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Effects of cover crops and irrigation on 'Tempranillo' grapevine and berry physiology: an experiment under the Mediterranean conditions of Southern Portugal

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ABSTRACT

In addition to irrigation, other viticultural practices such as soil management can be applied to improve grapevine (*Vitis vinifera* L.) quality responses and attenuate unfavourable environmental conditions. Cover crops in the interrow of irrigated vineyards change the dynamics of water extraction and it is expected that the patterns of vines' water relations will be modified, also changing their productive responses. This study took place over two seasons in 'Tempranillo' grapevines in a vineyard in South Portugal, where a cover crop was sown in the inter-rows of half the study area (SCC) while maintaining resident vegetation in the remaining (RV). Five water regime treatments were applied: full irrigation (200 mm irrigation amount–I_{200}); moderate irrigation (150 mm–I_{150}); deficit irrigation (100 mm–I_{100}); ultra-deficit irrigation (50 mm–I_{50}); rainfed (I_0). Measurements of predawn leaf water potential (Ψ_{PD}), stomatal conductance (gs), photosynthetic rate (An), and transpiration rate (E) were made during the final stages of the growth cycle. Data of soil water availability, yield and growth variables, and berries and wine composition were also used. Significant interactions between the effect of soil management and water regime were observed on Ψ_{PD}. A water competition effect exerted by the cover crop could be responsible for reduced water loss and carbon assimilation, whenever Spring rain is lower and/or the cover crop biomass development is not controlled. Differences in gs and An observed at midday and late measurements reflect the influence of the daily increase of atmospheric water demand. Stomatal closure of grapevines was less affected in plots of higher soil water storage capacity. The correlation between Ψ_{PD} and gs was higher in the midday and late measurements, pointing to the regulation of stomatal response in response to water availability and daily environmental conditions. Principal components analysis (PCA) evidenced an influence of water deficit on metabolic responses that benefit fruit and wine quality. The cluster analysis (CA) revealed that no significant cluster of cases was clearly controlled by soil management or water regime in the first season but, in the second, drier season, significant clustering more irrigation- than soil management-controlled showed that a predominant influence of irrigation should be expected for 'Tempranillo' grapevines grown under dry Mediterranean conditions.

KEYWORDS

'Tempranillo' grapevines, soil management, cover crops, irrigation, water relations, gas exchange parameters, Mediterranean environments

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INTRODUCTION

The total water consumption of vineyards varies from 300 to 700 mm, a range that is generally higher than the annual average precipitation in many viticultural areas, as is the case of Mediterranean regions (Medrano *et al.,* 2015). Among the environmental problems associated with viticulture, water scarcity is a critical issue and climate change may have a significant effect on temperatures and precipitations throughout the growing cycle, leading to more severe water shortages that affect yield and fruit composition (Fraga *et al.,* 2012; IPCC, 2018; van Leeuwen and Darriet, 2016). However, the grapevine is a traditionally non-irrigated crop, well adapted to drought-prone areas where irrigation was introduced to increase the low land yield (Cifre *et al.,* 2005; Fraga *et al.,* 2012) but is mostly managed following schedules optimized to improve water use efficiency. In fact, there is little doubt that deficit irrigation strategies, supported by physiologically based monitoring tools, like regulated deficit irrigation (RDI) or partial root drying (PRD) (Loveys *et al.,* 2000; Mccarthy *et al.,* 2000) are powerful options to balance vine vegetative development, yield, and fruit quality while improving the yield to water consumption ratio (Flexas *et al.* 2010).

In addition to irrigation, various viticultural practices such as soil and canopy management, choice of appropriate training systems and rootstocks, etc. can be applied to improve grape quality and to buffer unfavourable natural conditions (Naulleau *et al.,* 2021; Zhang *et al.,* 2014; Zsófi *et al.,* 2009). The use of cover crops in the interrow of vineyards is a well-known practice to promote reductions in vine vigour and improve berry composition (Bouzas-Cid *et al.,* 2018; Medrano *et al.,* 2015; Pou *et al.,* 2011). Cover crops are spontaneous vegetation and sown plant species associated with a perennial crop in the rows or inter-rows with a high potential to provide ecosystem services (Fernández-Mena *et al.,* 2021). Agri-environmental benefits from the use of cover crops in vineyard interrow include improved soil protection that contributes to reduce soil erosion (Bagagiolo *et al.,* 2018); climate change mitigation since they can contribute to carbon sequestration by increasing soil organic matter content and soil stability at the same time (Novara *et al.,* 2019; Schultz and Stoll, 2010); increased biodiversity with a positive effect on providing habitats for natural enemies of grapevine pests (Civitello *et al.,* 2015; Vukicevich *et al.,* 2016). The benefits of the use of cover crops in non-irrigated Mediterranean vineyards for grape and wine quality have been addressed in several studies, such as Celette *et al.* (2005), Monteiro and Lopes (2007), or Mercenaro *et al.* (2014). Despite these positive influences, the use of vegetation in the interrow may induce competition for resources, primarily water, especially in Mediterranean environments, whenever water availability is a concern (Beslic *et al.,* 2015; Cataldo *et al.,* 2020; Celette *et al.,* 2008; Lopes *et al.,* 2011). In irrigated vineyards, cover crops in the interrow may change the dynamics of soil water extraction. Tomaz *et al.* (2017) reported that water uptake by irrigated vines is not limited to the plantation row and that the thin roots of the year adjust their growth and activity as a function of available water in different soil compartments, with different depths and locations, within the row or in-between rows. As long as an accurate account of the total and available water holding capacities of the soil and the rooting depths of the crop is regarded, the restriction in vine water uptake induced by the presence of the cover crop can contribute to the control of excessive vigour and, thereby, to the improvement of grape and wine quality (Bouzas-Cid *et al.,* 2018; H. Medrano *et al.,* 2015; Pou *et al.,* 2011) especially when dealing with pedoclimatic conditions of high water availability (Tissot *et al.,* 2019; Tomaz *et al.,* 2017).

The measurement of relevant parameters of grapevine physiological status as leaf water potential and stomatal conductance can be used to assess the interactions between the plant and its growing conditions. These parameters have been thoroughly studied to understand the responses of different cultivars under water constraint and stress (e.g., Bota *et al.,* 2016; Chaves *et al.,* 2002; Collins *et al.,* 2010; Flexas *et al.,* 2002; Vaz *et al.,* 2016; Wang *et al.,* 2003; Zufferey *et al.,* 2020), providing knowledge based on their capacity to decouple leaf water potential from atmospheric demand, known as the iso/anisohydric behaviour (Tardieu and Simonneau, 1998), as well as tools for the delineation of appropriate irrigation strategies (Cifre *et al.,* 2005; Davies *et al.,* 2002; Dry *et al.,* 2001; Flexas *et al.,* 2010). Soil properties and management are also important factors affecting vine development and wine quality (Jackson and Lombard, 1993; Ubalde *et al.,* 2010). The properties of the soil that most influence the cultivation of the vine are those that control the water content of the soil and directly affect the balance between the vegetative vigour and the production of the vine (van Leeuwen *et al.,* 2004).

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Soil type can have significantly more influence on grapevine water status and berry composition than genotype, overriding differences between cultivars in determining the productive potential of a vineyard (Tramontini *et al.,* 2013, 2014). Furthermore, other environmental factors like soil-to-canopy hydraulic conductance and vapour pressure deficit play an important role in leading vines to shift from anisohydric to isohydric behaviour (Hochberg *et al.,* 2018). Thereby, the prediction of grapevine cultivars hydraulics cannot be made without accounting for the environment (Gambetta *et al.,* 2020).

Given the change in the dynamics of water extraction that the interaction between irrigation and cover crop introduces into the soil-plant system, it is expected that the patterns of plant water relations will change, also changing their yield responses. To contribute to the understanding of grapevine water relations and physiological responses to drought and agronomic practices, and considering the above, we aim to (i) study the influence of water regimes and soil management on grapevine (variety 'Tempranillo') water status and functioning using leaf water potential and gas exchange methods in a Mediterranean vineyard; (ii) examine the relationships between measurements of these variables during the development cycle and the grapevines growth, yield, berry and wine composition.

MATERIALS AND METHODS

1. Site description

Grapevines of the variety 'Tempranillo' were studied during two seasons, in a 4-ha area of a vineyard located in southern Portugal (37°58'11" N; 7°33'14" W; 190 m). Vines were 7-year-old, grafted on the SO4 rootstock, spaced at 2.8 m × 1 m and trained in VSP (vertical shoot position). The climate of the study area is Mediterranean or temperate with hot and dry summer (Csa in Köppen Classification). The long-term means for the period 1981–2010 of annual precipitation and annual mean temperature are, respectively, 558 mm and 16.9 °C, by Beja, the main town located near the study area (IPMA, 2020). Meteorological data were recorded in an automatic weather station (Figure 1). Total precipitation was 593 mm and 474 mm, in the first and second years, respectively. In the first season, precipitation in May was higher and occurred until the end of June. Maximum temperatures above 40 °C were registered in both seasons around the veraison stage. Soils in the vineyard were deep Vertisols (depth > 2.00 m), with high water holding capacity, thus capable of providing water through the vine vegetative stages of the cycle, whenever there was adequate precipitation during Spring (Tomaz *et al.,* 2017). Irrigation was applied by an automatic drip irrigation system, through emitters spaced 1 m with a flow of 2.2 L h^{-1}. Irrigation dates and main phenological stages can be observed in Figure 1.

2. Study design

Four main plots (1 ha) were defined in the vineyard. In two of them, a cover crop was sown between the rows (SCC), one year prior to the beginning of the study, with a commercial grass-legume mixture, mostly *Lolium* L. and *Medicago* L.; the remaining two plots were left with resident vegetation (RV), where a predominance of *Lolium* L. and some species of *Trifolium* L. and *Rumex* L. were observed (Appendix 1). The plots were also distinguished by soil type (Soil I and Soil II) to attend to a slight increase in depth and clay content along a gentle downslope, in the direction NW-SE. A C layer rich in secondary $CaCO_3$ resulting from altered gabbrodiorites was located at 80 cm and 115 cm depth in Soil I and II, respectively.

Therefore, each of the four main plots corresponded to a unit consisting of a soil cover management and soil type: resident vegetation in soil type I (RVI); resident vegetation in Soil type II (RVII); sown cover crop in Soil type I (SCCI); sown cover crop in Soil type II (SCCII). Results previously reported by Tomaz *et al.* (2015) showed that the biomass produced by the sown cover crop (where legumes became dominant during the first year) was about 2.5 times more than the biomass of the permanent resident vegetation. Within the main plots, five subplots corresponding to different water regimes were set, namely: full irrigation, with a 200 mm irrigation amount (I_{200}); moderate irrigation, with 150 mm (I_{150}); deficit irrigation, with 100 mm (I_{100}); ultra-deficit irrigation, with 50 mm (I_{50}); rainfed (I_0), only studied in the second season of the trial. The I_{100} and I_{50} treatments were conducted through a regulated deficit irrigation strategy (RDI), specifically: irrigation started when pre-dawn leaf water potential (Ψ_{PD}) registered in the less irrigated treatment ranged from –0.3 to –0.4 MPa; second and third irrigations were applied when Ψ_{PD} approached –0.5 MPa; the following irrigations took place at Ψ_{PD} values of –0.6 to –0.7 MPa (Deloire *et al.,* 2020).

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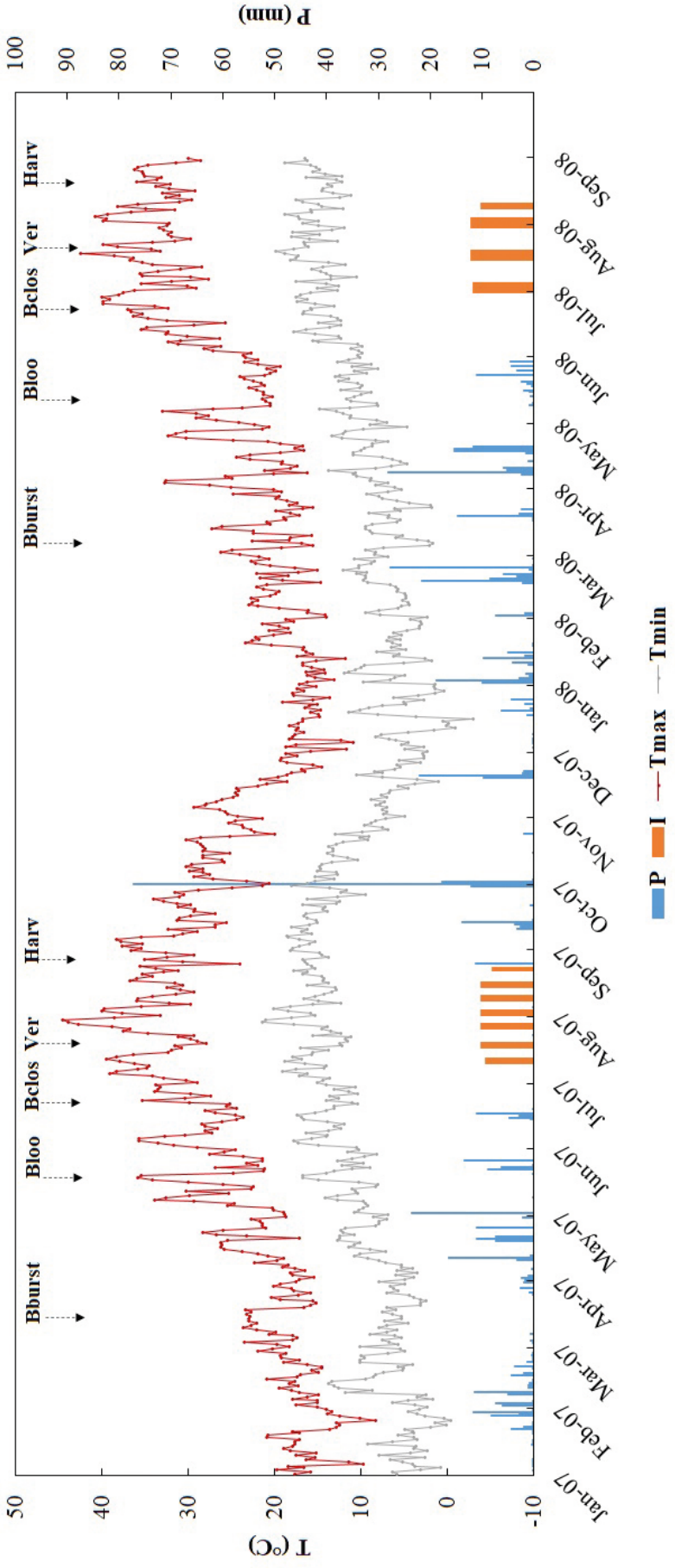


FIGURE 1. Daily maximum temperature (Tmax), minimum temperature (Tmin), precipitation (P), irrigation (I) and phenological stages during the two seasons of the study.
I–Daily irrigation in the I_{200} water regime treatment. Bburst–Bud burst; Bclos–Bunch closure; Ver–Veraison; Harv–Harvest

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3. Plant physiology measurements

Measurements of pre-dawn leaf water potential (Ψ_{PD}; MPa) were carried out on two adult well-exposed leaves, located in the middle third of the canopy, using a pressure chamber (Model 1000, PMS Instrument Co., Albany, OR, USA). Each season, eight measurements (two repetitions per measurement) were made starting at middle June, at different phenological stages, namely, one at bunch closure (Bclos), three during veraison (Ver1, Ver2 and Ver3), three during ripening (Rip1, Rip2 and Rip3) and one a few days before harvest (Harv). Net photosynthesis (An; μmol CO_2 m^{-2} s^{-1}), stomatal conductance (gs; mol H_2O m^{-2} s^{-1}) and transpiration rate (E; mol H_2O m^{-2} s^{-1}) were measured with an IRGA portable system (infrared gas analyzer, model LICOR-6400) using 1500 μmol m^{-2} s^{-1} of PAR radiation, which was previously found to reach photosynthetic saturation in this trial. The gas exchange measurements (three and two repetitions in the first and in the second season, respectively) were made at 9 am (E–Early), 2 pm (MD–Midday) and 6 pm (L–Late) at dates coinciding with some of the Ψ_{PD} measurements, namely: in the first season, during berry ripening (Rip1 and Rip2) and pre-harvest (Harv); in the second season, during veraison (Ver2), berry ripening (Rip1 and Rip2) and before harvest (Harv). Intrinsic (wue_i; μmol mol^{-1}) and instantaneous water use efficiency (wue_{inst}; μmol mol^{-1}) were obtained from the ratios An/gs and An/E, respectively.

4. Soil water monitoring

Soil water content was monitored using neutron probes (TROXLER® 4300, Troxler Electronic Laboratories, Inc., Durham, NC, USA) every 2 or 3 weeks and weekly when irrigation started, on 63 access tubes installed from 1.70 m to 2.70 m depth. Twelve tubes were located in the I_{200} sub-plots; eleven in I_{150}; eight in I_{100}; twelve in I_{50}; ten in I_0. The remaining ten tubes were distributed about equally between rows of the different sub-plots. The probe calibration was carried out by linear regression of the values of mean volumetric water content, calculated from the multiplication of the gravimetric water content by the bulk density and the mean normalized counts of the probe. The gravimetric water content and the bulk density were obtained in soil samples of the known volume collected near the access tube at each measurement level. Earlier results reported in Tomaz *et al.* (2017), indicated that the water extraction of the grapevines in CC plots occurred to depths > 2.70 m, whenever precipitation was enough to supply the entire pedologic profile. Since not all the access tubes reached this depth, for the purpose of this study, we opted to compute the available soil water (ASW) considering a 2.00 m depth, using Equation (1):

$$ASW_i = \theta_{h(0-200\ cm),i} - \theta_{h(0-200\ cm),min} \quad (1)$$

where ASW_i is the available soil water on day i (mm); $\theta_{h(0-200cm),i}$ is the soil water content in the 200 cm profile on day i (mm); $\theta_{h(0-200cm),min}$ is the minimum soil water content in the 200 cm profile (mm) registered on each season. θ_h values were obtained by multiplying the volumetric water content by the depth of each layer corresponding to the measurement levels of the probes with 20 cm step.

5. Vegetative growth, yield and quality parameters

Control areas of twenty vines, grouped in pairs formed by contiguous plants, were fixed in each subplot, thus corresponding to ten repetitions of two contiguous plants, taken together for the purposes of growth and yield measurements. The studied parameters of vine growth and yield were pruning weight (PW; kg $vine^{-1}$), yield (Y; kg $vine^{-1}$) and yield to pruning weight (IR).

The OIV (International Organisation of Vine and Wine) procedures (OIV, 2014) were used to determine the following parameters in berry and wine composition: total soluble solids of berries (°Brix); pH, titratable acidity (TA; g tartaric acid dm^{-3}); wine alcohol content (WAC; %), wine pH (WpH); wine titratable acidity (WTA; g tartaric acid dm^{-3}); wine volatile acidity (WVA; g acetic acid dm^{-3}); wine sugar content (WSC; g dm^{-3}). Furthermore, total polyphenol index (PF; %) and total anthocyanins (ANT; mg dm^{-3}), were determined according to (Cabrita *et al.,* 2003). The effects of the soil management and water regime on the grapevines' productive responses were discussed elsewhere by Tomaz *et al.* (2015) that found: both soil management and water regime affected vegetative growth and yield, pointing to a competition effect by the cover crop; in general, a positive significant effect of the sown cover crop in Soil I on berries and wine quality parameters, mainly in the second season of the trial.

6. Statistical analyses

All statistical analyses were made using *STATISTICA* 7 (StatSoft Inc., 2004). Two-way Analyses of Variance (ANOVA) were performed for the effects of soil management and water

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regime on predawn leaf water potential and gas exchange parameters at different times and dates. The ANOVA were conducted separately for each season. Differences between means were compared using Tukey's test ($p < 0.05$). Matrices of Pearson's correlations coefficients for the two seasons were computed to examine the relationships between soil water and plant physiological variables. A Principal Components Analysis (PCA) was computed with average values to examine patterns and to reduce de number of variables into a small number of independent variables (principal components). The PCA was made on standardized values of plant water status variables, using the growth, yield and quality parameters as supplementary variables. The principal components (PC) were retained after applying the Scree test (Cattell, 1966), considering PC with eigenvalues >1 that accounted for a proportion of variance > 10 %. The factor loadings of the first two PC, representing the correlation between the PC and the variables, were plotted accompanied by plots of PC scores of cases. Hierarchical agglomerative cluster analysis (CA) was performed with the factor scores of the two-component model to detect similarity groups between cases. The distance between clusters was evaluated using Ward's Method (Ward, 1963) for the amalgamation (linkage) rule. The Euclidean distance for similarity measures was used as linkage distance (dlink), expressed as the percentage of the range from the maximum to the minimum distance (dmax) in the data, dlink/dmax*100. Statistically significant clusters were identified considering Euclidean distances < 40 % and then represented in the two-dimensional plane defined by the PC model.

RESULTS AND DISCUSSION

1. Pre-dawn leaf water potential

Until after veraison and pre-harvest, values of Ψ_{PD} did not differentiate between soil management and water regime treatments during the first season (Table 1), showing that, despite irrigation, and due to a favourable amount of Spring rain, the soil water content during the early stages of development was still readily available and sufficient to maintain a favourable plant water status. The value of Ψ measured before dawn is the maximum plant water potential during the day, resulting from an equilibrium between soil and plant water potentials in the absence of water flux. Also, plants adapt the conductivity of their roots as well as that of the soil in their vicinity, to match the soil conditions and atmospheric water demand, to regulate plant water status and transpiration (Carminati and Javaux, 2020). During ripening, grapevines under deficit (I_{100}) and ultra-deficit (I_{50}) irrigation showed significant lower leaf water potential (thus, higher absolute values of Ψ_{PD}) than fully and moderately irrigated plants, with values < –0.40 MPa denoting moderate water stress (Carbonneau, 1998). Additionally, a significant interaction between soil management and water regime was observed and deficit irrigation coupled with resident vegetation cover in the interrow showed lower (more negative) Ψ_{PD} values, pointing to an accentuation of water competition caused by the presence of vegetation between the rows. Nevertheless, Ψ is an indicator used to strategize irrigation, seeking positive effects of moderate stress around veraison and at late stages that induce physiologic responses, like the production of abscisic acid (ABA), beneficial to specific metabolic responses, namely, the anthocyanins and flavonoids biosynthesis (Ferrandino and Lovisolo, 2014; Ojeda *et al.,* 2002).

During the second season, higher (less negative) significant values of Ψ_{PD} were observed, in general, in grapevines in the resident vegetation plots. As mentioned in the Materials and Methods, Section 5, a water competition effect of the sown cover crop, which presented high biomass development mostly in the second year, could have led to a decrease in soil water storage, mainly in the SCC plots, and, therefore, to reduced leaf water potentials.

The lowest (more negative, thereby, higher in absolute value) values were observed at the beginning of veraison, during the ripening period and at pre-harvest, a consequence of an increasing atmospheric water demand coupled with less soil water content. The values of Ψ_{PD} reached about –0.50 MPa and near –0.70 MPa at the final stages, respectively, in ultra-deficit water regime (I_{50}) and rainfed grapevines (I_0), denoting a moderate to severe water stress (Carbonneau, 1998; Deloire *et al.,* 2005; Deloire *et al.,* 2020). The interaction between factors was significant from the beginning of veraison, which could indicate that Ψ_{PD} under less or null irrigation amounts were more pronounced whenever grapevines developed in the sown cover crop plots.

2. Gas exchange parameters

The effects of soil management and irrigation on stomatal conductance measured at different times and dates can be observed in Table 2.

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TABLE 1. Two-way ANOVA for the effect of soil management and water regime on predawn leaf water potential (Ψ_{PD}; MPa) at different stages of the growth cycle (two repetitions per date of measurement).

Season	Source of variation		Bunch closure	Veraison 1st	Veraison 2nd	Veraison 3rd	Ripening 1st	Ripening 2nd	Ripening 3rd	Pre harvest
1	Soil management		NS	NS	NS	NS	*	*	*	NS
		RV-I	–0.250	–0.369	–0.275	–0.388	–0.444 b	–0.519 c	–0.331 a	–0.444
		RV-II	–0.288	–0.369	–0.269	–0.363	–0.431 ab	–0.381 a	–0.344 ab	–0.419
		SCC-I	–0.256	–0.394	–0.288	–0.369	–0.431 ab	–0.400 ab	–0.375 b	–0.419
		SCC-II	–0.231	–0.394	–0.269	–0.356	–0.388 a	–0.438 b	–0.344 ab	–0.438
	Water regime		NS	NS	*	*	*	*	*	*
		I_{200}	–0.263	–0.363	–0.206 a	–0.300 a	–0.338 a	–0.381 a	–0.250 a	–0.369 a
		I_{150}	–0.256	–0.381	–0.269 b	–0.306 ab	–0.406 b	–0.381 a	–0.325 b	–0.431 b
		I_{100}	–0.263	–0.400	–0.313 c	–0.381 b	–0.419 b	–0.506 b	–0.413 c	–0.475 b
		I_{50}	–0.244	–0.381	–0.313 c	–0.488 c	–0.531 c	–0.469 b	–0.406 c	–0.444 b
	Interaction		NS	NS	NS	NS	*	NS	*	NS
2	Soil management		*	*	*	*	*	*	*	*
		RV-I	–0.325 bc	–0.430 c	–0.295 b	–0.395 c	–0.486 b	–0.494 c	–0.442 a	–0.566 a
		RV-II	–0.264 a	–0.347 a	–0.269 ab	–0.275 a	–0.373 a	–0.403 a	–0.468 ab	–0.471 b
		SCC-I	–0.350 c	–0.537 d	–0.320 bc	–0.355 bc	–0.452 b	–0.541 b	–0.508 b	–0.551 a
		SCC-II	–0.304 b	–0.375 b	–0.345 c	–0.309 ab	–0.432 ab	–0.398 a	–0.414 a	–0.435 b
	Water regime		NS	*	*	*	*	*	*	*
		I_{200}	–0.324	–0.421 ab	–0.244 a	–0.220 a	–0.314 a	–0.349 a	–0.361 a	–0.399 a
		I_{150}	–0.290	–0.408 a	–0.256 a	–0.228 a	–0.356 ab	–0.346 a	–0.340 a	–0.445 a
		I_{100}	–0.319	–0.438 b	–0.259 a	–0.315 b	–0.419 b	–0.489 b	–0.449 b	–0.453 ab
		I_{50}	–0.303	–0.408 a	–0.328 b	–0.383 b	–0.523 c	–0.518 b	–0.508 b	–0.534 b
		I_0	–0.319	–0.438 b	–0.450 c	–0.523 c	–0.568 c	–0.598 c	–0.633 c	–0.699 c
	Interaction		NS	*	*	*	*	*	*	*

* Significance for $p < 0.05$; NS–No significance for $p < 0.05$. Different letters indicate statistically significant differences ($p < 0.05$) by the Tukey test. RV–Resident vegetation; SCC–Sown cover crop; I–Soil I ; II–Soil II ; I_{200}–200 mm water regime; I_{150}–150 mm water regime; I_{100}–100 mm water regime; I_{50}–50 mm water regime.´; I_0–rainfed.

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TABLE2. Two-way ANOVA for the effect of soil management and water regime on stomatal conductance (gs; mol H_2O m-2 s^{-1}) at different times of day and stages of the growth cycle (three and two repetitions per date of measurement in season 1 and 2, respectively).

Season	Source of variation	Veraison 2nd			Veraison 3rd			Ripening 1st			Ripening 2nd			Pre-harvest		
	Time	9:00 AM	02:00 PM	06:00 PM	9:00 AM	02:00 PM	06:00 PM	9:00 AM	02:00 PM	06:00 PM	9:00 AM	02:00 PM	06:00 PM	9:00 AM	02:00 PM	06:00 PM
1	Soil management							NS			NS	NS	NS	NS		
	RV-I							0.28			0.21	0.15	0.15	0.04		
	RV-II							0.23			0.24	0.12	0.17	0.05		
	Water regime							*			NS	*	*	NS		
	I_{200}							0.32 a			0.27	0.24 a	0.24 a	0.06		
	I_{150}							0.29 a			0.19	0.13 b	0.16 b	0.04		
	I_{100}							0.25 ab			0.23	0.09 b	0.11 b	0.03		
	I_{50}							0.16 b			0.21	0.07 b	0.13 b	0.02		
	Interaction							NS			NS	NS	NS	NS		
2	Soil management	NS	NS	*		NS	*	NS	NS	*	NS	NS		NS	*	NS
	RV-I	0.12	0.15	0.13 ab		0.17	0.09 b	0.11	0.09	0.07 b	0.22	0.09		0.12	0.08 b	0.08
	RV-II	0.14	0.15	0.15 ab		0.19	0.09 b	0.13	0.11	0.09 ab	0.20	0.07		0.13	0.09 b	0.08
	SCC-I	0.11	0.11	0.12 b		0.17	0.10 b	0.12	0.11	0.08 ab	0.19	0.08		0.15	0.10 b	0.11
	SCC-II	0.15	0.15	0.20 a		0.15	0.14 a	0.14	0.16	0.12 a	0.24	0.16		0.17	0.16 a	0.16
	Water regime	*	*	*		NS	*	*	*	*	*	*		*	*	*
	I_{200}	0.15 a	0.17 a	0.20 a		0.25	0.16 a	0.14 a	0.16 a	0.13 a	0.29 a	0.16 a		0.19 a	0.17 a	0.15 a
	I_{100}	0.14 a	0.15 a	0.15 a		0.11	0.12 b	0.14 a	0.12 b	0.09 b	0.20 b	0.09 b		0.15 a	0.09 b	0.11 ab
	I_0	0.10 b	0.09 b	0.08 b		0.15	0.06 c	0.09 b	0.06 c	0.05 c	0.14 b	0.04 c		0.08 b	0.05 c	0.05 b
	Interaction	*	NS	*		NS	*	*	*	*	NS	*		NS	*	NS

* Significance for $p < 0.05$; NS–No significance for $p < 0.05$. Different letters indicate statistically significant differences ($p < 0.05$) by the Tukey test. RV–Resident vegetation; SCC–Sown cover crop; I–Soil I ; II–Soil II; I_{200}–200 mm water regime; I_{150}–150 mm water regime; I_{100}–100 mm water regime; I_{50}–50 mm water regime.′; I_0–rainfed. Shaded columns–values not available

In the first season, no interaction was observed between factors, probably due to an insufficiency of data. Nonetheless, a decreasing pattern from the begging of ripening to harvest can be observed (Figure 2). The last measurements (pre-harvest), very low (0.02 to 0.06 mol H_2O m^{-2} s^{-1}), indicated severe water stress (Cifre *et al.,* 2005; Medrano *et al.,* 2002), mainly in the deficit and ultra-deficit irrigated grapevines, which led to a decline in the photosynthesis rate (An), more pronounced in the I_{50} treatment (Figure 2; Appendix 2).

In the second season, gs responded to irrigations (Figures 3 and 4), as an increase was observed in the second measurement during the ripening period, after an irrigation event. In general, a significant effect of water regime occurred at every measurement date and time, with the highest gs, representing mild to moderate stress (0.05 to 0.40 mol H_2O m^{-2} s^{-1}), observed in the I_{200} and I_{100} treatments, and rainfed grapevines presenting gs values indicating moderate to severe water deficits (Cifre *et al.,* 2005; Medrano *et al.,* 2002). Daily patterns were varied from date to date but, overall, gs values decreased during the day and the lowest stomatal conductance occurred at midday and late hours. Regarding soil management, significant differences were observed only at midday and late measurements, influenced by the daily increase of atmospheric water demand. Higher significant values of gs occurred, generally, in the SCC-II plots. Thereby, possibly due to a higher water availability in soil type II, stomatal closure was less affected.

The interaction between factors was significant, hence, a combined effect of soil management and water regime took place. Except for the early measurements in vines in SCC-I and midday measurements in RV-I, the temporal pattern of An, is not entirely parallel to gs, as no recovery of photosynthesis rate was observed at the second measurement during ripening when gs values increased (Figures 3 and 4; Appendix 2).

Significant effects of water regime, as well as a significant interaction between factors, were observed on An at midday and late measurements, (Appendix 2).

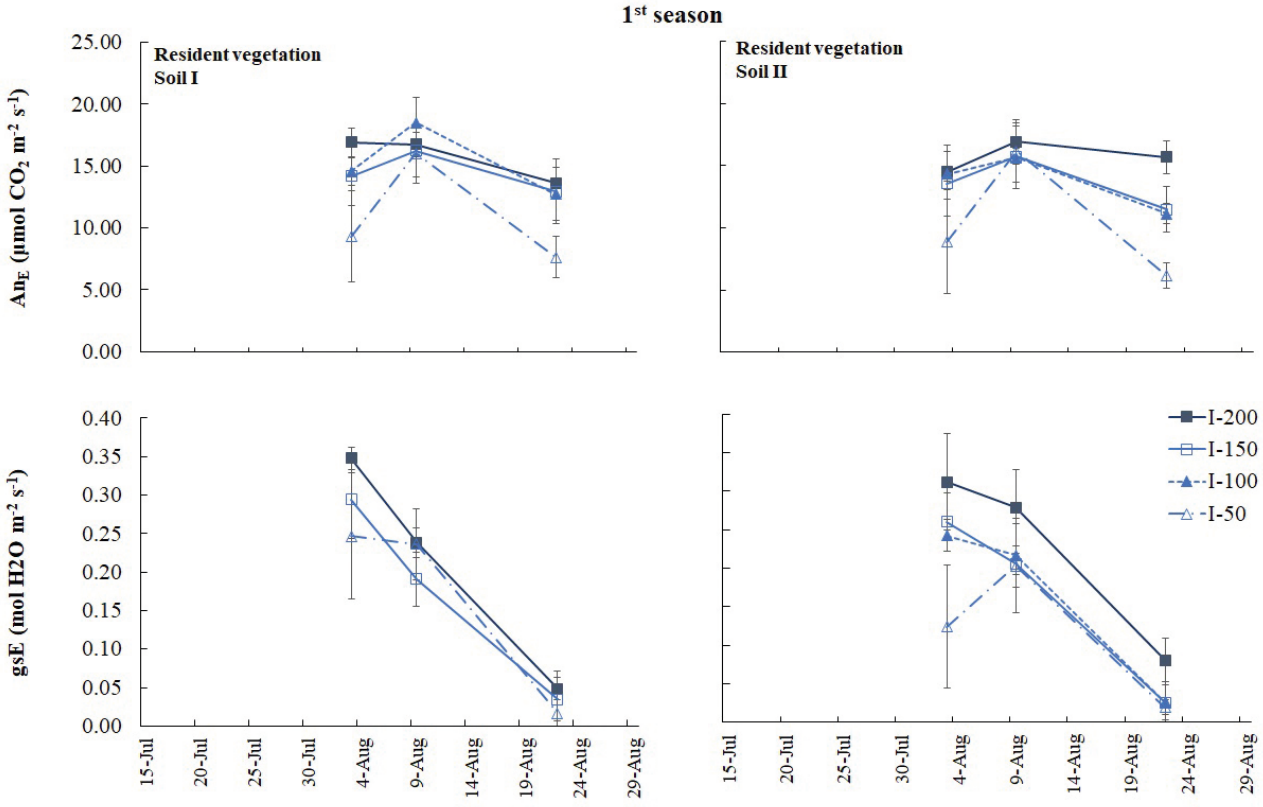


FIGURE 2. Temporal evolution of early (9 am) stomatal conductance (gs), and net photosynthesis (An) in the resident vegetation plots during the first season of the study. Marks represent the average of measurements performed in four water regimes at each soil management and soil type plot and whiskers represent the standard deviation (n = 3).

I_{200}–200 mm water regime; I_{150}–150 mm water regime; I_{100}–100 mm water regime; I_{50}–50 mm water regime.

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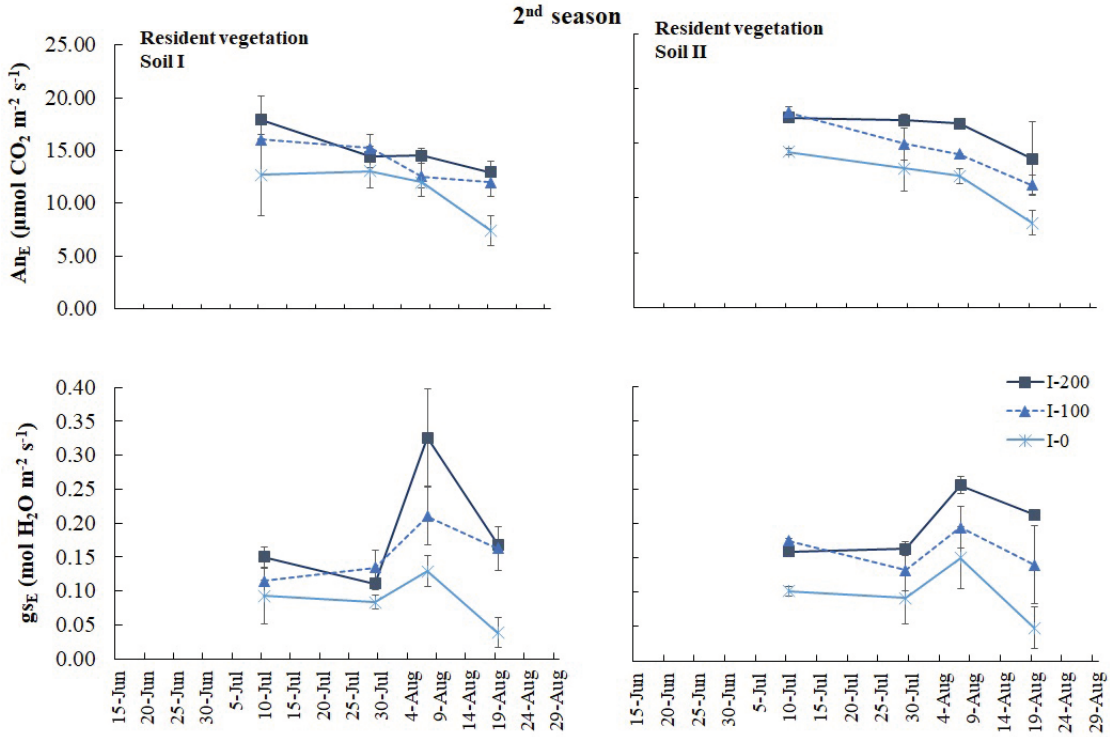


FIGURE 3. Temporal evolution of early (9 am) stomatal conductance (gs), and net photosynthesis (An) in the resident vegetation plots during the second season of the study. Marks represent the average of measurements performed in four water regimes at each soil management and soil type plot and whiskers represent the standard deviation (n = 2).

I_{200}–200 mm water regime; I_{100}–100 mm water regime; I_0–rainfed.

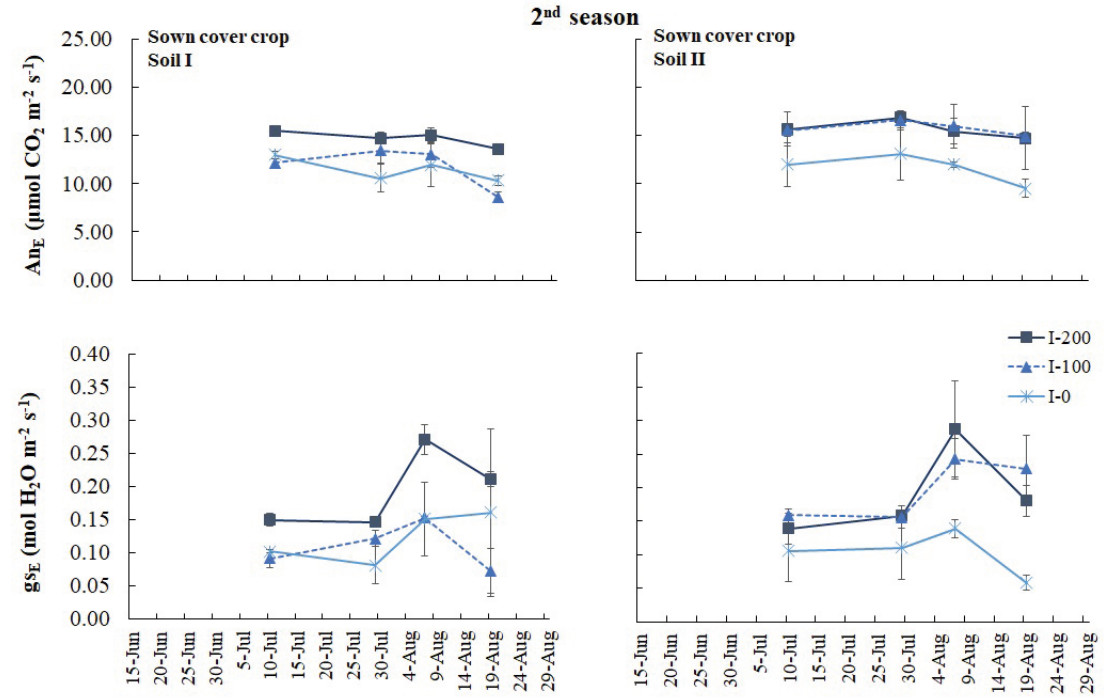


FIGURE 4. Temporal evolution of early (9 am) stomatal conductance (gs), and net photosynthesis (An) in the sown cover crop plots during the second season of the study. Marks represent the average of measurements performed in four water regimes at each soil management and soil type plot and whiskers represent the standard deviation (n = 2).

I200–200 mm water regime; I100–100 mm water regime; I0–rainfed.

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In fact, these observations are in accordance with the findings of Chaves *et al.* (2002) that reported on the influence of the evaporative demand in the atmosphere on carbon assimilation and water loss during the day, as drought progresses, and with the work of Lovisolo *et al.* (2010) that refer midday to afternoon depression of gs and An in many cultivars, even under sufficient soil water availability.

3. Correlation, principal components and cluster analyses

The correlation matrices of 17 variables of soil water availability, plant water status and gas exchange parameters at different times of day can be observed in Tables 3 and 4. In the first season, predawn water potential (Ψ_{PD}) and available soil water (ASW) showed a very high correlation (1.00) (Table 3).

Except for midday and late stomatal conductance (gs_{MD} vs. gs_L), no correlation was found between the same gas exchange parameters measured at different times of the day. Positive correlation coefficients, higher than 0.90, were found between early and midday stomatal conductance and transpiration rate (gs_E vs. E_E, and gs_{MD} vs. E_{MD}, respectively), midday intrinsic and instantaneous water use efficiency ($wue_{i\,MD}$ vs. $wue_{inst\,MD}$), late photosynthesis rate and transpiration rate (An_L vs. E_L) and late photosynthesis rate and stomatal conductance (An_L vs. gs_L). The highest correlations between gs and An occurred for the late measurements (0.959).

The correlation matrix for data of the second season (Table 4) shows, in general, more significant, and higher correlation coefficients. Possible explanations for this are, on one hand, the influence of more data obtained from gas exchange measurements plus the introduction of rainfed subplots, where water-stressed grapevines showed more differentiated responses, and, on the other hand, the contribution of the competition for water brought by an excessive biomass production of the sown cover crop that may have caused an imbalance in the vegetative growth of the vines. The highest correlation between ASW and early gas exchange measurements was found for the transpiration rate (E_E) (0.764). The Ψ_{PD} was moderately to highly (> 0.70) correlated with ASW, An_E, An_{MD}, gs_{MD}, E_{MD}, An_L, gs_L and E_L, denoting a stomatal response to plant water potential. This response is induced by a passive mechanism of hydraulic connection between epidermal and guard cells and/or an active mechanism through the production of hormones, such as ABA (Carminati and Javaux, 2020), and is dependent not only on the genotype (Tardieu and Simonneau, 1998) but also of the environmental conditions (Hochberg *et al.,* 2018). The correlation of gs with Ψ_{PD} is higher in the midday and late measurements, pointing to the regulation of stomatal response in response to plant water potential and environmental conditions, therefore, to a more isohydric-like (Medrano *et al.,* 2003; Sousa *et al.,* 2006) than anisohydric-like behaviour (Lovisolo *et al.,* 2010; Vaz *et al.,* 2016).

The PCA results from data of the first season can be observed in Figure 5. The first two principal components (PC1 and PC2) explain 65.3 % of the variance in the model. The gas exchange parameters used in the analysis (early measurements of An and gs at ripening and pre-harvest), as well as Ψ_{PD} from bunch closure to pre-harvest, yield (Y), pruning weight (PW), berries' titratable acidity (TA) and wine alcohol content (WAC) present negative loadings both in principal component 1 (PC1) and principal component 2 (PC2) (Figure 5a). Absolute values of Ψ_{PD} during veraison, ripening and pre-harvest positively load PC1, together with wine pH (WpH), must sugar content (WSC). The highest absolute factor loadings in PC1 occur for Ψ_{Ver2}, Ψ_{Ver3}, gs_{Rip1}, An_{Rip1}, An_{Harv}. PC2 had a high contribution of Ψ_{Ver1}, with a factor loading of –0.82.

Significant clustering of cases in the factor scores biplot (Figure 5b) evidences that during the first season, the variables were equally controlled by soil management and by water regimes as no cluster was predominantly composed of distinguished cases of soil management regardless of the water regime treatments. The cluster composed of I_{50} in RV plots shows that ultra-deficit irrigation with resident vegetation soil cover correlated with berries' pH, anthocyanins (ANT) and polyphenol content (PF), as well as with wine volatile acidity (WVA), pointing to an influence of water deficit on metabolic responses that benefit fruit and wine quality.

The PCA performed for the second season captured 75.8 % of the variance of data and both PC show higher factor loadings, not only of plant physiology variables but also of berries and wine parameters (Figure 6a). High positive factor loadings in PC1 and PC2 occur for all Ψ_{PD} measurements, WTA and WVA. An and gs measurements, Y and TA had high negative factor loadings (< –0.65) in PC1, while WpH negatively contributed to PC2 (–0.65).

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TABLE 3. Correlation matrix of soil and plant water status measurements in the first season.

	Ψ_{PD}	ASW	An_E	gs_E	E_E	$wuei_E$	$wueins_{MD}$	An_{MD}	gs_{MD}	E_{MD}	$wuei_{MD}$	$wueins_L$	An_L	gs_L	E_L	$wuei_L$	$wueins_L$
Ψ_{PD}	1.000																
ASW	**1.000**	1.000															
An_E	0.432	0.572	1.000														
gs_E	0.232	0.616	**0.665**	1.000													
E_E	0.179	0.529	0.505	**0.955**	1.000												
$wuei_E$	–0.282	–0.461	–0.473	**–0.829**	**–0.820**	1.000											
$wueins_E$	–0.256	–0.409	–0.345	**–0.770**	–0.782	**0.982**	1.000										
An_{MD}	–0.180	0.231	–0.274	0.101	0.060	0.119	0.108	1.000									
gs_{MD}	–0.360	–0.037	–0.433	0.034	0.043	0.109	0.082	**0.786**	1.000								
E_{MD}	–0.453	–0.081	–0.392	0.097	0.095	0.082	0.068	**0.819**	**0.958**	1.000							
$wuei_{MD}$	0.398	0.154	0.109	–0.030	0.000	–0.110	–0.125	–0.326	–0.590	–0.692	1.000						
$wueins_{MD}$	0.406	0.171	0.121	–0.001	0.034	–0.133	–0.145	–0.319	–0.616	–0.699	**0.996**	1.000					
An_L	0.289	0.325	–0.440	0.139	0.245	–0.248	–0.354	0.584	0.666	0.632	–0.141	–0.196	1.000				
gs_L	0.294	0.318	–0.453	0.039	0.149	–0.161	–0.265	0.530	**0.747**	0.633	–0.178	–0.297	**0.959**	1.000			
E_L	0.123	0.252	–0.392	0.277	0.373	–0.346	–0.439	0.679	0.580	0.658	–0.116	–0.088	**0.932**	**0.811**	1.000		
$wuei_L$	0.436	0.106	–0.044	–0.494	–0.468	0.434	0.426	–0.420	0.015	–0.269	–0.005	–0.207	–0.074	0.144	–0.422	1.000	
$wueins_L$	–0.253	–0.292	0.296	0.043	–0.019	0.099	0.173	–0.243	–0.673	–0.422	0.160	0.378	–0.623	**–0.809**	–0.350	–0.514	1.000

Ψ_{PD}–predawn leaf water potential; ASW–available soil water; An–net photosynthesis rate; gs–stomatal conductance; E–transpiration rate; wuei–intrinsic water use efficiency; wueinst–instant water use efficiency. Subscripts E, MD and L represent measurements at 9 am (Early), 2 pm (Midday) and 6 pm (Late), respectively. Significant correlations ($p < 0.05$) are highlighted with bold.

TABLE 4. Correlation matrix of soil and plant water status measurements in the second season.

	Ψ_{PD}	ASW	An_E	gs_E	E_E	$wuei_E$	$wueins_{MD}$	An_{MD}	gs_{MD}	E_{MD}	$wuei_{MD}$	$wueins_L$	An_L	gs_L	E_L	$wuei_L$	$wueins_L$
Ψ_{PD}	1.000																
ASW	**0.703**	1.000															
An_E	**0.783**	**0.696**	1.000														
gs_E	**0.394**	**0.404**	**0.543**	1.000													
E_E	**0.649**	**0.764**	**0.791**	**0.656**	1.000												
$wuei_E$	**–0.398**	**–0.556**	**–0.454**	**–0.570**	**–0.863**	1.000											
$wueins_E$	**–0.304**	–0.357	**–0.432**	**–0.887**	**–0.565**	**0.598**	1.000										
An_{MD}	**0.805**	**0.650**	**0.769**	**0.506**	**0.612**	–0.282	**–0.355**	1.000									
gs_{MD}	**0.786**	**0.668**	**0.691**	**0.496**	**0.626**	**–0.352**	**–0.345**	**0.835**	1.000								
E_{MD}	**0.777**	**0.725**	**0.673**	**0.375**	**0.672**	**–0.449**	–0.261	**0.750**	**0.959**	1.000							
$wuei_{MD}$	**–0.175**	–0.220	0.024	0.046	–0.202	**0.346**	–0.063	0.103	**–0.296**	**–0.461**	1.000						
$wueins_{MD}$	**–0.421**	**–0.363**	–0.212	–0.105	–0.223	0.110	–0.057	**–0.382**	**–0.518**	**–0.537**	**0.400**	1.000					
An_L	**0.804**	**0.757**	**0.740**	**0.574**	**0.704**	**–0.462**	**–0.477**	**0.897**	**0.889**	**0.854**	–0.074	**–0.601**	1.000				
gs_L	**0.732**	**0.596**	**0.630**	**0.604**	**0.659**	**–0.448**	**–0.488**	**0.787**	**0.748**	**0.697**	–0.065	**–0.513**	**0.856**	1.000			
E_L	**0.788**	**0.691**	**0.667**	**0.660**	**0.617**	**–0.378**	**–0.549**	**0.834**	**0.899**	**0.863**	–0.107	**–0.667**	**0.943**	**0.906**	1.000		
$wuei_L$	–0.105	0.045	0.150	–0.247	0.212	–0.277	0.198	–0.060	–0.228	–0.188	0.053	0.297	–0.053	–0.311	–0.355	1.000	
$wueins_L$	**–0.345**	–0.114	–0.232	**–0.475**	–0.286	0.176	**0.409**	**–0.433**	**–0.338**	–0.250	–0.081	0.166	**–0.372**	**–0.716**	**–0.514**	**0.533**	1.000

Ψ_{PD}–predawn leaf water potential; ASW–available soil water; An–net photosynthesis rate; gs–stomatal conductance; E–transpiration rate; wuei–intrinsic water use efficiency; wueinst–instant water use efficiency. Subscripts E, MD and L represent measurements at 9 am (Early), 2 pm (Midday) and 6 pm (Late), respectively. Significant correlations ($p < 0.05$) are highlighted with bold.

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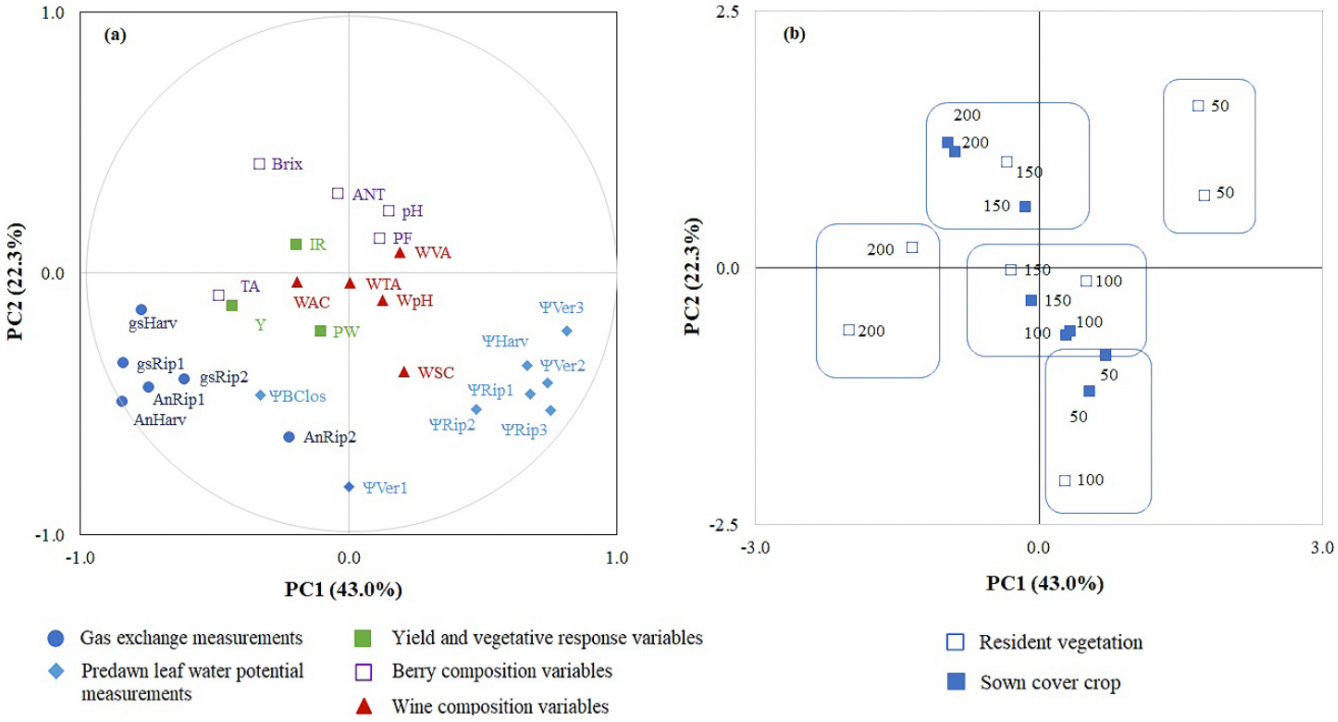


FIGURE 5. PCA results in the first season: (a) Loading plot of variables of the first two components (PC1 and PC2). (b) Score plot of cases of the first two components. Rounded squares represent significant clusters (dlink/dmax*100 < 40 %).

200–200 mm water regime; 150–150 mm water regime; 100–100 mm water regime; 50–50 mm water regime.

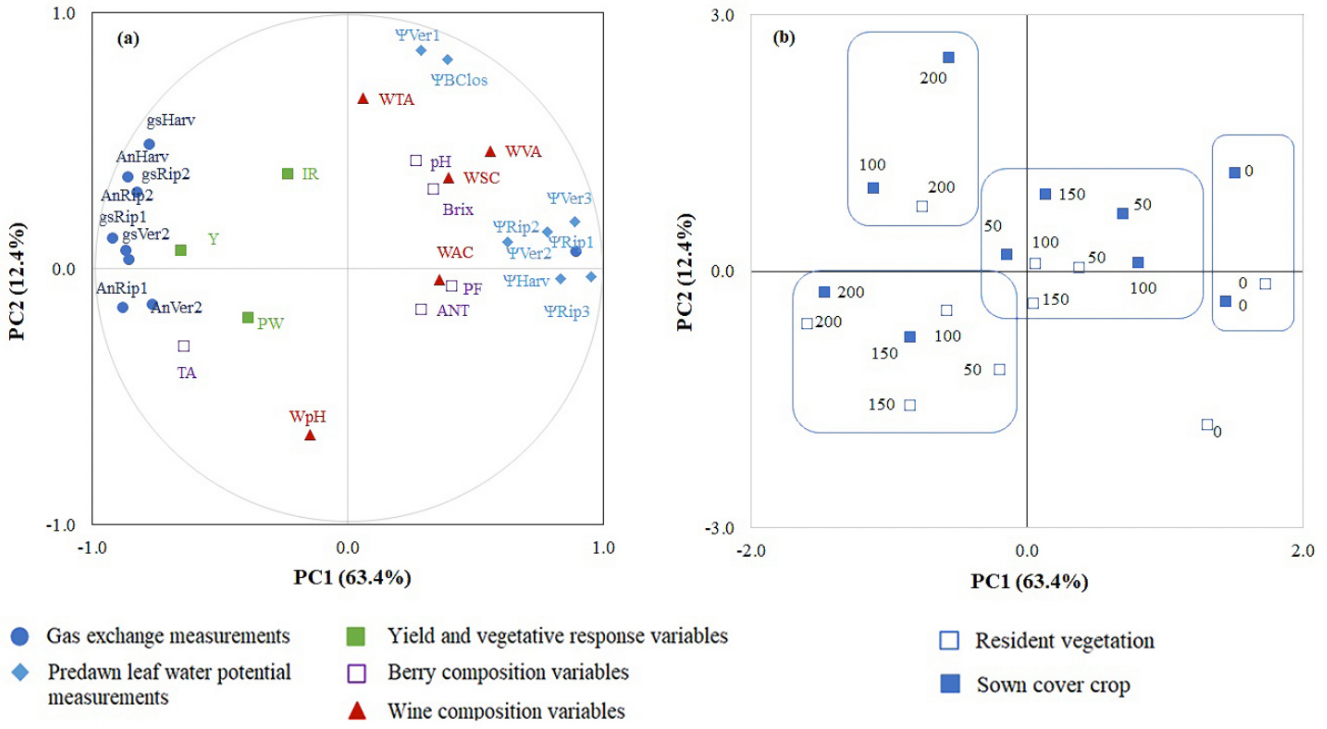


FIGURE 6. PCA results in the second season: (a) Loading plot of variables of the first two components (PC1 and PC2). (b) Score plot of cases of the first two components. Rounded squares represent significant clusters (dlink/dmax*100 < 40 %).

200–200 mm water regime; 150–150 mm water regime; 100–100 mm water regime; 50–50 mm water regime; 0–Rainfed.

A significant cluster of cases of I_0 water regime, both in RV and SCC plots in the positive quadrant of PC1 points to a positive relationship with plant water status (absolute values of Ψ_{PD}) and berries and wine composition. A cluster composed of I_{200} and I_{100}, both in RV and SCC plots in the PC1 < 0 and PC2 > 0 quadrant indicates a correlation between Y, Yield to pruning weight (IR) and gas exchange measurements. This grouping of cases pattern seems to imply a significant clustering which was more irrigation-controlled than soil management-controlled, therefore, regardless of the indisputable effects of soil cover previously discussed, a predominant influence of irrigation should be expected for 'Tempranillo' grapevines grown under dry Mediterranean conditions.

CONCLUSIONS

The current study provided insights about the combined effects of soil management and water regime (irrigation and rainfed conditions) on grapevine water status and functioning of 'Tempranillo' grown in a Mediterranean environment.

Significant interactions between the effect of soil management and water regime were observed on vine functioning by measuring the predawn leaf water potential, midday and late stomatal conductance and photosynthetic rate. A water competition effect exerted by the cover crop could be responsible for reduced transpiration and carbon assimilation, whenever Spring rain is lower and/or the cover crop biomass development is not controlled. Differences in stomatal conductance and net photosynthesis rate observed at midday and late measurements reflect the influence of the daily increase of atmospheric water demand (vapour pressure deficit). A combined effect of soil cover management and water regime was observed for midday and late stomatal conductance and photosynthetic rate but stomatal closure of grapevines was less affected in plots of higher soil water storage capacity. High to strong correlations were found between predawn leaf water potential and available soil water content. The correlation of stomatal conductance and leaf water potential was higher in the midday and late measurements, pointing to the regulation of stomatal response in response to soil water availability and daily environmental conditions (micro and mesoclimate).

The multivariate statistical approach with principal components analysis clearly showed that, in the first season, ultra-deficit irrigation with resident vegetation soil cover correlated with berries' pH, anthocyanins and polyphenol content, as well as with wine volatile acidity. In the second season, while positive correlations were found between yield and growth variables and gas exchange measurements, the rainfed treatment positively related with high absolute values of pre-dawn leaf water potential and berries and wine composition. Therefore, it was observed an influence of water deficit on berry metabolic responses that could benefit fruit and wine quality but may hinder vegetative growth and yield.

The CA analysis revealed that no significant cluster of cases was clearly controlled by soil management or water regime in the first season. In the second season, significant clustering more irrigation-controlled than soil management-controlled indicated that, whenever water availability is lower, either due to lower precipitation in the Spring or to water competition with interrow vegetation, a predominant influence of irrigation should be expected for 'Tempranillo' grapevines growing under dry Mediterranean conditions.

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