Influence of water stress on plant hydraulics, gas exchange, berry composition and quality of Pinot noir wines in Switzerland

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Abstract

Aims : The aims of this study were to investigate the physiological behavior (plant hydraulics, gas exchange) of the cultivar Pinot Noir in the field under progressively increasing conditions of water stress and analyze the effects of drought on grape and wine quality.

Methods and results : Grapevines of the variety *Vitis vinifera* L. cv. Pinot noir (clone 9-18, grafted onto 5BB) were subjected to different water regimes (irrigation treatments) over the growing season. Physiological indicators were used to monitor plant water status (leaf and stem water potentials and relative carbon isotope composition ($\delta^{13}C$) in must sugars). Leaf gas exchange (net photosynthesis A and transpiration E), leaf stomatal conductance (gs), specific hydraulic conductivity in petioles ($K_{petiole}$), yield components, berry composition at harvest, and organoleptic quality of wines were analyzed over a 7-year period, between 2009 and 2015, under relatively dry conditions in the canton of Wallis, Switzerland. A progressively increasing water deficit, observed throughout the season, reduced the leaf gas exchange (A and E) and gs in non-irrigated vines. The intrinsic water use efficiency (WUE_i, A/gs) increased during the growing season and was greater in water-stressed vines than in well-watered vines (irrigated vines). This rise in WUE_i was correlated with an increase in $\delta^{13}C$ in must sugars at harvest. Drought led to decreases in $K_{petiole}$, E and sap flow in stems. A decrease in vine plant vigor was observed in vines that had been subjected to water deficits year after year. Moderate water stress during ripening favored sugar accumulation in berries and caused a reduction in total acidic and malic contents in must and available nitrogen content (YAN). Wines produced from water-stressed vines had a deeper color and were richer in anthocyanins and phenol compounds compared with wines from well-watered vines with no water stress. The vine water status greatly influenced the organoleptic quality of the resulting wines. Wines made from non-irrigated vines with a water deficit presented more structure and higher-quality tannins. They were also judged to be more full-bodied and with blended tannins than those made from irrigated vines.

Conclusions : Grape ripening and resulting Pinot Noir wines were found to be largely dependent on the water supply conditions of the vines during the growing season, which influenced gas exchange and plant hydraulics.

Significance and impact of the study : Plant water status constitutes a key factor in leaf gas exchange, canopy water use efficiency, berry composition and wine quality.

Keywords: Water stress, gas exchange, stomatal conductance, plant hydraulics, water use efficiency (WUE), carbon isotope composition, berry composition, wine quality

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Introduction

Grapevines are regularly subjected to environmental constraints, which are mainly soil water availability limitations and supra-optimal temperatures during summer. Even in cool to temperate climates, conditions of water stress may periodically arise during summer months, depending on vineyard topography and rainfall amounts. The pedoclimatic situation (soil type, soil available water reserves, rainfall) and climate evolution both play a major role in the development of edaphic water deficits. Global warming and heat waves, observed over the last few decades, have further accentuated abiotic stress. The grapevine, originating from the Mediterranean region, is traditionally considered a drought-resistant plant (Carbonneau, 1998). Its ability to endure water scarcity comes from its capacity to reach down to great depths, thanks to a large and deep well-developed root system (Bauerle *et al*., 2008; Barrios-Masias *et al*., 2015). Furthermore, the vine's water needs are relatively modest compared with other crops (Pereira *et al*., 1998). Controlled vine yields and progressive, moderate water deficit are needed to obtain quality wines (Seguin, 1975; van Leeuwen and Seguin, 1994).

Vine sensitivity to water deficit depends on factors that are intrinsic to each site (soil type, mesoclimate) and varies according to genetic (rootstock/scion association) (Spring, 1997; Lovisolo *et al*., 2016), agronomic (cover crops, leaf-fruit ratio, irrigation) and other factors. Therefore, the environmental constraints imposed by topography, climate and its evolution sometimes require adaptations of management techniques. These adaptations are mainly irrigation to ensure yield and maintain or improve wine quality (Dry and Loveys, 1998; Chaves *et al*., 2007) in association with other practices (e.g., soil cover, grass management, leaf-fruit ratio; Celette and Gary, 2013).

Numerous studies have shown that limiting vine water availability affects photosynthesis (A) and leaf transpiration (E) (Chaves *et al*., 2010), plant (Stevens *et al*., 1995) and root development (Dry *et al*., 2000b), and leaf and berry mineral nutrition (Gonzalez-Dugo *et al*., 2010). Stomatal control of leaf transpiration constitutes a physiological drought-avoiding mechanism by optimizing crop water use while preventing embolism events (Lovisolo *et al*., 2002). High temperatures together with water deficit conditions can lead to leaf fall, in turn leading to a source-sink imbalance, a decrease in the plant canopy's capacity for photosynthesis, and incomplete ripening of berries due to limited carbohydrate availability (Chaves *et al*., 2007). It is also recognized that not only the severity of a drought but also the timing and duration influence the final berry size and composition (Deloire *et al*., 2004). Generally, moderate water stress during the ripening period is favorable for sugar accumulation (van Leeuwen *et al*., 2009) and increases the anthocyanin and tannin contents in berries (Matthews and Anderson, 1989; Koundouras *et al*., 2006). In temperate climates, conditions of water deficit are favorable for producing high-quality red wines (van Leeuwen *et al*., 2009).

Physiological indicators (leaf and stem water potentials, relative carbon isotope composition) that allow direct evaluations of vine water status during the season have been the object of much research (Choné *et al*., 2001). These indicators were also used in the present study to create different vine water regimes during the growing season by imposing deficit irrigation (DI) from flowering to ripening (irrigated vines with respect to maximum leaf water potential) and water stress without irrigation (non-irrigated vines). The effects of water supply on leaf gas exchange (A, E), water use efficiency (WUE), leaf stomatal conductance, petiole hydraulic conductivity, plant vigor, yield components, and Pinot noir grape and wine quality were analyzed in a field experiment on adult vines (> 10 years) under relatively dry and warm alpine valley conditions (Valais) in Switzerland.

Materials and Methods

1. Experimental site and plant material

The experiment was conducted during 2009-2015 at the Agroscope experimental station in Leytron, Switzerland (46°10' N, 7°12' E; 485 m asl), which is located in an alpine valley. The region has a continental climate with fluctuating rainfalls and temperatures over the last 150 years (Figure 1). Monthly rainfalls and temperatures from 2009 to 2015 (and long-term averages from 1981 to 2010) from the meteorological station in Leytron are presented in Tables 1 and 2. The planting material was the cultivar Pinot noir (clone 9-18) grafted onto *Vitis berlandieri* x *Vitis riparia* cv. Kober 5BB rootstock. Vines were planted in the Guyot training system (vertical shoot-positioned) with a planting density of 5500 vines ha^{-1} (planting distance: 1.8 x 1.0 m). Six shoots per vine were maintained. The experimental site in Leytron lies on very stony (peyrosol > 60% large elements, stones, blocks and gravel) and deep soil (> 2.5 m vine root depth) with a water-holding capacity estimated at 150 mm.

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Table 1. Monthly rates of precipitation (mm) at the experimental site Leytron (Switzerland) during the seven study years (2009-2015) compared with the long-term averages (1981-2010)

	2009	2010	2011	2012	2013	2014	2015	Long-term
January	109	11	22	57	21	42	55	51
February	28	29	7	0	59	79	11	47
March	23	27	14	5	29	5	63	42
April	37	8	5	51	45	29	12	35
May	25	120	43	52	83	34	123	49
June	40	15	40	37	24	17	34	54
July	87	73	69	51	52	106	35	58
August	16	45	22	65	30	87	78	57
September	18	22	42	52	45	15	14	44
October	11	14	34	39	67	30	29	52
November	68	36	2	53	95	44	42	52
December	108	70	168	152	17	42	4	64
Year	570	470	468	614	567	530	500	603

Table 2. Monthly mean temperatures (°C) at the experimental site Leytron (Switzerland) during the seven study years (2009-2015) compared with the long-term averages (1981-2010)

	2009	2010	2011	2012	2013	2014	2015	Long-term
January	-2.7	-1.5	0.2	1.5	1.0	2.6	1.4	-0.1
February	1.0	1.5	2.9	-1.7	0.0	4.2	1.3	1.8
March	5.9	6.1	7.9	9.1	5.2	8.4	7.9	6.5
April	12.4	11.8	14.2	10.9	10.9	12.8	12.2	10.4
May	16.4	14.0	17.0	16.1	12.5	15.6	15.6	14.9
June	18.4	18.9	18.8	20.0	18.1	20.1	20.6	18.1
July	20.5	21.8	18.6	20.3	21.6	19.3	24.0	20.1
August	21.6	18.5	21.0	21.3	20.2	18.4	20.9	19.2
September	16.8	14.8	17.8	15.8	16.3	16.9	14.9	15.2
October	10.3	10.3	10.4	11.5	12.7	13.0	10.5	10.3
November	6.7	5.5	5.2	6.4	3.8	8.1	5.9	4.3
December	1.0	-0.6	1.9	0.6	0.4	2.7	2.2	0.6
Year	10.7	10.1	11.3	11.0	10.1	11.7	11.5	10.1

2. Irrigation treatments

Three different irrigation treatments were established. In the first treatment, 9 L/m^2 soil (16 L/vine) was drip-fed weekly from bloom (~150 DOY) to fruit ripening (~215 DOY). This level of irrigation (deficit irrigation, DI) corresponded to an approximately weekly compensation of 30% evapotranspiration potential (ETP). The second treatment was no irrigation (rain-fed) throughout the entire growing season. The third treatment also involved no irrigation but included waterproof and non-reflecting plastic on the soil from bloom (~150 DOY) to harvest (~280 DOY) to eliminate the infiltration of water from precipitation events. The trial was conducted using 40 plants per treatment, which were set out in 4 split-plot randomized blocks of 10 vines each.

3. Plant water status and gas exchange measurements

Predawn leaf water potential (Ψ_{PD}) and midday stem water potential (Ψ_{STEM}) were measured using a pressure chamber (Scholander *et al*., 1965) according to Turner (1988). Ψ_{PD} was measured between 0400 and 0500 in the morning, in complete darkness, on eight mature, undamaged and non-senescent leaves. Midday Ψ_{STEM} measurements were performed between 1400 and 1500, when evapotranspiration was at a maximum, on eight leaves bagged with a plastic sheet and covered with aluminum foil to stop

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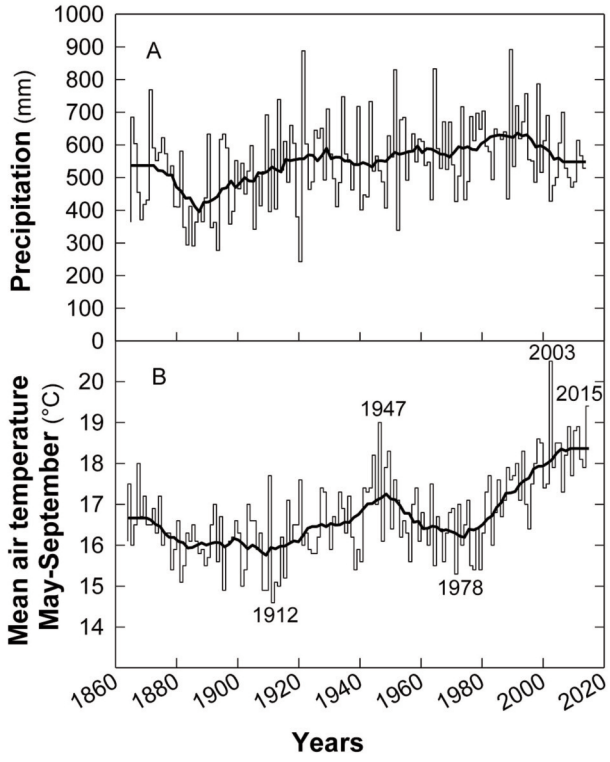


Figure 1. Evolution of annual rainfall (A) and mean temperatures (B) recorded from May to September from 1864 to 2015. Data from the meteorological station in Sion, Switzerland (46°13' N, 7°21' E; 510 m asl; MétéoSuisse database).

transpiration at least one hour before the measurement (Fulton *et al*., 2001).

Leaf gas exchange [net photosynthesis (A) and transpiration (E)], stomatal conductance (gs) and mesophyll resistance (r_m) were measured on healthy, fully expanded, mature and non-senescent leaves well exposed to direct sunlight (PFD > 1800 µmol $m^{-2}s^{-1}$) from June until mid-October. Eight leaves per irrigation treatment were measured in the morning (1000) on clear-sky days. Gas exchange was measured using a portable photosynthesis system (LI-6400, LI-COR Inc., Lincoln, NE, USA). R_m was calculated as $r_m = (C_i-\Gamma)/A$, where C_i is the intercellular partial pressure of CO_2, Γ is the CO_2 compensation point (corresponding to 50 ppm for adult leaves with a leaf temperature between 20-25°C; Schultz *et al*., 1996), and A is the net photosynthesis. Intrinsic water use efficiency (WUE_i, A/gs) and instantaneous water use efficiency (WUE_{inst}, A/E) were determined from single leaf gas exchange measurements that related the net photosynthesis rate (A) either to stomatal conductance for water vapor (gs), termed WUE_i (Osmond *et al*., 1980), or to leaf transpiration rate (E), termed WUE_{inst}.

Sap flow meter measurements (tissue heat balance, T4.2 device, Environmental Measuring Systems, Brno, Czech Republic) (Cermak and Kucera, 1981) were performed at the base of four shoots on four different vines per irrigation treatment during the 2009-2010 seasons. Hourly and daily sap flow rates (liters per hour and per leaf area, $L/h/m^2$) were determined on different days on shoots of irrigated and non-irrigated vines.

4. Relative carbon isotope composition ($\delta^{13}C$)

The stable carbon isotope composition ($\delta^{13}C$) in must sugars and leaf sugars (leaf carbon isotope signature) was determined at harvest at the Stable Isotope Laboratory of the University of Lausanne by elemental analysis-isotope ratio mass spectrometry (EA-IRMS) using a Carlo Erba 1108 Elemental Analyzer connected to a Thermo Fisher Scientific (Bremen, Germany) Delta V mass spectrometer. $\delta^{13}C$ is reported as per mille (‰) deviations of the isotope ratio relative to known standards as follows: $\delta = [(R_{sample} - R_{standard}) R_{standard}] \times 1000$, where R is the ratio of the heavy to light isotopes ($^{13}C/^{12}C$). The $R_{standard}$ value for ^{13}C in Vienna Pee Dee Belemnite limestone is 0.0112372 (Deléens *et al*., 1994).

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5. Specific hydraulic conductivity in petioles ($K_{petiole}$) and vulnerability to cavitation (PLC)

$K_{petiole}$ was measured using a xylem embolism meter (XYL'EM, Bronkhorst Instructec, Montigny-les-Cormeilles, France). The principle of the XYL'EM meter is to accurately measure the water flow (F; mmol s^{-1}) entering the petiole of a cut leaf when exposed to hydrostatic pressure (P; MPa) using a high-resolution liquid mass flow meter. For the measurement, shoots were cut at the base under water and were held under water for approximately 20 min to promote xylem tension relaxation; then, petioles of the apical zone were excised under water and connected to the XYL'EM apparatus. The initial hydraulic conductance (K_{init}) was determined with a hydrostatic pressure gradient of approximately 3 to 4 kPa. Distilled and degassed water was used as perfusion liquid for all measurements. $K_{petiole}$ (mmol m^{-1} s^{-1} MPa^{-1}) was calculated as $K_{petiole} = K_{init}$ x L/LA, where K_{init} is the initial hydraulic conductance described above (mmol s^{-1} MPa), L is the petiole length (m), and LA is the leaf blade area (m^2). The XYL'EM was interfaced with a computer to automatically log the data. Four leaves per replicate were used for the $K_{petiole}$ measurements.

Percentage loss of conductivity (PLC) figures were constructed using the average values obtained from four petioles and as many measurements representing Ψ_{STEM}. PLC versus Ψ_{STEM} curves were utilized to determine the vulnerability to cavitation, expressed as Ψ_{PLC50}, the xylem water potential inducing a 50% loss in hydraulic conductivity. Ψ_{PLC50} was estimated by fitting a sigmoid PLC curve versus Ψ_{STEM} data as follows: $PLC = 100/[1+ \exp (a (\Psi_{stem} - \Psi_{PLC50}))]$, where a represents the slope of the curve at the point of inflection.

6. Leaf area measurements and pruning weight

Leaf area (LA) in the field was determined non-destructively in 2009 and 2010 using measurements of the two secondary lateral vein (lamina) lengths (L_1, L_2) multiplied by a varietal coefficient j according to Carbonneau (1976), with $LA = j(L_1 + L_2)^2$. Planimetric measurements were performed to assess the varietal coefficient j to 0.488 for the cv. Chasselas (Zufferey, 2000). All leaves from two shoots of each vine (five vines per block) were measured to estimate the average leaf area per shoot. The average shoot leaf area was used to estimate the total vine leaf area by multiplying it by the number of shoots per vine. In winter, the total weight of pruned vine shoots was recorded (6 shoots per vine), representing 10 plants per replica and 40 plants per treatment.

7. Leaf and berry mineral nutrition

A foliar analysis was performed to determine the levels of leaf nitrogen (Kjeldahl method), potassium, phosphorous, calcium and magnesium. The samples consisted of 25 leaves gathered in the cluster zone at veraison. Leaves with petioles were washed, over-dried, ground and analyzed. The leaf chlorophyll index was measured using an N-tester apparatus (Yara, Nanterre, France) on adult leaves situated at the base of fruit-ripe branches. Yeast available nitrogen (YAN) was estimated by NIR spectroscopy (WineScan®, FOSS NIRSystems, USA). This method quantifies the N-compounds of juice assimilable by the yeasts during fermentation. YAN corresponds to the concentration of ammonium ion and primary amino acids, excluding proline.

8. Yield components, berry composition and wine analytics and testing

Bud fertility (the number of clusters per shoot) was observed each year shortly before flowering. At harvest, 50 berries per replica were randomly selected and weighed to determine the berry weight. The yield per plant (kg/vine) divided by the number of clusters per plant enabled the average weight of clusters at harvest time to be estimated. The fruit composition parameters at harvest included the soluble solid content (g/L), pH, titratable acidity (g tartrate/L) expressed as tartaric acid (g/L), and malic acid (g/L). Microvinification (60 kg of grape) was conducted identically for all irrigation treatments by the same winemaker. Wine composition was assessed at bottling using infrared spectroscopy. The anthocyanin content was evaluated using a decoloration step with sulfur dioxide and measuring the difference in wine absorbance at 520 nm (Ribéreau-Gayon *et al*., 1998). The total polyphenol index was calculated based on wine absorbance at 280 nm (Ribéreau-Gayon *et al*., 1998). A sensory analysis was conducted two months after bottling by a panel of 12 experienced tasters. The panelists rated the intensity of 23 sensory attributes, including appearance, bouquet and palate. Wines were evaluated on an unstructured line scale from 1 (no perception) to 7 (very intense perception).

9. Statistical analysis

The significance of each treatment was evaluated using an analysis of variance ($P<0.05$) followed by a single-comparison Newman–Keuls test using XLSTAT 2011.2.04 (Addinsoft, Paris, France).

OENO One, 2017, **51**, 1, 17-27
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Linear and non-linear regressions of Ψ_{PD} and Ψ_{STEM} and the different physiological parameters were determined using SigmaPlot software (version 13.0) and statistically analyzed using the SigmaStat program package.

Results

1. Climatic conditions

The irrigation trials were conducted in a relatively dry, internal valley in the Swiss Alps (canton of Wallis). Annual rainfall measurements (Figure 1A) and average temperatures between May and September (Figure 1B), recorded from 1864 to 2015, showed large interannual rainfall variations, with the annual average increasing from the beginning of the 20th century from approximately 400 to nearly 600 mm in the 1990s, followed by a downward trend over the last 20 years, stabilizing at approximately 550 mm. Similarly, mean temperatures recorded during the growth period of the vine showed strong interannual variations over the 150-year observation period. The years 1930-1950 were characterized by warm temperatures compared with the cooler years recorded around 1910 and prior years. Another cooler episode followed during 1960-1980. Since the middle of the 1980s, rising annual temperatures have been observed, with a particularly hot year in 2003 (the hottest year in the last 150 years, followed by 2015 and 1947).

Over the 7-year study period (2009-2015), climatic conditions (monthly precipitations and temperatures) varied considerably (Tables 1 and 2). Overall, the annual precipitation from 2009 to 2015 was slightly below the long-term average (600 mm), with the exception of 2012. In 2010, 2011 and 2015, precipitation was well under the long-term average by approximately 100 to 130 mm, with recorded rainfall between 470 and 500 mm per year. Measurements of summer rainfall (August-September), observed during grape ripening, also showed great contrast. Little summer rain was measured in 2009 and 2011. For the other vintages, summer rain was close to the long-term average measurement at approximately 40 to 60 mm per month. The year 2014 was an exception, with high precipitation in July (106 mm) and August (87 mm), well above the mean. The average annual temperatures observed during this study period were approximately 0.6 to 1.6°C greater than the average long-term temperature, with the exception of 2010

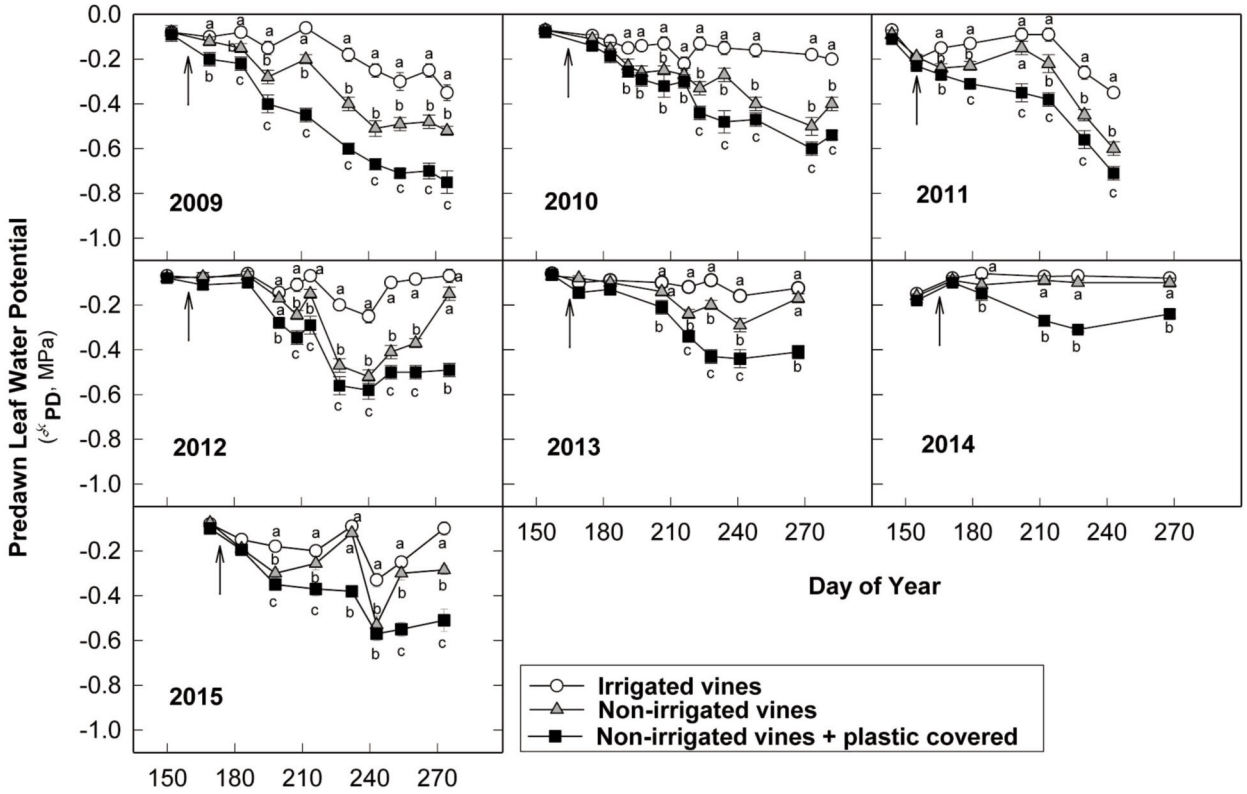


Figure 2. Seasonal evolution of predawn leaf water potential (Ψ_{PD}) for different irrigation treatments.
Arrows indicate irrigation onset. Means +/- SE for eight leaves. Letters: statistically significant at the 5% level of probability. Pinot noir, Leytron (Switzerland), 2009-2015.

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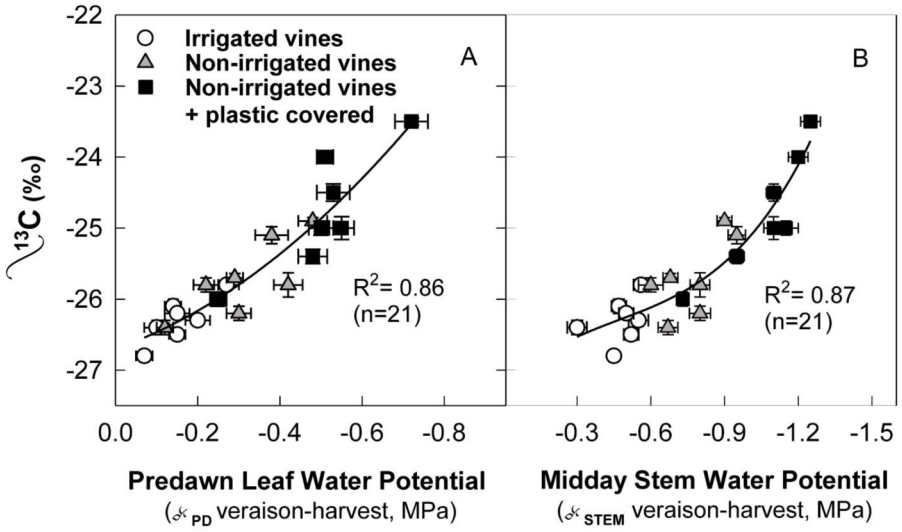


Figure 3. Relationship between predawn leaf water potential (Ψ_{PD}, A) and midday stem water potential (Ψ_{STEM}, B) measured during the veraison-harvest period and relative carbon isotope composition ($\delta^{13}C$) in must sugars at harvest for different irrigation treatments.
Means +/- SE. Pinot noir, Leytron (Switzerland), 2009-2015.

and 2013, when annual temperatures were comparable to the average (10.1°C, Table 2). The study period was characterized by summer temperatures (July-September) that were globally higher, and sometimes considerably higher, than the long-term average temperature, particularly in 2009, 2011, 2012 and 2015.

2. Plant water status

Seasonal courses of $\Psi_{PD,}$ measured between 2009 and 2015, highlighted significant differences between irrigated and non-irrigated vines (Figure 2). No water stress was observed in well-watered vines, with Ψ_{PD} values between -0.05 and -0.25 MPa throughout the season. On the other hand, non-irrigated vines (rain-fed) presented Ψ_{PD} values that became increasingly negative from the end of July (DOY 210). These values ranged between -0.3 and -0.5 MPa, reflecting moderate water stress from veraison (DOY 220) to the end of the ripening period, except for 2014, when the water deficit was small. Water stress was accentuated even more in non-irrigated vines where the soil was covered by a plastic waterproof sheet. In this case, water stress generally developed from veraison, with Ψ_{PD} values < -0.5 MPa, especially during the hot, dry summers of 2009, 2011, 2012 and 2015. In contrast, water stress was moderate in 2010, 2013 and 2014 due to cooler temperatures and greater rainfall (Tables 1 and 2), thus occasioning a lower ETP and a less rapid depletion of water soil resources.

The Ψ_{PD} and Ψ_{STEM} values measured during the veraison-harvest period correlated well (R^2 = 0.86, P<0.01 and R^2 = 0.87, P<0.01, respectively) with the relative carbon isotope composition ($\delta^{13}C$) of must sugars at harvest (Figure 3). δC^{13} values were between -23 ‰ (high water stress) in non-irrigated vines and -27 ‰ (no water stress) in irrigated vines during the study period. In addition, a correlation was observed between Ψ_{PD} values and midday Ψ_{STEM} values (R^2 = 0.80, P<0.01), measured at solar noon, and a vapor pressure deficit (VPD) between 2.5 and 3.5 kPa during the 7-year study period (results not presented).

3. Water and gas exchange relationship

Figure 4 illustrates the impacts of the different water regimes, estimated by Ψ_{PD} during the night or Ψ_{STEM} at midday (Figures 4A, B), on gs (Figure 4C), mesophyll resistance (r_m; Figure 4D), net photosynthesis A (Figure 4E) and leaf transpiration E (Figure 4G) measured at midday during the 2009 season. Non-irrigated vines presented lower values of gs, A and E than irrigated vines from the end of July (DOY 210) and particularly in September, with a decrease in gas exchange of nearly 40% compared with irrigated vines. There was a progressive increase in r_m during the season, with an important rise as water stress increased in non-irrigated vines. In water-stressed vines where the soil was covered with an impermeable plastic sheet, major reductions in gas exchange (A, E) and gs were measured from the end of July. Very low levels of gs, A and E were

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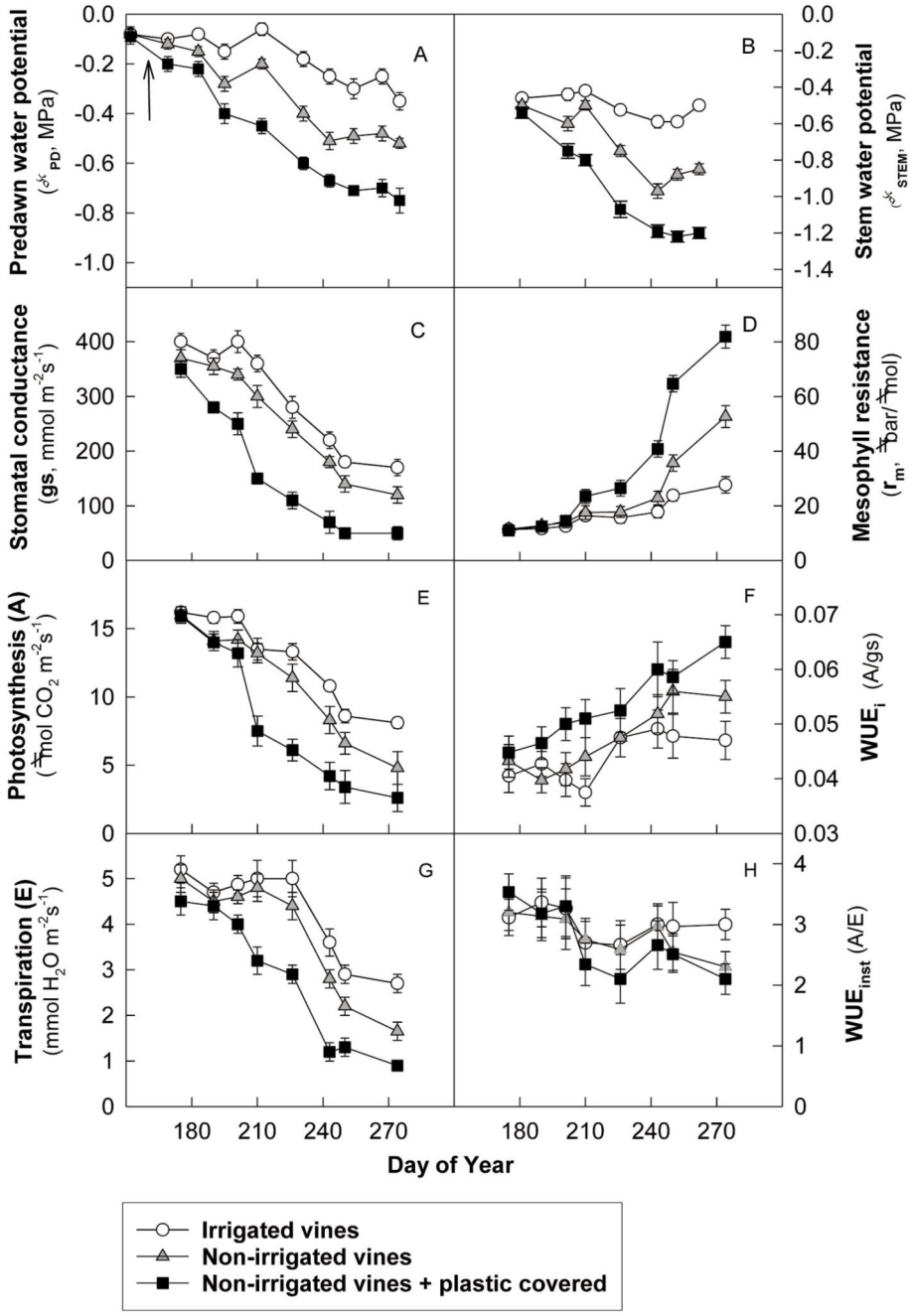


Figure 4. Changes in predawn leaf water potential (Ψ_{PD}, A), stem water potential (Ψ_{STEM}, B), stomatal conductance (gs, C), mesophyll resistance (r_m, D), photosynthetic rate (A, E), intrinsic water use efficiency (WUE_i, F), transpiration rate (E, G) and instantaneous water use efficiency (WUE_{inst}, H) during the 2009 season.
Means +/- SE for eight leaves. Pinot noir, Leytron (Switzerland).

recorded during the grape ripening phase (August-September), generally corresponding to residual conductance g_{res} (~30 mmol $m^{-2}s^{-1}$) and to rates of photosynthesis and leaf transpiration of approximately 2 µmol CO_2 $m^{-2}s^{-1}$ and 1 mmol H_2O $m^{-2}s^{-1}$, respectively. Gas exchange (A, E) and gs in adult non-senescent leaves, measured at midday during periods covering bloom through to mid-ripening, generally correlated with Ψ_{PD} values: correlation coefficients (R^2) rose to approximately 0.92 (P<0.01) for A, 0.90 (P<0.01) for E and 0.91 (P<0.01) for gs.

WUE_i (A/gs) was found to increase progressively during the growing season (Figure 4F) and was greatest in vines where water deficit was highest (non-irrigated vines with a covered soil) compared to

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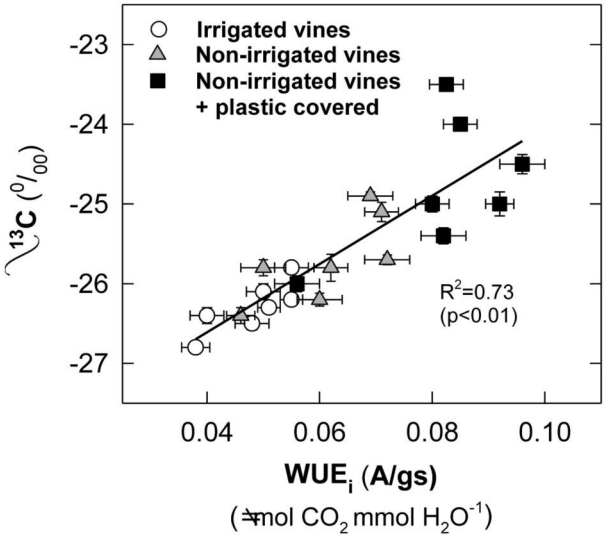


Figure 5. Relationship between intrinsic water use efficiency (WUE_i) and relative carbon isotope composition ($\delta^{13}C$) in must sugars at harvest for different irrigation treatments.
Means +/- SE. Pinot noir, Leytron (Switzerland), 2009-2015.

irrigated vines. WUE_{inst} (A/E), however, tended to decrease during the growing phase (Figure 4H) and was found to be slightly lower in non-irrigated vines, which presented the greatest water deficit at the end of the season. A correlation between WUE_i and $\delta^{13}C$ in must sugars was noted during the seven years of observation (Figure 5). The increase in WUE_i was associated with that in $\delta^{13}C$.

Daily rates of leaf transpiration E (Figure 6B) and stem sap flow (global shoot transpiration; Figure 6C) were greatly dependent on vine water status (Ψ_{PD} values) and daytime climatic conditions, such as solar radiation, air temperature and relative humidity (Figure 6A). E and sap flow values rose rapidly in the morning as solar radiation was intercepted and air temperatures increased. Nevertheless, a lapse was observed in the early hours of the morning (lag phase) between sap flow values, which remained very low despite light conditions, and leaf transpiration on the external part of the canopy. The maximum sap flow values (0.17 L/h/m²) were recorded during the afternoon, when air temperatures were highest and air humidity was lowest (greatest VPD), in well-watered vines with Ψ_{PD} of -0.06 MPa. In non-irrigated vines, the maximum E and sap flow values were lower, particularly in the afternoon at the hottest times. During most of the daytime, sap flow rates measured in water-stressed vines (Ψ_{PD} = -0.55 MPa) represented approximately 30 to 40% of values recorded in well-watered vines.

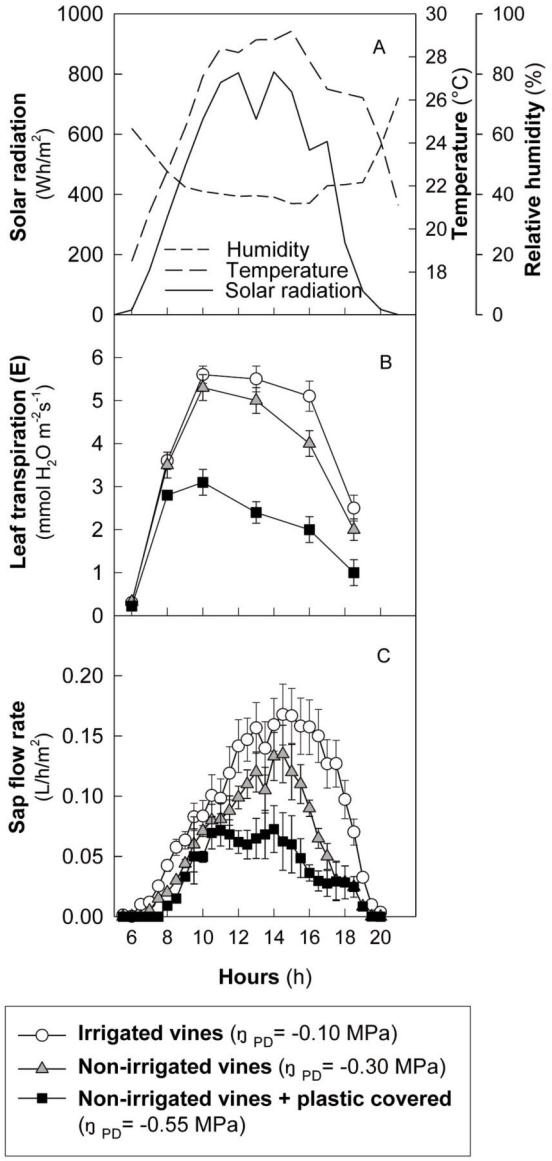


Figure 6. Diurnal course of solar radiation (A), mean air temperature (A), relative humidity (A), leaf transpiration rate (B) and sap flow rate (C) through the shoots for different irrigation treatments during the day of 26 July 2009.
Means +/- SE of eight leaves (leaf transpiration) and four vines (sap flow rate). Pinot noir, Leytron (Switzerland).

4. Cavitation vulnerability

The specific hydraulic conductivity in petioles ($K_{petiole}$) was found to be highest when Ψ_{STEM} values were above -0.5 MPa (Figure 7A), in the absence of water stress. There was a large decrease in $K_{petiole}$ as water deficit increased, and notably with Ψ_{STEM} values less than 1.2 MPa, observed in non-irrigated vines with plastic-covered soils. A cavitation

OENO One, 2017, **51**, 1, 17-27
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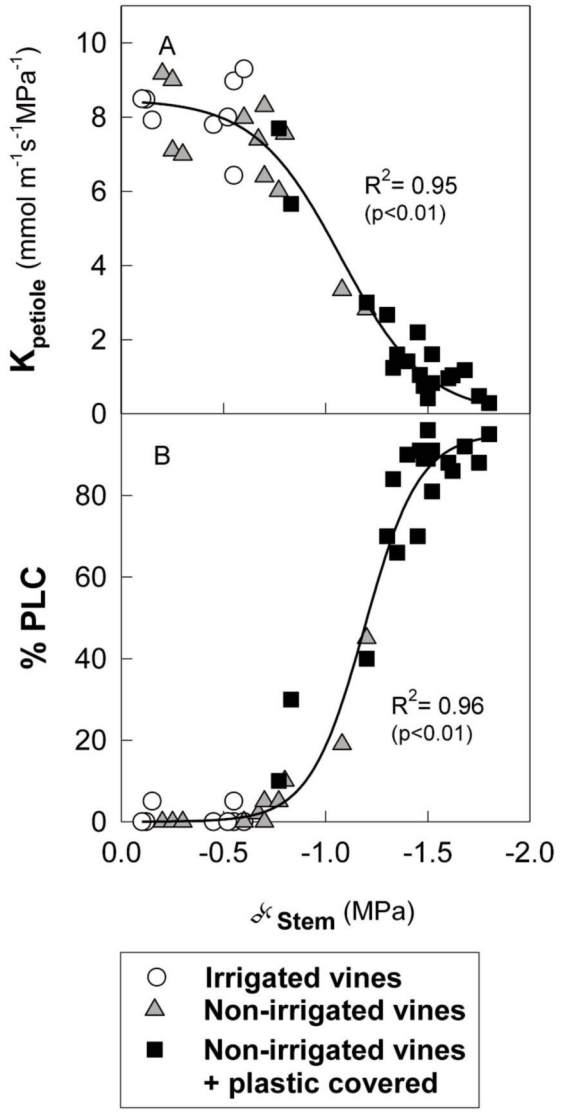


Figure 7. Specific hydraulic conductivity in petioles ($K_{petiole}$, A) and vulnerability to cavitation (PLC, percent loss of conductivity, B) versus stem water potential (Ψ_{STEM}) for grapevine leaf petioles measured in situ for different irrigation treatments.
Pinot noir, Leytron (Switzerland), 2013.

vulnerability curve (Figure 7B) was constructed by plotting PLC in relation to Ψ_{STEM}. At Ψ_{STEM} = -1.0 MPa, a PLC of approximately 20% was noted. The 50% PLC threshold was reached when Ψ_{STEM} was approximately -1.25 MPa, according to the fitted function parameters. Non-irrigated vines with plastic-covered soils showed PLC values > 60% in petioles when Ψ_{STEM} was less than -1.3 MPa. Irrigated vines presented very low vulnerability to cavitation with Ψ_{STEM} values > -0.7 MPa. An intermediate situation was observed in non-irrigated vines (rain-fed vines).

5. Mineral supply to the vine

Table 3 presents the results of mineral element analysis from leaf blades, leaf chlorophyll index at veraison, and YAN in must at harvest. The leaf nitrogen values showed a tendency to decrease as water stress rose: indeed, leaf nitrogen values were lowest in non-irrigated vines with plastic-covered soils. The chlorophyll index followed a similar pattern. Levels of phosphorus in leaves were highest in irrigated vines with no water stress compared with non-irrigated vines. No significant differences were recorded for K, Ca or Mg in leaves, which were related to the vine water status. The lowest YAN values in must at harvest were observed from non-irrigated vines with plastic-covered soils, where water deficit was the greatest.

6. Leaf area and plant vigor (pruning weight)

The seasonal evolution of total leaf area (LA) per vine, in relation to the different irrigation treatments, is presented in Figure 8. An increase in LA through the end of July (~DOY 210) was observed in all three irrigation treatments. After this date (one week before veraison), a progressive decrease was observed initially, followed by a sharp drop in LA in vines subjected to major water stress (non-irrigated vines with plastic-covered soils). In these vines, loss of leaves in the basal zone of shoots, due to drought, largely explains the fall in LA, which went from ~2.5 m^2/vine (end of July) to ~1.2 m^2/vine (end of September). An intermediate situation was again found in non-irrigated vines where a slight decrease in LA/vine was observed at the very end of the season.

Vine water status also influenced plant vigor, which was estimated from the pruning weight obtained in winter (Table 4). Moderate to high water stress (non-irrigated vines with plastic-covered soils) diminished plant vigor (lower pruning weights), compared with well-watered vines (irrigated vines). On average, over the years of experimentation (2009-2015), plant vigor decreased as vines were subjected to increasing water stress. Compared with irrigated vines, a decrease of nearly 20% in pruning weight was observed in non-irrigated vines with plastic-covered soils, and of 7% in non-irrigated vines (rain-fed).

7. Yield components and must characteristics at harvest

Table 5 provides the yearly averages for the period 2009-2015 of bud fertility monitoring, berry and cluster weights, cluster removal intensity and yield. No significant differences were observed between

Table 3. Mineral supply to the vine: leaf nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) content at veraison; leaf chlorophyll index (N-tester measurements) at veraison; and yeast available nitrogen (YAN) content in must at harvest.

Letters: statistically significant at the 5% level of probability. Averages 2009-2015, Leytron (Switzerland).

	Leaf analysis (% D.M)					N-tester	YAN
	N	P	K	Ca	Mg		(mg N/L)
Irrigated vines	2.40a	0.41a	1.01a	4.48a	0.36a	655a	214a
Non-irrigated vines	2.35ab	0.34b	1.05a	4.31a	0.34a	652a	210a
Non-irrigated vines + plastic covered	2.19b	0.34b	1.04a	4.30a	0.32a	634b	172b

Table 4. Pruning weight (g/vine) per year and the 2009-2015 mean.

Letters: statistically significant at the 5% level of probability. Leytron (Switzerland).

	Pruning weight (g/vine)							Mean
	2009	2010	2011	2012	2013	2014	2015	2009-2015
Irrigated vines	701a	750a	720a	903a	807a	717a	788a	770a
Non-irrigated vines	722a	735a	592b	763b	819a	671a	700b	715ab
Non-irrigated vines + plastic covered	689a	696a	423c	727b	681b	575b	622b	630b

the different irrigation treatments concerning yield components, with the exception of average berry weight (significance at P=0.10) and average cluster weight (significance at P=0.15), which were found to be slightly lower in non-irrigated vines with plastic-covered soils, which had suffered water stress.

In Table 6, a strong influence of water supply on soluble solids (% Brix or mg per berry) in must can be observed. The highest sugar content was observed in non-irrigated vines when the water stress was moderate to high during the ripening period. Total acid content (expressed by tartaric acid) and malic acid content were found to be lowest in non-irrigated vines, with or without soil cover, compared to irrigated vines. The pH and tartaric acid content of must were not influenced by differing water treatments. In wines, values of pH, total acidity and tartaric acid were very similar among the various irrigation treatments and no significant differences were observed (results not presented).

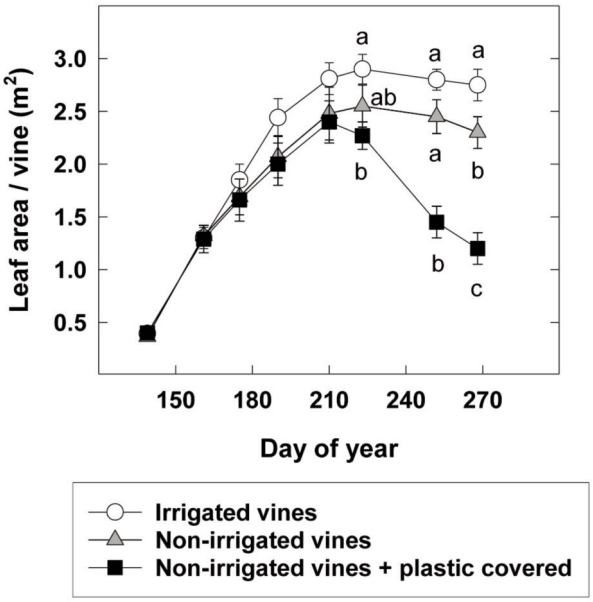


Figure 8. Seasonal evolution of leaf area per vine for different irrigation treatments. Means +/- SE.

Letters: statistically significant at the 5% level of probability. Pinot noir, Leytron (Switzerland) 2009.

8. Phenolic compounds and wine tasting

Analyses of total phenol index (DO 280) and anthocyanins were performed according to Ribéreau-Gayon *et al*. (1998). Figure 9 illustrates that the wines from non-irrigated vines were distinguished by their deeper colors and were thus richer in anthocyanins (Figure 9A) and phenolic compounds (Figure 9B) than wines from well-watered vines (irrigated vines). The main anthocyanins analyzed in wines were malvidin 3-*0*-ß glucoside and peonidin 3-*0*-ß glucoside, which represented approximately 80% of the proportion of the five anthocyanidins present in wines (results not presented).

Figure 10 shows the wine tasting results, performed a few weeks after bottling, for the four following key characteristics: bouquet (quality of aroma), wine structure, quality of tannins, and overall wine appreciation. Globally, the wines from non-irrigated vines were more appreciated for their superior tannin quality (smooth and supple), stronger structure and

OENO One, 2017, **51**, 1, 17-27
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Table 5. Yield components: bud fertility (number of inflorescences per shoot), cluster removal per vine, berry and cluster weight at harvest, and yield (per m²).
Letters: statistically significant at the 5% level of probability. Means 2009-2015, Leytron (Switzerland).

	Bud fertility (inflo/shoot)	Cluster removal (-x clusters per vine)	Berry weight (g)	Cluster weight (g)	Yield (kg/m²)
Irrigated vines	1.9a	-4a	1.2a	172a	0.82a
Non-irrigated vines	1.9a	-4a	1.2a	165a	0.75a
Non-irrigated vines + plastic covered	1.9a	-4a	1.1a	158a	0.77a

Table 6. Harvest characteristics: sugar content (soluble solids), pH and titratable acidity (total acidity, tartaric and malic acid) in musts.
Letters: statistically significant at the 5% level of probability. Means 2009-2015, Leytron (Switzerland).

	Soluble solids		pH	Total acidity	Tartaric acid	Malic acid
	(% Brix)	(mg/berry)		(g/L)	(g/L)	(g/L)
Irrigated vines	23.2a	276a	3.20a	8.5a	6.5a	3.9a
Non-irrigated vines	24.0ab	290b	3.22a	7.8b	6.3a	3.3ab
Non-irrigated vines + plastic covered	24.5b	286b	3.19a	7.6b	6.4a	2.9b

more asserted varietal aromas than wines from irrigated vines. The latter were judged to be of lower quality during 2009-2013, and again in 2015, but in a less pronounced way (no significant difference). In 2014, high summer rainfall and the absence of water stress in all three irrigation treatments resulted in wines with highly similar taste characteristics.

Discussion

1. Physiological indicators of plant water status

The different levels of irrigation tested in this study (regulated deficit irrigation, non-irrigated vines and non-irrigated vines with plastic-covered soils) led to highly contrasting vine water status. Regulated deficit irrigation, with a water supply compensating 30% of ETP from bloom to veraison, allowed a non-limiting vine water status to be maintained throughout the season, confirmed by Ψ_{PD} and Ψ_{STEM} measurements and $\delta^{13}C$ values. The lack of irrigation caused a moderate water deficit (Ψ_{PD} values between -0.3 and -0.5 MPa and Ψ_{STEM} values between -0.9 and -1.1 MPa), which was triggered around veraison in most years and continued until harvest, according to summer rainfall. Lastly, the lack of irrigation combined with soil cover by waterproof plastic sheets led to moderate to strong water stress in vines (Ψ_{PD} values between -0.5 and -0.8 MPa and Ψ_{STEM} values between -1.1 and -1.4 MPa), depending on the year and summer weather conditions.

The various physiological indicators of plant water status, such as Ψ_{PD}, Ψ_{STEM} and $\delta^{13}C$, enabled an accurate interpretation of vine water status over the growing season (Choné *et al*., 2000, 2001; van Leeuwen *et al*., 2009). Furthermore, good correlation between these different physiological indicators was not only found in the present study, but has also been highlighted in many others (van Leeuwen *et al*., 2001a,b, 2009; Souza *et al*., 2005a). The joint use of these indicators has the advantage of characterizing plant water status at different key moments in the day and/or the season. Leaf water potential, measured at predawn (Ψ_{PD}) when leaf transpiration is very low, tends to reflect the wettest portion of the soil and thus the soil water availability to the root system (edaphic stress). When Ψ_{STEM} is measured during the day and under canopy transpiration, not only edaphic stress is evaluated but also the atmospheric demand (i.e., VPD level). Many studies have highlighted the importance of the advantages and/or limitations of these two approaches to evaluating plant water status (van Leeuwen *et al*., 2009). Regarding $\delta^{13}C$ analyzed in must sugars at harvest, this indicator has the advantage of integrating water deficit during the phase of sugar accumulation in berries (Gaudillère *et al*., 2002; Souza *et al*., 2005b; Herrero-Langreo *et al*., 2013; Santesteban *et al*., 2015).

2. Physiological responses to progressive water deficit

a. Plant water status and gas exchange

A gradual increase in water deficit observed in non-irrigated vines over the growing season led to a progressive closure of stomata (decrease in gs), thus reducing water loss by transpiration (E) and carbon assimilation (A). Stomatal regulation of gas exchange

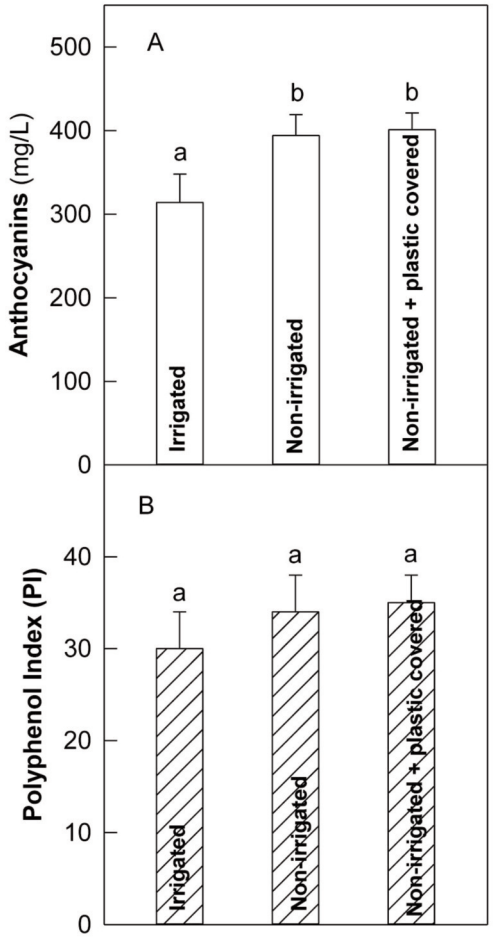


Figure 9. Anthocyanin content (A) and total polyphenol index (PI, B) in wines from different irrigation treatments. Means +/- SE.
Letters: statistically significant at the 5% level of probability.
Pinot noir, Leytron (Switzerland) 2009-2015.

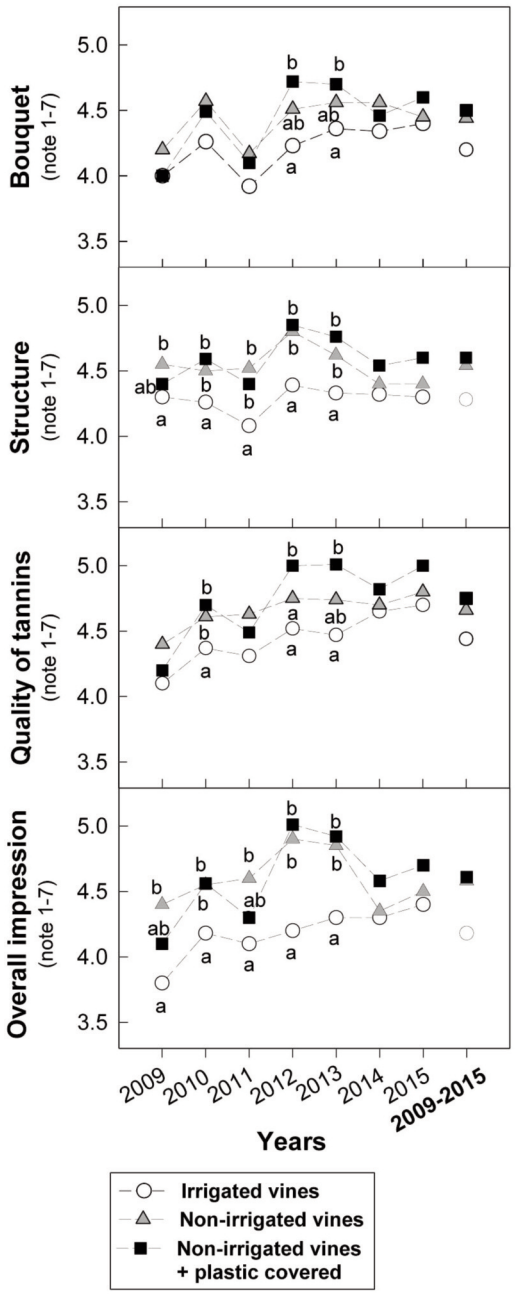


Figure 10. Evaluation of wine quality at tasting according to different sensory variables: olfactive (bouquet), gustatory (structure, tannin quality) and overall impression for the different irrigation treatments. Perception scale from 1 (poor) to 7 (high).
Letters: statistically significant at the 5% level of probability.
Pinot noir, Leytron (Switzerland) 2009-2015.

(A, E) in water stress conditions provides a rapid and early plant response, which has been reported in numerous studies (Chaves *et al*., 2003, 2010). Indeed, physiological drought-avoiding mechanisms, such as the stomatal control of transpiration and resulting risks linked to embolism events (Lovisolo *et al*., 2002; Zufferey *et al*., 2011), form short-term adaptation by plants to water stress. Under the conditions of the present study, net photosynthesis (A) decreased less rapidly than gs, when the vine was subjected to increasing water deficit during the growing season. Consequently, the intrinsic water use efficiency (WUE_i or A/gs) was higher in vines where water stress was moderate to high, compared with irrigated vines. The rise in WUE_i under drought conditions, tested in semi-arid Mediterranean climate, has been observed in many studies (Schultz, 1996; Bota *et al*., 2001; Cifre *et al*., 2005; Chaves *et al*., 2007; Pou *et al*., 2008; Flexas *et al*., 2010; Schultz and Stoll, 2010). As water stress becomes more important, however, a decrease in WUE_i has been noted (Prieto *et al*., 2010), which suggests an increase in mesophyll limitation for CO_2 transfer inside the leaf (rise in mesophyll resistance r_m), which would reduce assimilation (Flexas *et al*., 2002, 2007).

OENO One, 2017, **51**, 1, 17-27
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In general, a good correlation between WUE_i and $\delta^{13}C$ in berry sugars has been noted (Medrano *et al*., 2005; Souza *et al*., 2005a; Chaves *et al*., 2007; Bchir *et al*., 2016), which is confirmed by the present study. Indeed, non-irrigated vines showed higher levels of $\delta^{13}C$, associated probably with a lower discrimination against ^{13}C and an enrichment of ^{13}C in must (lower C_i/C_a), which has been correlated to an increase in WUE_i, with respect to irrigated vines (no water stress). The highest $\delta^{13}C$ values, observed in berries compared with leaves in our study (results not presented), are probably due to a lower ^{13}C discrimination in the organic acids of the fruit pulp and sugars. The latter were imported from leaves after veraison when the water stress was high and stomata virtually closed, thus supplying photo-assimilates with a higher ^{13}C and confirming observations of other authors (Souza *et al*., 2005a). There are, however, differences between C-isotope signatures in leaves and fruits undergoing water stress (Chaves *et al*., 2007; Bchir *et al*., 2016). Indeed, differences in dissimilation processes (leaf-berry respiration) may contribute to modifications in the ^{13}C isotope signature of the different vine organs.

The decline in gs with the rise of water deficit in non-irrigated vines was accompanied by an almost linear decrease in E. Thus, the A/E ratio, called instantaneous water use efficiency (WUE_{inst}), was slightly lower in non-irrigated vines with plastic-covered soils, than in irrigated vines, and decreased over the season. Moreover, several studies on grapevines have demonstrated that gs is highly sensitive to environmental factors, such as water stress, and air vapor pressure deficit (VPD) (Düring, 1987; Spring, 1997; Prieto *et al*., 2010; Zufferey and Smart, 2012). An increase in VPD generally leads to a progressive stomata closure and an increase in E, resulting finally in a drop in WUE_{inst}. VPD has a negative effect on WUE_{inst} over a wide range of water deficits due to decreases in gs and A, but not on WUE_i (Schultz and Stoll, 2010); under drought conditions and high VPD, this may result in opposing trends between the two parameters, as is the case in the present study. Such behavior was evidenced by Schultz and Stoll (2010), where non-irrigated vines presented WUE_{inst} values that were sometimes identical to those of irrigated vines (diurnal gas exchange data), and sometimes lower in water-stressed vines when the water deficit was acute.

Water stress also reduced mesophyll conductance (g_m), or, in other terms, increased mesophyll resistance (r_m), the resistance of CO_2 transfer from the sub-stomatal cavity towards CO_2 fixation sites (chloroplasts) where photosynthetic enzymes are located (Flexas *et al*., 2002). A reduction in gs, combined with a rise in r_m as water stress intensifies, leads to less CO_2 available in the chloroplasts (C_c). Under high solar radiation, the low concentration in C_c coupled with an increase in leaf temperature under water stress (results not presented) results in a rise in photorespiration (Zufferey *et al*., 2000; Hochberg *et al*., 2013) and heat dissipation by consumption of excess excitation energy: under these conditions, these two phenomena thus provide photoprotection of the photosynthetic apparatus (Medrano *et al*., 2002; Flexas *et al*., 2009).

b. Hydraulic conductivity and cavitation vulnerability

Under water stress conditions, the progressive closure of stomata occurs when VPD rises and hydraulic conductance along the soil-plant pathway (K_{plant}) decreases; therefore, Ψ_{leaf} remains above the critical threshold required to prevent hydraulic rupture and the risk of embolism formation (Tyree and Sperry, 1988). In the present study, petiole hydraulic conductivity ($K_{petiole}$) decreased as water stress intensified and when Ψ_{STEM} dropped below -1.0 MPa in non-irrigated vines. When Ψ_{STEM} values were close to -1.5 MPa, $K_{petiole}$ was very low and fell to approximately 1 mmol $m^{-1}s^{-1}MPa^{-1}$. The vulnerability to cavitation (PLC) subsequently increased with water stress to reach high values > 60% when Ψ_{STEM} was lower than -1.3 MPa.

According to the hypothesis of hydraulic segmentation (Charrier *et al*., 2016; Hochberg *et al*., 2016), it is known that leaf and petiole hydraulic conductivities may form a major bottleneck in the hydraulic system (Sack *et al*., 2003) and thus limit water transfer, whereas shoots generally present a high hydraulic conductivity (Lovisolo *et al*., 2007). The progressive stomatal closure, observed in the present study with increasing water stress, probably responded to a decrease in $K_{petiole}$, but other factors (hydraulic or chemical signals; Stoll *et al*., 2000; Pantin *et al*., 2013) cannot be excluded. A positive relationship between hydraulic conductance and gs has been described for different plant species (Saliendra *et al*., 1995), including grapevine (Schultz, 2003; Lovisolo *et al*., 2010; Zufferey and Smart, 2012), when Ψ_{leaf} remains constant, which would suggest a retroactive link between gs and some form of hydraulic signal. Furthermore, it is suggested that greater sensitivity of stomata to water stress would counterbalance greater vulnerability to cavitation during drought. The size of vessels and xylem pits, which depend on the cultivar, may play an equal role in cavitation vulnerability (Chouzouri and Schultz, 2005; Pagay *et al*., 2016).

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c. Shoot growth and plant mineral nutrition

A decrease in leaf area (LA) per vine occurred in non-irrigated vines with plastic-covered soils, subjected to moderate water stress, shortly before veraison. An intensification of water deficit after veraison resulted in leaf fall from the basal zone of shoots and a lowering of LA by almost half, compared with irrigated vines. A decrease in leaf and shoot growth is one of the perceptible signs of water stress in the vine (Stevens *et al*., 1995). In general, root growth reduction is less important than in shoots (Dry *et al*., 2000a,b), under water stress developing gradually, leading to a higher root/shoot ratio and thus ensuring an adequate supply of nutrients and water to shoots. Shoot growth inhibition has been used as a highly sensitive and pertinent indicator of vine water status (Pellegrino *et al*., 2005; Lebon *et al*., 2006). The cessation of vegetative growth (especially secondary shoots) and leaf loss, which limits global plant transpiration while reducing drying out of the soil, both help to maintain a stable Ψ_{leaf} at the end of the season, as observed in the present study. Year after year, vines that had been subjected to moderate to strong water stress showed diminishing shoot vigor, compared with irrigated vines without water stress. The smaller size of shoot vessels observed in non-irrigated vines (results not presented) tended to prevent excessive water losses by reducing their xylem hydraulic conductivity and may well contribute to avoid embolism events (Salleo *et al*., 1985).

Overall, a rise in water deficit brought about a fall in the content of nutritive elements in leaves at veraison, particularly for nitrogen and phosphorus. The leaf chlorophyll index (N-tester values) and available nitrogen content in berries were also affected by water stress in non-irrigated vines, having lower values than those in irrigated vines. Nutrient uptake from the soil depends greatly on water flow along the soil-root-shoot pathway (Gonzalez-Dugo *et al*., 2010; Keller, 2015), in other words, on canopy transpiration. Drying of the soil, together with high summer temperatures, may have a negative effect on the mineralization of nutrients (particularly nitrogen), with a corresponding reduction in microbial activity (Celette *et al*., 2009), and on their absorption in the plant's transpiration flow. Various authors (Reynard *et al*., 2011; Spring *et al*., 2012) have demonstrated the effect of water deficit, either climatic or edaphic, during the summer period on the nitrogen content in leaves and berries.

d. Berry growth and composition

Water deficit influences berry development, metabolism and composition (Chaves *et al*., 2010). The progressive water stress that prevailed from veraison until harvest in non-irrigated vines resulted in a small reduction in berry and cluster weights, compared with well-watered vines (although differences were not significant). Yield per vine, or yield expressed as a soil unit (m^2), was consequently unaffected by the water deficit occurring during grape ripening, with the exception of the very dry years (2009, 2011 and 2015) when non-irrigated vines presented slightly lower yields than irrigated vines (results not presented). Furthermore, a considerable decrease in photosynthesis, imposed by an acute water stress, may affect long-term production, and especially bud fertility and flower formation should the carbon and/or nitrogen balance have been inadequate the previous year (Guilpart *et al*., 2014). No change of bud fertility was noted during the period under study in non-irrigated vines, indicating that C and N reserves in the perennial parts of the vine had not been too depleted by the post-veraison water deficit.

It is known that not only the intensity of water stress but also the timing and duration have an influence on berry size and composition. During the initial phase of berry development (stage I pre-veraison; Coombe, 1976), berries are exclusively connected to the parent vine by the xylem: water stress would supposedly have an impact on berry growth directly by changes in water influx via the xylem, leading to a decrease in turgor of the mesocarp cells (Thomas *et al*., 2006). Water stress conditions developing from fruit set up to veraison thus inhibit berry expansion (McCarthy, 1997; Ollat *et al*., 2002) during the early phase of berry growth (Ojeda *et al*., 2001, 2002). It is also possible that ABA synthesized under water stress limits cell division (Chaves *et al*., 2010) and, consequently, produces smaller berries. After veraison and throughout the entire ripening period, the connection between berries and the parent vine is mainly – but not exclusively – assured by the phloem (Greenspan *et al*., 1994; Keller *et al*., 2006; Thomas *et al*., 2006). A post-veraison water stress (which was the case in this study) may indirectly reduce berry size by a decline in canopy photosynthesis capacity and thus cause a reduction of sugar accumulation in berries (Wang *et al*., 2003), the driving force for berry growth. Additionally, a post-veraison water deficit increases the proportion of whole berry fresh mass, represented by the seeds and skin (Roby *et al*., 2004), and therefore gives a higher ratio of skin to pulp (Kennedy *et al*., 2002).

OENO One, 2017, **51**, 1, 17-27
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Moderate water deficit favors the accumulation of sugars (van Leeuwen *et al*., 2009), either as a consequence of the cessation of secondary shoot growth, which leads to a reallocation of carbohydrates towards berries, or as the direct effect of ABA, signaling berry ripening (Deluc *et al*., 2009). Some authors have indicated that the impact of water stress on sugar content in grapevines may also depend on the cultivar (Ojeda *et al*., 2002; Castellarin *et al*., 2007). The higher concentration of sugars in berries observed in non-irrigated vines, which had undergone moderate water stress during ripening, indicates that the Pinot noir variety reacts positively to a moderate to strong post-veraison water deficit, by increasing the sugar content in berries, compared to well-watered vines. It should also be noted that the source-sink ratio has a strong influence on berry sugar content (Dai *et al*., 2009; Etchebarne *et al*., 2010) and thus determines the berry development and composition facing water scarcity, depending on the timing of its appearance, intensity and duration.

In the present study, non-irrigated vines showed a lower content of titratable acidity and malic acid than irrigated vines. According to some other authors (Matthews and Anderson, 1989; Esteban *et al*., 1999), no change in titratable acidity was observed in must from vines subjected or not to water stress. On the other hand, other experiments have reported a decrease in total acidity and a degradation in malic acid due to water deficit (Souza *et al*., 2005b; Santos *et al*., 2007) and/or to changes in microclimate (rise in temperature of sun-exposed berries) in non-irrigated vines because of the loss of leaves in the cluster zone (Santos *et al*., 2003). Must pH was not modified by water stress, in accordance with other observations (McCarthy, 2000).

e. Polyphenols and wine quality

It has been well documented that a water deficit during ripening can greatly influence berry polyphenol content and composition, including flavonoids (particularly the anthocyanin family), and wine quality (Kennedy *et al*., 2002). In general, moderate water stress leads to an increase in total anthocyanins and stilbenes in berries, compared to irrigated vines where there is no water deficit (Matthews and Anderson, 1989; Ojeda *et al*., 2002; Castellarin *et al*., 2007; Deluc *et al*., 2009, 2011). In the present study, vines subjected to moderate to strong water stress during ripening produced wines that were richer in anthocyanins and total polyphenols than wines from irrigated vines. Castellarin *et al*. (2007) have likewise shown that the expression of some enzymes from the phenylpropanoid synthetic pathway rose with increasing water stress, leading to a stimulation of anthocyanin hydroxylation (Mattivi *et al*., 2006) and the biosynthesis of various tri-hydroxylated anthocyanins. In this study, the main anthocyanins synthetized in berries and analyzed in the wine were malvidin 3-*0*-ß glucoside and peonidin 3-*0*-ß glucoside (results not shown here), which represented almost 80% of the five anthocyanins (delphinidin, cyanidin, peonidin, petunidin and malvidin) found in berries of *Vitis vinifera*. The exact proportion of these different anthocyanin forms depends on cultivar (Roggero *et al*., 1988), and the Pinot noir variety appears not to contain acylated anthocyanins (Fong *et al*., 1971). In addition, water supply had no impact on the proportion of these two main anthocyanins in wines from this study. The accumulation of proanthocyanidins and flavanols in grapes is little affected by water deficits, according to some studies (Downey *et al*., 2006; Castellarin *et al*., 2007), with the exception of one study conducted on the Tempranillo cultivar (Zarrouk *et al*., 2012).

Numerous studies have underlined the beneficial effect of a progressive water deficit during the ripening phase on the color of wines (Roby *et al*., 2004; Koundouras *et al*., 2006; Chalmers *et al*., 2010; Reynard *et al*., 2011). In the present study, Pinot noir wines made from non-irrigated vines had a deeper and more intense color than wines from irrigated vines. Moderate water stress led to more fruity wines with high aroma complexity compared with wines from well-watered vines, thus confirming observations of other authors (Chapman *et al*., 2005; Spring and Zufferey, 2009; Reynard *et al*., 2011). Matthews *et al*. (1990) and Hakimi-Rezaei and Reynolds (2010) have also highlighted the positive effect of a limited vine water status on wine bouquet. In the present study, wine structure and tannin quality (sweet and well-blended tannins from non-irrigated vines) were judged to be superior where a moderate water deficit had led to improved grape ripening and phenol compounds (as evaluated by sensory analysis). Globally, vine water status appears to constitute a determining factor in wine quality, especially in red wines (van Leeuwen *et al*., 2009), with positive effects from moderate water stress developing from veraison and continuing during ripening (Koundouras *et al*., 1999; Choné *et al*., 2001).

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