_{PD}$ - Ψ_{stem} (MPa)		$K_{root\text{-}stemt}$ (mmol $H_2O \cdot m^{-2} \cdot s^{-1} \cdot MPa^{-1}$)		K_{plant} (mmol $H_2O \cdot plant^{-1} \cdot s^{-1} \cdot MPa^{-1}$)	
Block 1	**1103P**	-0.21 ± 0.02	ab	0.58 ± 0.03	c	15.1 ± 1.2	cd	52.6 ± 5.7	cde
	110R	-0.21 ± 0.02	b	0.47 ± 0.03	ab	16.1 ± 1.2	de	58.7 ± 6.1	def
	140Ru	-0.15 ± 0.02	c	0.44 ± 0.03	a	19.2 ± 1.3	e	68.8 ± 6.1	ef
	420A	-0.21 ± 0.02	ab	0.49 ± 0.03	abc	14.4 ± 1.3	cd	60.9 ± 6.4	def
	RG2	-0.21 ± 0.02	ab	0.70 ± 0.03	d	8.6 ± 1.2	ab	16.9 ± 5.7	a
	RG3	-0.26 ± 0.02	a	0.58 ± 0.03	c	12.8 ± 1.2	cd	43.4 ± 5.7	cd
	RG4	-0.23 ± 0.02	ab	0.56 ± 0.03	bc	16.2 ± 1.2	de	63.7 ± 5.7	ef
	RG6	-0.19 ± 0.02	bc	0.57 ± 0.03	bc	13.0 ± 1.2	cd	43.1 ± 5.7	cd
	RG7	-0.20 ± 0.02	bc	0.57 ± 0.03	bc	7.5 ± 1.2	a	19.5 ± 5.7	ab
	RG8	-0.19 ± 0.02	bc	0.41 ± 0.03	a	19.4 ± 1.2	e	73.9 ± 5.7	f
	RG9	-0.23 ± 0.02	ab	0.55 ± 0.03	bc	11.9 ± 1.2	bc	35.6 ± 5.7	bc
	SO4	-0.21 ± 0.02	ab	0.56 ± 0.03	bc	13.7 ± 1.2	cd	56.2 ± 5.7	def
	CV	12%		14%		26%		37%	
Block 2	**1103P**	-0.39 ± 0.02	a	0.61 ± 0.03	abc	11.2 ± 0.8	d	29.0 ± 2.8	e
	110R	-0.31 ± 0.02	d	0.58 ± 0.03	ab	6.2 ± 0.8	a	11.1 ± 2.8	ab
	140Ru	-0.37 ± 0.02	abc	0.67 ± 0.03	bcd	8.3 ± 0.8	abc	24.0 ± 2.8	de
	420A	-0.32 ± 0.02	cd	0.59 ± 0.03	abc	8.0 ± 0.9	abc	18.5 ± 2.9	bcd
	RG2	-0.31 ± 0.02	d	0.65 ± 0.03	abcd	8.4 ± 0.8	abc	6.6 ± 2.9	a
	RG3	-0.32 ± 0.02	cd	0.75 ± 0.03	de	7.0 ± 0.8	ab	9.9 ± 2.8	ab
	RG4	-0.38 ± 0.02	ab	0.79 ± 0.03	e	7.7 ± 0.8	abc	17.7 ± 2.8	bcd
	RG6	-0.32 ± 0.02	d	0.69 ± 0.03	cd	9.1 ± 0.8	bcd	22.1 ± 2.8	cde
	RG7	-0.28 ± 0.02	d	0.56 ± 0.03	a	8.1 ± 0.8	abc	13.9 ± 2.8	abc
	RG8	-0.33 ± 0.02	bcd	0.68 ± 0.03	bcd	9.9 ± 0.8	cd	21.3 ± 2.8	cde
	RG9	-0.34 ± 0.02	abcd	0.65 ± 0.03	abcd	7.9 ± 0.8	abc	10.6 ± 2.8	ab
	SO4	-0.31 ± 0.02	d	0.63 ± 0.03	abc	11.6 ± 0.8	d	27.5 ± 2.8	e
	CV	10%		11%		19%		41%	
Significance of effects	**R**	ns (2%)		*** (12%)		*** (11%)		*** (19%)	
	Block	*** (22%)		*** (14%)		*** (19%)		*** (38%)	
	R*B	ns (3%)		** (10%)		** (9%)		*** (8%)	

Data are averages and standard errors of six plants per rootstock and block in two dates across the season. Within each column and block, different letters indicate significant differences (Duncan test; $p>0.05$) and CV the coefficient of variation. *, **, *** and ns indicate significant differences at the 0.05, 0.01, 0.001 levels of probability and non-significant, respectively. Within each factor, the percentage of explained variance is indicated between brackets.

3.3.2. Hydraulic conductance

Our results confirmed that under a mild soil water deficit (i.e. $\Psi_{PD} > -0.4$ MPa), the rootstock genotype plays an important role in the hydraulic conductance of the vines (Table 3) (Labarga et al., 2023). In the $K_{root\text{-}stem}$, the CV among rootstocks was 26% and 19% in Block 1 and 2, respectively, while in the K_{plant} was 37% and 41%, respectively. It is noteworthy that both hydraulic conductances were in good agreement with each other, despite the fact that the $K_{root\text{-}stem}$ calculation does not take into account the leaf area of the vine, in contrast to the K_{plant}. This indicates the importance of the hydraulic conductance for the vegetative vigour of the scion. Thus, RG2 and RG7, which had low vigour, g_s and A_N, also had low $K_{root\text{-}stem}$ and K_{plant}, whereas the invigorating RG8 and 140Ru tended to have the highest values of the hydraulic conductances (Table 3 and Supplementary Table 2). The latter, as indicated above, stood out for their good stomatal regulation. Overall, the lower $K_{root\text{-}stem}$ and K_{plant} observed in the RG than in the commercial rootstocks has been reported to indicate a lower water supply to the shoots, explained by a lower water status (Romero et al., 2010a; de Souza et al., 2022). Nevertheless, the significant interaction between rootstock and block for these hydraulic parameters highlights the importance of the soil in modulating the effect of the rootstock genotype on the physiological response.

3.4. Rootstock genotype effects on vegetative parameters and yield components

3.4.1. Vegetative growth

The effect of the rootstock genotype on the vegetative development and the yield components across seasons showed a range of variation similar to that of gas exchange parameters between rootstocks (Tables 2 and 4). The mean values of total leaf area (LA) for all the seasons ranged from 1.7 to 4.1 m^2/vine, with 140Ru, 110 R and RG8 being the rootstocks with the highest vigour and RG2, RG3 and RG9 the lowest (Table 4). The CV of LA among rootstocks accounted for 21%. Consistent differences among rootstocks were found in the pruning mass (CV of 39%) and shoots section (CV of 17%), but also trunk section (CV of 25%). Rootstock genotype had a strong effect on vine vigour, with pruning mass ranging from 1.2 (140Ru) to 0.2 $kg \cdot vine^{-1}$ (RG2), and the sum of shoot cross-sectional areas ranging from 436 to 918 mm^2. However, no significant effect was found on the number of shoots per vine. This is, to some extent, an expected result, since in a spur pruned unilateral cordon, pruners usually attempt to maintain equal the number of spurs per vine, regardless of the vigour of the vine. It is remarkable that the differences in vegetative development among rootstocks in LA, pruning mass and shoots section do not seem to be exclusive to the three experimental seasons, as the trunk section already showed a cumulative effect on the vigour of the vines in the first season (data not shown).

3.4.2. Yield components

Among the yield components recorded over the three seasons, rootstock genotype strongly influenced the number of clusters per vine (CV of 23%), the cluster mass (CV of 31%) and the yield (CV of 42%) (Table 4), but not berry mass (data not shown). Thus, the RG2 rootstock led to a decrease in the number of clusters per vine, and also to the lowest cluster mass and consequently to the lowest yield. This rootstock induced a very poor vine performance in this scion, as already reported by Marín et al. (2022a), although these authors did not report such a strong effect when grafted on Syrah. This fact could be a direct consequence of variability in the scion × rootstock interaction, but a certain degree of incompatibility between RG2 and Tempranillo cannot be discarded (Tedesco et al., 2022). On the other hand, RG8, RG3, and especially, 140Ru were the rootstocks that increased the yield components. Overall, the other RG rootstocks consistently showed a reduction in both vegetative development and yield components compared to the commercial rootstocks. The rootstock can indeed influence bud fertility (Guilpart et al., 2014), which usually shows a positive relationship with

Table 4
Mean values of vine performance parameters of ‘Tempranillo’ grapevines grafted onto 12 rootstocks grown in block 1 at Miranda de Arga, Navarra, Spain, in the 2018, 2019, and 2020 seasons.

Year	Rootstock	LA($m^2 \cdot vine^{-1}$)	Pruningmass($kg \cdot vine^{-1}$)	Trunksection(cm^2)	Shootssection($mm^2 \cdot vine^{-1}$)	Clusterspervine	Clustermass(g)	Yield($kg \cdot vine^{-1}$)	LA − to − yield($m^2 \cdot kg^{-1}$)	WP_c($kg \cdot m^{-3}$)
2018-2020	1103P	3.4 ± 0.1 b-e	0.9 ± 0.1 c-f	9.5 ± 1.0 bc	818.4 ± 37 c-e	11.4 ± 0.0 bc	319 ± 46 b-d	3.6 ± 0.2 cd	1.0 ± 0.1 a	4.9 ± 0.6 cd
	110R	3.7 ± 0.4 de	1.0 ± 0.1 d-f	10.6 ± 1.2 cd	844.6 ± 52 de	12.9 ± 0.4 c	295 ± 44 b-d	3.8 ± 0.2 cd	1.0 ± 0.1 a	5.1 ± 0.6 cd
	140Ru	4.1 ± 0.4 e	1.2 ± 0.1 f	10.2 ± 0.7 bc	918.2 ± 38 e	13.9 ± 0.6 c	399 ± 64 d	5.6 ± 0.3 e	0.8 ± 0.1 a	7.6 ± 1.3 e
	420A	3.2 ± 0.4 b-e	0.9 ± 0.2 c-e	7.5 ± 0.6 b	781.2 ± 80 b-e	12.1 ± 0.3 c	308 ± 61 b-d	3.8 ± 0.3 cd	0.9 ± 0.1 a	5.1 ± 0.9 cd
	RG2	1.7 ± 0.2 a	0.2 ± 0.0 a	4.0 ± 0.5 a	435.5 ± 31 a	4.7 ± 1.5 a	85 ± 2 a	0.4 ± 0.2 a	5.0 ± 1.4 b	0.5 ± 0.2 a
	RG3	3.1 ± 0.2 b-d	0.7 ± 0.1 b-d	8.8 ± 0.9 bc	761.6 ± 27 b-d	14.1 ± 0.7 c	279 ± 26 b-d	3.9 ± 0.2 de	0.8 ± 0.1 a	5.4 ± 0.7 de
	RG4	3.1 ± 0.4 b-d	0.6 ± 0.1 b-d	11.2 ± 1.1 cd	721.0 ± 44 b-d	13.2 ± 0.8 c	237 ± 20 bc	3.1 ± 0.2 b-d	1.0 ± 0.1 a	4.2 ± 0.3 b-d
	RG6	2.7 ± 0.2 bc	0.6 ± 0.1 bc	8.3 ± 0.8 bc	695.0 ± 49 b-d	11.2 ± 1.1 bc	255 ± 41 bc	2.9 ± 0.3 b-d	1.0 ± 0.2 a	3.9 ± 0.8 b-d
	RG7	2.5 ± 0.1 ab	0.4 ± 0.1 ab	7.4 ± 0.3 b	633.3 ± 24 b	10.7 ± 1.8 bc	190 ± 9 ab	2.0 ± 0.2 a-c	1.3 ± 0.2 a	2.8 ± 0.5 a-c
	RG8	3.7 ± 0.2 de	1.1 ± 0.1 ef	13.1 ± 1.5 d	848.2 ± 17 de	13.0 ± 0.6 c	322 ± 29 b-d	4.2 ± 0.2 de	0.9 ± 0.1 a	5.8 ± 1.0 de
	RG9	2.6 ± 0.2 b	0.6 ± 0.1 b-d	9.1 ± 0.9 bc	677.0 ± 60 b-d	8.4 ± 0.8 b	202 ± 28 ab	1.6 ± 0.2 ab	1.6 ± 0.0 a	2.2 ± 0.1 ab
	SO4	3.5 ± 0.3 c-e	1.0 ± 0.1 d-f	8.9 ± 0.8 bc	813.7 ± 56 c-e	11.2 ± 1.7 bc	339 ± 45 cd	3.8 ± 0.2 cd	1.0 ± 0.2 a	5.1 ± 0.8 cd
CV		21%	39%	25%	17%	5%	23%	42%	87%	42%
Significance effect		***	***	***	***	***	***	***	***	***

Data are averages and standard errors of ten vines of the block 1 per rootstock and season. indicate significant differences at the 0.001 level of probability. Within each column, different letters indicate significant differences (Duncan test; p>0.05) and CV the coefficient of variation.

the invigorating effect of the rootstock (Romero et al., 2018; Marín et al., 2019). The contrasting response of RG2 and RG8 to the other RG rootstocks is notable as the parentals are the same. Therefore, given the general response of some of the RG rootstocks, the hybridization carried out did not improve the performance of the ‘Tempranillo’ scion in comparison with the most widely used commercial rootstocks. Nevertheless, the significant differences in the vegetative and reproductive growth of the vines among the rootstocks did not have a significant effect on the vine equilibrium indexes, since no differences were found in the LA-to-yield ratio, except for RG2 (Table 4).

WP_c, was also influenced by the rootstock genotype (Table 4). The RG2 rootstock showed the lowest WP_c values, whereas 140Ru resulted in the highest. Overall, the commercial rootstocks along with RG3 and RG8 tended to have a higher WP_c than the other RG rootstocks. Some grapevine genotypes can show very low WUE_i but relatively high yield, as that WP_c can be decoupled from the WUE_i in grapevine (Tomás et al., 2012; Merli et al., 2015; Medrano et al., 2015b; Tortosa et al., 2020; Buesa et al., 2021). Therefore, biomass was explained by the net carbon assimilation (A_N) of the leaves rather than its efficiency ($A_N/g_s = WUE_i$).

3.5. *Vine nutritional status*

In order to assess whether if differences among rootstocks in vine performance and physiology could be explained by differences in vine nutritional status, petiole analysis of macronutrients (N, P, K and Mg) and micronutrients (Fe, and Mn) were conducted during ripening stage (Supplementary Table 3). The results showed that the petiole nutrient concentrations were adequate for this cultivar and growing area (García-Escudero et al., 2013; Romero et al., 2010b). Even for Mg, where an antagonism with the high soil K levels would be expected (Stockdale et al., 2013), no deficiencies were found. In addition, little difference was observed among the rootstocks, except for a higher concentration of N in RG9, RG7 and RG2 compared to 110R and a higher content of K in RG8 compared to RG9. The effect of rootstock genotype on N content has been reported by several authors (Fisarakis et al., 2004; Köse et al., 2016; Somkuwar et al., 2015; Williams and Smith, 1991; Wooldridge et al., 2010: Bianchi et al., 2018), although this is not always confirmed (Angyal et al., 2002; Bavaresco et al., 1993). The K increment has been identified as a mechanism to enhance tolerance to water stress (Bianchi et al., 2018). In contrast, Bianchi et al. (2020) found a significant effect of the genotype of a new “G series” of *Vitis* hybrids on the petiole content of N, K, Ca, Mg, Na, Mn and Cu.

These results suggest that rootstock genotype hardly modulates the petiole nutrient content of Tempranillo cultivar and therefore does not explain the different behaviour found among rootstocks in terms of vine physiology and performance.

3.6. *Relationship between ecophysiological traits and agronomic performance*

A correlation matrix between pairs of physiological and vine performance variables was performed, and linear relationships were shown (Supplementary Figure 2). Vine water status, gas exchange parameters and vegetative and reproductive growth parameters were positively correlated, but WUE_i was negatively correlated with all parameters. It is worth noting that all relationships are statistically significant, with mean Pearson’s coefficients between physiological and agronomic parameters greater than 0.50. These relationships confirm that the timing of the physiological measurements was representative of the seasons. This was also supported by the relationship between $\delta^{13}C$ and WUE_i depicted in Fig. 2. The measurement of the berry juice $\delta^{13}C$ is recognised as a good indicator of the seasonal water deficit (Gaudillère et al., 2002; Santesteban et al., 2015). In this regard, it is worth noting the wide range of variation observed in the $\delta^{13}C$ values due to the rootstock effect. In our trial, the WUE_i and the berry must $\delta^{13}C$ also showed a highly significant linear relationship, as reported by previous researchers in

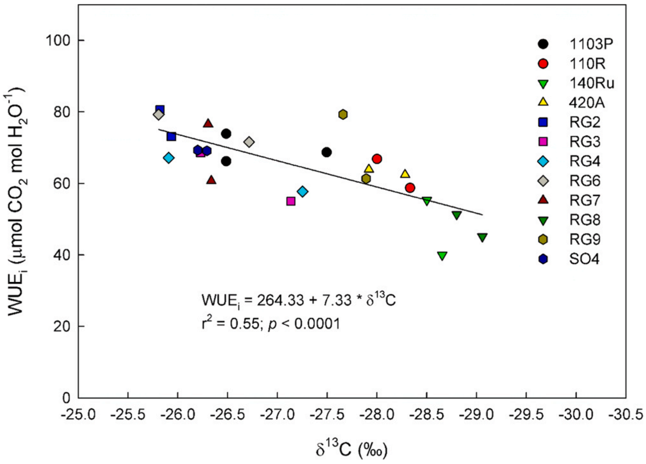


Fig. 2. Relationships between carbon isotope discrimination ($\delta^{13}C$) measured at harvest and mean intrinsic water use efficiency (WUE_i) in a 'Tempranillo' vineyard grafted onto 12 rootstocks across the 2018 and 2019 seasons in Miranda de Arga, Navarra, Spain.

studies with Tempranillo, Grenache and Cabernet Sauvignon cultivars (Bchir et al., 2016; Torres et al., 2021; Buesa et al., 2022b). These results also highlighted that, despite the interaction between rootstock and season, all physiological parameters were strongly related to vine performance, resulting in good indicators of the WP_c.

Closer examination of the relationships between grapevine WP_c and vine water status (g_s and Ψ_{stem}) for the full dataset (Fig. 3A, B) showed that Ψ_{stem} explained vine yield responses to a lesser extent than g_s. On the other hand, WP_c and WUE_i showed a negative relationship across seasons (Fig. 3C). This implies that, despite improvements in net carbon assimilation efficiency at the leaf level, rootstocks that were able to maintain higher photosynthetic rates were more efficient in terms of grape yield (Merli et al., 2016; Romero et al., 2018). This could be explained by a greater capacity to uptake and transport water from the soil to the plant, since most yielding rootstocks were also the most vigorous. Indeed, when K_{plant} increased by 10 mmol H_2O $plant^{-1}\cdot s^{-1}\cdot MPa^{-1}$, WP_c increased by 1.1 $Kg\cdot m^{-3}$ (Fig. 4B). Therefore, rootstocks maintaining a better water status induced a high performance of the scion, and thus a higher transpiration potential (Fig. 3). In any case, it should be noted that a less vigorous rootstock is not necessarily less efficient in the use of resources, but in some circumstances, it may simply use resources at a different pace (Simonneau et al., 2017). In this case, water and nutrient resources may remain available in the soil for later stages of the season or for future seasons.

We aimed to know how the vigour-inducing rootstocks could maintain better water status and photosynthetic rates than the low vigour-inducers. Fig. 4A shows the significant linear relationship between K_{plant} and g_s, suggesting that the differences among rootstocks in vine water status are presumably related to hydraulic signalling (Tombesi et al., 2015). This result confirms that the rootstock genotype affects vine growth through shifts in vine hydraulic traits (de Herralde et al., 2006). Similarly, the K_{plant} showed a linear positive and strong relationship with the WP_c (Fig. 4B). Therefore, the large differences found in K_{plant} among rootstocks are shown to be key to vine performance. Further studies are needed to elucidate the causes of these remarkable differences in K_{plant}. They could arise from differences in soil exploration capacity, root morphology, vascular anatomy, root osmotic adjustment, water uptake dynamics, or even in the affinity with the scion cultivar

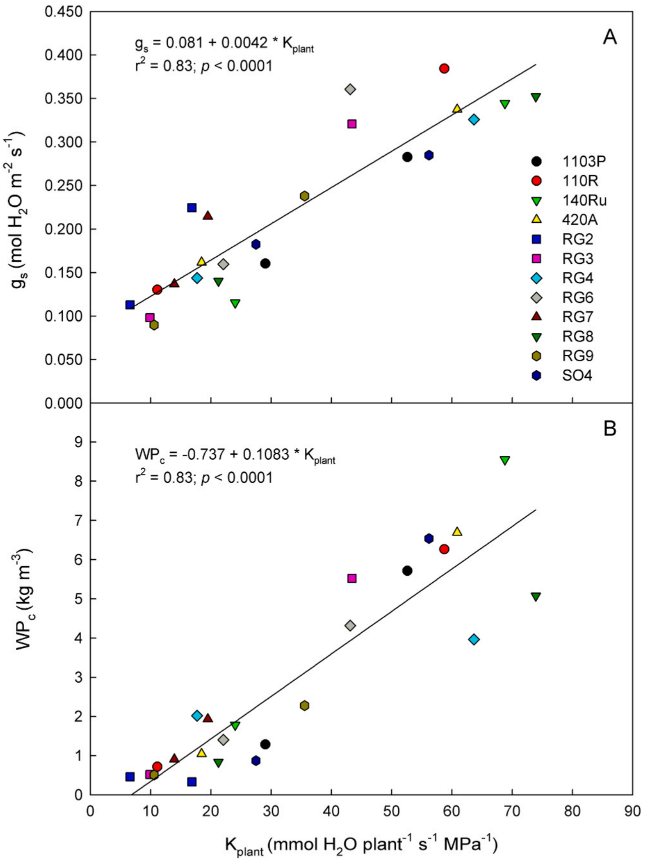


Fig. 4. Relationships between plant hydraulic conductance (K_{plant}) and (A) stomatal conductance (g_s) and (B) crop productivity (WP_c) in the block 1 and 2 of a 'Tempranillo' vineyard grafted onto 12 rootstocks in 2020 in Miranda de Arga, Navarra, Spain.

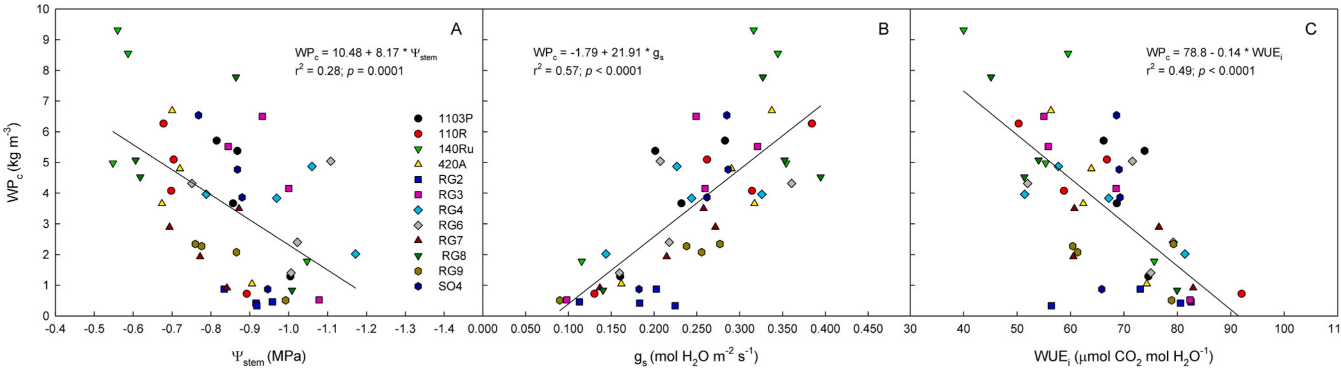


Fig. 3. Relationships between physiological variables (A; stem water potential (Ψ_{stem}), B; stomatal conductance (g_s) and C; intrinsic water use efficiency (WUE_i)) and crop water productivity (WP_c) across 2018–20 seasons in a 'Tempranillo' vineyard grafted onto 12 rootstocks in Miranda de Arga, Navarra, Spain.

and/or graft quality (Southey and Archer, 1988; Santarosa et al., 2016; Shtein et al., 2017; Gautier et al., 2018; Yıldırım et al., 2018; de Souza et al., 2022; Marín et al., 2022b; Tedesco et al., 2022). It should be noted that the determination of root characteristics and dynamics remains a major technical challenge (Marín et al., 2021).

Furthermore, the hydraulic conductances estimated in this study (K_{plant} and $K_{root\text{-}stem}$) revealed significant correlations with the slope of g_s-Ψ_{stem} regression (Fig. 5). This is noteworthy because higher absolute slopes indicate greater stomatal sensitivity of the genotype to vine water status (Bota et al., 2016). Thus, a regression slope greater than 0.25 tends towards an isohydric behaviour, stronger "water savers", which showed higher values of hydraulic conductance than those with a more anisohydric behaviour (g_s-Ψ_{stem} regression slope below 0.25) (Fig. 1B). Therefore, rootstocks that conferred a higher K_{plant} also induced a more isohydric behaviour in the scion. This implies that those with a better scion performance may have a greater capacity to uptake and transport water by keeping Ψ_{stem} values higher, but with a high stomatal closure regulation of the scion when they decrease it. This would confirm that iso/anisohydric behaviour is an adaptive response to the environment that can be regulated by the rootstock (Hochberg et al., 2018; Gambetta et al., 2020). In fact, vines can even exhibit iso/anisohydric behaviour depending on the intensity of the water deficit (Levin et al., 2020). In this sense, it would be expected that rootstocks with higher K_{plant} rates under moderate stress conditions would have larger xylem vessels and therefore might be more vulnerable to embolism (Simonneau et al., 2017; Plavcová et al., 2019). This, in turn could lead to isohydric-like behaviour under more severe water deficit conditions (Lamarque et al., 2023).

On the other hand, chemical signals, i.e. abscisic acid (ABA), are also known to play a key role in the regulation of the stomatal responses (Soar et al., 2006; Pou et al., 2008; Rogiers et al., 2012). Indeed, Labarga et al. (2023) recently reported a negative exponential correlation between leaf ABA content and hydraulic conductance of Tempranillo vines grafted onto 1103P, 110R and 161–49 Couderc. Nevertheless, hydraulic mechanisms play a dominant role in the stomatal regulation under soil water deficit compared to chemical signalling (Rodrigues et al., 2008; Tombesi et al., 2015). In our trial, the increase in hydraulic conductance seems to be related both to the ability to keep the difference between Ψ_{stem} and Ψ_{PD} small (Table 3) and thus to maintain higher g_s rates for a given Ψ_{stem} (Fig. 1B). Nevertheless, whether it is hydraulics that drives gas exchange or vice versa remains a matter of debate (Meinzer et al., 2009; Flexas et al., 2018).

Contrary to our results, Pou et al. (2012) reported in Grenache and Syrah onto 110R and Chardonnay onto 1103P that the isohydric or near-isohydric behaviour did not perform better than the anisohydric behaviour under similar water stress levels as in our experiment. These authors explained their findings by the strong adjustment of g_s associated with the isohydric behaviour, which was mediated by a reduction in leaf hydraulic conductance. Other studies have drawn similar conclusions regarding isohydric and anisohydric behaviour in grapevine cultivars, indicating that anisohydric behaviour leads to high g_s and WUE_i regardless of vine water status (Poni et al., 2014; Tombesi et al., 2014). However, beyond a certain threshold of soil water deficit, anisohydric behaviour may not remain favourable, as reported for Syrah and Chardonnay (Alsina et al., 2007). In any case, these conclusions were obtained by comparing cultivars and not by assessing the capacity of the rootstock to transport water to the scion. In this sense, Pou et al. (2008) reported that the fine regulation of the 110R rootstock resulted in very high WUE_i.

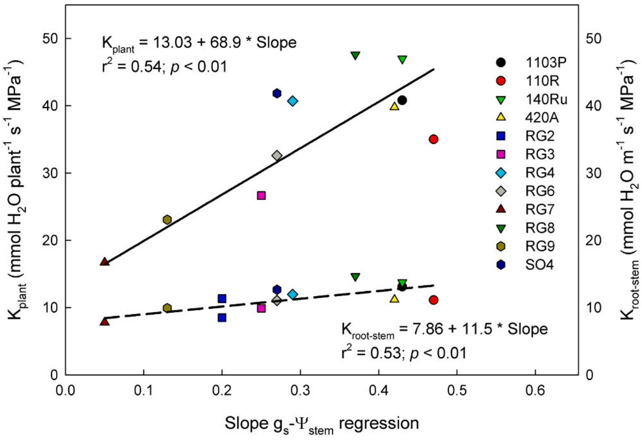


Fig. 5. Relationship between the slope of stomatal conductance (g_s) versus stem water potential (Ψ_{stem}) equation for each of the 12 rootstocks across the 2018–2020 seasons and the hydraulic conductance of the whole vine in 2020 (K_{plant}; solid line) and of the root-to-stem transect ($K_{root\text{-}stem}$; dash line).

3.7. Overall evaluation of rootstock effects on water behaviour and clustering

3.7.1. Principal component analysis

PCA analysis was conducted to determine general trends between rootstocks over the seasons with the full data set (Supplementary Figure 3). PC1 accounted for 68.8% of the total variance, while PC2 accounted for 8.8%. The distribution of rootstock genotypes in PC1 was mainly explained by differences in vegetative and reproductive growth and WUE_i, while the separation in PC2 was explained by vine water status, photosynthetic performance and shoot number (Supplementary Figure 3A). In addition, the year was mainly separated by PC2 (Supplementary Figure 3B). However, there was no clear difference between years, consistent with the interactive effect of rootstock × year on ecophysiology (Table 2).

In order to establish similar behaviour among rootstock genotypes, a further PCA was conducted with the means of all the seasons after removing highly correlated variables (Fig. 6). The first two principal components (PC1 and PC2) explained 66.2% and 12.0% of the total variance, respectively (Fig. 6A). PC1 mainly reflects the expected behaviour of a scion, i.e., a positive relationship between growth, yield and water availability, which at the same time is negatively related to $\delta^{13}C$ and WUE_i. In this component, 140Ru, RG8 stand out as inducers of high yield and vegetative development, while RG2 and, to a much lesser extent, RG7 and RG9 confer lower development and productivity and higher WUE_i. At this point, PC2 shows that although Ψ_{stem} and Ψ_{PD} are positively correlated on axis 1, they are strongly opposed on axis 2. Thus, the rootstocks with the highest score for PC2 (RG4 and RG6) would be expected to have higher Ψ_{stem} values for a given $\Psi_{PD,}$ whereas the rootstocks with the lowest (RG8, 140Ru and 110R) would behave in the opposite way, suggesting a high capacity for water uptake and transport. These behaviours were indeed confirmed by the estimation of hydraulic conductance, with RG8, 140Ru and 110R showing higher values compared to RG6 and RG4 (Table 3).

3.7.2. Hierarchical clustering

To improve the visualisation and understanding of the relationships between genotypes, HCPC was performed on the first three PCs. The results were plotted in a phylogenetic tree (Fig. 6B), which showed a clear differentiation between rootstock genotypes was revealed. Six clusters were identified; the first cluster was composed of 110R and 420A rootstocks, the second cluster included RG8 and 140Ru, RG3 and 1103P belonged to the third cluster, RG4, RG6 and SO4 clustered together in the fourth, the fifth consisted of RG2, and finally, the sixth cluster included RG7 and RG9. Broadly speaking, this cluster analysis summarises the similar behaviour of some of the RG genotypes, with the exception of RG8, which has a very similar agronomic (Table 4) and physiological behaviour to 140Ru (Fig. 1B and Tables 2 and 3). These results show that the traditional breeding of rootstocks through common parentals can generate highly contrasted progeny, as already reported

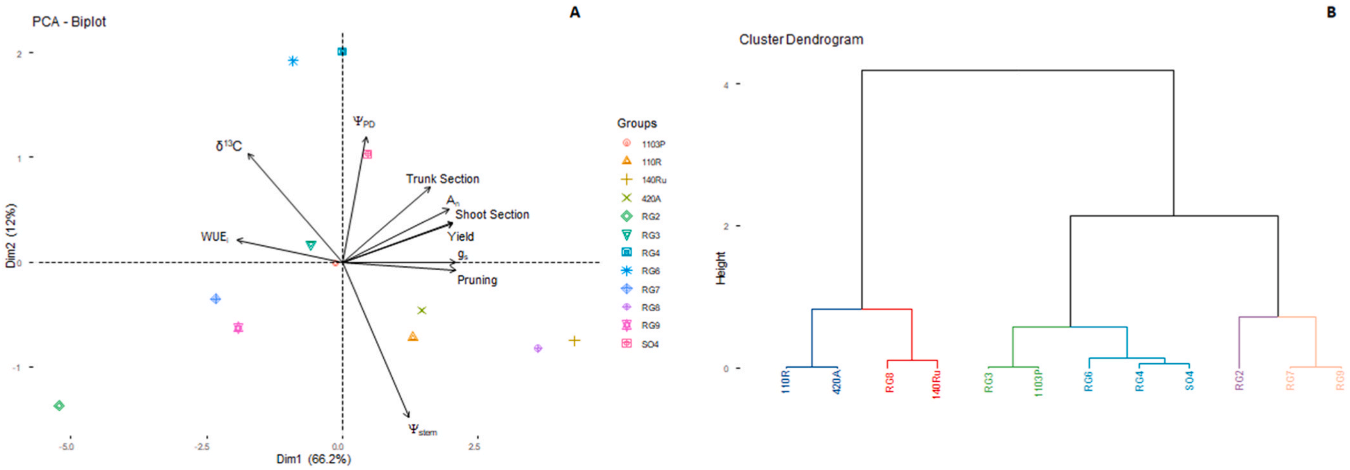


Fig. 6. Principal component analysis (PCA) of the mean values for the physiological and agronomic variables of ‘Tempranillo’ scions grafted on 12 rootstocks during the experimental years of 2018, 2019, and 2020 and phylogenetic tree resulting from the hierarchical clustering performed on the first three components of the PCA. Different colours indicate belonging to a different cluster.

for the RG series by Marín et al. (2022a). These authors observed that RG genotypes, when grafted with Tempranillo and Syrah cultivars, strongly affected vine vigour, yield and berry quality parameters. Under mild soil water deficit conditions, most of the RG rootstocks reduced vine performance in both cultivars compared to their parents, except for RG8 (Marín et al., 2022a). The RG genotypes that induce low vigour in the scion might become more interesting under more restrictive scenarios due to their greater tolerance to water stress (Zhang et al., 2016). That is, rootstocks that improve vine performance under mild water stress may not be the most resilient during the longer and more severe water deficit periods predicted for the future (Döll, 2002). In this sense, rootstocks that induce low vigour in the scion, such as RG2, RG6, RG7 and RG9, increased WUE_i and would also reduce vine evapotranspiration (Edwards et al., 2022; Pérez-Álvarez et al., 2023). This in turn could help to conserve potentially available soil water in more demanding scenarios (Zhang et al., 2016; Bonada et al., 2018). In our trial, the rootstocks with the highest hydraulic conductance were those with the most isohydric stomatal behaviour ("water savers"), due to their likely higher hydraulic vulnerability (Fig. 5) (Lamarque et al., 2023). These concerns, together with the explanation for the large differences in hydraulic conductance between rootstocks, will need to be addressed in the future (Lovisolo et al., 2016; Zhang et al., 2016). Similarly, the interaction between rootstock and scion needs to be considered (Serra et al., 2014; Santarosa et al., 2016; Clingeleffer et al., 2019).

4. Conclusions

In the current climate change scenario, new grapevine rootstocks may be a possible strategy to improve the vineyard response to soil water deficit. Our results show a wide range of intrinsic water use efficiency, carbon isotope ratios and crop water productivity in the Tempranillo cultivar when grafted onto different rootstock genotypes. Rootstocks strongly influenced water relations and leaf gas exchange, with up to fourfold differences in whole-plant hydraulic conductance among rootstocks. Furthermore, this study revealed a coordination between hydraulic conductance and iso/anisohydric behaviour, identifying rootstocks such as RG2, RG7 and RG9, which conferred an anisohydric behaviour and low K_{plant} to the scion, and other rootstocks such as RG8 or 140Ru, which conferred the opposite. Overall, the RG rootstocks showed a reduction in the vine performance of the ‘Tempranillo’ scion compared to the most widely used commercial rootstocks, with the notable exception of RG8, as reported by Marín et al. (2022a) in their agronomic evaluation of the RG series rootstocks. Furthermore, our results showed a strong positive relationship between ecophysiological responses and vine performance, suggesting that the rootstock water uptake and transport capacity determine scion vigour and crop water productivity. Our work also highlighted the importance of seasonal conditions and soil type in modulating vine response, implying that a rootstock may be better suited to one environment or another. Therefore, this study highlighted the high potential of rootstocks to adapt to the challenges of viticulture by improving vineyard performance and providing physiological insights for future studies and breeding programmes.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agwat.2023.108560.

References

Alsina, M., De Herralde, F., Aranda, X., Save, R., Biel, C., 2007. Water relations and vulnerability to embolism are not related: experiments with eight grapevine cultivars. Vitis 46, 1.

Alsina, M.M., Smart, D.R., Bauerle, T., de Herralde, F., Biel, C., Stockert, C., Negron, C., Save, R., 2011. Seasonal changes of whole root system conductance by a drought-tolerant grape root system. J. Exp. Bot. 62, 99–109. https://doi.org/10.1093/jxb/erq247.

Angyal, M., Lehoczky, É., Kocsis, L., 2002. Examination of the nutrient uptake by the view of grapevine rootstock-scion interaction. Acta Biol. Szeged 46, 189–190.

Bavaresco, L., Fraschini, P., Perino, A., 1993. Effect of the rootstock on the occurrence of lime-induced chlorosis of potted *Vitis vinifera* L. cv.' Pinot blanc. Plant Soil 305–306.

Bchir, A., Escalona, J.M., Galléc, A., Hernández-Montes, E., Tortosa, I., Brahama, M., et al., 2016. Carbon isotope discrimination (d^{13}C) as an indicator of vine water status and water use efficiency (WUE): looking for the most representative sample and sampling time. Agric. Water Manag. 167, 11–20. https://doi.org/10.1016/j.agwat.2015.12.018.

Bianchi, D., Grossi, D., Tincani, D.T.G., Simone Di Lorenzo, G., Brancadoro, L., Rustioni, L., 2018. Multi-parameter characterization of water stress tolerance in *Vitis* hybrids for new rootstock selection. Plant Physiol. Biochem 132, 333–340. https://doi.org/10.1016/j.plaphy.2018.09.018.

Bianchi, D., Grossi, D., Simone Di Lorenzo, G., Zi Ying, Y., Rustioni, L., Brancadoro, L., 2020. Phenotyping of the "G series" *Vitis* hybrids: first screening of the mineral composition. Sci. Hortic. 264, 109155 https://doi.org/10.1016/j.scienta.2019.109155.

Bonada, M., Buesa, I., Moran, M.A., Sadras, V.O., 2018. Interactive effects of warming and water deficit on Shiraz vine transpiration. OENO One 52. https://doi.org/10.20870/oeno-one.2018.52.2.2141.

Bota, B.J., Flexas, J., Medrano, H., 2001. Genetic variability of photosynthesis and water use in Balearic grapevine cultivars. Ann. Appl. Biol. 138, 353–361. https://doi.org/10.1111/j.1744-7348.2001.tb00120.x.

Bota, J., Tomás, M., Flexas, J., Medrano, H., Escalona, J.M., 2016. Differences among grapevine cultivars in their stomatal behavior and water use efficiency under progressive water stress. Agric. Water Manag. 164, 91–99. https://doi.org/10.1016/j.agwat.2015.07.016.

Buesa, I., Escalona, J.M., Tortosa, I., Marín, D., Loidi, M., Santesteban, L.G., Douthe, C., Medrano, H., 2021. Intracultivar genetic diversity in grapevine: water use efficiency variability within cv. Grenache. Physiol. Plant 173, 2226–2237. https://doi.org/10.1111/ppl.13573.

Buesa, I., Romero-Azorín, P., Escalona, J.M. and Intrigliolo D.S., {C}2022a{C}. Vineyard water balance and use, in: {C}{C}{C}Costa J.M. {C}, {C}Catarino S. {C}, {C} Escalona J.M. {C}, {C}Comuzzo P. {C}{C}{C} (2022) Improving Sustainable Viticulture and Winemaking Practices Academic Press. ISBN: 9780323851503.

Buesa, I., Hernández-Montes, E., Tortosa, I., Baraldi, G., Rosselló, M., Medrano, H., Escalona, J.M., 2022b. Unraveling the physiological mechanisms underlying the intracultivar variability of water use efficiency in *Vitis vinifera* "Grenache". Plants 11, 3008. https://doi.org/10.3390/plants11213008.

Chaves, M.M., Maroco, J.P., Pereira, J.S., 2003. Understanding plant responses to drought from genes to the whole plant. Funct. Plant Biol. 30, 239–264. https://doi.org/10.1071/fp02076.

Chaves, M.M., Zarrouk, O., Francisco, R., Costa, J.M., Santos, T., Regalado, A.P., et al., 2010. Grapevine under deficit irrigation: hints from physiological and molecular data. Ann. Bot. 105, 661–676. https://doi.org/10.1093/aob/mcq030.

Cifre, J., Bota, J., Escalona, J., Medrano, H., Flexas, J., 2005. Physiological tools for irrigation scheduling in grapevine (*Vitis vinifera* L.): an open gate to improve water-use efficiency. Agric. Ecosyst. Environ. 106, 159–170.

Clingeleffer, P., Morales, N., Davis, H., Smith, H., 2019. The significance of scion × rootstock interactions: this article is published in cooperation with the 21th GIESCO International Meeting, June 23-28 2019, Thessaloniki, Greece. Guests editors: Stefanos Koundouras and Laurent Torregrosa. OENO One 53. https://doi.org/10.20870/oeno-one.2019.53.2.2438.

Costa, J.M., Vaz, M., Escalona, J., Egipto, R., Lopes, C., Medrano, H., Chaves, M.M., 2016. Modern viticulture in southern Europe: vulnerabilities and strategies for adaptation to water scarcity. Agric. Water Manag. 164, 5–18. https://doi.org/10.1016/j.agwat.2015.08.021.

Döll, P., 2002. Impact of climate change and variability on irrigation requirements: a global perspective. Clim. Change 54, 269–293. https://doi.org/10.1023/a:1016124032231.

Edwards, E.J., Betts, A., Clingeleffer, P.R., Walker, R.R., 2022. Rootstock-conferred traits affect the water use efficiency of fruit production in Shiraz. Aust. J. Grape Wine Res. 28, 316–327. https://doi.org/10.1111/ajgw.12553.

Fereres, E., Soriano, M.A., 2007. Deficit irrigation for reducing agricultural water use. J. Exp. Bot. 58, 147–159. https://doi.org/10.1093/jxb/erl165.

Fisarakis, I., Nikolaou, N., Tsikalas, P., Therios, I., Stavrakas, D., 2004. Effect of salinity and rootstock on concentration of potassium calcium magnesium phosphorus and nitrate-nitrogen in Thompson seedless grapevine. J. Plant Nutr. 27, 2117–2134. https://doi.org/10.1081/LPLA-200034662.

Flexas, J., Bota, J., Escalona, J.M., Sampol, B., Medrano, H., 2002. Effects of drought on photosynthesis in grapevines under field conditions: an evaluation of stomatal and mesophyll limitations. Funct. Plant Biol. 29, 461–471. https://doi.org/10.1071/PP01119.

Flexas, J., Galmés, J., Gallé, A., Gulías, J., Pou, A., Ribas-Carbo, M., et al., 2010. Improving water use efficiency in grapevines: potential physiological targets for biotechnological improvement. Aust. J. Grape Wine Res. 16, 106–121. https://doi.org/10.1111/j.1755-0238.2009.00057.x.

Flexas, J., Carriquí, M., Nadal, M., 2018. Gas exchange and hydraulics during drought in crops: who drives whom. J. Exp. Bot. 69, 3791–3795. https://doi.org/10.1093/jxb/ery235.

Fraga, H., García de Cortázar Atauri, I., Malheiro, A.C., Santos, J.A., 2016. Modelling climate change impacts on viticultural yield phenology and stress conditions in Europe. Glob. Change Biol. 22, 3774–3788. https://doi.org/10.1111/gcb.13382.

Frioni, T., Biagioni, A., Squeri, C., Tombesi, S., Gatti, M., Poni, S., 2020. Grafting cv. Grechetto gentile vines to New M4 Rootstock improves leaf gas exchange and water status as compared to commercial 1103 P rootstock. Agronomy 10, 708. https://doi.org/10.3390/agronomy10050708.

Gambetta, G.A., Manuck, C.M., Drucker, S.T., Shaghasi, T., Fort, K., Matthews, M.A., Walker, M.A., McElrone, A.J., 2012. The relationship between root hydraulics and scion vigour across *Vitis* rootstocks: what role do root aquaporins play. J. Exp. Bot. 63, 6445–6455. https://doi.org/10.1093/jxb/ers312.

Gambetta, G.A., Herrera, J.C., Dayer, S., Feng, Q., Hochberg, U., Castellarin, S.D., 2020. The physiology of drought stress in grapevine: towards an integrative definition of drought tolerance. J. Exp. Bot. 71, 4658–4676. https://doi.org/10.1093/jxb/eraa245.

García-Escudero, E., Romero, I., Benito, A., Domínguez, N., Martín, I., 2013. Reference levels for leaf nutrient diagnosis of cv. Tempranillo grapevine in the Rioja Appellation. Commun. Soil Sci. Plant Anal. 44, 645–654. https://doi.org/10.1080/00103624.2013.745385.

Gaudillère, J.P., Van Leeuwen, C., Ollat, N., 2002. Carbon isotope composition of sugars in grapevine, an integrated indicator of vineyard water status. J. Exp. Bot. 53, 757–763. https://doi.org/10.1093/jexbot/53.369.757.

Gautier, A.T., Chambaud, C., Brocard, L., Ollat, N., Gambetta, G.A., Delrot, S., Cookson, S.J., 2018. Merging genotypes: graft union formation and scion–rootstock interactions. J. Exp. Bot. 70, 747–755. https://doi.org/10.1093/jxb/ery422.

Guilpart, N., Metay, A., Gary, C., 2014. Grapevine bud fertility and number of berries per bunch are determined by water and nitrogen stress around flowering in the previous year. Eur. J. Agron. 54, 9–20.

Guiot, J., Cramer, W., 2016. Climate change: the 2015 Paris agreement thresholds and mediterranean basin ecosystems. Science 354, 465–468. https://doi.org/10.1126/science.aah5015.

de Herralde, F., del Mar Alsina, M., Aranda, X., Savé, R., Biel, C., 2006. Effects of rootstock and irrigation regime on hydraulic architecture of *Vitis vinifera* L. cv. Tempranillo. OENO One 40, 133–139. https://doi.org/10.20870/oeno-one.2006.40.3.868.

Hochberg, U., Rockwell, F.E., Holbrook, N.M., Cochard, H., 2018. Iso/anisohydry: a plant–environment interaction rather than a simple hydraulic trait. Trends Plant Sci. 23, 112–120. https://doi.org/10.1016/j.tplants.2017.11.002.

Keller, M., 2010. The science of grapevines: Anatomy and physiology. Academic press, Elsevier,. ISBN: 978-0-12-419987-3.

Keller, M., Mills, L.J., Harbertson, J.F., 2012. Rootstock effects on deficit-irrigated winegrapes in a dry climate: vigor, yield formation, and fruit ripening. Am. J. Enol. Vitic. 63, 29–39. https://doi.org/10.5344/ajev.2011.11078.

Köse, B., Horuz, A., Akınoğlu, G., 2016. Phenological changes of leaf nutrients in *Vitis labrusca* L. Grape grafted on different rootstocks in heavy clay soil conditions. ErwerbsObstbau 58, 211–217. https://doi.org/10.1007/s10341-016-0279-5.

Koundouras, S., Tsialtas, I.T., Zioziou, E., Nikolaou, N., 2008. Rootstock effects on the adaptive strategies of grapevine (*Vitis vinifera* L. cv. Cabernet–Sauvignon) under contrasting water status: leaf physiological and structural responses. Agric. Ecosyst. Environ. 128, 86–96. https://doi.org/10.1016/j.agee.2008.05.006.

Labarga, D., Mairata, A., Puelles, M., Martín, I., Albacete, A., García-Escudero, E., Pou, A., 2023. The rootstock genotypes determine drought tolerance by regulating aquaporin expression at the transcript level and phytohormone balance. Plants 12, 718. https://doi.org/10.3390/plants12040718.

Lamarque, L.J., Delmas, C.E.L., Charrier, G., Burlett, R., Dell'Acqua, N., Pouzoulet, J., Gambetta, G.A., Delzon, S., 2023. Quantifying the grapevine xylem embolism resistance spectrum to identify varieties and regions at risk in a future dry climate. Sci. Rep. 13, 7724. https://doi.org/10.1038/s41598-023-34224-6.

Lavoie-Lamoureux, A., Sacco, D., Risse, P.-A., Lovisolo, C., 2017. Factors influencing stomatal conductance in response to water availability in grapevine: a meta-analysis. Physiol. Plant. 159, 468–482. https://doi.org/10.1111/ppl.12530.

Lê, S., Josse, J., Husson, F., 2008. FactoMineR: an R package for multivariate analysis. J. Stat. Softw. 25, 1–18. https://doi.org/10.18637/jss.v025.i01.

Levin, A.D., Williams, L.E., Matthews, M.A., 2020. A continuum of stomatal responses to water deficits among 17 wine grape cultivars (*Vitis vinifera*). Funct. Plant Biol. 47, 11–25 https://doi.org/10.1071/FP19073.

Lovisolo, C., Hartung, W., Schubert, A., 2002. Whole-plant hydraulic conductance and root-to-shoot flow of abscisic acid are independently affected by water stress in grapevines. Funct. Plant Biol. 29, 1349–1356. https://doi.org/10.1071/FP02079.

Lovisolo, C., Perrone, I., Carra, A., Ferrandino, A., Flexas, J., Medrano, H., Schubert, A., 2010. Drought-induced changes in development and function of grapevine (*Vitis* spp.) organs and in their hydraulic and non-hydraulic interactions at the whole-plant level: a physiological and molecular update. Funct. Plant Biol. 37, 98–116. https://doi.org/10.1071/FP09191.

Lovisolo, C., Lavoie-Lamoureux, A., Tramontini, S., Ferrandino, A., 2016. Grapevine adaptations to water stress: new perspectives about soil/plant interactions. Theor. Exp. Plant Physiol. 28, 53–66. https://doi.org/10.1007/s40626-016-0057-7.

Marguerit, E., Brendel, O., Lebon, E., van Leeuwen, C., Ollat, N., 2012. Rootstock control of scion transpiration and its acclimation to water deficit are controlled by different genes. New Phytol. 194, 416–429. https://doi.org/10.1111/j.1469-8137.2012.04059.x.

Marín, D., García, R., Eraso, J., Urrestarazu, J., Miranda, C., Royo, J., Abad, J., Santesteban, L.G., Gonzalez, I., 2019. Evaluation of the agronomic performance of 'Syrah' and 'Tempranillo' when grafted on 12 rootstocks. Vitis -Geilweilerhof- 58, 111–118. https://doi.org/10.5073/vitis.2019.58.special-issue.111-118.

Marín, D., Armengol, J., Carbonell-Bejerano, P., Escalona, J.M., Gramaje, D., Hernández-Montes, E., Intrigliolo, D.S., Martínez Zapater, J.M., Medrano, H., Mirás-Avalos, J.M., Palomares-Rius, J.E., Romero-Azorín, P., Savé, R., Santesteban, L.G., de Herralde, F., 2020. Challenges of viticulture adaptation to global change: tackling the issue from the roots. Aust. J. Grape Wine Res. 27, 8–25. https://doi.org/10.1111/ajgw.12463.

Marín, D., Miranda, C., Abad, F.J., Urrestarazu, J., Mayor, B., Villa-Llop, A., Santesteban, L.G., 2022a. Agronomic evaluation of eight 41 B × 110 richter grapevine genotypes as rootstock candidates for mediterranean viticulture. Hortic. Plant J. https://doi.org/10.1016/j.hpj.2022.10.002.

Marín, D., Santesteban, L.G., Dayer, S., Villa-Llop, A., Abad, F.J., Gambetta, G.A., Torres-Ruiz, J.M., Torres, N., 2022b. Connection matters: exploring the implications of scion–rootstock alignment in grafted grapevines. Aust. J. Grape Wine Res. 284, 561–571. https://doi.org/10.1111/ajgw.12559.

May, P., 1994. Using grapevine rootstocks: the Australian perspective, first ed. Winetitles, Adelaide.

McCarthy, M.G., Cirami, R.M., Furkaliev, D.G., 1997. Rootstock response of Shiraz (*Vitis vinifera*) grapevines to dry and drip-irrigated conditions. Aust. J. Grape Wine Res. 3, 95–98. https://doi.org/10.1111/j.1755-0238.1997.tb00121.x.

Medrano, H., Escalona, J.M., Cifre, J., Bota, J., Flexas, J., 2003. A ten-year study on the physiology of two Spanish grapevine cultivars under field conditions: effects of water availability from leaf photosynthesis to grape yield and quality. Funct. Plant Biol. 30, 607–619.

Medrano, H., Tomás, M., Martorell, S., Escalona, J.M., Pou, A., Fuentes, S., et al., 2015a. Improving water use efficiency of vineyards in semi-arid regions. A review. Agron. Sustain. Develop. 35, 499–517. https://doi.org/10.1007/s13593-014-0280-z.

Medrano, H., Tomás, M., Martorell, S., Flexas, J., Hernández, E., Rosselló, J., et al., 2015b. From leaf to whole-plant water use efficiency (WUE) in complex canopies: limitations of leaf WUE as a selection target. Crop J. 3, 220–228. https://doi.org/10.1016/j.cj.2015.04.002.

Meggio, F., Prinsi, B., Negri, A.S., Simone Di Lorenzo, G., Lucchini, G., Pitacco, A., Failla, O., Scienza, A., Cocucci, M., Espen, L., 2014. Biochemical and physiological responses of two grapevine rootstock genotypes to drought and salt treatments. Aust. J. Grape Wine Res. 20, 310–323. https://doi.org/10.1111/ajgw.12071.

Meinzer, F.C., Johnson, D.M., Lachenbruch, B., McCulloh, K.A., Woodruff, D.R., 2009. Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. Funct. Ecol. 23, 922–930. https://doi.org/10.1111/j.1365-2435.2009.01577.x.

Merli, M.C., Magnanini, E., Gatti, M., Pirez, F.J., Buesa, I., Intrigliolo, D.S., Poni, S., 2016. Water stress improves whole-canopy water use efficiency and berry composition of cv. Sangiovese (*Vitis vinifera* L.) grapevines grafted on the new drought-tolerant rootstock M4. Agric. Water Manag. 169, 106–114. https://doi.org/10.1016/j.agwat.2016.02.025.

Migicovsky, Z., Cousins, P., Jordan, L.M., et al., 2021. Grapevine rootstocks affect growth-related scion phenotypes. Plant Direct 5, e00324. https://doi.org/10.1002/pld3.324.

Mira de Orduña, R., 2010. Climate change associated effects on grape and wine quality and production. Food Res. Int. 43, 1844–1855. https://doi.org/10.1016/j.foodres.2010.05.001.

Nardini, A., Salleo, S., 2000. Limitation of stomatal conductance by hydraulic traits: sensing or preventing xylem cavitation. Trees 15, 14–24. https://doi.org/10.1007/s004680000071.

Ollat, N., Bordenave, L., Tandonnet, J.P., Boursiquot, J.M., Marguerit, E., 2016. Grapevine rootstocks: origins and perspectives. Acta Hortic. 1136, 11–22. https://doi.org/10.17660/ActaHortic.2016.1136.2.

Peiró, R., Jiménez, C., Perpiñà, G., Soler, J.X., Gisbert, C., 2020. Evaluation of the genetic diversity and root architecture under osmotic stress of common grapevine rootstocks and clones. Sci. Hortic. 266, 109283 https://doi.org/10.1016/j.scienta.2020.109283.

Pérez-Álvarez, E.P., Intrigliolo, D.S., Martínez-Moreno, A., García-Sánchez, F., Parra, M., Buesa, I., 2023. Ecophysiological responses of grapevine rootstocks to water deficit. Vitis 62, 59–74. https://doi.org/10.5073/vitis.2023.62.59-74.

Plavcová, L., Gallenmüller, F., Morris, H., Khatamirad, M., Jansen, S., Speck, T., 2019. Mechanical properties and structure–function trade-offs in secondary xylem of young roots and stems. J. Exp. Bot. 70, 3679–3691. https://doi.org/10.1093/jxb/erz286.

Poni, S., Galbignani, M., Magnanini, E., Bernizzoni, F., Vercesi, A., Gatti, M., Merli, M.C., 2014. The isohydric cv. Montepulciano (*Vitis vinifera* L.) does not improve its whole-plant water use efficiency when subjected to pre-veraison water stress. Sci. Hortic. 179, 103–111. https://doi.org/10.1016/j.scienta.2014.09.021.

Pou, A., Flexas, J., Alsina Mdel, M., Bota, J., Carambula, C., de Herralde, F., et al., 2008. Adjustments of water use efficiency by stomatal regulation during drought and recovery in the drought-adapted *Vitis* hybrid Richter-110 (*V. berlandieri* × *V. rupestris*). Physiol. Plant. 134, 313–323. https://doi.org/10.1111/j.1399-3054.2008.01138.x.

Pou, A., Medrano, H., Tomas, M., Martorell, S., Ribas-Carbo, M., Flexas, J., 2012. Anisohydric behaviour in grapevines results in better performance under moderate water stress and recovery than isohydric behaviour. Plant Soil 359, 335–349. https://doi.org/10.1007/s11104-012-1206-7.

Rahmani, H., Rasoli, V., Abdossi, V., Jahromi, M.G., 2023. Ch1 (*Vitis vinifera* L.) rootstock control of scion response to water stress in some commercial grapevine cultivars. South Afr. J. Enol. Vitic. 44, 1–8. https://doi.org/10.21548/44-1-5325.

Ramírez-Cuesta, J.M., Intrigliolo, D.S., Lorite, I.J., Moreno, M.A., Vanella, D., Ballesteros, R., Hernández-López, D., Buesa, I., 2023. Determining grapevine water use under different sustainable agronomic practices using METRIC-UAV surface energy balance model. Agric. Water Manag. 281, 108247 https://doi.org/10.1016/j.agwat.2023.108247.

Renouf, V., Tregoat, O., Roby, J.P., Van Leeuwen, C., 2010. Soils, rootstocks and grapevine varieties in prestigious Bordeaux vineyards and their impact on yield and quality. J. Int. Sci. Vigne Vin. 44, 127–134. https://doi.org/10.20870/oeno-one.2010.44.3.1471.

Riaz, S., Pap, D., Uretsky, J., Laucou, V., Boursiquot, J.M., Kocsis, L., Walker, M.A., 2019. Genetic diversity and parentage analysis of grape rootstocks. Theor. Appl. Genet. 132, 1847–1860. https://doi.org/10.1007/s00122-019-03320-5.

Rienth, M., Vigneron, N., Darriet, P., Sweetman, C., Burbidge, C., Bonghi, C., Walker, R.P., Famiani, F., Castellarin, S.D., 2021. Grape berry secondary metabolites and their modulation by abiotic factors in a climate change scenario–a review. Front. Plant Sci. 12. https://doi.org/10.3389/fpls.2021.643258.

Rodrigues, G.C., Pereira, L.S., 2009. Assessing economic impacts of deficit irrigation as related to water productivity and water costs. Biosys. Eng. 103, 536–551. https://doi.org/10.1016/j.biosystemseng.2009.05.002.

Rodrigues, M.L., Santos, T.P., Rodrigues, A.P., de Souza, C.R., Lopes, C.M., Maroco, J.P., Pereira, J.S., Chaves, M.M., 2008. Hydraulic and chemical signalling in the regulation of stomatal conductance and plant water use in field grapevines growing under deficit irrigation. Funct. Plant Biol. 35, 565–579. https://doi.org/10.1071/FP08004.

Rogiers, S.Y., Greer, D.H., Hatfield, J.M., Hutton, R.J., Clarke, S.J., Hutchinson, P.A., Somers, A., 2012. Stomatal response of an anisohydric grapevine cultivar to evaporative demand available soil moisture and abscisic acid (Mar). Tree Physiol. 32 (3), 249–261. https://doi.org/10.1093/treephys/tpr131.

Romero, P., Fernández-Fernández, J.I., Martinez-Cutillas, A., 2010a. Physiological thresholds for efficient regulated deficit-irrigation management in winegrapes grown under semiarid conditions. Am. J. Enol. Vitic. 61, 300–312. https://doi.org/10.5344/ajev.2010.61.3.300.

Romero, I., García-Escudero, E., Martín, I., 2010b. Effects of leaf position on blade and petiole mineral nutrient concentration of Tempranillo grapevine (*Vitis vinifera* L.). Am. J. Enol. Vitic. 61, 544–550. https://doi.org/10.5344/ajev.2010.09091.

Romero, P., Botía, P., Navarro, J.M., 2018. Selecting rootstocks to improve vine performance and vineyard sustainability in deficit irrigated Monastrell grapevines under semiarid conditions. Agric. Water Manag. 209, 73–93. https://doi.org/10.1016/j.agwat.2018.07.012.

Romero, P., Navarro, J.M., Ordaz, P.B., 2022. Towards a sustainable viticulture: the combination of deficit irrigation strategies and agroecological practices in Mediterranean vineyards. A review and update. Agric. Water Manag. 259, 107216 https://doi.org/10.1016/j.agwat.2021.107216.

Rossdeutsch, L., Edwards, E., Cookson, S.J., Barrieu, F., Gambetta, G.A., Delrot, S., Ollat, N., 2016. ABA-mediated responses to water deficit separate grapevine genotypes by their genetic background. BMC Plant Biol. 16, 91. https://doi.org/10.1186/s12870-016-0778-4.

Sadras, V., Moran, M., Petrie, P., 2017. Resilience of grapevine yield in response to warming. OENO One 51, 381–386. https://doi.org/10.20870/oeno-one.2017.51.4.1913.

Santarosa, E., Dutra de Souza, P.V., de Araujo, M.J.E., Lourosa, G.V., 2016. Physiological interaction between rootstock-scion: effects on xylem vessels in cabernet sauvignon and merlot grapevines. Am. J. Enol. Vitic. 67, 65–76. https://doi.org/10.5344/ajev.2015.15003.

Santesteban, L., Miranda, C., Barbarin, I., Royo, J., 2015. Application of the measurement of the natural abundance of stable isotopes in viticulture: a review. Aust. J. Grape Wine Res. 21, 157–167.

Santesteban, L.G., Miranda, C., Royo, J.B., 2010. Vegetative growth, reproductive development and vineyard balance. In: Delrot, S., Medrano, H., Or, E., Bavaresco, L., Grando, S. (Eds.), Methodologies and results in grapevine research. Springer Netherlands, Dordrecht, The Netherlands, pp. 45–56.

Serra, I., Strever, A., Myburgh, P.A., Deloire, A., 2014. Review: the interaction between rootstocks and cultivars (*Vitis vinifera*L.) to enhance drought tolerance in grapevine. Aust. J. Grape Wine Res. 20, 1–14. https://doi.org/10.1111/ajgw.12054.

Shtein, I., Hayat, Y., Munitz, S., Harcavi, E., Akerman, M., Drori, E., Schwartz, A., Netzer, Y., 2017. From structural constraints to hydraulic function in three *Vitis* rootstocks. Trees 31. https://doi.org/10.1007/s00468-016-1510-6.

Simonneau, T., Lebon, E., Coupel-Ledru, A., Marguerit, E., Rossdeutsch, L., Ollat, N., 2017. Adapting plant material to face water stress in vineyards: which physiological targets for an optimal control of plant water status. OENO One 51, 167–179. https://doi.org/10.20870/oeno-one.2017.51.2.1870.

Smart, D.R., Schwass, E., Morano, L., Lakso, A.N., 2006. Grapevine root distributions: a comprehensive analysis and review. Am. J. Enol. Vitic. 57, 89–104.

Soar, C.J., Speirs, J., Maffei, S.M., Penrose, A.B., McCarthy, M.G., Loveys, B.R., 2006. Grape vine varieties Shiraz and Grenache differ in their stomatal response to VPD: apparent links with ABA physiology and gene expression in leaf tissue. Aust. J. Grape Wine Res. 12, 2–12. https://doi.org/10.1111/j.1755-0238.2006.tb00038.x.

Somkuwar, R.G., Taware, P.B., Bhange, M.A., Sharma, J., Khan, I., 2015. Influence of different rootstocks on growth photosynthesis biochemical composition and nutrient contents in 'Fantasy seedless' grapes. Int. J. Fruit. Sci. 15, 251–266. https://doi.org/10.1080/15538362.2015.1031564.

Southey, J.M., Archer, E., 1988. The effect of rootstock cultivar on grapevine root distribution and density. In: Van Zyl, J.L. (Ed.), The grapevine root and its environment. Tech comm. Dept. Agric. Water Supply. Pretoria, SA, 215, pp. 57–63.

de Souza, C.R., Gindro, K., Verdenal, T., Spring, J.-L., Spangenberg, J.E., Zufferey, V., 2022. Water deficit responses of field-grown Pinot noir mediated by rootstock genotypes in a cool climate region. OENO One 56, 136–148. https://doi.org/10.20870/oeno-one.2022.56.2.3567.

Stockdale, E.A., Goulding, K.W.T., George, T.S., Murphy, D.V., 2013. Soil fertility. Soil Cond. Plant Growth 49–85.

Tedesco, S., Fevereiro, P., Kragler, F., Pina, A., 2022. Plant grafting and graft incompatibility: a review from the grapevine perspective. Sci. Hortic. 299. https://doi.org/10.1016/j.scienta.2022.111019.

Tomás, M., Medrano, H., Pou, A., Escalona, J.M., Martorell, S., Ribas-Carbó, M., et al., 2012. Water-use efficiency in grapevine cultivars grown under controlled conditions: effects of water stress at the leaf and whole-plant level. Aust. J. Grape Wine Res. 18, 164–172. https://doi.org/10.1111/j.1755-0238.2012.00184.x.

Tombesi, S., Nardini, A., Farinelli, D., Palliotti, A., 2014. Relationships between stomatal behavior xylem vulnerability to cavitation and leaf water relations in two cultivars of *Vitis vinifera*. Physiol. Plant. 152, 453–464. https://doi.org/10.1111/ppl.12180.

Tombesi, S., Nardini, A., Frioni, T., Soccolini, M., Zadra, C., Farinelli, D., Poni, S., Palliotti, A., 2015. Stomatal closure is induced by hydraulic signals and maintained by ABA in drought-stressed grapevine. Sci. Rep. 24, 12449. https://doi.org/10.1038/srep12449.

Torres, N., Yu, R., Martínez-Lüscher, J., Kostaki, E., Kurtural, S.K., 2021. Effects of irrigation at different fractions of crop evapotranspiration on water productivity and flavonoid composition of cabernet sauvignon grapevine. Front. Plant Sci. 12, 712622 https://doi.org/10.3389/fpls.2021.712622.

Tortosa, I., Escalona, J.M., Bota, J., Tomás, M., Hernández, E., García-Escudero, E., Medrano, H., 2016. Exploring the genetic variability in water use efficiency: evaluation of inter and intra cultivar genetic diversity in grapevines. Plant Sci. 251, 35–43. https://doi.org/10.1016/j.plantsci.2016.05.008.

Tortosa, I., Escalona, J., Douthe, C., Pou, A., García-Escudero, E., Toro, G., Medrano, H., 2019. The intra-cultivar variability on water use efficiency at different water status as a target selection in grapevine: influence of ambient and genotype. Agric. Water Manag. 223, 105648 https://doi.org/10.1016/j.agwat.2019.05.032.

Tortosa, I., Escalona, J.M., Toro, G., Douthe, C., Medrano, H., 2020. Clonal behavior in response to soil water availability in tempranillo grapevine cv: from plant growth to water use efficiency. Agronomy 10, 862. https://doi.org/10.3390/agronomy10060862.

Tramontini, S., Vitali, M., Centioni, L., Schubert, A., Lovisolo, C., 2013. Rootstock control of scion response to water stress in grapevine. Environ. Exp. Bot. 93, 20–26. https://doi.org/10.1016/j.envexpbot.2013.04.001.

Tsuda, M., Tyree, M.T., 2000. Plant hydraulic conductance measured by the high pressure flow meter in crop plants. J. Exp. Bot. 51, 823–828. https://doi.org/10.1093/jexbot/51.345.823.

van Leeuwen, C., Destrac-Irvine, A., 2017. Modified grape composition under climate change conditions requires adaptations in the vineyard. Oeno One 51, 147–154. https://doi.org/10.20870/oeno-one.2016.0.0.1647.

van Leeuwen, C., Trégoat, O., Choné, X., Bois, B., Pernet, D., Gaudillère, J.-P., 2009. Vine water status is a key factor in grape ripening and vintage quality for red Bordeaux wine. How can it be assessed for vineyard management purposes. OENO One 43, 121–134. https://doi.org/10.20870/oeno-one.2009.43.3.798.

Verslype, N.I., Nascimento, A.C.Ad, Musser, Rd.S., Caldas, R.Md.S., Martins, L.S.S., Leão, P.Cd.S., 2023. Drought tolerance classification of grapevine rootstock by machine learning for the São Francisco Valley. Smart Agric. Technol. 4, 100192 https://doi.org/10.1016/j.atech.2023.100192.

Vilanova, M., Genisheva, Z., Tubío, M., Alvarez, K., Lissarrague, J.R., Oliveira, J.M., 2021. Rootstock effect on volatile composition of albariño wines. Appl. Sci. 11 (5), 2135. https://doi.org/10.3390/app11052135.

Villalobos-González, L., Muñoz-Araya, M., Franck, M., Pastenes, C., 2019. Controversies in midday water potential regulation and stomatal behavior might result from the environment, genotype, and/or rootstock: evidence from Carménère and Syrah grapevine varieties. Front. Plant Sci. 10, 1522. https://doi.org/10.3389/fpls.2019.01522.

Villalobos-Soublett, E., Verdugo-Vásquez, N., Díaz, I., Zurita-Silva, A., 2022. Adapting grapevine productivity and fitness to water deficit by means of naturalized rootstocks. Front. Plant Sci. 13. https://doi.org/10.3389/fpls.2022.870438.

Wang, P., Zhao, F., Zheng, T., Liu, Z., Ji, X., Zhang, Z., Pervaiz, T., Shangguan, L., Fang, J., 2023. Whole-genome re-sequencing, diversity analysis, and stress-resistance analysis of 77 grape rootstock genotypes. Front. Plant Sci. 14. https://doi.org/10.3389/fpls.2023.1102695.

Williams, L.E., Smith, R.J., 1991. The effect of rootstock on the partitioning of dry weight, nitrogen and potassium, and root distribution of cabernet sauvignon grapevines. Am. J. Enol. Vitic. 42, 118–122.

Wooldridge, J., Louw, P.J.E., Conradie, W.J., 2010. Effects of rootstock on grapevine performance, petiole and must composition and overall wine score of *Vitis vinifera* cv. Chardonnay and pinot noir. South Afr. J. Enol. Vitic. 31, 45–48.

Yıldırım, K., Yağcı, A., Sucu, S., Tunç, S., 2018. Responses of grapevine rootstocks to drought through altered root system architecture and root transcriptomic regulations. Plant Physiol. Biochem. 127, 256–268. https://doi.org/10.1016/j.plaphy.2018.03.034.

Zhang, L., Marguerit, E., Rossdeutsch, L., Ollat, N., Gambetta, G.A., 2016. The influence of grapevine rootstocks on scion growth and drought resistance. Theor. Exp. Plant Physiol. 28, 143–157. https://doi.org/10.1007/s40626-016-0070-x.

Zúñiga, M., Ortega-Farías, S., Fuentes, S., Riveros-Burgos, C., Poblete-Echeverría, C., 2018. Effects of three irrigation strategies on gas exchange relationships, plant water status, yield components and water productivity on grafted carménère grapevines. Front. Plant Sci. 9, 992. https://doi.org/10.3389/fpls.2018.00992.