



Optimizing deficit irrigation in Monastrell vines grafted on rootstocks of different vigour under semi-arid conditions

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ABSTRACT

A progressive irrigation reduction was applied during five years (from 2017 to 2021) by using regulated deficit irrigation (RDI) and partial root-zone drying irrigation (PRD) in field-grown mature Monastrell grapevines grafted on five different rootstocks (140Ru, 1103P 41B, 110R, and 161–49C) in the semi-arid wine-growing region of D.O. Bullas, South-Eastern (SE) Spain. The main goal was to adjust the irrigation volume applied during the growing season for each rootstock depending on the drought tolerance/vigour/productivity of the rootstock. Thus, the annual irrigation volume was progressively reduced (from 104 mm year⁻¹ [2017] to 45 mm year⁻¹ [2018–2019] and 15 mm year⁻¹ [2020–2021] in the most drought-tolerant, vigorous, and productive rootstocks [1103P, 140Ru], and from 104 mm year⁻¹ [2017] to 74 mm year⁻¹ [2018–2019] and 58 mm year⁻¹ [2020–2021] in the less drought-tolerant, vigorous, and productive rootstocks [110R, 161–49C, 41B]). A severe reduction of the irrigation in 140Ru and 1103P substantially reduced vigour, productivity, and berry weight and increased water productivity (WP) (220% and 97%, respectively) and phenolic berry quality (50% and 92%, respectively). Medium/low-vigour rootstocks also had a decrease in vigour, yield, and berry weight in response to an irrigation reduction, enhancing WP (between 17% [41B] and 41% [161–49C]) and phenolic berry quality (between 11% [161–49C] and 46% [110R]). With a low water volume DI (53–77 mm year⁻¹), vines grafted on 161–49C delivered the highest berry quality compared to other rootstocks. Physiological changes produced by very low water volume PRD were reflected in a reduced root water and nutrient uptake and leaf gas exchange and a slightly increased technological berry quality compared to RDI. However, PRD did not produce a significant improvement in WP, phenolic concentration, and global berry quality compared to RDI.

1. Introduction

To face the risks associated with climate change (CC) and to achieve an environmentally sustainable viticulture, selecting rootstocks based on a better adaptation and tolerance to the new climatic conditions has been proposed as an effective measure of adaptation in the medium/long term in order to mitigate the negative effects of climate change, enhancing resistance against drought stress (Fraga et al., 2012; Berdeja et al., 2015). This genetic diversity of the vine should be exploited to increase the diversity of vineyards and overcome the threats of CC (Wolkovich et al., 2018). Besides, genetic variability was important among three of the most-commonly-used rootstocks (110 R, 140Ru, and 1103 P and a higher genetic variability is convenient to overcome constraints associated to climate change (Peiró et al., 2020).

Rootstocks offer resistance to *Phylloxera*, nematodes, and fungal

pathogens, aside from showing a varying tolerance to abiotic stresses (e. g., water and salt stress) (Marín et al., 2021). Genotypic differences in the vigour of the rootstocks induce morphological and anatomical modifications and changes in the distribution of the root system, which may influence the soil volume that is explored, the availability of water for the plant, and the capacity to extract water from drying soils. In this sense, rootstock can affect the regulation of soil-plant water relations and leaf gas exchange (Alsina et al., 2011; Jones, 2012; Marguerit et al., 2012; Bianchi et al., 2020), leaf area development, yield components, and water productivity (WP) (Marín et al., 2021), as well as fruit composition, including the accumulation of phenolic compounds and changes in volatile profile (Berdeja et al., 2014; Habran et al., 2016; Stevens et al., 2016; Gutierrez-Gamboa et al., 2021; Awale et al., 2021; Zhang et al., 2022).

A major factor associated with water deficit tolerance in *Vitis*

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genotypes (e.g., rootstocks) has been associated with the maintenance of a better water status in the vine and higher stomatal conductance and photosynthesis values during soil water deficit, as a consequence of a greater rooting depth and a higher uptake of water from the soil (Cochetel et al., 2020; Prinsi et al., 2021; Villalobos-Soublett et al., 2022). Although there are recent studies about the effects of deficit irrigation (DI)/water stress on the performance of vines grafted on different rootstocks (Palai et al., 2021; Caruso et al., 2023; Villalobos-Soublett et al., 2022; Labarga et al., 2023), studies on the optimisation of deficit irrigation strategies and the adjustment of irrigation water volume depending on the physiological/agronomical rootstock characteristics in field conditions are very scarce (Romero et al., 2022).

In previous five-year studies, Romero et al. (2018) and Romero et al. (2019) evaluated the interactive effects of deficit irrigation (DI) methods (regulated deficit irrigation [RDI] and partial root-zone drying irrigation [PRD]) and rootstocks (invigorating and non-invigorating) on physiological and agronomical Monastrell vine performance and berry and wine quality. They concluded that the application of low water volumes (85–90 mm year⁻¹) with DI strategies for Monastrell vines grafted on low-vigour rootstocks (161–49 C, 110 R) resulted in moderate yields (7400–9900 kg ha⁻¹) with a higher global berry and wine quality and a greater nutraceutical potential, compared to high-vigour rootstocks (140Ru, 1103 P) under semi-arid conditions in SE Spain (Romero et al., 2018). In contrast, in invigorating rootstocks, yield and WP were substantially increased (e.g., in 140Ru, +72% in WP, compared to the average of the other rootstocks), allowing the production of a greater volume of wine, but at the expense of a poorer polyphenolic content, nutraceutical potential, and chromatic characteristics, as a consequence, among other factors, of a greater berry weight and dilution effects (Romero et al., 2019). Rootstocks conferring high vigour maintained a greater root water uptake capacity and leaf photosynthesis rate, and increased resources accumulated in organs during the growing season (Romero et al., 2018). Low vigour rootstocks, however, presented a better balance between sink/source organs, as well as lower berry weight and dilution effects that could contribute to improve vineyard resilience to climate change, making this adaptation compatible with grape quality under semi-arid conditions (Romero et al., 2018). Therefore, based on these results, we hypothesise that in invigorating drought-tolerant rootstocks (140Ru and 1103 P), irrigation water volume could be further reduced under more restricted DI strategies in order to control the excess of vigour and yield, to reduce berry weight and dilution effects, and to increase WP and berry quality. Accordingly, in order to optimise the irrigation for each rootstock, the aim of this study was to adjust the volumes of water depending on the vigour/productivity of the rootstock, irrigating the most vigorous and productive rootstocks (1103 P, 140Ru) with a lower annual water volume, and comparing them with the less vigorous and productive rootstocks (110 R, 161–49 C, 41B), which were irrigated with a greater annual water volume. This allowed us to evaluate the gradual adaptation of each rootstock/scion combination to more restrictive deficit irrigation conditions under RDI and PRD. In this 5-year study, we focussed on soil-plant water relations and leaf gas exchange, vegetative development, mineral nutrition, yield, and berry quality response.

2. Material and methods

2.1. Field conditions, plant materials, and irrigation treatments

This research was carried out from 2017 to 2021 in a 0.4-ha vineyard at the IMIDA experimental station in Cehegín, Murcia, SE of Spain (38° 6′ 38.13″ N, 1° 40′ 50.41″ W, 432 m a. s. l.). The soil of the plot was an 80-cm deep clay loam (31% clay, 38% silt, and 32% sand) and had an organic C content of 1.02%, a pH (PTA-FQ/004, pH-metre) of 7.4, an electrical conductivity (PTA-FQ/005, conductivity metre) of 0.40 dS m⁻¹, an active CaCO₃ of 15%, and a cation exchange capacity of 20.6 meq/100 g.

Irrigation water was taken from a well and had a pH of 8.0 and an electrical conductivity of 0.81 dS m⁻¹. Climate is Mediterranean semi-arid, with hot and dry summers, a high ETo, and a scarce annual rainfall (around 300 mm year⁻¹, with some exceptions) (Table 1). Grapevines (*Vitis vinifera* L, var. Monastrell, syn. Mourvedre, a local red wine variety) were 20 + years-old and were grafted on five different commercial rootstocks: 140Ru (*V. rupestris* x *V. berlandieri*), 1103 P (*V. rupestris* x *V. berlandieri*), 41B (*V. vinifera* x *V. berlandieri*), 161–49 C (*V. berlandieri* x *V. riparia*), and 110 R (*V. rupestris* x *V. berlandieri*). The training system was bilateral cordon (double Royat) trellised to a three-wire vertical system. Vine rows ran NW-SE, and planting density was 3 m between rows and 1.25 m between vines (2667 vines ha⁻¹). Six two-bud spurs (12 nodes) were left after pruning, whereas in May, green non-productive shoots were removed from each vine in the same way for all of the treatments, according to the grower's practice in the area.

Each rootstock was drip irrigated during five consecutive years (2017–2021) using two different deficit irrigation techniques: regulated deficit irrigation (RDI) and partial root-zone drying (PRD). In 2017, all of the rootstocks were irrigated with similar annual water volumes and applying the same deficit irrigation strategy (Table 2). After that, annual irrigation volume was reduced in a progressive way (from 104 mm year⁻¹ [2017] to 45 mm year⁻¹ [2018,2019] and 15 mm year⁻¹ [2020,2021] in the most vigorous and productive rootstocks [1103 P, 140Ru] and from 104 mm year⁻¹ [2017] to 74 mm year⁻¹ [2018,2019] and 58 mm year⁻¹ [2020,2021] in the less vigorous and productive rootstocks [110 R, 161–49 C, 41B]). Therefore, high-vigour rootstocks (1103 P, 140Ru) were irrigated with a 40% less water than low/medium-vigour rootstocks (110 R, 161–49 C, 41B) (years 2018, 2019) and between 71% and 75% less water than low-vigour rootstocks (years 2020, 2021) (Table 2).

Crop evapotranspiration [ET_c = (E_{to} × K_c)] was estimated using varying crop coefficients (K_c) based on those proposed by the FAO and adjusted for the Mediterranean area and reference evapotranspiration (E_{to}) values (Table 1). The applied K_c values were 0.35 in April, 0.45 in May, 0.52 in June, 0.75 in July-mid August, 0.60 in mid-August-early September, and 0.45 in mid-September-October. Reference evapotranspiration (E_{to}) was calculated weekly from the mean values of the experimental period and preceding 12–15 years using the Penman Monteith-FAO method (Allen et al., 1998) and the daily climatic data collected in the meteorological station (CR-32) (Campbell mod. CR 10X) located at the experimental vineyard belonging to the Servicio de Información Agraria de Murcia (SIAM, IMIDA).

The experimental design consisted of four replicates per rootstock-irrigation combination (a total of 8 repetitions for each rootstock) in a completely randomised 4-block design. Each replicate contained 5 vines, but only the three central plants were monitored. Where possible, border vines in each row were excluded from the study to eliminate potential edge effects.

Irrigation was applied every year, from April to October, during the late evening-night period (20:00–23:00) and between two to five times per week, depending on the phenological period. Control was automatic. Each irrigation event lasted between 1 and 3 h, according to the phenological stage and vine water needs, in order to avoid deep water percolation. The amount of water applied to each irrigation system (PRD and RDI) was measured with flow-metres (model M170, Elster Iberconta, Basque Country, Spain). All of the rootstock-irrigation system combinations received the same annual low amount of fertilisers (30 kg of N, 20 kg of P, 30 kg of K, and 16 kg of Mg per ha), which were supplied through the irrigation drip system from April to August. Besides, at the beginning of the growing season, a liquid organic matter-amino acid complex was applied. Water was applied by one pressure-compensated emitter per plant (2 L h⁻¹) with one drip-irrigation line per row for the conventional drip irrigation in RDI and a double line per row for the PRD with emitters (4 L h⁻¹) to apply the same amount of water in PRD and RDI. To apply less water in plants grafted on 140Ru and 1103 P under RDI and PRD, in 2018, low-water volume pressure-compensated

Table 1

Mean values of several climatic parameters in different phenological periods for every year of the experiment in the study area.

| Phenological period | Period of the year | ET _o (mm) | VPD (kPa) | Rainfall (mm) | T _{max} (°C) | T _{med} (°C) | T _{min} (°C) | Solar rad. (W m ⁻²) |
|-----------------------------|--------------------|-------------------------|--------------|------------------|--------------------------|--------------------------|--------------------------|------------------------------------|
| Year 2017 | 15 April-14 June | 284 | 1.16 | 29.8 | 25.5 | 17.7 | 8.7 | 281 |
| Budburst-fruit set | 15 June-31 July | 297 | 2.10 | 0.90 | 33.4 | 25.3 | 15.6 | 312 |
| Fruit set-veraison | 1 August-20 Sept. | 237 | 1.40 | 46 | 30.8 | 23.2 | 15.5 | 241 |
| Veraison-harvest | 21 Sept.–31 Octob. | 110 | 0.89 | 0.1 | 26.1 | 17.4 | 9.3 | 184 |
| Postharvest | 1 Nov.–14 April. | 306 | 0.60 | 129.0 | 16.0 | 8.3 | 1.1 | 142 |
| Dormancy period | | 1234 | 1.23 | 206 | 26.4 | 18.4 | 10.0 | 232 |
| Total/annual average | | | | | | | | |
| Year 2018 | | | | | | | | |
| Budburst-fruit set | 15 April-14 June | 265 | 0.98 | 78 | 23.7 | 16.7 | 8.8 | 268 |
| Fruit set-veraison | 15 June-31 July | 291 | 2.00 | 0.1 | 32.8 | 24.6 | 14.4 | 328 |
| Veraison-harvest | 1 August-20 Sept. | 219 | 1.39 | 57 | 31.0 | 23.76 | 16.43 | 229 |
| Postharvest | 21 Sept.–31 Octob. | 97 | 0.77 | 26.8 | 23.8 | 16.5 | 9.93 | 165 |
| Dormancy period | 1 Nov-14 April | 289 | 0.52 | 126.3 | 17.03 | 8.3 | 0.60 | 147 |
| Total/annual average | | 1161 | 1.13 | 288.2 | 25.67 | 19.97 | 10.03 | 227 |
| Year 2019 | | | | | | | | |
| Budburst-fruit set | 15 April-14 June | 280 | 1.06 | 119 | 24.2 | 16.9 | 8.6 | 280 |
| Fruit set-veraison | 15 June-31 July | 280 | 2.04 | 1.4 | 32.9 | 24.5 | 14.2 | 313 |
| Veraison-harvest | 1 August-20 Sept. | 219 | 1.43 | 170 | 30.5 | 23.3 | 15.7 | 234 |
| Postharvest | 21 Sept.–31 Octob. | 95 | 0.79 | 39 | 25.0 | 16.9 | 9.3 | 180 |
| Dormancy period | 1 Nov-14 April | 261 | 0.45 | 289 | 16.7 | 9.34 | 2.75 | 133 |
| Total/annual average | | 1135 | 1.15 | 618 | 25.9 | 18.2 | 10.10 | 228 |
| Year 2020 | | | | | | | | |
| Budburst-fruit set | 15 April-14 June | 255 | 1.06 | 27 | 25.1 | 17.7 | 9.3 | 264 |
| Fruit set-veraison | 15 June-31 July | 266 | 1.92 | 6 | 33.2 | 24.6 | 14.4 | 316 |
| Veraison-harvest | 1 August-20 Sept. | 231 | 1.71 | 6 | 32.2 | 23.5 | 13.8 | 258 |
| Postharvest | 21 Sept.–31 Octob. | 99 | 0.99 | 9 | 24.5 | 15.2 | 5.8 | 181 |
| Dormancy period | 1 Nov-14 April | 261 | 0.45 | 233 | 16.6 | 9.0 | 2.2 | 135 |
| Total/annual average | | 1112 | 1.23 | 281 | 26.3 | 18.0 | 9.10 | 231 |
| Year 2021 | | | | | | | | |
| Budburst-fruit set | 15 April-14 June | 253 | 0.94 | 113 | 24.3 | 17.1 | 9.2 | 259 |
| Fruit set-veraison | 15 June-31 July | 247 | 1.75 | 53 | 32.1 | 23.8 | 13.8 | 306 |
| Veraison-harvest | 1 August-20 Sept. | 206 | 1.63 | 3 | 32.3 | 24.1 | 15.5 | 234 |
| Postharvest | 21 Sept.–31 Octob. | 94 | 0.79 | 16 | 24.8 | 17.2 | 10.05 | 162 |
| Dormancy period | 1 Nov-21 March | 173 | 0.48 | 201 | 16.2 | 8.06 | 0.80 | 120 |
| Total/annual average | | 973 | 1.12 | 386 | 25.94 | 18.05 | 9.87 | 216 |

Abbreviations: ET_o, Reference evapotranspiration; VPD, atmospheric vapour pressure deficit; T_{max}, daily maximum temperature; T_{med}, average daily temperature; T_{min}, daily minimum temperature. Solar rad., incident solar radiation.

emitters were used in RDI (0.5 L h⁻¹) and PRD (2 × 0.5 L h⁻¹). In the PRD layout, the two pipelines were joined on both sides of the trunk and placed underneath each vine row. In each pipeline in the PRD treatments, there were alternate zones with and without emitters to create dry and wet root zones within each vine row. In the PRD treatments, water was supplied to one single side of the root system at a time, alternating every 14–16 days. In the RDI treatments, irrigation water was supplied simultaneously to the entire root system. We applied 13–14 drying-re-watering PRD cycles during the whole season (from early-mid April to the end of October) every year.

2.2. Soil water content and root water uptake rate

From 2017 to 2021, volumetric soil water content (θ_v) was generally measured between 9:00–10:00 a.m. (always 10–12 h after irrigation), once a week (daily in specific periods) with a Diviner 2000 portable soil moisture probe (Sentek Pty Ltd., Stepney, SA, Australia). PVC access tubes were installed at a depth of 100 cm in one (RDI) or both (PRD) parts of the root zone, with a total of 60 access tubes. Readings were taken close to the vines, 10–15 cm away from the drip head and with a perpendicular orientation with regards to the drip lines, at depths ranging from 10 to 100 cm (maximum depth) for four replicates per rootstock-irrigation system combination (one per plot). At the beginning of the experiment (2017), a soil texture analysis was made in different soil profiles (45 soil samples) in the whole experimental vineyard. Scaled frequency (SF) values were converted to θ_v using a capacitance probe calibration equation ($SF = 0.2352\theta_v^{0.3672}$) for clay loam soil (Paraskevas et al., 2012), with a similar texture to that of our vineyard soil. During different phenological periods, the root water uptake rates

($\Delta\theta_v \Delta t^{-1}$, mm day⁻¹) of the soil profile (10–50 cm) were estimated, using the discrete readings of soil moisture probes (DIVINER 2000) to determine the changes in θ_v (stock 10–50 cm) with time between consecutive days with irrigation (R) and no irrigation (NR) and between consecutive days with no irrigation (NR-NR). Root water uptake was estimated using a methodology similar to that used by IrriMax® version 9.1.1 Sentek (2012) software for continuous θ_v FDR measurements (EnviroSCAN, Sentek Pty Ltd), adapted for discrete FDR measurements (Romero et al., 2018).

2.3. Vine water status, leaf gas exchange, and hydraulic conductance

Each year, the stem water potential (Ψ_s) was determined weekly or fortnightly from the beginning of the vegetative growth until leaf fall. From six to ten healthy, fully exposed, and expanded mature leaves from the main shoots in the middle and upper part of the vine canopy were taken per rootstock. Leaves were enclosed in aluminium foil and covered with plastic at least 2 h before the midday measurement. Ψ_s was measured at noon (12:00–13:30 h) using a pressure chamber (Model 600; PMS Instrument Co., Albany, OR, USA).

Net leaf photosynthesis was measured between 09:00 h and 10:30 h and between 12:30 h and 14:00 h every 14 days from May to October, from 2017 to 2021, on selected clear and sunny days. Measurements were taken on healthy, fully expanded mature leaves exposed to the sun (one leaf on each of 8–16 vines per rootstock, depending on the year) and from main shoots located on the exterior canopy. Leaf gas exchange rates (leaf photosynthesis, A ; stomatal conductance, g_s ; and transpiration rate, E) were measured at the early morning (9:00–10:30 a.m.) and midday (12:30–13.45 p.m.) with a portable photosynthesis

Table 2

Deficit irrigation strategy and water volume applied for each irrigation method (partial root-zone drying irrigation, PRD and regulated deficit irrigation, RDI) and rootstock in each phenological period and total for every year in the period 2017–2021.

| Year | Rootstock | Irrig. system | Budburst-fruitset (mm) | Fruit set-veraison (mm) | Veraison-harvest (mm) | Postharvest (mm) | Total annual water volume applied (mm year ⁻¹) | %ETc* applied annually |
|----------------------------|----------------|---------------|---------------------------|----------------------------|-----------------------------------|---------------------------|---|------------------------|
| | | | April-May | June-July | Beginning of August-mid September | Mid-September-end October | | |
| DI strategy | | | | | | | | |
| 2017 | All rootstocks | PRD | 20.7 | 34.6 | 36.0 | 15.1 | 106.4 | 19% |
| | | RDI | 20.0 | 32.8 | 34.3 | 14.8 | 101.8 | 18% |
| Optimisation Period | | | | | | | | |
| 2018 | 110 R | PRD | 21.5 | 20.8 | 21.6 | 9.0 | 73.0 | 13% |
| | 41B | | | | | | | |
| | 161-49 C | RDI | 21.5 | 20.1 | 21.9 | 9.0 | 72.5 | 13% |
| 2018 | 1103 P 140Ru | PRD | 12.9 | 12.1 | 13.2 | 5.4 | 43.5 | 8% |
| | | RDI | 12.9 | 12.1 | 13.2 | 5.4 | 43.5 | 8% |
| 2019 | 110 R | PRD | 30.9 | 26.4 | 13.8 | 5.9 | 77 | 14% |
| | 41B | RDI | 30.9 | 26.4 | 13.8 | 5.9 | 77 | 14% |
| | 161-49 C | | | | | | | |
| 2019 | 1103 P 140Ru | PRD | 18.5 | 15.9 | 8.3 | 3.5 | 46.2 | 8% |
| | | RDI | 18.5 | 15.9 | 8.3 | 3.5 | 46.2 | 8% |
| 2020 | 110 R | PRD | 22.6 | 24.8 | 13 | 2.87 | 63.3 | 11% |
| | 41B | RDI | 22.6 | 24.8 | 13 | 2.87 | 63.3 | 11% |
| | 161-49 C | | | | | | | |
| 2020 | 1103 P | PRD | 5.7 | 6.2 | 3.3 | 0.72 | 15.9 | 3% |
| | 140Ru | RDI | 5.7 | 6.2 | 3.3 | 0.72 | 15.9 | 3% |
| 2021 | 110 R | PRD | 17.0 | 22.2 | 7.3 | 6.2 | 52.7 | 9% |
| | 41B | RDI | 17.0 | 22.2 | 7.3 | 6.2 | 52.7 | 9% |
| | 161-49 C | | | | | | | |
| 2021 | 1103 P | PRD | 4.8 | 6.0 | 2.4 | 2.1 | 15.2 | 3% |
| | 140Ru | RDI | 4.8 | 6.0 | 2.4 | 2.1 | 15.2 | 3% |

* 100% ETc (crop evapotranspiration) estimated in the study area (567.36 mm year⁻¹)

measurement system (LI-6400, Li-Cor, Lincoln, NE, USA) equipped with a broadleaf chamber (6.0 cm²).

On the 2nd-3rd of August, 2018, an estimate of whole-plant hydraulic conductance (K_{plant}) was obtained using the evaporative flux (EF) method (Nardini and Salleo, 2000): $K_{\text{plant}} = E_{\text{max}}/(\Psi_{\text{soil}} - \Psi_{\text{lmin}})$, where E_{max} is the maximum transpiration rate and Ψ_{soil} and Ψ_{lmin} are soil (pre-dawn leaf water potential) and minimum diurnal leaf water potential, respectively. Maximum values for E_{max} and minimum values for Ψ_{l} (measured at noon, between 12:00–17:00 h on sunny days) were taken to calculate K_{plant} . K_{plant} was then scaled to the total leaf area of the vine.

2.4. Leaf mineral analysis

Leaf samples were collected in July 2019 for mineral analysis. About 40 leaves were collected from eight vines per treatment. Leaves were washed immediately, dried at 65 °C for one week, and milled. After plant tissue was digested, ashes were dissolved in HNO₃, and K, Mg, Ca, Na, P, Fe, Mn, Zn, and B were analysed with an inductively coupled plasma optical emission spectrometer (Varian MPX Vista, Palo Alto, CA). Nitrogen concentration was determined using the LECO FP-428 protein detector.

2.5. Vine vigour and total and exposed leaf area

From 2017 to 2021, the total leaf area per vine was estimated pre- and post-veraison, in 8 or 16 vines per rootstock-irrigation method combination (depending on the year), using a non-destructive method, by developing a first order polynomial equation in which main shoot length (SL) and total leaf area (TLA) were related for each rootstock. Total leaf area per plant was calculated selecting five representative main shoots per vine and determining the average main shoot length. Total shoot length was measured with a tape. The number of total main shoots per vine was also measured each year at the end of June in the same vines. Total leaf area per plant was estimated by multiplying the average shoot leaf area by the total main shoot number of the vine, according to Romero et al. (2018).

The exposed leaf area was estimated every year (2017–2020) during the pre-veraison periods, in 16 vines per treatment (the same vines used for total leaf area and shoot growth measurements), by measuring the external perimeter of the leaf area (the height and width of the canopy). Measurements were made with a tape, from the beginning of the leaf layer on one side of the vine (East) to the end of the leaf layer on the other side of the vine (West). Four measurements per vine were taken. To calculate the exposed leaf area per vine, the average of four external perimeter measurements (m) was multiplied by the distance between vines (1.25 m).

In winters (2017–2020), pruning weight (PW) measurements were taken from 24 vines per rootstock (including the same vines from which leaf area and shoot measurements were calculated).

2.6. Yield response, sink/source ratios, and water productivity (WP)

Each year, at harvest, yield components were measured for 24 vines per rootstock (12 vines per irrigation method). Harvest date was determined according to the grower's practice in the area, when °Brix were around 23–24. Yield per vine, number of clusters per vine, cluster weight, berry number per cluster, and berry weights were calculated.

Vegetative growth and productive data of the different years were used to calculate several vine vigour indices and sink/source ratios, such as yield/pruning weight, total leaf area/yield, and exposed leaf area/total leaf area. Besides, water productivity (WP) was expressed as the mass of fresh grapes produced per m³ of applied water, per vine.

2.7. Berry quality

2.7.1. Physicochemical determinations in grapes

Samples of mature berries were collected from each grapevine in September 2017, 2018, 2019, 2020, and 2021, when maturity was around 23–24°Brix (concurring with harvest time), and transported to the laboratory. Harvest dates were determined on the basis of weekly analyses of grape composition (°Brix and total acidity). Samples consisted of approximately 800–900 g of berries randomly collected from different clusters in each vine. The rest of the berries were crushed with an automatic blender (Coupe 550GT), avoiding seed breakage. A first sub-sample of this crushed sample of grapes was centrifuged, and juice was used to analyse pH, TSS, solutes per berry (g), titratable acidity, and organic acids (tartaric acid and malic acid), as previously described in detail in Romero et al. (2013, 2015). A second sub-sample of crushed grapes was kept frozen (–20 °C) until the analysis of phenolic compounds was carried out.

2.7.2. Phenolic potential of grapes and berry quality indices

The phenolic potential of grapes was calculated according to the method described by Saint-Cricq et al. (1998), in which grapes are macerated overnight at two pH values (3.6 and 1.0). The extractable and total anthocyanin contents of the two solutions were then chemically assayed by measuring the absorbance of the samples at pH 3.6 and pH 1.0, respectively, whereas the total phenol content (TPC) was calculated by measuring the absorbance of the solution at pH 3.6 and 280 nm. Phenolic potential was calculated as described by Ribéreau-Gayon et al. (2006). In addition, we calculated the berry quality indices ($QI_{\text{technological berry}}$, $QI_{\text{phenolic berry}}$ and $QI_{\text{overall berry}}$) as previously described by Romero et al. (2018).

2.8. Statistical analysis

Data were analysed using analysis of variance (ANOVA) procedures, and means were separated by Duncan's multiple range test, using the Statgraphics 2.0 Plus software (Statistical Graphics Corporation, USA). A two-way ANOVA procedure was used to discriminate the effect of rootstocks and irrigation methods.

3. Results

3.1. Evolution of soil water content, root water uptake rate, and whole-plant hydraulic conductance

Total soil water content (θ_v) in the soil profile (10–50 cm deep) gradually decreased in all of the rootstocks as the irrigation water volume declined, especially in 140Ru and 1103 P, from 2017 to 2021, and significantly lower values of θ_v in 2020 and 2021 were observed with regards to the other rootstocks (Fig. 1A). Besides, root water uptake rates ($\Delta\theta_v \Delta t^{-1}$) were significantly greater in 140Ru in 2017 compared to 41B or 161–49 C (Fig. 1B). However, in 2019, $\Delta\theta_v \Delta t^{-1}$ from 140Ru rootstock was significantly lower than in 41B (Fig. 1B).

In addition, when a more in-detail study of the contribution of the root and dry wet root zone in PRD to root water uptake rate ($\Delta\theta_v \Delta t^{-1}$) over the years was made, we observed that, at the beginning, in 2017 (with all of the rootstocks irrigated with the same water volume), 140Ru and 1103 P had a significantly greater $\Delta\theta_v \Delta t^{-1}$ than the other rootstocks in the wet root zone (Fig. 1G), but not in the dry root zone (Fig. 1H). However, in 2018 and 2019, rootstocks irrigated with less water, that is, 140Ru and 1103 P, showed similar or even lower $\Delta\theta_v \Delta t^{-1}$ than other rootstocks in both wet and dry root zones. This was emphasised in 2020 and 2021, when still much less water was used for irrigation and these two rootstocks (140Ru and 1103 P) showed a significantly lower $\Delta\theta_v \Delta t^{-1}$ compared to other rootstocks, both in the wet and dry root zones (Fig. 1G and H), as a consequence of the very small volume of water that was applied (Table 2).

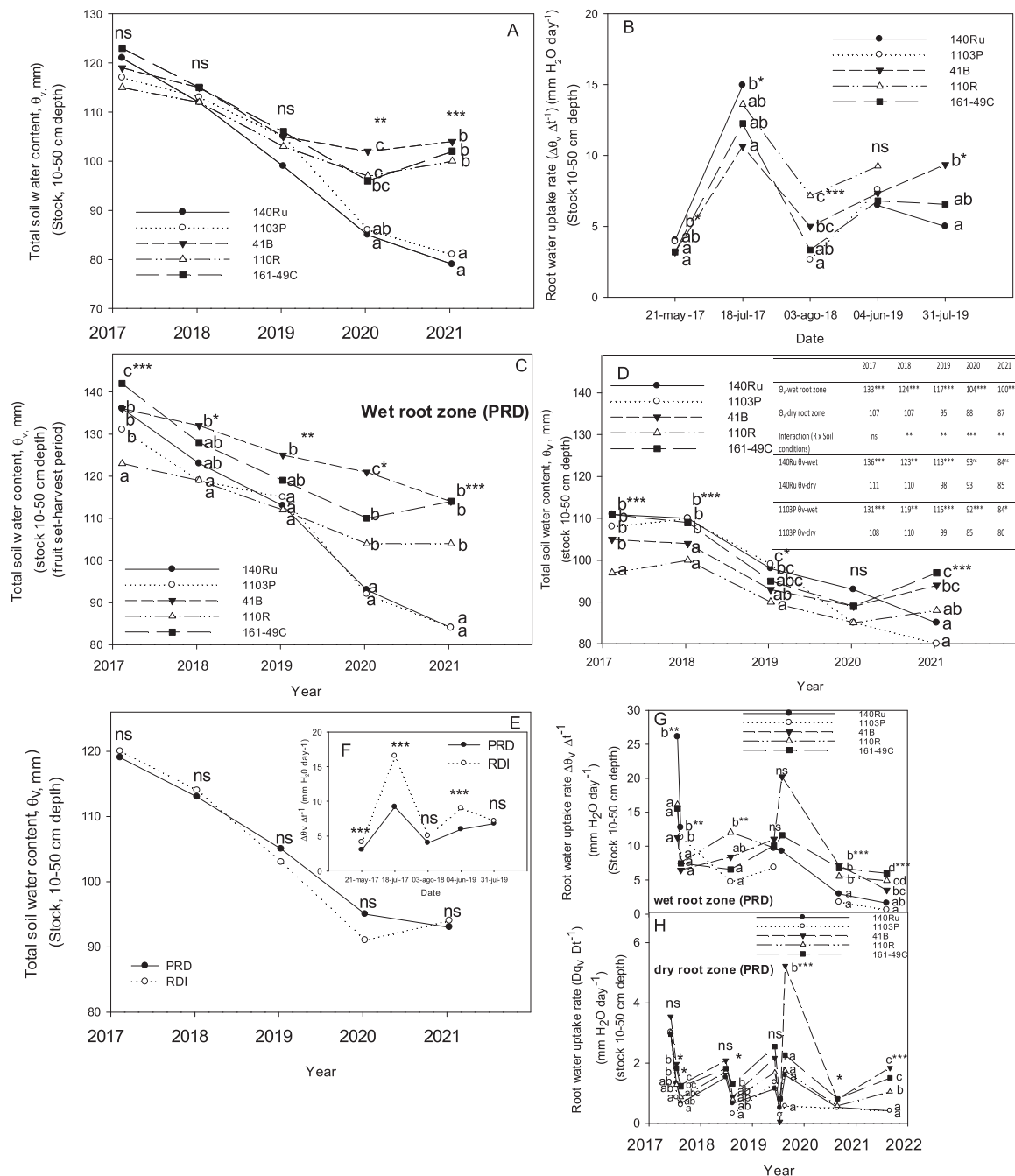


Fig. 1. A. Evolution of total soil water content (θ_v) in the stock 10–50 cm deep (measured in the rhizosphere) for each rootstock throughout the years (2017–2021) for the fruit set-harvest period. B. Root water uptake rates ($\Delta\theta_v \Delta t^{-1}$) estimated from the stock 10–50 cm deep, for each rootstock during the experimental period. C, D. Evolution of total soil water content (θ_v) in the stock 10–50 cm deep for each rootstock in partial root-zone drying irrigation (PRD) treatment, in the wet root zone (C) and the dry root zone (D). Inside graphic D, values in the table represent the average of the total soil water content maintained every year (from fruit set to harvest) in the wet and dry root zones in PRD, and in 140Ru and 1103 P rootstocks during the experimental period 2017–2021. E. Evolution of total soil water content (θ_v) in the stock 10–50 cm deep (from fruit set to harvest period) for PRD and regulated deficit irrigation (RDI) treatments during the experimental period (2017–2021). F. Average root water uptake rates ($\Delta\theta_v \Delta t^{-1}$) estimated from the stock 10–50 cm deep for PRD and RDI during the experimental period (2017–2019). G, H. Root water uptake rates in the soil profile 10–50 cm deep in PRD vines in the wet root zone (G) and dry root zone (H) for each rootstock during the experimental period 2017–2021. Each point is the average of four plants (soil tubes). ANOVA: ns, not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. For each year, the separation of means was made by Duncan’s multiple range test at a 95% confidence level.

Besides, vines grafted on high-vigour rootstocks with greater $\Delta\theta_v \Delta t^{-1}$ also showed significantly higher whole-plant hydraulic conductance (K_{plant} , measured in 2018) (140Ru followed by 1103 P), compared to low-vigour rootstocks 161–49 C and 41B (supplemental Fig. S1).

3.2. Evolution of vine water status

The evolution of Ψ_s throughout the years revealed that 2020, followed by 2019, were the years in which vines suffered more water stress during the growing cycle (Fig. 2A and B). The possible reason is that in 2020, a drastic reduction in irrigation was combined with very little rain from bud break to harvest (Table 1).

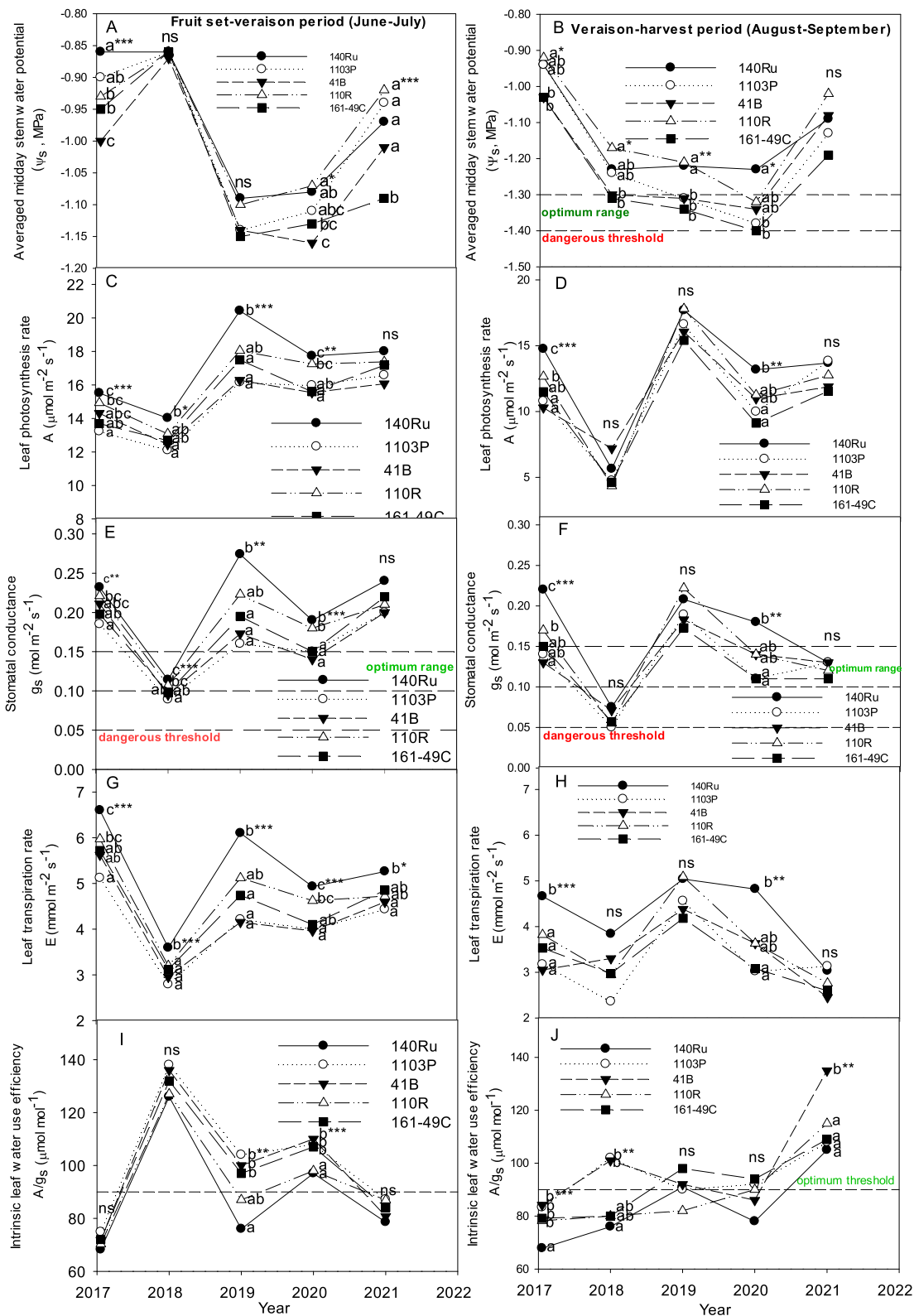


Fig. 2. A, B. Evolution of midday stem water potential during 2017–2021, in two phenological periods for each rootstock. C, D. Evolution of leaf photosynthesis rate (A) during 2017–2021, in two phenological periods for each rootstock measured at early morning. E, F. Evolution of stomatal conductance (g_s) during 2017–2021, in two phenological periods for each rootstock measured at early morning. G, H. Evolution of leaf transpiration rate (E) during 2017–2021, in two phenological periods for each rootstock measured at early morning. I, J. Evolution of intrinsic leaf water use efficiency (A/g_s) during 2017–2021, in two phenological periods for each rootstock measured at early morning. Short horizontal dashed lines represent optimum and dangerous thresholds values of different parameters. Each point is the average of several measurements taken during the phenological period. ANOVA: ns, not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. For each year, the separation of means was made by Duncan’s multiple range test at a 95% confidence level.

In 2017, with the same water volume applied to all of the rootstocks, vines grafted on 140Ru showed a better water status than 41B, 110 R, and 161–49 C (Fig. 2A and B). In 2018, there were no clear differences in vine water status among rootstocks. However, in 2019, during the post-veraison period, 140Ru and 110 R experienced a lower water stress than the other rootstocks (Fig. 2B). Besides, in 2019, the annual average Ψ_s in these two rootstocks (140Ru and 110 R) was also significantly higher (less negative) than that of 161–49 C, which showed the most negative Ψ_s (Table 3). Interestingly, in 2020 (pre- and post-veraison periods), vines grafted on 140Ru showed a significantly higher Ψ_s (less negative) than 41B (pre-veraison) and 1103 P and 161–49 C (post-veraison), in spite of using much less water for irrigation (Fig. 2A and B). Vines grafted on 161–49 C, followed by 1103 P rootstocks, were the most water stressed vines in all of the years, showing significantly lower Ψ_s than the other rootstocks (pre-veraison and annual average) (Fig. 2A, Table 3).

3.3. Evolution of leaf gas exchange at the early morning and midday

In 2017, leaf gas exchange (A , g_s , and E) at the early morning was significantly higher in vines grafted on 140Ru than on 1103 P, 41B, and 161–49 C (Fig. 2C–H). This difference increased during the veraison-harvest period. Besides, WUE_{leaf} (A/g_s) (veraison-harvest) was also significantly lower in 140Ru compared to the rest of the rootstocks (Fig. 2I and J).

During 2018 and 2019 (when 140Ru and 1103 P were irrigated with less water), vines grafted on 140Ru maintained greater leaf gas exchange rates at the early morning than the other rootstocks (1103 P, 41B, and 161–49 C), especially during the fruit set-veraison period (Fig. 2C–2 H). A/g_s was also significantly lower in 140Ru compared to 1103 P, 41B, and 161–49 C (fruit set-veraison period, 2019, and veraison harvest period, 2018) (Fig. 2I and J). The most stressed vines were grafted on 41B, followed by 1103 P, which showed lower g_s , E values and a higher A/g_s .

In 2020, 140Ru also showed greater leaf gas exchange rates (A , g_s , E) than 41B and 1103 P, and a lower A/g_s than 1103 P, during the budburst-fruit set period (Table 3). This response was intensified during the fruit set-veraison and veraison-harvest periods, where 140Ru showed a significantly higher leaf gas exchange and lower A/g_s compared to 1103 P, 41B, and 161–49 C (Fig. 2C–2J). Vines with the lowest leaf gas exchange and the highest A/g_s during the growing season were 1103 P and 41B.

Generally speaking, in 2021, there were no significant differences in leaf gas exchange among rootstocks (Fig. 2 and Table 3). Only during the fruit set-veraison period, E was significantly higher in 140Ru vines than in 1103 P and 41B vines (Fig. 2G), and during the veraison-harvest period, A/g_s and A/E were significantly higher in 41B (Fig. 2J and Table 3). As a consequence of irrigation reduction, A/g_s progressively increased in all of the rootstocks from 2017 to 2021 during the veraison harvest period, reaching values above $110 \mu\text{mol mol}^{-1}$ (Fig. 2J and Table 3).

Besides, leaf gas exchange rates (A , g_s , and E) measured at midday in different phenological periods and years (2017–2020) were also significantly higher in 140Ru vines (compared to 41B, 1103 P or 161–49 C), especially during veraison-harvest periods (Table 3).

3.4. Leaf mineral nutrition

In 2019, there were no significant differences in leaf N content among rootstocks. However, vines grafted on low-vigour rootstock 161–49 C showed a significantly lower concentration of P, K, and Zn and higher concentration of Ca in leaves compared to other rootstocks in 2019 and 2021 (Table 4). Vines grafted on 41B also showed a lower concentration of Ca (2019) and B (2021) compared to the rest of the rootstocks. In contrast, vines grafted on high-vigour rootstocks had a significantly higher concentration of K (140Ru) and Mg (1103 P) and

lower concentration of Na and Cu (140Ru) (2019), compared to the rest of the rootstocks (Table 4).

3.5. Evolution of vegetative development

Essentially, in all of the rootstocks there was a gradual decrease in TLA and exposed leaf area (ELA), main shoot length (MSL), and pruning weight (PW) throughout the years, being this more accused in 140Ru and 1103 P (Fig. 3A, B, C, and E), as a consequence of the greater reduction in water volume. In general, yield/PW ratio gradually increased throughout the years in all of the rootstocks, whereas the TLA/yield ratio progressively decreased in all of the rootstocks, except for 1103 P (Fig. 3D and F).

In 2017, vegetative development (MSL, TLA, and PW) was significantly higher in 140Ru, followed by 1103 P, compared to the rest of the rootstocks. The lowest vegetative development was found in 110 R and 41B rootstocks. Yield/PW ratios were significantly higher in 41B and 110 R compared to the rest of the rootstocks, whereas the TLA/yield ratio was the highest in plants grafted on 161–49 C (Fig. 3D and F).

In 2018 and 2019, plants grafted on 140Ru also maintained significantly higher MSL, TLA, ELA, and PW values than those of the rest of the rootstocks. In contrast, plants grafted on 110 R showed the lowest vegetative growth (Fig. 3A–3E). Yield/PW ratios were significantly higher in 110 R (2018, 2019) and 41B (2019) compared to the rest of the rootstocks (Fig. 3D). Furthermore, TLA/yield ratio was significantly higher in 1103 P (2018) and 161–49 C (2018, 2019) compared to the other rootstocks, whereas 110 R showed the lowest TLA/yield ratio (Fig. 3F).

In 2020, vines grafted on 140Ru continued to maintain a greater vegetative development (MSL, TLA, PW) than the other rootstocks, and even than 1103 P (Fig. 3). In contrast, 110 R rootstock was the one that showed the lowest vegetative development. Besides, yield/PW ratio was the highest in 110 R and 41B, and the lowest in 161–49 C (Fig. 3D). In contrast, the TLA/yield ratio was significantly higher in plants grafted on 161–49 C compared to the rest of the rootstocks (Fig. 3F). In 2021, although there was a general decrease in growth in all of the rootstocks, plants grafted on 140Ru showed a significantly higher MSL than 1103 P and 41B, and a higher TLA and PW than the rest of the rootstocks (Fig. 3A–3E). There were no significant differences in the TLA/yield ratio among rootstocks (Fig. 3F), but yield/PW ratio significantly increased in 140Ru and 110 R, showing the lower value in 161–49 C (Fig. 3D).

3.6. Evolution of yield response and WP

A gradual reduction in yield response was found throughout the years in vines grafted on all of the rootstocks, but specially on 1103 P and 140Ru, from 2019 to 2021 (with a more drastic irrigation reduction) (Fig. 4). Thus, yield reduction in this period (2019–2021) was around 66% (1103 P) and 53% (140Ru), being higher than in the rest of the rootstocks (around 45% in 41B, 34% in 110 R, and 33% in 161–49 C) (Fig. 4A). All of the yield components were affected by irrigation reduction (especially the number of clusters per vine in 140Ru, 1103 P, and 41B), cluster weight (in all of the rootstocks), and berry number per cluster (Fig. 4A–D). Berry weight was also reduced by irrigation restriction, but to a lesser extent (Fig. 4E). Thus, from 2017 to 2021, berry weight was reduced around 20% in 140Ru, 16% in 110 R, 13% in 1103 P and 41B, and 8% in 161–49 C.

As a consequence of irrigation reduction, the evolution of water productivity (WP) showed a substantial increase throughout the years in all of the rootstocks, but especially in 140Ru and 1103 P, reaching very high efficiencies in 2020 (Fig. 4F). Thus, for the period 2017–2021, WP was increased by 223% in 140Ru, 97% in 1103 P, 41% in 161–49 C, 29% in 110 R, and 17% in 41B.

In 2017, yield components (yield, number of clusters, cluster weight, berry weight, number of berries per cluster) were significantly higher in plants grafted on 140Ru than in the rest of the rootstocks (Fig. 4). In

Table 3

Midday stem water potential (Ψ_s) and leaf gas exchange parameters (A, E, g_s , A/E, A/ g_s) measured in different phenological periods and at different times of the day during each year for the different rootstocks and irrigation methods (partial root-zone drying irrigation, PRD and regulated deficit irrigation, RDI).

| 2017 | | | | | | | | | | |
|------------------------|--------------|---|------------------------------------|------------------------------------|-----------------------------|-----------------------------|----------------------------------|---------------------------|----------|---------------------------|
| | Annual aver. | Budburst-fruit set period (early morning) | Budburst-Fruit set period (midday) | Fruit set-veraison period (midday) | | | Veraison-harvest period (midday) | | | |
| Rootstock (R) | Ψ_s | A | E | A | g_s | E | A | g_s | E | A/ g_s |
| 140Ru | -0.89b | 19.04b | 5.72b | 12.16b | 0.152c | 6.60c | 15.25c | 0.230c | 6.19b | 68a |
| 1103 P | -0.91b | 18.01a | 4.74ab | 9.74a | 0.120ab | 4.90a | 12.87a | 0.178ab | 4.86a | 75b |
| 41B | -1.00a | 17.85a | 4.58a | 9.88a | 0.117a | 5.07a | 11.83a | 0.156a | 4.53a | 77b |
| 110 R | -0.93b | 18.56ab | 4.63a | 11.50b | 0.142bc | 5.85b | 14.00b | 0.199b | 5.35a | 72ab |
| 161-49 C | -0.98a | 17.81a | 5.36ab | 10.89ab | 0.133abc | 5.77b | 12.26a | 0.167a | 4.72a | 76b |
| Irrigation method (IM) | | | | | | | | | | |
| PRD | -0.94 | 17.95 | 5.05 | 10.97 | 0.135 | 5.78 | 13.17 | 0.185 | 5.07 | 74 |
| RDI | -0.95 | 18.56 | 4.96 | 10.70 | 0.130 | 5.50 | 13.32 | 0.188 | 5.19 | 73 |
| ANOVA | | | | | | | | | | |
| Rootstock (R) | *** | * | * | *** | *** | **** | **** | **** | **** | * |
| Irrigation method (IM) | ns | ** | ns | ns | ns | ns | ns | ns | ns | ns |
| Interaction (R x IM) | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| 2018 | | | | | | | | | | |
| | Annual aver. | Budburst-fruit set (early morning) | | | Fruit set-veraison (midday) | | | Veraison-harvest (midday) | | |
| Rootstock (R) | Ψ_s | g_s | E | A/ g_s | A | g_s | E | E | A/ g_s | A/E |
| 140Ru | -1.05 | 0.155b | 4.01b | 117.9ab | 14.02b | 0.114c | 3.59b | 3.84 | 76a | 1.53a |
| 1103 P | -1.05 | 0.136ab | 3.29a | 122.0ab | 12.10a | 0.089a | 2.79a | 2.36 | 102b | 2.31b |
| 41B | -1.08 | 0.128a | 3.28a | 126.0b | 12.45a | 0.095ab | 2.95a | 3.30 | 101b | 2.20b |
| 110 R | -1.01 | 0.153ab | 3.77ab | 112.6a | 13.08ab | 0.107bc | 3.20a | 2.94 | 80ab | 1.51a |
| 161-49 C | -1.09 | 0.160b | 3.95b | 112.4a | 12.68ab | 0.098ab | 3.12a | 2.97 | 80ab | 1.53a |
| Irrigation method (IM) | | | | | | | | | | |
| PRD | -1.07 | 0.147 | 3.63 | 118.9 | 12.57 | 0.098 | 3.05 | 3.46 | 82 | 1.61 |
| RDI | -1.05 | 0.145 | 3.69 | 117.4 | 13.16 | 0.104 | 3.21 | 2.70 | 94 | 2.02 |
| ANOVA | | | | | | | | | | |
| Rootstock (R) | ns | * | ** | * | * | *** | *** | ns | ** | ** |
| Irrigation method (IM) | ns | ns | ns | ns | ns | ns | ns | * | * | ** |
| Interaction (R x IM) | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| 2019 | | | | | | | | | | |
| | Annual aver. | Fruit set-veraison (midday) | | | | | Veraison-harvest (midday) | | | |
| Rootstock (R) | Ψ_s | A | g_s | E | A/ g_s | A/E | A | g_s | E | A/ g_s |
| 140Ru | -1.15b | 15.91b | 0.157b | 4.76b | 103a | 3.36a | 14.54b | 0.154b | 5.52b | 98 |
| 1103 P | -1.22ab | 13.03ab | 0.107ab | 3.44a | 127b | 3.94b | 12.94ab | 0.127ab | 4.79ab | 108 |
| 41B | -1.22ab | 11.53a | 0.096a | 3.02a | 132b | 4.03b | 12.05ab | 0.119ab | 4.34ab | 106 |
| 110 R | -1.15b | 14.37ab | 0.137ab | 4.10ab | 112ab | 3.61ab | 15.01b | 0.154b | 5.44b | 99 |
| 161-49 C | -1.24a | 14.51ab | 0.131ab | 4.07ab | 116ab | 3.61ab | 11.19a | 0.102a | 4.00a | 117 |
| Irrigation method (IM) | | | | | | | | | | |
| PRD | -1.20 | 13.76 | 0.122 | 3.82 | 121 | 3.72 | 13.27 | 0.133 | 4.86 | 105 |
| RDI | -1.19 | 13.98 | 0.129 | 3.93 | 115 | 3.70 | 13.02 | 0.130 | 4.77 | 106 |
| ANOVA | | | | | | | | | | |
| Rootstock (R) | * | * | * | ** | ** | ** | * | * | * | ns |
| Irrigation method (IM) | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| Interaction (R x IM) | ns | ns | ns | ns | ns | ns | ns | * | * | ns |
| 2020 | | | | | | | | | | |
| | Annual aver. | Budburst-fruit set (early morning) | | | | Budburst-fruit set (midday) | Fruit set-veraison (midday) | | | Veraison-harvest (midday) |

(continued on next page)

Table 3 (continued)

| 2017 | | | | | | | | | | | | | |
|------------------------|--------------|---|------------------------------------|------------------------------------|----------|-------------------------------------|----------------------------------|---------|----------|----------------------------------|--------|----------|--------|
| | Annual aver. | Budburst-fruit set period (early morning) | Budburst-fruit set period (midday) | Fruit set–veraison period (midday) | | | Veraison-harvest period (midday) | | | | | | |
| Rootstock (R) | Ψ_s | A | g_s | E | A/ g_s | g_s | E | A | g_s | E | A | g_s | E |
| 140Ru | -1.12 | 21.05b | 0.211b | 4.29b | 101a | 0.131bc | 4.22b | 11.17b | 0.123b | 5.48b | 10.52b | 0.129b | 6.74b |
| 1103 P | -1.18 | 17.36a | 0.150a | 3.10a | 124b | 0.120abc | 3.60ab | 9.72ab | 0.097a | 4.41a | 8.40a | 0.081a | 4.24a |
| 41B | -1.20 | 18.21ab | 0.162a | 3.30a | 115ab | 0.099a | 3.13a | 9.16a | 0.092a | 4.23a | 8.88ab | 0.099a | 4.92a |
| 110 R | -1.13 | 19.64ab | 0.189ab | 3.77ab | 107ab | 0.134c | 3.87b | 11.22b | 0.114ab | 5.00ab | 8.18a | 0.086a | 4.43a |
| 161-49 C | -1.20 | 19.03ab | 0.174ab | 3.71ab | 115ab | 0.105ab | 3.51ab | 10.41ab | 0.106ab | 4.85ab | 7.67a | 0.083a | 4.59a |
| Irrigation method (IM) | | | | | | | | | | | | | |
| PRD | -1.18 | 19.30 | 0.180 | 3.72 | 113 | 0.126 | 3.86 | 10.30 | 0.106 | 4.80 | 8.83 | 0.095 | 4.94 |
| RDI | -1.16 | 18.82 | 0.174 | 3.55 | 113 | 0.110 | 3.48 | 10.37 | 0.107 | 4.79 | 8.63 | 0.097 | 5.03 |
| ANOVA | | | | | | | | | | | | | |
| Rootstock (R) | ns | * | * | * | * | ** | ** | * | * | ** | ** | *** | **** |
| Irrigation method (IM) | ns | ns | ns | ns | ns | * | * | ns | ns | ns | ns | ns | ns |
| Interaction (R x IM) | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| 2021 | | | | | | | | | | | | | |
| | Annual aver. | Budburst-fruit set (early morning) | | | | Fruit set –veraison (early morning) | | | | Veraison-harvest (early morning) | | | |
| Rootstock (R) | Ψ_s | A | g_s | E | A/ g_s | A | g_s | E | A/ g_s | g_s | E | A/ g_s | A/E |
| 140Ru | -1.01b | 20.36 | 0.27 | 5.52 | 77 | 18.00 | 0.24 | 5.26b | 78.61 | 0.13 | 3.03 | 105a | 4.51a |
| 1103 P | -1.01b | 18.71 | 0.24 | 4.79 | 81 | 16.57 | 0.20 | 4.43a | 87.14 | 0.13 | 3.13 | 108a | 4.38a |
| 41B | -1.03b | 18.86 | 0.24 | 4.91 | 80 | 16.07 | 0.20 | 4.59a | 80.77 | 0.13 | 2.45 | 135b | 5.06b |
| 110 R | -0.96b | 18.87 | 0.23 | 4.78 | 85 | 17.38 | 0.21 | 4.72ab | 86.95 | 0.12 | 2.76 | 115a | 4.69ab |
| 161-49 C | -1.12a | 19.31 | 0.25 | 5.03 | 81 | 17.18 | 0.22 | 4.85ab | 84.12 | 0.11 | 2.59 | 109a | 4.47a |
| Irrigation method (IM) | | | | | | | | | | | | | |
| PRD | -1.07 | 19.05 | 0.24 | 4.99 | 81 | 16.66 | 0.20 | 4.61 | 85.14 | 0.116 | 2.75 | 113 | 4.63 |
| RDI | -0.98 | 19.40 | 0.25 | 5.02 | 80 | 17.42 | 0.22 | 4.93 | 81.90 | 0.132 | 2.83 | 115 | 4.61 |
| ANOVA | | | | | | | | | | | | | |
| Rootstock (R) | *** | ns | ns | ns | ns | ns | ns | * | ns | ns | ns | ** | ** |
| Irrigation method (IM) | *** | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| Interaction (R x IM) | ** | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |

Abbreviations: Ψ_s , midday stem water potential (MPa); A, net leaf photosynthesis rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$); g_s , leaf stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$); E, leaf transpiration rate ($\text{mmol m}^{-2} \text{s}^{-1}$); A/ g_s , intrinsic leaf water use efficiency ($\mu\text{mol mol}^{-1}$); A/E, instantaneous leaf water use efficiency ($\mu\text{mol mmol}^{-1}$). 'ns' not significant; *, **, and *** indicate significant differences at the 0.05, 0.01, and 0.001 levels of probability, respectively. In each column and for each factor, different letters indicate significant differences according to Duncan's multiple range test at a 95% confidence level.

contrast, plants grafted on 161–49 C, followed by 110 R and 41B, had the lowest yield response. Besides, WP was significantly greater in 140Ru vines, followed by 1103 P, and the lowest values were found in 161–49 C (Fig. 4F).

In 2018 and 2019, 140Ru vines also maintained a significantly higher yield, number of clusters, cluster weight, number of berries per cluster, and berry weight than 1103 P and the rest of the rootstocks (Fig. 4). Besides, in 140Ru vines, WP was significantly increased (between 51% and 76% 2018 and 47% and 76% in 2019), compared to the other rootstocks. Vines grafted on 161–49 C showed the lowest yield and WP.

In 2020 and 2021, vines grafted on 140Ru still maintained a significantly greater yield (in all of the yield components, except for berry weight; Fig. 4E) compared to other rootstocks. However, there were no significant differences in the yield response among the other rootstocks. Besides, as a consequence of irrigation reduction in 2020–2021, WP was increased between 56–89% in 140Ru vines compared to the other rootstocks, reaching values of 90 kg m^{-3} in 2020 and 58 kg m^{-3} in 2021. In this regard, 140Ru was followed by 1103 P (51 kg m^{-3} in 2020

and 22 kg m^{-3} , in 2021). The lowest WP was observed in 161–49 C (10 kg m^{-3}) in 2020 (Fig. 4F).

3.7. Evolution of berry quality

In 2017, with all of the rootstocks irrigated with the same water volume, there were no differences in °Brix among rootstocks (Table 5). In contrast, pH and malic acid were significantly lower in 161–49 C, and higher in 140Ru and 1103 P. The tartaric acid/malic acid ratio was also higher in 161–49 C compared to the rest of the rootstocks. The percentage of must was also significantly higher in 140Ru than in the rest of the rootstocks (Table 5), whereas colour intensity was higher in 161–49 C (with lower a*, b*, C*, and h; Table 6) than in 41B or 140Ru. Polyphenol content was also the lowest in 140Ru vines (Table 6). The analysis of nutrient concentration in must carried out in 2017 (Table 7) also revealed that 140Ru and 1103 P vines had significantly higher values of P (140Ru, 1103 P), K (1103 P), Zn (140Ru) than the other rootstocks (especially 41B and 161–49 C). In contrast, 140Ru and 1103 P had lower Ca and Mn values than 41B and 161–49 C (Table 7).

Table 4

Leaf mineral concentration of Monastrell plants at veraison in five different rootstocks (140Ru, 1103 P, 41B, 110 R, and 161–49 C) and two different irrigation systems (partial root-zone drying irrigation, PRD and regulated deficit irrigation, RDI) in 2019 and 2021. N, P, K, Ca, Mg, and Na in %, Fe, Cu, Mn, Zn, and B in ppm.

| 2019 | | | | | | | | | | | | |
|-------------------------------|-----|------|--------|---------|--------|--------|--------|--------|-------|-------|--------|--------|
| Rootstock (R) | | N | P | K | Ca | Mg | Na | Fe | Cu | Mn | Zn | B |
| 140Ru | | 2.40 | 0.100b | 0.433c | 1.66bc | 0.434a | 0.035a | 77.2 | 22.6a | 128 | 28.7b | 50.5b |
| 1103 P | | 2.30 | 0.100b | 0.358ab | 1.60b | 0.486b | 0.042b | 78.2 | 31.7b | 120 | 29.3b | 50.2b |
| 41B | | 2.29 | 0.101b | 0.346ab | 1.073a | 0.435a | 0.052b | 79.5 | 31.6b | 114 | 27.3b | 31.5a |
| 110 R | | 2.33 | 0.103b | 0.375bc | 1.73bc | 0.437a | 0.044b | 76.1 | 32.3b | 122 | 27.5b | 55.9b |
| 161-49 C | | 2.25 | 0.089a | 0.308a | 1.93c | 0.440a | 0.043b | 82.3 | 33.7b | 131 | 23.2a | 57.8b |
| Irrigation method (IM) | | | | | | | | | | | | |
| PRD | | 2.32 | 0.097 | 0.359 | 1.77 | 0.445 | 0.043 | 77.0 | 28.4 | 120 | 27.6 | 54.0 |
| RDI | | 2.31 | 0.100 | 0.369 | 1.43 | 0.448 | 0.043 | 80.4 | 32.3 | 126 | 26.8 | 44.3 |
| Interaction (R x IM) | | | | | | | | | | | | |
| 140Ru | PRD | 2.35 | 0.095 | 0.416 | 2.11 | 0.432 | 0.035 | 76.1 | 24.9 | 120 | 28.9 | 63.2 |
| | RDI | 2.46 | 0.104 | 0.450 | 1.21 | 0.437 | 0.034 | 78.4 | 20.4 | 136 | 28.5 | 37.7 |
| 1103 P | PRD | 2.30 | 0.099 | 0.338 | 1.76 | 0.507 | 0.045 | 79.1 | 30.4 | 115 | 29.8 | 55.5 |
| | RDI | 2.31 | 0.100 | 0.378 | 1.44 | 0.466 | 0.040 | 77.4 | 33.1 | 125 | 28.7 | 44.9 |
| 41B | PRD | 2.30 | 0.100 | 0.380 | 1.15 | 0.417 | 0.050 | 78.2 | 29.4 | 120 | 29.5 | 33.9 |
| | RDI | 2.29 | 0.101 | 0.311 | 1.00 | 0.454 | 0.054 | 80.8 | 33.7 | 109 | 25.0 | 29.1 |
| 110 R | PRD | 2.39 | 0.105 | 0.345 | 1.67 | 0.436 | 0.043 | 74.2 | 26.3 | 125 | 27.1 | 52.8 |
| | RDI | 2.28 | 0.101 | 0.405 | 1.80 | 0.438 | 0.045 | 77.9 | 38.3 | 119 | 27.9 | 59.0 |
| 161-49 C | PRD | 2.27 | 0.088 | 0.315 | 2.14 | 0.432 | 0.043 | 77.2 | 31.2 | 121 | 22.5 | 64.7 |
| | RDI | 2.23 | 0.091 | 0.302 | 1.73 | 0.448 | 0.043 | 87.5 | 36.2 | 140 | 23.9 | 50.9 |
| ANOVA | | | | | | | | | | | | |
| Rootstock (R) | | ns | *** | ** | *** | * | * | ns | ns | ns | *** | ns |
| Irrigation method (IM) | | ns | ns | ns | *** | ns | ns | ns | ns | ns | ns | ns |
| R x IM | | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| 2021 | | | | | | | | | | | | |
| Rootstock (R) | | | P | K | Ca | Mg | Na | Fe | Cu | Mn | Zn | B |
| 140Ru | | | 0.111 | 0.40b | 1.76ab | 0.35a | 0.127 | 67.2 | 11.7 | 93.8 | 28.8b | 60.8ab |
| 1103 P | | | 0.104 | 0.37ab | 1.74ab | 0.40b | 0.134 | 71.0 | 12.3 | 98.0 | 29.3b | 72.5b |
| 41B | | | 0.112 | 0.34ab | 1.83b | 0.36a | 0.126 | 71.9 | 13.2 | 102.5 | 24.6a | 44.1a |
| 110 R | | | 0.107 | 0.40b | 1.64a | 0.33a | 0.130 | 69.5 | 12.8 | 98.0 | 28.2ab | 63.9b |
| 161-49 C | | | 0.103 | 0.30a | 1.90b | 0.35a | 0.134 | 68.5 | 12.6 | 96.8 | 25.2a | 78.4b |
| Irrigation method (IM) | | | | | | | | | | | | |
| PRD | | | 0.106 | 0.36 | 1.75 | 0.35 | 0.132 | 70.3 | 12.2 | 98.4 | 27.4 | 72.0 |
| RDI | | | 0.108 | 0.36 | 1.80 | 0.37 | 0.128 | 68.9 | 12.8 | 97.3 | 27.1 | 55.9 |
| Interaction (R x IM) | | | | | | | | | | | | |
| 140Ru | PRD | | 0.109 | 0.38 | 1.76 | 0.34 | 0.135 | 71.2ab | 11.6 | 91.3 | 29.8 | 79.1 |
| | RDI | | 0.112 | 0.41 | 1.76 | 0.36 | 0.120 | 63.1a | 11.8 | 96.3 | 27.7 | 42.5 |
| 1103 P | PRD | | 0.101 | 0.37 | 1.81 | 0.40 | 0.144 | 72.8ab | 12.3 | 106.8 | 30.3 | 84.4 |
| | RDI | | 0.107 | 0.38 | 1.66 | 0.40 | 0.125 | 69.2ab | 12.2 | 89.1 | 28.3 | 60.7 |
| 41B | PRD | | 0.110 | 0.36 | 1.72 | 0.35 | 0.127 | 74.8b | 13.0 | 100.6 | 24.4 | 43.6 |
| | RDI | | 0.114 | 0.32 | 1.93 | 0.37 | 0.125 | 68.9ab | 13.3 | 104.4 | 24.7 | 44.5 |
| 110 R | PRD | | 0.108 | 0.41 | 1.57 | 0.30 | 0.137 | 63.5a | 12.3 | 98.9 | 25.9 | 69.6 |
| | RDI | | 0.106 | 0.38 | 1.71 | 0.36 | 0.122 | 75.5b | 13.2 | 97.2 | 30.6 | 58.3 |
| 161-49 C | PRD | | 0.103 | 0.29 | 1.87 | 0.34 | 0.120 | 69.3ab | 11.7 | 94.3 | 26.4 | 83.3 |
| | RDI | | 0.103 | 0.31 | 1.92 | 0.37 | 0.148 | 67.7ab | 13.5 | 99.4 | 24.0 | 73.6 |
| ANOVA | | | | | | | | | | | | |
| Rootstock (R) | | | ns | * | * | *** | ns | ns | ns | ns | * | ** |
| Irrigation method (IM) | | | ns | ns | ns | * | ns | ns | ns | ns | ns | ** |
| R x IM | | | ns | ns | ns | ns | ns | * | ns | ns | ns | ns |

'ns' not significant; *, **, and *** indicate significant differences at the 0.05, 0.01, and 0.001 levels of probability, respectively. In each column and for each factor or interaction, different letters indicate significant differences according to Duncan's multiple range test at a 95% confidence level.

Besides, $QI_{overall\ berry}$ was significantly higher in 161–49 C compared to the other rootstocks (mainly due to a higher $QI_{phenolic\ berry}$) (Fig. 4H and J).

In 2018, pH was significantly higher in 1103 P compared to 161–49 C (which had the lowest pH) (Table 5). The concentration of malic acid was significantly higher in 140Ru and 1103 P compared to the rest of the rootstocks, while tartaric acid/malic acid ratio was higher in 161–49 C, compared to 140Ru, 1103 P, and 41B (Table 5). Extractable anthocyanins and polyphenol content in 161–49 C vines was significantly higher than in the rest of the rootstocks, and SM was significantly lower (Table 6). As a consequence, $QI_{overall\ berry}$ and $QI_{technological\ berry}$ were also significantly higher in 161–49 C than in the other rootstocks (Fig. 4H and J). The analysis of nutrient concentration in the must in 2018 also revealed that the most vigorous rootstocks (140Ru and 1103 P) had a higher concentration of P (140Ru, 1103 P),

Mg (1103 P), K (1103 P), and Zn (140Ru) compared to the rest of the rootstocks (Table 7).

In 2019, MI was significantly higher in 41B than in the rest of the rootstocks (Table 5). Besides, the concentration of malic acid and the tartaric acid/malic acid ratio were significantly increased in 161–49 C compared to the rest of the rootstocks (Table 5). The analysis of phenolic maturity in the must also indicated that vines grafted on 161–49 C had significantly higher CI, extractable and total anthocyanins, total polyphenols, CM, and SM values compared to the rest of the rootstocks (Table 6). In contrast, more vigorous rootstocks showed lower CI (1103 P), total and extractable anthocyanins (1103 P, 140Ru), polyphenols content (140Ru), and tannins (140Ru) values than the rest of the rootstocks. CM and SM were lower in 110 R compared to 161–49 C, 41B or 1103 P (Table 6). Therefore, $QI_{technological}$ and $QI_{overall\ berry}$ were also significantly increased in 161–49 C compared to the rest of the

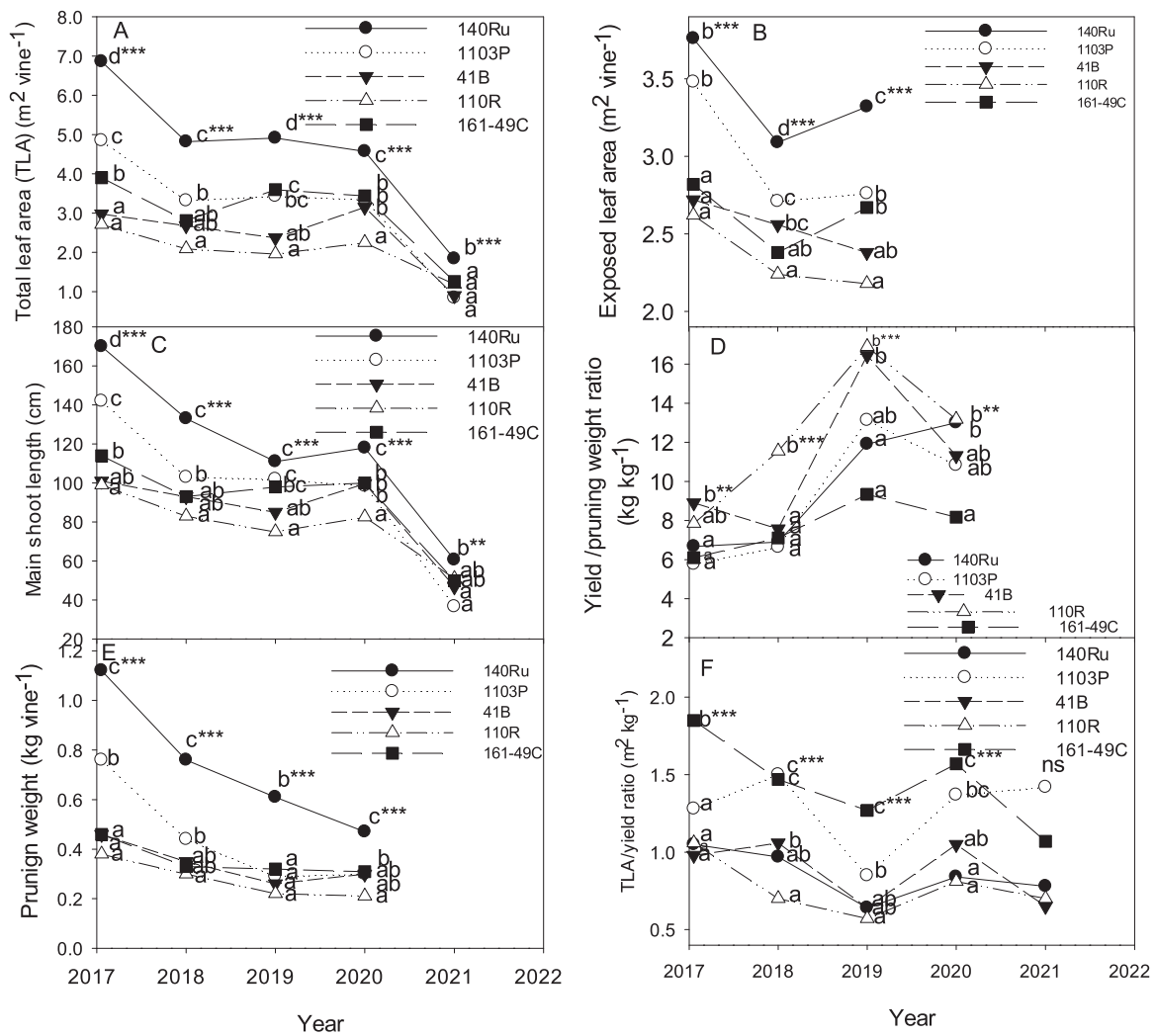


Fig. 3. A. Evolution of total leaf area (TLA) for each rootstock during the experimental period 2017–2021. B. Evolution of exposed leaf area for each rootstock during the experimental period 2017–2019. C. Evolution of main shoot length for each rootstock during the experimental period 2017–2021. D. Evolution of yield/pruning weight ratio for each rootstock during the experimental period 2017–2020. E. Evolution of pruning weight for each rootstock during the experimental period 2017–2020. F. Evolution of TLA/yield ratio for each rootstock during the experimental period 2017–2021. ANOVA: ns, not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. For each year, the separation of means was made by Duncan's multiple range test at a 95% confidence level.

rootstocks (Fig. 4H and J). In 2019, 110 R vines had a higher concentration of P and 1103 P had more K than the rest of the rootstocks (Table 7). In contrast, 161–49 C vines had a lower concentration of P (compared to 110 R, 41B, and 1103 P), K (compared to 1103 P), and Cu (compared to the rest of the rootstocks) and a higher concentration of Ca (compared to 110 R) and B (compared to 110 R, 41B, and 140Ru) (Table 7).

In 2020, pH and content of malic acid of the must significantly decreased in 161–49 C compared to the other rootstocks. In contrast, tartaric acid/malic acid ratio increased in 161–49 C, compared to other rootstocks (Table 5). The analysis of phenolic quality in 2020 (Table 6) reported no significant differences in colour intensity, chromatic parameters (CIELab parameters) or total anthocyanins between rootstocks. However, extractable anthocyanins and polyphenol content significantly increased in 161–49 C (compared to 110 R or 140Ru), whereas CM and SM indices were lower on it than in the rest of the rootstocks (Table 6). In contrast, 41B had the greatest tannin concentration in must. In 2020, there were no significant differences in $QI_{\text{technological}}$ and $QI_{\text{phenolic berry}}$ among rootstocks, but $QI_{\text{overall berry}}$ significantly increased in 161–49 C compared to the rest of the rootstocks (Fig. 4H and J). Rootstocks 110 R and 41B also showed a higher concentration of P in the must, meanwhile 161–49 C had a lower concentration of P, Zn, and Cu

compared to other rootstocks and higher B compared to (41B and 140Ru). In contrast, 140Ru had a higher Ca, Zn, and Cu concentration than other rootstocks (Table 7).

In 2021, there were no significant differences in TSS, pH, total acidity or MI among rootstocks (Table 5). However, the concentration of malic and tartaric acids increased in 1103 P and 110 R compared to 140Ru or 41B. Tartaric acid/malic acid ratios significantly decreased in 1103 P and 110 R compared to 41B (Table 5). The percentage of water in the berries and the percentage of must was progressively decreasing from 2017, reaching minimum values in 2021 in all of the rootstocks (Table 5). There were no significant differences in phenolic quality parameters (Table 6) and berry quality indices among rootstocks (Fig. 4), except in the CM index, where 140Ru and 1103 P had a lower CM than 41B or 161–49 C (Table 6). Besides, although CI and polyphenolic content was similar among rootstocks, some chromatic characteristics such as CIELab parameters b^* and h significantly increased in 161–49 C and 140Ru (Table 6). In addition, 110 R had a higher concentration of P and Zn in the must, whereas 140Ru and 161–49 C showed a lower concentration of P, K (140Ru), and Zn (161–49 C) (Table 7). However, vines grafted on 1103 P showed a significantly higher concentration of Mg, K, Mn, Zn, and B in the must compared to the rest of the rootstocks (Table 7).

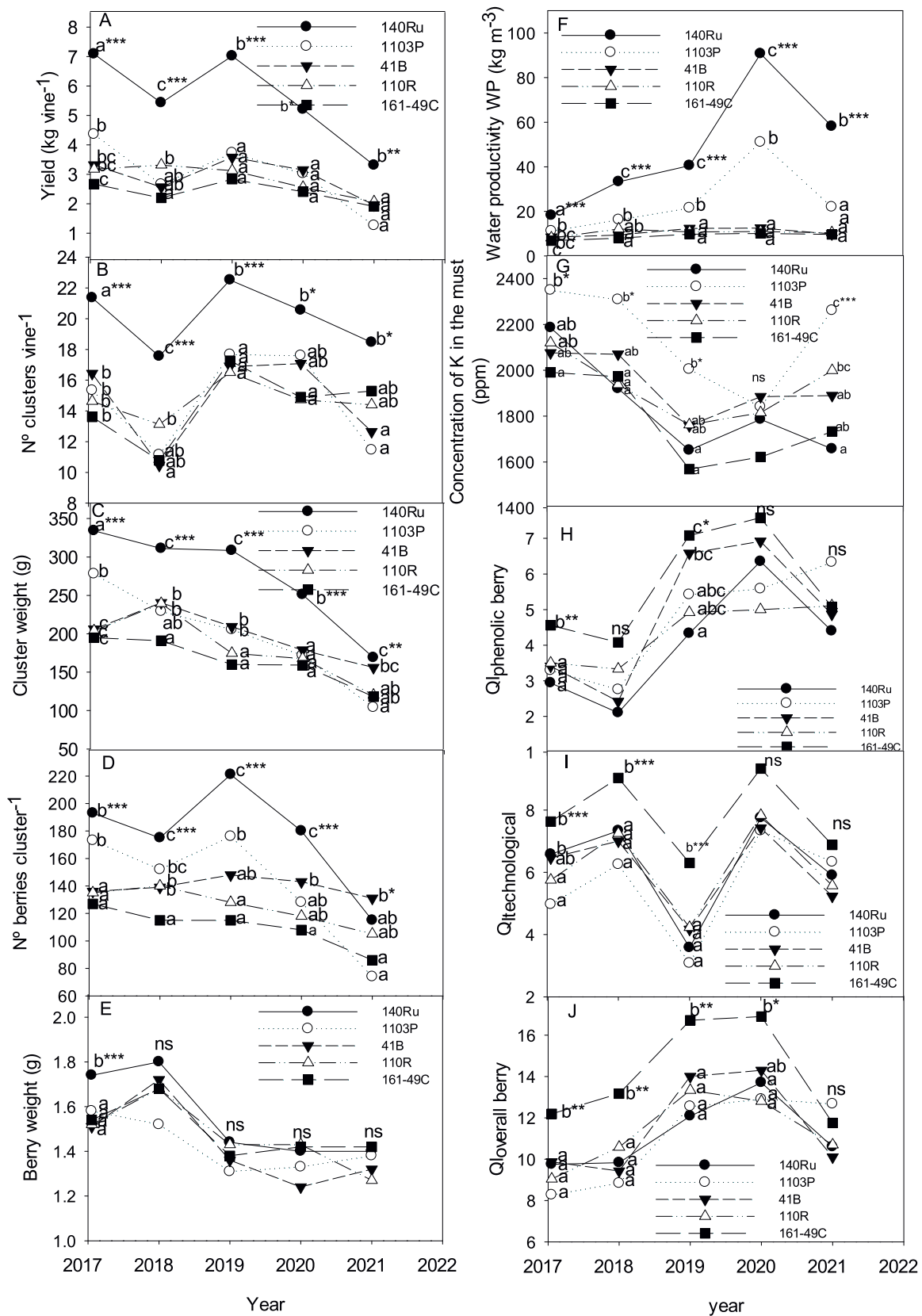


Fig. 4. Evolution of yield (A), number of clusters per vine (B), cluster weight (C), number of berries per cluster (D), berry weight (E), water productivity (WP) (F), concentration of K in the must (G), phenolic quality index ($QI_{phenolic\ berry}$) (H), technological quality index ($QI_{technological\ berry}$) (I), and quality index ($QI_{overall\ berry}$) (J), for each rootstock during the experimental period 2017–2021. ANOVA: ns, not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. For each year, the separation of means was made by Duncan's multiple range test at a 95% confidence level.

Table 5

Mean values of technological parameters of the must made from Monastrell grapes at harvest in different rootstocks (140Ru, 1103 P, 41B, 110 R, and 161–49 C) and two different irrigation methods (partial root-zone drying irrigation, PRD and regulated deficit irrigation, RDI) for each year (period 2017–2021). TSS (total soluble solids, °Brix), total acidity (g tartaric acid L⁻¹), MI (maturity index), tartaric acid (g L⁻¹), malic acid (g L⁻¹).

| 2017 | | | | | | | | | |
|-------------------------------|-------------|--------|---------------|-------|---------------|------------|--------------------------------|------------------------------------|--------|
| Rootstock (R) | TSS (°Brix) | pH | Total acidity | MI | Tartaric acid | Malic acid | Tartaric acid/malic acid ratio | %H ₂ O _{berry} | % must |
| 140Ru | 22.9 | 3.95ab | 3.53 | 6.61 | 4.57 | 1.89c | 2.06a | 73.7 | 70.0b |
| 1103 P | 22.7 | 4.09c | 3.32 | 6.95 | 4.55 | 1.96c | 2.37ab | 73.4 | 67.5a |
| 41B | 22.4 | 3.91ab | 3.29 | 7.00 | 4.26 | 1.52ab | 2.90bc | 73.5 | 67.7a |
| 110 R | 22.3 | 3.98b | 3.41 | 6.61 | 4.49 | 1.56b | 3.04c | 73.6 | 68.2a |
| 161-49 C | 22.6 | 3.87a | 3.61 | 6.51 | 4.52 | 1.37a | 3.44d | 74.0 | 68.8ab |
| Irrigation method (IM) | | | | | | | | | |
| PRD | 22.4 | 3.93 | 3.55 | 6.44 | 4.51 | 1.66 | 2.74 | 73.6 | 68.6 |
| RDI | 22.8 | 3.99 | 3.32 | 7.04 | 4.45 | 1.66 | 2.79 | 73.6 | 68.3 |
| ANOVA | | | | | | | | | |
| Rootstock (R) | ns | *** | ns | ns | ns | *** | *** | ns | * |
| Irrigation method (IM) | ns | ** | ** | ** | ns | ns | ns | ns | ns |
| Interaction (R x IM) | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| 2018 | | | | | | | | | |
| Rootstock (R) | TSS (°Brix) | pH | Total acidity | MI | Tartaric acid | Malic acid | Tartaric acid/malic acid ratio | %H ₂ O _{berry} | % must |
| 140Ru | 23.4 | 3.99ab | 3.56 | 6.61 | 4.04 | 1.49b | 2.56a | 75.0 | 69.6 |
| 1103 P | 22.9 | 4.18c | 3.87 | 5.88 | 4.15 | 1.58b | 2.77ab | 75.2 | 68.7 |
| 41B | 23.3 | 4.05bc | 3.64 | 6.57 | 3.82 | 1.17a | 3.03ab | 74.7 | 69.2 |
| 110 R | 23.3 | 4.06bc | 3.75 | 6.51 | 4.07 | 1.26a | 3.39bc | 75.0 | 69.4 |
| 161-49 C | 23.9 | 3.85a | 3.84 | 6.36 | 3.75 | 1.06a | 3.70c | 74.1 | 68.7 |
| Irrigation method (IM) | | | | | | | | | |
| PRD | 23.2 | 4.00 | 3.71 | 6.32 | 3.91 | 1.30 | 3.16 | 75.1 | 69.3 |
| RDI | 23.5 | 4.05 | 3.76 | 6.45 | 4.02 | 1.32 | 3.02 | 74.5 | 69.0 |
| ANOVA | | | | | | | | | |
| Rootstock (R) | ns | ** | ns | ns | ns | *** | ** | ns | ns |
| Irrigation method (IM) | ns | ns | ns | ns | ns | ns | ns | * | ns |
| Interaction (R x IM) | ns | ns | ns | ns | * | ns | *** | ns | ns |
| 2019 | | | | | | | | | |
| Rootstock (R) | TSS (°Brix) | pH | Total acidity | MI | Tartaric acid | Malic acid | Tartaric acid/malic acid ratio | %H ₂ O _{berry} | % must |
| 140Ru | 21.2 | 4.05 | 3.06 | 7.05a | 3.67 | 1.86b | 2.21a | 78.8 | 65.1 |
| 1103 P | 20.3 | 4.07 | 3.13 | 6.62a | 4.08 | 1.94b | 2.12a | 79.6 | 63.3 |
| 41B | 21.7 | 4.03 | 2.95 | 7.49b | 3.25 | 1.70b | 2.54a | 78.2 | 63.1 |
| 110 R | 21.8 | 4.01 | 3.24 | 6.69a | 3.74 | 1.95b | 1.98a | 78.4 | 65.9 |
| 161-49 C | 21.9 | 3.96 | 3.32 | 6.64a | 2.96 | 0.99a | 3.49b | 78.0 | 62.8 |
| Irrigation method (IM) | | | | | | | | | |
| PRD | 21.1 | 3.99 | 3.15 | 6.75 | 3.69 | 1.86 | 2.56 | 79.4 | 63.7 |
| RDI | 21.7 | 4.06 | 3.13 | 7.04 | 3.39 | 1.94 | 2.38 | 77.8 | 64.4 |
| ANOVA | | | | | | | | | |
| Rootstock (R) | ns | ns | ns | * | ns | ** | *** | ns | ns |
| Irrigation method (IM) | ns | ns | ns | ns | ns | ns | ns | * | ns |
| Interaction (R x IM) | ns | ns | ns | * | ns | ns | ns | ns | ns |
| 2020 | | | | | | | | | |
| Rootstock (R) | TSS (°Brix) | pH | Total acidity | MI | Tartaric acid | Malic acid | Tartaric acid/malic acid ratio | %H ₂ O _{berry} | % must |
| 140Ru | 24.0 | 4.10b | 3.86 | 6.16 | 4.04 | 1.28b | 3.84a | 71.1 | 64.0b |
| 1103 P | 23.7 | 4.15b | 3.78 | 6.36 | 3.99 | 1.11ab | 3.91a | 71.2 | 60.4ab |
| 41B | 24.0 | 4.10b | 3.67 | 6.60 | 3.86 | 1.03a | 3.92a | 71.1 | 57.0a |
| 110 R | 23.9 | 4.06ab | 4.06 | 6.01 | 3.66 | 1.04ab | 3.79a | 71.8 | 64.8b |
| 161-49 C | 24.8 | 3.99a | 4.12 | 6.09 | 3.93 | 0.87a | 4.93b | 70.7 | 60.5ab |
| Irrigation method (IM) | | | | | | | | | |
| PRD | 24.0 | 4.05 | 3.95 | 6.16 | 3.84 | 1.01 | 4.34 | 71.2 | 62.3 |
| RDI | 24.1 | 4.12 | 3.85 | 6.33 | 3.95 | 1.12 | 3.81 | 71.2 | 60.4 |
| ANOVA | | | | | | | | | |
| Rootstock (R) | ns | * | ns | ns | ns | * | ** | ns | * |
| Irrigation method (IM) | ns | * | ns | ns | ns | ns | * | ns | ns |
| Interaction (R x IM) | ns | ns | * | ns | ns | ns | * | ns | * |
| 2021 | | | | | | | | | |
| Rootstock (R) | TSS (°Brix) | pH | Total acidity | MI | Tartaric acid | Malic acid | Tartaric acid/malic acid ratio | %H ₂ O _{berry} | % must |
| 140Ru | 22.9 | 4.11 | 4.06 | 5.65 | 2.78a | 1.77a | 1.86ab | 69.2 | 56.5 |
| 1103 P | 23.2 | 4.29 | 3.96 | 5.74 | 3.24b | 2.16b | 1.55a | 67.2 | 49.6 |
| 41B | 23.3 | 4.21 | 3.92 | 6.14 | 3.09ab | 1.53a | 2.08b | 67.6 | 52.8 |
| 110 R | 23.1 | 4.12 | 3.87 | 6.01 | 3.22b | 2.01b | 1.67a | 65.3 | 54.4 |
| 161-49 C | 22.2 | 4.19 | 3.94 | 5.73 | 2.91ab | 1.60a | 1.85ab | 67.8 | 54.8 |
| Irrigation method (IM) | | | | | | | | | |
| PRD | 22.4 | 4.21 | 3.93 | 5.77 | 3.07 | 1.83 | 1.83 | 68.2 | 53.8 |
| RDI | 23.5 | 4.16 | 3.98 | 5.94 | 3.03 | 1.79 | 1.78 | 66.7 | 53.5 |
| ANOVA | | | | | | | | | |
| Rootstock (R) | ns | ns | ns | ns | * | * | * | ns | ns |
| Irrigation method (IM) | ** | ns | ns | ns | ns | ns | ns | ns | ns |
| Interaction (R x IM) | * | ns | ns | ns | ns | ns | ns | ns | ns |

'ns' not significant; *, ** and *** indicate significant differences at the 0.05, 0.01, and 0.001 levels of probability, respectively. In each column and for each factor, different letters indicate significant differences according to Duncan's multiple range test at a 95% confidence level.

3.8. Effects of low/very low water volume RDI and PRD and their interaction with the rootstock in vine performance and berry quality

The evolution of total θ_v (10–50 cm deep) throughout the years in the wet and root zone in PRD vines revealed a gradual decrease in θ_v as a consequence of a progressive reduction in irrigation volume; this was more accentuated in 140Ru and 1103 P in 2020 and 2021 (wet root zone, $P < 0.05$) and even in the dry root zone (2021, $P < 0.05$) (Fig. 1C and D). In addition, the analysis of mean values of total θ_v (10–50 cm deep) maintained in PRD during fruit-set harvest period showed that the heterogeneity in soil moisture (between dry and wet root zones) was maintained throughout the years in PRD (Fig. 1D; see table inside the figure). However, in 1103 P and in 140Ru, soil moisture heterogeneity decreased progressively, until the disappearance of the PRD effect, especially in 140Ru (similar $\theta_{v_{wet}}$ and $\theta_{v_{dry}}$ values) as a consequence of a drastic reduction of irrigation volumes in the last two years (2020 and 2021) (Fig. 1D; see table inside Fig. 1D). Besides, when all of the rootstocks are included, the evolution of total θ_v (10–50 cm deep) maintained in the PRD (average dry and wet root zone) was similar (no significant differences) to RDI throughout the years (Fig. 1E). However, in some periods, average $\Delta\theta_v \Delta t^{-1}$ was significantly higher in RDI compared to PRD (Fig. 1F). Additionally, there was no compensation effect in the wet root zone in PRD vines; therefore, $\Delta\theta_v \Delta t^{-1}$ in the wet root zone in PRD vines was significantly lower than $\Delta\theta_v \Delta t^{-1}$ in the wet root zone in RDI vines under both conditions: higher irrigation water volume (2017) and lower irrigation water volume (2018–2019) (Supplemental Table 1). It was also noticed that there were no differences in the whole-plant hydraulic conductance between PRD and RDI vines and the interaction (R x IM) in 2018 (supplemental Fig. S1).

During post-veraison in 2018 and 2021 and pre-veraison in 2021, and in the annual average calculated in 2021, PRD vines showed a significantly more negative Ψ_s (greater water stress) than RDI vines, although this depended also on the rootstock, especially in 161–49 C, 1103 P, and 140Ru (significant interaction, $P < 0.05$) (Fig. 5A and B, Table 3). The irrigation method also affected leaf gas exchange in different ways. Firstly, in 2017, PRD vines had a significantly higher A , g_s , and E than RDI vines during fruit set-veraison period (Fig. 5C and G). In 2018 and 2019, there were no significant differences in leaf gas exchange between PRD and RDI during the fruit set-veraison period. However, during the veraison-harvest period at the early morning and midday in 2018, a significantly higher E and lower A/g_s and A/E was observed in PRD vines with regards to RDI vines (Fig. 5H–5 J, Table 3). In contrast, in 2020 (with a lower water volume), the opposite effect was detected: during the fruit set-veraison period, PRD vines had a significantly lower g_s and E and higher A/g_s at the early morning than RDI vines (Fig. 5E, G and I).

On the whole, there were no significant differences between irrigation methods (PRD vs. RDI) and the interaction (R x IM) in leaf mineral concentration. Only PRD vines showed a significantly higher concentration of Ca (2019) and B (2021) and lower concentration of Mg (2021) in the leaves than RDI vines (Table 4). Besides, the analysis of the average mineral concentration of the must maintained during the experimental period 2017–2021 also showed that PRD vines had a significantly higher Ca, Mg, and B and lower K, P, and Cu than RDI vines. Significant interactions also revealed that PRD increased Ca (140Ru, 161–49 C), Mg (1103 P), and B (41B, 161–49 C) concentrations with regards to RDI (Supplemental Table 2).

Generally speaking, it was also noticed that in 2017, PRD vines had a significantly higher vegetative development (MSL, TLA, ELA) and TLA/yield than RDI vines (Fig. 6A and C). In contrast, yield/pruning weight ratio was significantly lower in PRD than in RDI vines (Fig. 6E). In 2018, however, TLA/yield ratio was significantly lower in PRD than in RDI. The rest of the years, there were no significant differences in vegetative

development between PRD and RDI, although there were some significant interactions (R x IM) in MSL, TLA, ELA, and PW. Therefore, vines grafted on 1103 P and 140Ru showed a significant reduction in TLA, MSL, and PW (1103 P, 140Ru) in 2018, and in TLA (140Ru) in 2021, under PRD compared to RDI (data not shown). In contrast, vines grafted on 110 R in 2018 and 2021 showed a significantly higher TLA, MSL, ELA, and PW (2018) and TLA (2021) in PRD compared to RDI (data not shown).

Overall, there were no significant differences between PRD and RDI vines in yield components and WP in any year (Fig. 6G and K), except for a higher cluster weight in 2020 and a lower berry weight at harvest in 2019 in PRD vines compared to RDI vines (Fig. 6I and J). Significant interactions were also observed occasionally in 2019 in the number of clusters per vine and cluster weight (data not shown). Thus, 140Ru had a significantly lower number of clusters in PRD, but a higher cluster weight compared to RDI, whereas 110 R under PRD had a higher number of clusters per vine than RDI (data not shown).

In 2017, PRD vines showed a lower pH and MI and a higher total acidity than RDI (Table 5). In general, PRD vines also had a significantly lower CM index, lower tone, and concentration of P in the must than RDI vines (Tables 6 and 7). Besides, significant interactive effects revealed that PRD vines grafted on 1103 P and 110 R had a lower concentration of total anthocyanins (1103 P, 110 R) and total polyphenol content (110 R) than RDI vines. Apart from that, PRD vines grafted on 140Ru also showed a significantly lower concentration of P than RDI vines. In contrast, 41B PRD vines had a higher concentration of total, extractable anthocyanins and polyphenol content than RDI vines, and 161–49 C PRD vines had a higher level of extractable anthocyanins than RDI (Supplemental Table 3).

In 2018, there were no significant differences in technological and phenolic quality (similar berry quality indices, Fig. 7) between RDI and PRD, except for a higher $\%H_2O_{berry}$ in PRD (Tables 5 and 6). The significant interaction also revealed that 1103 P PRD vines had a significantly lower concentration of tartaric acid, tartaric acid/malic acid ratio, colour intensity, and tone, and higher CIElab parameters (a^* and C^*) than RDI vines (Supplemental Table 4). In contrast, 161–49 C PRD vines had a significantly higher tartaric acid/malic acid ratio than RDI vines. Besides, 140Ru vines under PRD had a significantly lower concentration of P than RDI vines, whereas 1103 P vines under PRD had a significantly higher concentration of Ca than RDI vines (data not shown).

In 2019, PRD significantly increased the $\%H_2O_{berry}$ and the content of Mg, Mn, and B, while decreasing berry weight and P content in the must (Tables 5, 6, and 7), although this depended also on the rootstock (significant interaction, $P < 0.05$). Therefore, compared to RDI, PRD significantly decreased MI (1103 P, 110 R), CI, B content, and extractable anthocyanins (110 R), CM index and P content (140Ru) in the must (Supplemental Tables 5 and 6). In contrast, PRD increased colour intensity and the concentration of extractable anthocyanins (140Ru), Mg content (1103 P), and B content (140Ru and 161–49 C) in the must compared to RDI (Supplemental Tables 5 and 6).

In 2020, PRD vines showed a significantly lower pH and a higher tartaric acid/malic acid ratio in the must than RDI vines (Table 5). In addition, polyphenol content and the concentration of P, K, Zn, and Cu in the must significantly decreased also in PRD vines, whereas the concentration of B increased (Tables 6 and 7). Interactions (R x IM) also revealed that PRD significantly increased the percentage of must (41B), tartaric acid/malic acid ratio (140Ru, 161–49 C), and Ca content in the must (140Ru) compared to RDI. In contrast, PRD decreased CI (110 R) and Zn content (140Ru, 41B) (Supplemental Table 7). There were no significant differences in berry quality indices between irrigation methods (Fig. 7).

In 2021, in general, PRD decreased TSS, and $QI_{technological}$ berry

Table 6

Phenolic maturity parameters of the must made from Monastrell grapes at harvest in different rootstocks (140Ru, 1103 P, 41B, 110 R, and 161–49 C) and two different irrigation methods (partial root-zone drying irrigation, PRD and regulated deficit irrigation, RDI) for each year (period 2017–2021). Total anthocyanins (mg L⁻¹), extractable anthocyanins (mg L⁻¹), polyphenols content (mg L⁻¹), tannins (mg g⁻¹FW), CM Index (Cellular Maturity Index, %), SM Index (Seed Maturity Index, %), CIELab parameters (L*, a* b*, C*, h).

| 2017 | | | | | | | | | | | | | |
|-------------------------------|------------------|--------------------|--------------------------|---------------------|---------|----------|----------|--------|------|--------|--------|-------|--------|
| Rootstock (R) | Colour intensity | Total anthocyanins | Extractable anthocyanins | Polyphenols content | Tannins | CM Index | SM Index | Tone | L* | a* | b* | C* | h |
| 140Ru | 5.59b | 518 | 234 | 27.2a | 1.88 | 48.3 | 64.7 | 0.83c | 23.8 | 20.7bc | 6.16bc | 20.9a | 17.2bc |
| 1103 P | 5.83bc | 550 | 266 | 31.2b | 2.46 | 48.5 | 65.8 | 0.81bc | 22.3 | 17.9a | 5.10ab | 19.3a | 14.8a |
| 41B | 4.72a | 562 | 278 | 33.8b | 2.86 | 48.8 | 67.6 | 0.72a | 23.6 | 23.4c | 7.23c | 24.4b | 17.9c |
| 110 R | 5.53b | 550 | 288 | 34.0b | 2.82 | 47.3 | 66.2 | 0.79bc | 22.8 | 19.3ab | 5.62ab | 20.1a | 15.8ab |
| 161-49 C | 6.52c | 616 | 294 | 34.1b | 2.78 | 51.1 | 65.1 | 0.74ab | 23.0 | 17.2a | 4.54a | 17.8a | 14.6a |
| Irrigation method (IM) | | | | | | | | | | | | | |
| PRD | 5.63 | 545 | 282 | 32.2 | 2.43 | 45.1 | 64.8 | 0.76 | 23.1 | 20.1 | 5.96 | 20.6 | 16.2 |
| RDI | 5.64 | 573 | 262 | 31.9 | 2.68 | 52.4 | 67.0 | 0.79 | 23.0 | 19.3 | 5.49 | 20.4 | 15.9 |
| ANOVA | | | | | | | | | | | | | |
| Rootstock (R) | ** | ns | ns | ** | ns | ns | ns | ** | ns | *** | ** | ** | *** |
| Irrigation method (IM) | ns | ns | ns | ns | ns | ** | ns | * | ns | ns | ns | ns | ns |
| Interaction (R x IM) | ns | ** | * | *** | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| 2018 | | | | | | | | | | | | | |
| Rootstock (R) | Colour intensity | Total anthocyanins | Extractable anthocyanins | Polyphenols content | Tannins | CM Index | SM Index | Tone | L* | a* | b* | C* | h |
| 140Ru | 4.82 | 488 | 218a | 26.1a | 1.74 | 55.0 | 67.5b | 0.85b | 24.7 | 20.6 | 6.8 | 21.8 | 18.2 |
| 1103 P | 5.19 | 492 | 223a | 26.8a | 1.61 | 60.1 | 68.7b | 0.91c | 24.3 | 18.6 | 6.1 | 19.6 | 17.6 |
| 41B | 4.66 | 471 | 273a | 29.3ab | 1.71 | 44.2 | 64.7ab | 0.82b | 24.8 | 20.8 | 7.1 | 22.0 | 18.7 |
| 110 R | 4.84 | 548 | 252a | 35.8b | 1.37 | 49.9 | 70.4b | 0.81b | 24.8 | 20.6 | 7.2 | 21.9 | 18.5 |
| 161-49 C | 5.31 | 643 | 377b | 35.7b | 1.37 | 44.5 | 59.6a | 0.69a | 24.2 | 20.2 | 6.6 | 21.3 | 18.1 |
| Irrigation method (IM) | | | | | | | | | | | | | |
| PRD | 4.98 | 551 | 272 | 29.8 | 1.54 | 53.6 | 65.4 | 0.80 | 24.3 | 20.1 | 6.5 | 21.2 | 18.0 |
| RDI | 4.95 | 505 | 266 | 31.7 | 1.58 | 47.9 | 67.0 | 0.84 | 24.8 | 20.3 | 7.0 | 21.5 | 18.4 |
| ANOVA | | | | | | | | | | | | | |
| Rootstock (R) | ns | ns | *** | ** | ns | ns | ** | *** | ns | ns | ns | ns | ns |
| Irrigation method (IM) | ns | ns | ns | ns | ns | ns | ns | * | ns | ns | ns | ns | ns |
| Interaction (R x IM) | * | ns | ns | ns | ns | ns | ns | * | ns | * | ns | * | ns |
| 2019 | | | | | | | | | | | | | |
| Rootstock (R) | Colour intensity | Total anthocyanins | Extractable anthocyanins | Polyphenols content | Tannins | CM Index | SM Index | Tone | L* | a* | b* | C* | h |
| 140Ru | 3.11ab | 858ab | 343a | 37.7a | 3.04a | 58.7ab | 63.4ab | 0.98b | 26.7 | 28.2 | 13.0 | 31.0 | 24.4 |
| 1103 P | 2.88a | 744a | 346a | 51.6bc | 4.49b | 56.8ab | 73.0c | 0.91ab | 25.7 | 28.9 | 12.9 | 31.6 | 24.0 |
| 41B | 3.38bc | 949b | 432b | 56.9c | 5.12b | 57.0ab | 69.0bc | 0.88a | 25.7 | 28.4 | 12.6 | 31.0 | 23.6 |
| 110 R | 3.29ab | 898ab | 403ab | 41.0ab | 3.95ab | 52.4a | 59.0a | 0.86a | 26.5 | 29.4 | 13.7 | 32.3 | 24.3 |
| 161-49 C | 3.88c | 1305c | 467b | 63.6c | 4.27ab | 64.3b | 71.1c | 0.86a | 23.7 | 26.3 | 10.9 | 28.5 | 22.0 |
| Irrigation method (IM) | | | | | | | | | | | | | |
| PRD | 3.45 | 967 | 397 | 51.4 | 4.53 | 57.5 | 67.6 | 0.89 | 25.7 | 27.9 | 12.4 | 30.5 | 23.5 |
| RDI | 3.16 | 934 | 399 | 48.8 | 3.82 | 58.2 | 66.6 | 0.91 | 25.7 | 28.6 | 12.8 | 31.3 | 23.8 |
| ANOVA | | | | | | | | | | | | | |
| Rootstock (R) | ** | *** | ** | ** | * | * | *** | * | ns | ns | ns | ns | ns |
| Irrigation method (IM) | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| Interaction (R x IM) | * | ns | ** | ns | ns | * | ns | ns | ns | ns | ns | ns | ns |
| 2020 | | | | | | | | | | | | | |
| Rootstock (R) | Colour intensity | Total anthocyanins | Extractable anthocyanins | Polyphenols content | Tannins | CM Index | SM Index | Tone | L* | a* | b* | C* | h |
| 140Ru | 5.59 | 1015 | 359a | 29.5a | 1.21a | 63.1b | 56.5ab | 1.24bc | 26.6 | 19.3 | 8.37 | 21.1 | 23.6 |
| 1103 P | 6.29 | 788 | 337a | 41.5abc | 1.25a | 57.2b | 66.9b | 1.30c | 25.5 | 17.6 | 7.01 | 18.9 | 21.9 |
| 41B | 5.63 | 1031 | 447ab | 43.5bc | 1.76b | 54.9ab | 59.8b | 1.19b | 25.9 | 19.0 | 7.96 | 20.7 | 22.2 |
| 110 R | 5.54 | 750 | 301a | 31.5ab | 1.15a | 62.8b | 65.1b | 1.19bc | 26.0 | 20.1 | 8.70 | 21.9 | 22.4 |
| 161-49 C | 5.11 | 1199 | 610b | 47.1c | 1.27a | 47.3a | 49.1a | 1.06a | 25.7 | 20.7 | 8.56 | 22.4 | 22.2 |

(continued on next page)

Table 6 (continued)

| 2017 | | | | | | | | | | | | | |
|-------------------------------|------------------|--------------------|--------------------------|---------------------|---------|----------|----------|---------|------|------|------|------|-------|
| Rootstock (R) | Colour intensity | Total anthocyanins | Extractable anthocyanins | Polyphenols content | Tannins | CM Index | SM Index | Tone | L* | a* | b* | C* | h |
| Irrigation method (IM) | | | | | | | | | | | | | |
| PRD | 5.43 | 933 | 403 | 35.1 | 1.42 | 56.1 | 58.0 | 1.15 | 25.9 | 19.8 | 8.25 | 21.5 | 22.4 |
| RDI | 5.83 | 981 | 419 | 42.2 | 1.24 | 58.0 | 60.9 | 1.24 | 25.9 | 18.9 | 7.99 | 20.6 | 22.6 |
| ANOVA | | | | | | | | | | | | | |
| Rootstock (R) | ns | ns | ** | * | ** | ** | ** | *** | ns | ns | ns | ns | ns |
| Irrigation method (IM) | ns | ns | ns | * | ns | ns | ns | ** | ns | ns | ns | ns | ns |
| Interaction (R x IM) | ** | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| 2021 | | | | | | | | | | | | | |
| Rootstock (R) | Colour intensity | Total anthocyanins | Extractable anthocyanins | Polyphenols content | Tannins | CM Index | SM Index | Tone | L* | a* | b* | C* | h |
| 140Ru | 3.74 | 674 | 505 | 17.8 | 2.01 | 41.7a | 58.4a | 0.99bc | 27.0 | 26.5 | 14.1 | 30.9 | 28.3b |
| 1103 P | 3.90 | 734 | 508 | 21.7 | 3.03 | 44.7a | 66.4b | 1.04c | 24.0 | 24.0 | 12.2 | 26.9 | 26.4a |
| 41B | 3.55 | 685 | 447 | 17.3 | 3.15 | 60.6c | 64.2b | 0.87a | 25.3 | 25.6 | 12.5 | 28.3 | 26.2a |
| 110 R | 3.43 | 690 | 493 | 19.0 | 3.02 | 43.1ab | 63.9ab | 0.95ab | 25.2 | 25.8 | 12.8 | 28.8 | 25.6a |
| 161-49 C | 2.98 | 715 | 460 | 19.0 | 2.65 | 51.5bc | 65.1b | 0.96abc | 27.7 | 28.2 | 15.6 | 32.3 | 28.9b |
| Irrigation method (IM) | | | | | | | | | | | | | |
| PRD | 3.49 | 722 | 474 | 18.3 | 2.85 | 53.8 | 63.9 | 0.99 | 25.5 | 26.0 | 13.1 | 29.4 | 26.9 |
| RDI | 3.56 | 677 | 491 | 19.6 | 2.70 | 42.9 | 63.3 | 0.94 | 26.2 | 26.1 | 13.7 | 29.5 | 27.2 |
| ANOVA | | | | | | | | | | | | | |
| Rootstock (R) | ns | ns | ns | ns | ns | * | * | * | ns | ns | ns | ns | * |
| Irrigation method (IM) | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| Interaction (R x IM) | ns | ns | ns | ns | ns | ns | ns | ** | ns | ns | ns | ns | * |

‘ns’ not significant; *, ** and *** indicate significant differences at the 0.05, 0.01, and 0.001 levels of probability, respectively. In each column and for each factor, different letters indicate significant differences according to Duncan’s multiple range test at a 95% confidence level.

compared to RDI (Fig. 7A and Table 5). There were no significant differences in polyphenolic content, $QI_{phenolic}$ quality, and $QI_{overall}$ berry quality between PRD and RDI (Table 6 and Figs. 7B and 7C). The analysis of the interaction (R x IM) also revealed a drastic reduction in TSS and MI, and an increase in tone in 161–49 C under PRD compared to RDI (Supplemental table 8). Additionally, in rootstock 140Ru, the parameter CIElab h^* significantly decreased in PRD compared to RDI. Besides, PRD increased the concentration of Ca (161–49 C) and Mn (1103 P) in the must compared to RDI (Supplemental table 8).

4. Discussion

4.1. Rootstock affects root water and nutrient uptake capacity under severe DI

Rootstock had a significant impact on the ability to extract water and nutrients from the soil and, as a consequence, on vine water status, leaf photosynthesis, leaf/must mineral content, vigour, productivity, WP, and berry quality of Monastrell vines, as had been observed in other varieties (Paranychianakis et al., 2010; Walker et al., 2010).

Under a greater irrigation water volume (2017), high-vigour rootstocks 140Ru and 1103 P were able to maintain a higher $\Delta\theta_v \Delta t^{-1}$ in the root zone than low/moderate-vigour rootstocks, especially in the wet root zone (in PRD) and in RDI (Fig. 1B). A greater vegetative growth also meant larger water needs of the vines (Keller, 2010). As a consequence, 1103 P and 140Ru depleted soil water faster than 161–49 C or 41B, with a higher decrease of θ_v in the soil profile under high-irrigated conditions (Romero et al., 2018) (Fig. 1A–1 C). However, with moderate (2018, 2019) or severe irrigation reductions (2020, 2021) and a drastic decrease in total soil water availability (especially in 2020 and 2021,

Fig. 1), 140Ru and 1103 P substantially reduced $\Delta\theta_v \Delta t^{-1}$ in the root zone (10–50 cm deep) compared to 161–49 C, 110 R, or 41B (Fig. 1B, G, and H). Surprisingly, even in severe deficit irrigated conditions with scarce soil water availability, these rootstocks (especially 140Ru) were able to supply larger amounts of water to the scion and to maintain a better vine water status and a greater leaf gas exchange, yield, and vegetative growth than low-vigour rootstocks (Figs. 2 and 3). The fact that, despite the lower rates of water uptake by the roots, these vines maintained higher rates of transpiration and a greater development of the leaf area may suggest the presence of a more extensive and deeper root system of 140Ru, able to extract water from a larger volume of soil, which indicates the existence of a more efficient root system architecture and/or uptake and transport mechanisms (Albacete et al., 2015), as well as a greater drought tolerance (Prinsi et al., 2021). It has been reported that vigorous and drought-tolerant rootstocks such as 140Ru or 1103 P have larger, more extensive, and deeper root systems and/or a greater root hydraulic conductance, and, as a consequence, show a greater capacity of the whole-root system to extract water from drying soils when water deficit develops (Alsina et al., 2011; Tramontini et al., 2013; Gambetta et al., 2020; Caruso et al., 2023). In our study, although $\Delta\theta_v \Delta t^{-1}$ was similar under soil water deficit conditions between 140Ru and 1103 P, K_{plant} was significantly higher in 140Ru vines than in 1103 P and the other rootstocks (Fig. S1), which could also explain the better vine water status and leaf gas exchange maintained in this rootstock. It has been reported that more vigorous rootstocks trigger a lower leaf water potential and a higher leaf gas exchange and K_{plant} than the less vigorous ones (Labarga et al., 2023).

In spite of a drastic reduction of irrigation, vines grafted on 1103 P and 140Ru had similar or higher water contents in the berries and a greater % of must; besides, they showed a significantly higher

Table 7

Nutrient concentration (in ppm) of the must obtained from Monastrell grapes at harvest in five different rootstocks (140Ru, 1103 P, 41B, 110 R, and 161–49 C) and two different irrigation methods (partial root-zone drying irrigation, PRD and regulated deficit irrigation, RDI) for each year during the period 2017–2021.

| 2017 | | | | | | | | |
|-------------------------------|---------|---------|--------|--------|---------|---------|---------|---------|
| Rootstock (R) | P | Mg | Ca | K | Mn | Zn | Cu | B |
| 140Ru | 415c | 107.4 | 157a | 2186ab | 0.681a | 0.591b | 0.483c | 17.3 |
| 1103 P | 373c | 107.1 | 151a | 2349b | 0.681a | 0.472a | 0.393b | 17.7 |
| 41B | 329b | 107.2 | 175b | 2076a | 0.793b | 0.528a | 0.364b | 16.1 |
| 110 R | 370bc | 105.9 | 159a | 2120ab | 0.712ab | 0.462a | 0.412b | 18.7 |
| 161-49 C | 285a | 105.8 | 178b | 1991a | 0.794b | 0.474a | 0.295a | 20.9 |
| Irrigation method (IM) | | | | | | | | |
| PRD | 333 | 107.8 | 165 | 2195 | 0.732 | 0.500 | 0.372 | 18.7 |
| RDI | 376 | 105.6 | 163 | 2094 | 0.733 | 0.511 | 0.407 | 17.6 |
| ANOVA | | | | | | | | |
| Rootstock (R) | *** | ns | *** | * | * | *** | *** | ns |
| Irrigation method (IM) | ** | ns | ns | ns | ns | ns | ns | ns |
| Interaction (R x IM) | * | ns | ns | ns | ns | ns | ns | ns |
| 2018 | | | | | | | | |
| Rootstock (R) | P | Mg | Ca | K | Mn | Zn | Cu | B |
| 140Ru | 110.5c | 89.1abc | 83.7 | 1920a | 0.657 | 0.375b | 0.210b | 14.1ab |
| 1103 P | 110.5c | 96.8c | 87.6 | 2308b | 0.601 | 0.270a | 0.188b | 17.6c |
| 41B | 101.3bc | 86.3a | 86.0 | 2070ab | 0.577 | 0.325ab | 0.137ab | 12.7a |
| 110 R | 89.2ab | 95.7bc | 83.9 | 1938a | 0.611 | 0.276a | 0.189b | 16.1bc |
| 161-49 C | 80.4a | 87.3ab | 98.8 | 1973a | 0.570 | 0.333ab | 0.110a | 16.2bc |
| Irrigation method (IM) | | | | | | | | |
| PRD | 96.0 | 90.5 | 89.0 | 1970 | 0.601 | 0.320 | 0.160 | 15.4 |
| RDI | 100.8 | 91.6 | 87.0 | 2114 | 0.605 | 0.311 | 0.173 | 15.3 |
| ANOVA | | | | | | | | |
| Rootstock (R) | *** | * | ns | * | ns | * | * | ** |
| Irrigation method (IM) | ns | ns | ns | ns | ns | ns | ns | ns |
| Interaction (R x IM) | * | ns | * | ns | ns | ns | ns | ns |
| 2019 | | | | | | | | |
| Rootstock (R) | P | Mg | Ca | K | Mn | Zn | Cu | B |
| 140Ru | 94.1ab | 85.1 | 84.4ab | 1651a | 0.845 | 0.391 | 0.492b | 10.2ab |
| 1103 P | 120.7b | 90.3 | 84.3ab | 2004b | 0.802 | 0.387 | 0.596b | 11.6 cd |
| 41B | 99.1b | 82.9 | 89.4b | 1758ab | 0.817 | 0.386 | 0.463b | 9.1a |
| 110 R | 128.3c | 83.3 | 78.1a | 1762ab | 0.699 | 0.344 | 0.545b | 10.9bc |
| 161-49 C | 84.5a | 82.2 | 91.4b | 1569a | 0.826 | 0.343 | 0.368a | 12.3d |
| Irrigation method (IM) | | | | | | | | |
| PRD | 100.1 | 88.6 | 88.2 | 1698 | 0.840 | 0.370 | 0.470 | 11.4 |
| RDI | 110.6 | 81.0 | 82.8 | 1799 | 0.756 | 0.371 | 0.515 | 10.2 |
| ANOVA | | | | | | | | |
| Rootstock (R) | *** | ns | * | * | ns | ns | ** | ** |
| Irrigation method (IM) | * | * | ns | ns | * | ns | ns | * |
| Interaction (R x IM) | * | * | * | ns | ns | ns | ns | ** |
| 2020 | | | | | | | | |
| Rootstock (R) | P | Mg | Ca | K | Mn | Zn | Cu | B |
| 140Ru | 97.7b | 83.5 | 85.1b | 1786 | 1.09 | 0.390c | 0.488d | 11.6a |
| 1103 P | 99.1b | 85.5 | 72.6a | 1840 | 1.13 | 0.311b | 0.329b | 14.3b |
| 41B | 104.2b | 77.6 | 75.8a | 1885 | 1.11 | 0.322b | 0.367bc | 10.7a |
| 110 R | 121.8c | 82.9 | 72.1a | 1815 | 0.97 | 0.309b | 0.428c | 12.3ab |
| 161-49 C | 80.9a | 75.0 | 76.0a | 1622 | 1.15 | 0.247a | 0.247a | 14.6b |
| Irrigation method (IM) | | | | | | | | |
| PRD | 92.5 | 81.8 | 76.9 | 1675 | 1.08 | 0.291 | 0.336 | 13.6 |
| RDI | 108.9 | 80.0 | 75.8 | 1904 | 1.10 | 0.341 | 0.408 | 11.9 |
| ANOVA | | | | | | | | |
| Rootstock (R) | *** | ns | ** | ns | * | *** | *** | ** |
| Irrigation method (IM) | *** | ns | ns | *** | ns | ** | *** | * |
| Interaction (R x IM) | ns | ns | * | ns | ns | * | ns | ns |
| 2021 | | | | | | | | |
| Rootstock (R) | P | Mg | Ca | K | Mn | Zn | Cu | B |
| 140Ru | 126.7ab | 91.2a | 86.0 | 1622a | 0.82a | 0.30ab | 0.47 | 10.6a |
| 1103 P | 143.7bc | 108.5b | 92.2 | 2261c | 1.04b | 0.34b | 0.55 | 14.0b |
| 41B | 130.8b | 88.5a | 86.3 | 1935b | 0.83a | 0.27ab | 0.49 | 9.9a |
| 110 R | 156.1c | 93.0a | 91.3 | 1999bc | 0.79a | 0.33b | 0.51 | 11.8a |
| 161-49 C | 107.5a | 86.8a | 98.5 | 1733ab | 0.84a | 0.24a | 0.45 | 11.2a |
| Irrigation method (IM) | | | | | | | | |
| PRD | 129.7 | 96.5 | 94.7 | 1885 | 0.93 | 0.32 | 0.48 | 12.0 |
| RDI | 136.3 | 90.7 | 87.0 | 1935 | 0.80 | 0.27 | 0.50 | 11.0 |
| ANOVA | | | | | | | | |
| Rootstock (R) | ** | ** | ns | ** | * | * | ns | ** |
| Irrigation method (IM) | ns | ns | ns | ns | * | ns | ns | ns |
| Interaction (R x IM) | ns | ns | ** | ns | ** | ns | ns | ns |

'ns' not significant; *, ** and *** indicate significant differences at the 0.05, 0.01, and 0.001 levels of probability, respectively. In each column and for each factor, different letters indicate significant differences according to Duncan's multiple range test at a 95% confidence level.

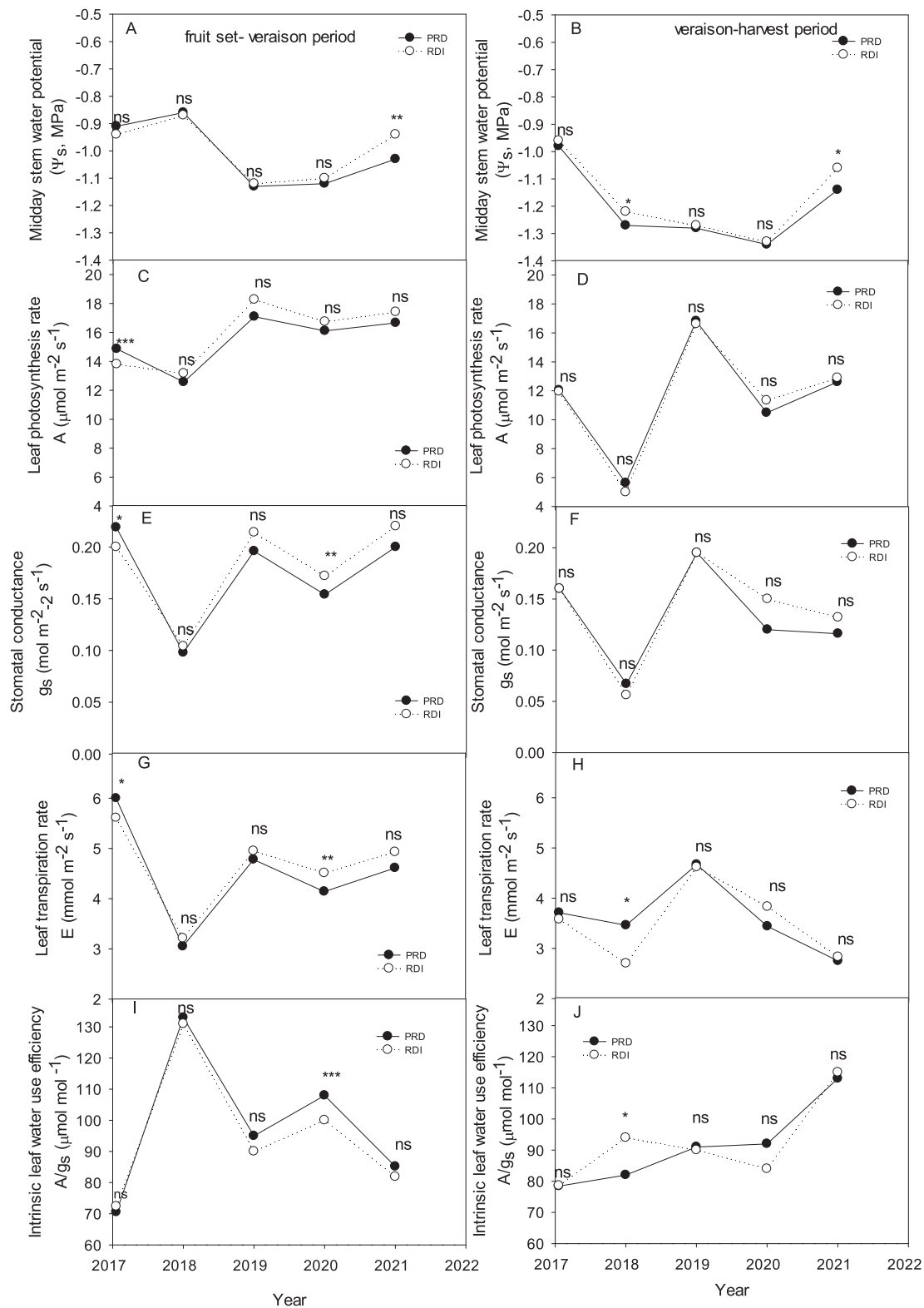


Fig. 5. A, B. Evolution of midday stem water potential (Ψ_s) during 2017–2021, in two phenological periods for each irrigation method (partial root-zone drying irrigation, PRD vs. regulated deficit irrigation, RDI). C, D. Evolution of leaf photosynthesis rate (A) during 2017–2021, in two phenological periods for each irrigation method (PRD vs. RDI) measured at the early morning. E, F. Evolution of stomatal conductance (g_s) during 2017–2021, in two phenological periods for each irrigation method (PRD vs. RDI) measured at the early morning. G, H. Evolution of leaf transpiration rate (E) during 2017–2021, in two phenological periods for each irrigation method (PRD vs. RDI) measured at the early morning. I, J. Evolution of intrinsic leaf water use efficiency (A/g_s) during 2017–2021, in two phenological periods for each irrigation method (PRD vs. RDI), measured at the early morning. Each point is the average of several measurements taken during the phenological period. ANOVA: ns, not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. For each year, the separation of means was made by Duncan’s multiple range test at a 95% confidence level.

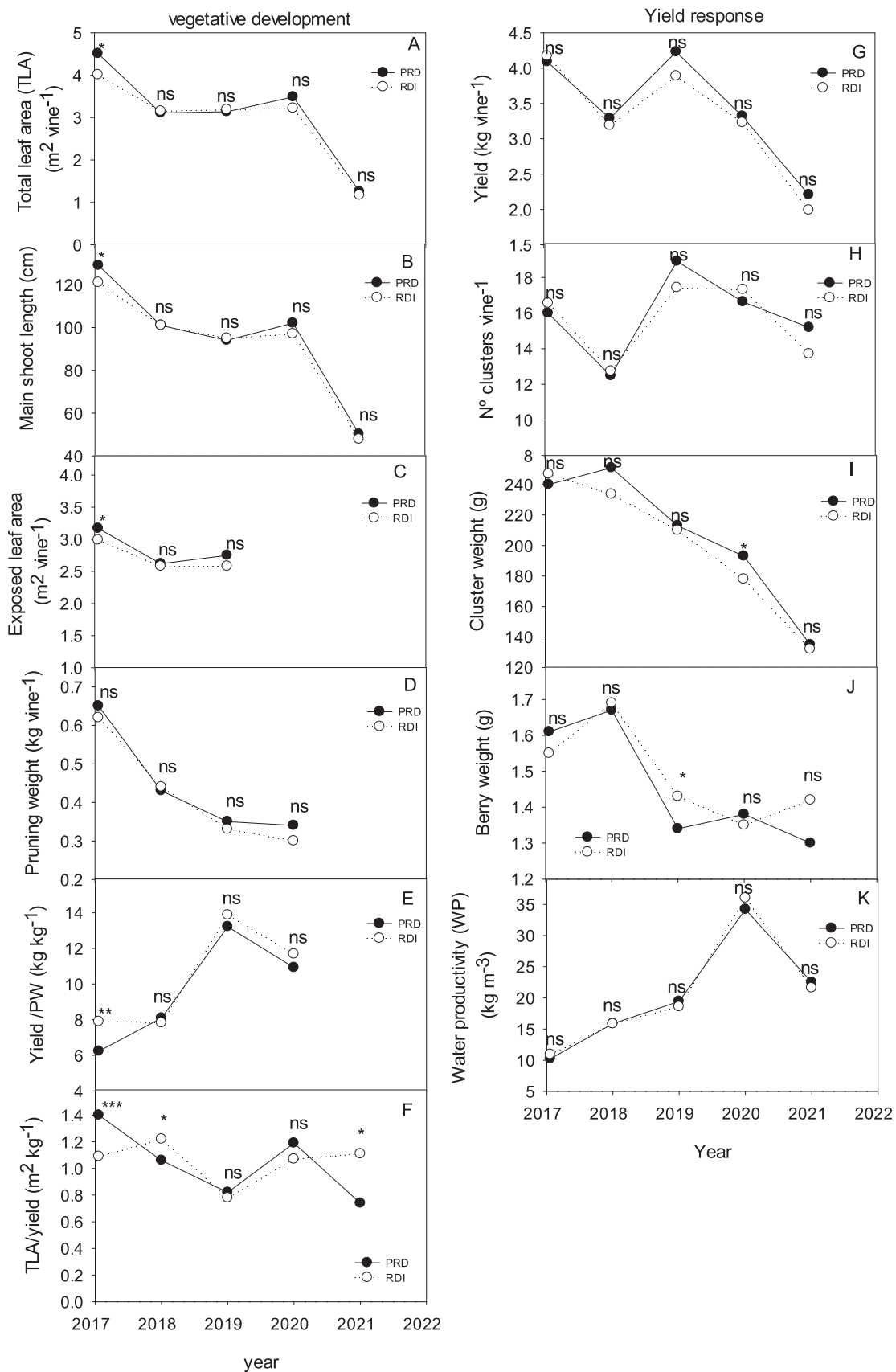


Fig. 6. Evolution of total leaf area (TLA) (A), main shoot length (B), exposed leaf area (C), pruning weight (D), yield/pruning weight ratio (E), total leaf area/yield ratio (F), yield (G), number of clusters per vine (H), cluster weight (I), berry weight (J), and water productivity (WP) (K) for each irrigation method (partial root-zone drying irrigation, PRD vs. regulated deficit irrigation, RDI) during the experimental period (2017–2021). ANOVA: ns, not significant; * P < 0.05; ** P < 0.01; *** P < 0.001. For each year, the separation of means was made by Duncan's multiple range test at a 95% confidence level.

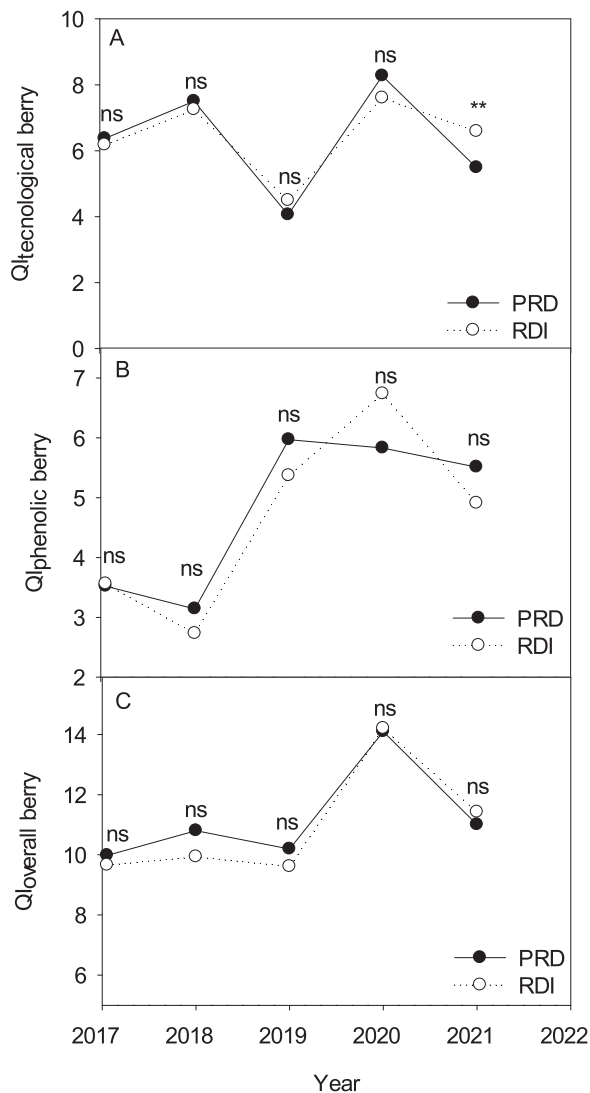


Fig. 7. Evolution of berry quality indices (A, technological quality ($QI_{\text{technological berry}}$), B, phenolic quality ($QI_{\text{phenolic berry}}$), and C, overall berry quality ($QI_{\text{overall berry}}$) at harvest for each irrigation method (partial root-zone drying irrigation, PRD vs. regulated deficit irrigation, RDI) during the experimental period 2017–2021. ANOVA: ns, not significant; * * $P < 0.01$. For each year, the separation of means was made by Duncan's multiple range test at a 95% confidence level.

concentration of some mineral elements in the must and leaves. Thus, under higher (2017) and lower irrigation (2018–2021), these high-vigour rootstocks showed a higher concentration of mineral elements in the must (P, K, Mg, Mn, and B [1103 P], and P, K, Zn, Cu, and Ca [140Ru]) and the leaves (K and Zn [140Ru], and Mg and Zn [1103 P] [2019,2021]), compared to medium/low-vigour rootstocks (Tables 4 and 7). This indicates a greater capacity for soil nutrient and water uptake, transport and translocation from the roots to shoot, leaves, and berries under prolonged soil water deficit. Among these high-vigour rootstocks, 1103 P showed the highest average concentrations of mineral elements in the must during the whole experimental period (K, Mg, P, and B) compared to 140Ru, which suggests the presence of a highly nutrient-efficient rootstock (Albacete et al., 2015) (Supplemental Table 2). In contrast, 161–49 C vines, despite being irrigated with more water, showed a lower nutrient uptake capacity and had the lowest contents of P, K, Zn (leaves, must), and Cu (must), but higher B and Ca (leaves, must) levels than other rootstocks (Tables 4 and 7). Nutrient content (K^+ , N, Ca^{++}) in vine organs is greatly affected by several

factors, including the rootstock, vine water status, and modifications in sink-source ratio (Martins et al., 2012). The greater leaf Ca content in 161–49 C vines (compared to the other rootstocks, Table 4) may indicate a stronger adjustment to a greater water stress intensity, as Ca is an important player in most cellular signalling processes, including increasing resistance to pathogens (Martins et al., 2012), and acts as a secondary signal provoked by many different environmental stresses (Kacperska, 2004). Grapevine rootstocks also determine the accumulation of micronutrients in vine organs (Martins et al., 2012). Greater concentrations of Zn and Cu in 140Ru can also be related with the greater mass upward flow of water in the xylem, as a consequence of a higher root water uptake capacity, K_{plant} , and leaf transpiration rates (Martins et al., 2012). Besides, even in the absence of significantly higher values of leaf N content (Table 4), the maintenance of a greater total leaf area and yield in 140Ru (Figs. 3A and 4A) would indicate a higher N content per plant, and thus a greater root N uptake, translocation, and assimilation than in the other rootstocks. It has been reported that high-vigour rootstocks tend to acquire more N (Habran et al., 2016), and 140Ru is more effective at assimilating N than other rootstocks (Keller et al., 2001).

4.2. Rootstock controls vine water status and leaf gas exchange under DI

The low volume of water that was applied annually (DI strategy) (Table 2) was enough to maintain vine water status (Ψ_s) and leaf stomatal conductance rate (g_s) in values close to or within the optimum physiological thresholds and ranges proposed for Monastrell grapevines (Ψ_s was within the optimum range, i.e., between -1.2 and -1.4 MPa in all of the rootstocks) (Fig. 2A, B, E, and F), in order to increase WP and berry quality and to avoid severe functional damage of roots and leaves (Romero et al., 2010).

A drastic irrigation reduction in vines grafted on 140Ru induced only a mild water stress (-1.09 MPa $>$ minimum $\Psi_s >$ -1.23 MPa, and 0.21 mol $m^{-2} s^{-1} >$ average g_s [2017–2021] $>$ 0.16 mol $m^{-2} s^{-1}$), whereas in vines grafted on 1103 P, it induced a moderate water stress (-1.14 MPa $>$ minimum $\Psi_s >$ -1.38 MPa and 0.16 mol $m^{-2} s^{-1} >$ average g_s [2017–2021] $>$ 0.12 mol $m^{-2} s^{-1}$) (Romero et al., 2022). It was observed that, in spite of an increased stomatal closure and a more reduced leaf area, Ψ_s was also substantially reduced in 1103 P vines (near-anisohydric behaviour), as opposed to the response that is frequently observed in anisohydric species (Tardieu and Simonneau, 1998). In contrast, in 140Ru vines, a greater stomatal aperture and total leaf area and a less negative Ψ_s under progressive soil water deficit indicate a more isohydric behaviour. A tight regulation of Ψ_s is not necessarily associated with a greater stomatal control nor with a more constrained assimilation during drought (Lavoie-Lamoureux et al., 2017). Variation in (an)-isohydric may result from an imbalance between transpiration rate (controlled by stomatal aperture and transpirable surface area), root water uptake rate, and whole-plant hydraulic conductance. Therefore, the drop in water potential may suggest a low value of root water uptake rate and hydraulic conductance that is limiting water uptake and transport on the path from the soil through the plant to the leaves (Simonneau et al., 2017; Schultz, 2003), and it is not enough to offset the water losses by transpiration (Keller, 2005).

The analysis of leaf gas exchange regulation also revealed that: 1) In general, A decreased substantially less than g_s and E in all of the rootstocks during the development of soil water deficit (from 2017 to 2021), and not was severely impaired by water stress, enhancing water use efficiency in the leaf (A/g_s , A/E); 2) leaf gas exchange was more down-regulated during the veraison-harvest period (ripening period) than during the fruit set-veraison period; 3) in the veraison-harvest period, A was upregulated from 2017 to 2021 in all of the rootstocks (between 0.52% in 161–49 C and 28% in 1103 P), except for 140Ru, where A decreased around 7%; and 4) during the 2017–2021 period, g_s and E also decreased substantially more in 140Ru in the ripening period (41% and 35%, respectively) compared to 1103 P (7% and 1%, respectively) and

other rootstocks (between 0%–29% in g_s , and between 20%–28% in E). These results revealed that genotypes such as 1103 P showed an “elastic” behaviour, as they maintained a less changed g_s and E under progressive soil water deficit (Bianchi et al., 2020). However, regardless of a more intense down-regulation of A , g_s , and E in 140Ru under soil water deficit, these vines still maintained a greater stomatal aperture, leaf gas exchange rates, total leaf area, and plant water use, and were systematically more productive every year than 1103 P and the rest of the rootstocks, in spite of using much less water for watering. This suggests that differences are also truly fixed at a genetic level, irrespective of the irrigation conditions, as observed in other *Vitis* genotypes (Tortosa et al., 2019; Romero et al., 2023).

4.3. Rootstock modifies sink/source relationships, yield response, and water productivity

Water productivity (WP) was substantially increased by the progressive reduction of irrigation. Thus, vines grafted on 140Ru and, to a lesser extent, on 1103 P, were also those with a higher water productivity. An 85% of the irrigation reduction (from 2017 to 2021) in 140Ru and 1103 P produced, respectively, a reduction of around 53% and 71% in yield, as well as an increment in WP of 220% and 97%. Therefore, WP reached very high values in 2020 and 2021 (> 90 – 58 kg m^{-3} , respectively [140Ru], and > 51 – 22 kg m^{-3} , respectively [1103 P]), values that, to our best knowledge, had not been previously reported in literature.

In contrast, as observed in other genotypes, vines grafted on 140Ru were the least efficient at the leaf level (the lowest A/g_s), indicating a lower vine water stress (Medrano et al., 2015). Differences in carbon partitioning and sink/source adjustments due to the varying resource distribution could have been involved (Buesa et al., 2022).

Rootstock, which is a potential sink, has a strong impact on source activity, affecting the morphology and activity of the aerial part of the plant (Davies et al., 2012). Therefore, as an adaptive measure to progressive soil water deficit, Monastrell vines were less vigorous and productive every year, modifying sink/source relationships (leaf area/fruit ratio decreased, whereas yield/PW ratio increased; Fig. 3D and F). In all of the rootstocks, there was a stronger reduction in total leaf area than in fruit load. Grapevine growth is widely known to be very sensitive to water deficit; more than photosynthesis and yield (Keller, 2005; Chaves et al., 2010). It was also noticed that high high-vigour rootstocks (140Ru, 1103 P) irrigated with much less water had a more intense down regulation of the vegetative and reproductive development than medium/low-vigour rootstocks (41B, 110 R or 161–49 C) during progressive soil water deficit, suggesting a stronger adjustment to severe water deficit in these two rootstocks. Thus, vines grafted on 1103 P were the most sensitive to water deficit, and, during the 2017–2021 period, they had a higher reduction of TLA and yield (83% and 71%, respectively) than vines grafted on 140Ru (73% and 53%, respectively). As a consequence, the TLA/yield ratio was systematically higher in 1103 P than in 140Ru (Fig. 3F), which indicates that 1103 P vines under WS allocated more resources to maintain TLA, rather than yield, whereas 140Ru vines allocated more resources to the yield. The rest of the rootstocks also reduced TLA between 56% (110 R) and 70% (41B), and fruit load between 28% (161–49 C) and 41% (41B). Probably, the higher Zn content in 140Ru vines (Table 7) could also be related with increases in PW, cluster number, and overall vine yield (Martins et al., 2012).

Down-regulation of all of the yield components due to a progressive increase in soil water deficit was observed in all of the rootstocks (Fig. 4), but more markedly in high-vigour rootstocks with a greater soil water deficit (mainly in 1103 P, followed by 140Ru). Therefore, in vines grafted on 1103 P and 140Ru, cluster weight was substantially reduced from 2017 to 2021 (between 63% and 49%, respectively); the same occurred to the number of berries per cluster (between 57% and 40%, respectively) and, to a lesser extent, to the number of clusters per vine

(between 25% and 13.5%, respectively) and berry weight (between 13% and 19.5%, respectively).

Medium/low-vigour rootstocks also increased WP between 17% [41B] and 41% [161–49 C]) in response to a progressive irrigation reduction (from 2017 to 2021) and besides, the reduction in yield components was not so intense: number of clusters per vine (between 1.57% [110 R] and 23% [41B]), cluster weight (between 24% [41B] and 41% [110 R]), number of berries per cluster (between 3.67% [41B] and 32% [161–49 C]) and berry weight (between 8% [161–49 C] and 16% [110 R]). It is well known that, in many cases, RDI produces yield losses (averaging between 10% and 24%) compared to conventional, standard irrigation or full irrigation practices (Romero et al., 2022), which is reflected in a reduction of the different yield components. Greater carryover effects produced by a severe and prolonged soil water deficit could also affect long-term productivity (Keller, 2005), as observed especially in 1103 P, followed by 140Ru, by the stronger reduction in yield components (Fig. 4). In our study, bud fruitfulness, inflorescence formation, cluster and flower induction, and berry set could be affected by water stress, as indicated by the stronger decrease in cluster weight, number of berries per cluster, and number of clusters per vine observed during soil water deficit progression, mainly on less watered rootstocks in 2020–2021 (Fig. 4), as previously reported in other RDI studies (Girona et al. (2006); Shellie (2006); Shellie and Bowen (2014); Santesteban et al. (2011); Romero and Martínez-cutillas (2012)), although not always all of the yield components are reduced by RDI (Santos et al. (2007); Shellie (2014); Zúñiga et al. (2018)).

Nevertheless, our results also indicate that very low water volume DI (between 15–46 mm year^{-1}) was suitable for Monastrell grapevines grafted on 140Ru under semi-arid conditions. These vines were still productive with very little irrigation water (average yield in the 2020–2021 period: 11,596 kg ha^{-1}) suggesting a greater drought tolerance and irrigation water productivity than those found in 1103 P and medium/low-vigour rootstocks. These results also point out to the possibility that these vines can adapt well to rainfed conditions, as well as reduce reliance on supplemental irrigation and make vineyards more sustainable in semi-arid areas for dry farming (Romero et al., 2023). In contrast, vines grafted on 1103 P were the ones that accused the drastic reduction of irrigation the most (average yield in the 2020–2021 period: 5714 kg ha^{-1}) suggesting greater carryover effects produced by a severe and prolonged soil water deficit.

4.4. Reducing irrigation in rootstocks of different vigour improves berry quality

Even if source/sink relationships were significantly affected by rootstock and irrigation reduction, final sugar concentration in berries was not significantly altered (Table 5). Interestingly, although leaf area (m^2)/fruit yield (kg) values were in most cases within an optimum range above 1 $\text{m}^2 \text{ kg}^{-1}$ for well-balanced vines (Kliewer and Dokoozlian, 2005), leaf area/fruit ratios were $< 1 \text{ m}^2 \text{ kg}^{-1}$ in some rootstocks (e.g., 110 R, 140Ru or 41B in 2019, 2020, 2021; Fig. 3F), indicating a decreased total leaf area and vines that were not well balanced. The leaf/area fruit ratio is a critical factor for berry sugar level (Davies et al., 2012), and values of 1.2–1.8 $\text{m}^2 \text{ kg}^{-1}$ have been proposed to obtain satisfactory sugar levels. However, lower leaf area and higher yield ratios may have also stimulated photosynthesis (Paranychianakis et al., 2004), and greater photosynthesis rates maintained in 140Ru or 110 R compared to 1103 P or 161–49 C could also help preserve satisfactory sugar levels in the berries, counteracting the effects of lower TLA/yield ratios. In addition, sugar accumulation has been reported to be less sensitive to water stress than berry growth (Matthews and Anderson, 1988). In spite of a drastic cutback of irrigation in 140Ru and 1103 P, berry growth did not show a substantially higher reduction in vines bearing a heavy crop (e.g., 140Ru) than in vines with a lighter crop load (e.g., 161–49 C), suggesting a high $\Delta\Psi$ driving water uptake by those berries, and no reduced sugar availability per berry (Keller, 2005).

Besides, a greater concentration of B in 1103 P and 161–49 C could also explain the increased sugar content in berries, despite the fact that 1103 P and especially 161–49 C plants had lower photosynthesis rates and total leaf area than other rootstocks (Romero et al., 2018). Boron is linked to photoassimilate synthesis and partitioning in the vine, especially that of sucrose from the leaves to the roots and fruiting bodies, thus increasing the sugar content in the fruit (Batukaev et al., 2016).

Traditionally, high vine vigour (with large and dense canopies) and yields are associated with grapes and wines of low quality (Keller, 2005; Cortell et al., 2008). The hypothesis that we considered in this work was the following: 1) that, by reducing vigour, yield, cluster compactation, and berry weight through a more restrictive DI strategy in high-vigour rootstocks we could optimise irrigation, save water, and have better balanced vines in order to improve berry quality and WP; and 2) that applying a lighter irrigation reduction in medium/low-vigour rootstocks could also improve WP and berry quality. Our results indicate that, by applying a more severe DI strategy and reducing the irrigation in 140Ru and 1103 P, vigour, cluster compactation (cluster weight, and number of berries per cluster), productivity, and berry weight were substantially reduced, and WP and berry quality indices (particularly, phenolic quality, and global berry quality) were increased. Thus, from 2017 to 2021, $QI_{\text{phenolic berry}}$ increased by 50% in 140Ru vines and by 92% in 1103 P vines, whereas $QI_{\text{overall berry}}$ increased by 9% in 140Ru vines and 53% in 1103 P vines (Fig. 4H, I, and J). Medium/low-vigour rootstocks also increased phenolic berry quality (between 11% [161–49 C] and 46% [110 R]), in response to a progressive irrigation reduction (Fig. 4). Probably, higher reductions of berry weight (greater skin/pulp ratio) and lower % of must (especially in 140Ru and 1103 P, Fig. 4E and Table 5) could produce a greater concentration effect, increasing phenolic compounds (Roby and Matthews, 2004), although this depended also on the year. For instance, in 2021 (with no differences in berry weight), the reduction in berry quality (especially phenolic quality) observed in almost all of the rootstocks could be due to: 1) a lower annual vine water stress (pre- and post-veraison; Fig. 2A and B); 2) a highly reduced total leaf area and, as a consequence, lower photoassimilate accumulation for primary (sugars and acids) and secondary (flavonoids) metabolism; 3) long-term carryover effects of water stress in fertility, productivity, and secondary metabolism; and 4) an excessive berry sun exposure. It has also been noticed that $QI_{\text{technological}}$ was not improved by irrigation reduction, and it even slightly decreased in 2021, except for 1103 P (Fig. 4I).

No significant differences were observed in pH, total acidity, tartaric acid, and Cielab parameter L^* in must among rootstocks in any year, but some quality attributes were modified by irrigation reduction, which can be beneficial or detrimental for the quality of the grape. For instance, in 140Ru and 161–49 C vines, K content in the must showed a decrease around 24% and 13% from 2017 to 2021, respectively (Fig. 4G). Our results point out that progressive soil water deficit in 140Ru vines induced a lower K root uptake and translocation into the clusters, reducing K content in the must. Some rootstocks show the ability to reduce potassium uptake by vines and berries (Martins et al., 2012), which is important and can be beneficial, considering that grape juice pH is correlated with juice potassium, and a high pH has negative consequences for flavour, wine stability, and colour (Rogiers et al., 2017). Besides, in 140Ru, changes were found in other quality attributes when irrigation was reduced; for example, lower malic acid and higher tartaric acid/malic acid ratio in the must (2020), which can also be beneficial to quality (Conde et al., 2007). In contrast, 1103 P vines showed the opposite effect, with a higher K content and malic acid and lower tartaric acid/malic acid ratio (2021), which can be detrimental for technological quality (Rogiers et al., 2017), indicating that this rootstock is a high K cumulative rootstock. Besides, 1103 P and 41B showed a higher incidence of wood disease (e.g., Esca) during the experimental period (19–26% of affectation) compared to other rootstocks (between 8–11% of affectation) (data not shown), which can be detrimental for vine performance and berry quality.

A lower K content in the must in 161–49 C vines was also related with other positive quality attributes, such as a lower pH, malic acid, and tone, as well as higher total acidity, IM, tartaric acid/malic acid ratio, colour intensity, total and extractable anthocyanins, and total polyphenol content, and, as a consequence, to greater QI_s than those found in other rootstocks (Fig. 4H and J). Vines grafted on 161–49 C maintained the highest values of leaf area/fruit ratio every year (around $1.5\text{--}1.7\text{ m}^2\text{ kg}^{-1}$), which in Monastrell vines has been closely related to a higher berry phenolic quality (Romero et al., 2016). An increased exposure of the cluster to the sun, due to a lower vine vigour and leaf area development and a greater water stress during the pre-veraison and ripening periods (as observed in 161–49 C), could also increase the anthocyanin and flavonoids synthesis and accumulation (Navarro et al., 2021).

4.5. Low-water volume deficit irrigation under PRD affect negatively vine performance compared to RDI

The root system of Monastrell grapevines can compensate for the decreased water availability on the non-irrigated side of the vine during PRD by increasing root water uptake on the irrigated side in periods when the wet root zone has a high soil water content ($\theta_{v\text{-wet}} > 30\%$ at 10–60 cm) (Romero et al., 2012, 2014). However, in our study, a compensation effect in the root water uptake in the wet root zone was not observed, indicating that the applied irrigation water was insufficient to maintain a more favourable supply of water and nutrients in PRD compared to RDI. For instance, in 140Ru and 1103 P rootstocks, during 2017 (year with a higher irrigation volume), average $\theta_{v\text{-wet}}$ in the soil profile (10–50 cm deep) was maintained around 25–24% (data not shown), well below the established optimal threshold ($> 30\%$). Conversely, the low irrigation volume applied led to a decrease in the θ_v availability in the wet root zone and the total $\Delta\theta_v \Delta t^{-1}$ of PRD plants compared to RDI plants, probably due to limited sap flow from roots in drying soil, when θ_v was too low and wet soil volume was too small (Romero et al., 2014). In agreement with this, $\theta_{v\text{-dry}}$ (in 2021) was also significantly lower in 140Ru and 1103 P than in other rootstocks, which also translated into significantly lower root water uptake rates in the dry root zone (Fig. 1D, G, and H).

As a consequence of the low water volume that was applied, a deeper water percolation through the soil PRD (60–100 cm deep) (data not shown) was not clearly observed, unlike what frequently occurs in PRD vines (Santos et al., 2007; Collins et al., 2010). In addition, it was noticed that the very low water volume applied in 2020 and 2021 in 140Ru and 1103 P produced a loss of heterogeneity in soil moisture and, therefore, the disappearance of the full effect of PRD (chiefly in 140Ru; see Fig. 1D and Table inside) due to an important reduction in wet soil volume (Keller, 2005). It has been reported that the benefits of PRD relative to RDI depend on factors such as 1) the genotypic variation in root distribution and the proportion of root biomass exposed to drying soil (Martín-Vertedor and Dodd, 2011), which can depend on the genotype of the rootstock, and 2) the volumetric soil water content maintained in the wet root zone ($\theta_{v\text{-wet}}$) (Hutton and Loveys, 2011; Einhorn et al., 2012), which is determined by irrigation management (irrigation frequencies and volumes). According to Wang et al. (2012), $\theta_{v\text{-wet}}$ should be maintained relatively high to improve vine performance, whereas in the drying zone it should not be very low. Both conditions are crucial to maintain high soil and plant water statuses while sustaining ABA signalling under long-term PRD in semi-arid conditions (Romero and Martínez-cutillas (2012)). In our study, after a higher irrigation volume in 2017, PRD vines showed a significantly higher leaf gas exchange and total leaf area than RDI vines during the fruit set-veraison period (Figs. 5 and 6). It was also noticed that PW, yield response, and WP were not significantly altered by the irrigation method during progressive soil water deficit (2017–2021). As a consequence, in 2017, TLA/yield ratio was higher, whereas yield/PW ratio was lower in PRD vines (compared to RDI). This positive PRD effect in soil plant water relations and

vegetative growth was occasional and it was not observed in other years with a lower irrigation water volume (2018–2021).

Besides, as a consequence of the significantly lower θ_{v-wet} and θ_{v-dry} and the reduced $\Delta\theta_v \Delta t^{-1}$, PRD vines also had a lower concentration of some nutrients in the must (mainly P and K, Zn, Cu) and the leaves (Mg, Tables 4 and 7), which indicates a lower root nutrient uptake/translocation capacity than that found in RDI vines (Romero et al., 2018), mainly when soil water deficit was more intense (2019–2021). However, in the must there was a higher content of Ca (also in leaf), B, Mn, and Mg in PRD (compared to RDI) (Table 7). In other species (e.g., tomatoes), it has been reported that PRD boosts root and fruit Ca uptake, which has been associated with a greater xylem sap abscisic acid concentration, a lower stomatal conductance, and a higher plant water status compared to DI (Sun et al., 2013). In our study, the accumulation of Ca and other nutrients, such as B, in the must was not related to a greater $\Delta\theta_v \Delta t^{-1}$ or a better vine water status in PRD, nor was it related to a higher concentration effect in PRD, because it had a similar yield, berry weight, water content in the berries, and % must compared to RDI. Rather, it was associated with lower Ψ_s (2018, 2021), g_s , and E values, as well as a higher A/g_s , indicating a greater vine water stress, stomatal closure, and WUE at the leaf level in PRD vines compared to RDI vines. These physiological changes produced by low water volume PRD were also reflected in a slightly increased technological berry quality compared to RDI (lower pH, berry weight, and CM and increased tartaric acid and tartaric acid/malic acid ratio). However, very low water volume PRD did not produce an improvement in phenolic concentration and global berry quality compared to RDI, and polyphenol content (2020), TSS, and $QI_{\text{technological berry}}$ (2021, Table 5, Fig. 7) were even decreased, probably as a consequence of the lower synthesis and accumulation of carbohydrates (lower TLA/yield ratio in PRD than in RDI in 2018 and 2021, Fig. 6F). This confirms the previous results obtained in PRI Monastrell grapevines receiving a low irrigation volume (Romero et al., 2015).

5. Conclusions

Severe DI strategy in high-vigour/productive rootstocks 140Ru and 1103 P reduced vigour, productivity, and berry weight and increased significantly water productivity and berry quality. Very low water volume DI was suitable for Monastrell grapevines grafted on 140Ru under semi-arid conditions, which were still very productive with very little irrigation water. Besides, based on these results, we recommend the use of this high water use efficient rootstock under rainfed conditions in semiarid areas, as a measure of adaptation to climate change. In contrast, vines grafted on 1103 P were the ones that accused the drastic reduction of irrigation the most, suggesting greater carryover effects produced by a severe and prolonged soil water deficit, which could also have a wider impact on long-term productivity. Medium/low-vigour rootstocks (41B, 161–49 C, and 110 R) also decreased vigour, yield, and berry weight in response to a progressive irrigation reduction, enhancing water productivity between 17% and 41% and phenolic berry quality between 11% and 46%. With low water volume DI, vines grafted on 161–49 C generated the highest berry quality.

A severe DI strategy with very low water volume was not suitable for the implementation of the PRD in Monastrell vines under semi-arid conditions because of the following reasons: 1) there is a strong decrease in root water and nutrient uptake capacity; 2) PRD effect (soil moisture heterogeneity) can be lost due to a very reduced θ_v and a scarce wet soil volume, and 3) it did not produce substantial improvements in vine performance (yield, global berry quality, and WP) compared to RDI.

Nevertheless, to achieve a better adaptation of the vineyards to climate change, in addition to a more efficient use of water and fertilisers (nitrogen) through deficit irrigation techniques and the use of more efficient and drought-tolerant rootstocks, it will also be necessary the implementation of more sustainable soil management, as well as other

beneficial agroecological practices, in order to design vineyards that are more resilient to climate change in the short, medium and long term.

CRedit authorship contribution statement

Navarro Acosta Josefa: Methodology, Investigation. **Romero Pascual:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Botia Ordaz Pablo:** Supervision, Methodology. **Morote Elisa:** Methodology.

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.2024.108669](https://doi.org/10.1016/j.agwat.2024.108669).

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