

The impact of plant water status on the gas exchange, berry composition and wine quality of Chasselas grapes in Switzerland

Vivian Zufferey^{1,*}, Thibaut Verdenal¹, Agnès Dienes¹, Sandrine Belcher¹, Fabrice Lorenzini¹, Carole Koestel¹, Johannes Rösti¹, Katia Gindro¹, Jorge E. Spangenberg², Olivier Viret³ and Jean-Laurent Spring¹

¹Agroscope, Swiss Agricultural Research Institute, Route de Duillier 50, 1260 Nyon, Switzerland

²Institute of Earth Surface Dynamics IDYST, University of Lausanne, Lausanne, CH-1015, Switzerland

³Service de l'Agriculture et de la Viticulture (SAVI), Avenue de Marcelin 29, CH-1110 Morges, Switzerland

Abstract

Aims: The aim of this research was to study the physiological and agronomical behaviors (leaf gas exchange, plant vigor, mineral supply, and yield components) of the Chasselas grapevine subjected to different water regimes during the growing season. The resulting grape and wine qualities were also determined.

Methods and results: Adult vines of *Vitis vinifera* L. cv. Chasselas (clone 14/33-4, grafted onto 5BB) were subjected to different water regimes (various levels of irrigation) during the growing season. Physiological indicators were used to monitor the plant water status [the predawn leaf (Ψ_{PD}) and stem (Ψ_{STEM}) water potentials and the carbon isotope composition ($\delta^{13}C$) in the must]. Leaf photosynthesis (A) and transpiration (E), stomatal conductance (gs), vulnerability to cavitation, yield parameters, berry composition at harvest, and organoleptic quality of wines were analyzed over a period of eight consecutive years between 2009 and 2016, under the relatively dry conditions of the Canton of Wallis, Switzerland.

In non-irrigated vines, the progressively increasing water deficit observed over the season reduced the leaf gas exchange (A and E) and gs. The intrinsic water use efficiency (WUE_i , A/gs) increased over the season and was greater in vines that had suffered water restriction than in irrigated vines. The rise in WUE_i was correlated with an increase in $\delta^{13}C$ in the must sugars at harvest. Vulnerability to cavitation (embolism phenomenon) increased with increasing water deficit in the non-irrigated vines with covered soils. A decrease in plant vigor was observed in the vines that had been subjected to water restrictions over multiple years. Moderate water stress during fruit ripening was favorable for sugar accumulation in berries and lowered the contents of total and malic acidity in the musts and the content of available nitrogen (YAN). Overall, the organoleptic characteristics and quality of Chasselas wines were little influenced by the vine water regimes, with the exception of the hot, dry season in 2009 (and, to a lesser degree, in 2011). In those years, the quality of the wines from the irrigated vines, which had not suffered any water stress, received a better appreciation. Bitterness was generally greater in samples from the non-irrigated vineyards that had suffered from drought than in samples from the irrigated vines. No significant differences in the aroma and wine structure were measured during the study period, regardless of the vine irrigation status.

Conclusions: The physiological behavior (gas exchange, plant vigor, and mineral supplies) and grape ripening in Chasselas vines were largely dependent on the water supply conditions in the vineyard during the growing season.

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

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

Received: 23 March 2018; Accepted: 7 August 2018; Published: 31 December 2018

doi: /10.20870/oeno-one.2018.52.4.2181

Introduction

Vine sensitivity to water deficit depends on a number of factors intrinsic to the vineyard site (soil characteristics, soil available water reserves, and mesoclimate) and varies according to genetic (grape variety, rootstock) and agronomical factors, including cultivation techniques (cover crop, plant density, leaf-fruit ratio). It has been known for many years, due to studies carried out on different “terroirs” (Seguin, 1975; van Leeuwen *et al.*, 1994), that plant water status has a major influence on the physiological behavior of vines (photosynthesis, mineral supply, growth) and the quality of grapes and wines. Moreover, the capacity of a large and deep, well-developed root system in some vineyards enables vines to endure water scarcity. Severe water stress, however, leads to reduced gas exchange (photosynthesis and transpiration) through stomatal and hydraulic controls (probably sustained by a chemical signal, ABA), consequently decreasing early plant growth (Dry *et al.*, 2000a,b; Chaves *et al.*, 2010). The stomatal regulation of transpiration, together with a reduction in vessel hydraulic conductivity, tends to optimize water use efficiency, while reducing the risk of physiological disorders, such as embolism in vessels during severe drought (Lovisolo *et al.*, 2016). By limiting water flow throughout the plant, and thus limiting canopy development (decreasing leaf area by leaf fall), the plant is able to maintain leaf water potentials above threshold values, thus avoiding the onset of cavitation (the appearance of air bubbles in vessels) under high water deficit conditions (Tyree and Sperry, 1988).

The effects of water deficit on yield components depend on the timing, the intensity and the duration of water stress (Deloire *et al.*, 2004). Water stress early in the season leads to a smaller number of berries per cluster; severe stress developing between the fruit set and veraison period causes a reduction in berry weight (Ojeda *et al.*, 2001) and increases the heterogeneity of berry size. No water stress, combined with high soil water availability, often develops vigorous plant growth and increases the risk of fungal diseases, altering the harvest quality (increased yield, increased competition in the sugar allocation between the vegetative and reproductive vine parts, dilution phenomena, and reduced wine color). On the other hand, a progressively increasing and moderate water stress (after fruit set) leads to a slow stop in plant growth around the veraison, promoting the production of berries richer in sugars, anthocyanins and phenol compounds, with less acids (van Leeuwen *et al.*, 2009; Zufferey *et al.*, 2017). For the elaboration of high-quality white wines, it is well

known that vines should experience no mineral nutrient deficiencies, particularly nitrogen deficiencies (Bell and Henschke, 2005; Lacroux *et al.*, 2008). For this reason, vines should not be exposed to a water deficit that is too severe (Choné *et al.*, 2006) which may result in a loss of aromatic compounds and wine quality (Reynolds *et al.*, 2010; Reynard *et al.*, 2011).

In the present study, the impact of water supply to vines on plant behavior was analyzed by creating different water regimes during the growing season. The experiments included three levels of irrigation: a deficit irrigation that compensated approximately 30% of evapotranspiration potential (ETP) from flowering to the onset of ripening (veraison); no water supply (no irrigation, rain-fed vines) throughout the whole season; and water stress imposed by covering the soil with a plastic, impermeable, non-reflecting sheet during the growing period (April-October). The vine water status was monitored by using physiological indicators, such as leaf and stem water potentials and carbon isotope composition in the must sugars at harvest. The influence of the water regime on the vine physiology (gas exchange, stomatal and hydraulic conductances, plant vigor, leaf and berry mineral nutrition) and agronomical behavior (yield components) and the quality of the resulting wines was observed in adult vines of the cultivar Chasselas over a period of eight consecutive years on the experimental Agroscope vineyard, which is located in a relatively dry alpine region of Switzerland (Valais).

Materials and methods

1. Study site and plant material

The experiments were conducted from 2009-2016 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 planting material was the cultivar Chasselas (clone 14/33-4), grafted onto *Vitis berlandieri* x *Vitis riparia* cv. Kober 5BB rootstock. Vines were trained in the Guyot 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 (> 2.5 m vine root depth) soil with a water-holding capacity estimated at 150 mm. Monthly rainfalls and temperatures from 2009 to 2016 (and long-term averages from 1981 to 2010) from the meteorological station in Leytron are presented in Tables 1 and 2.

2. Irrigation treatments

Three different irrigation treatments were established. In the first treatment, 9 L/m² of 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 approximate weekly compensation of 30% ETP. The second treatment applied no irrigation throughout the entire growing season (plants were rain fed). The third treatment also involved no irrigation; in addition, waterproof and non-reflecting plastic sheeting was placed 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 four split-plot randomized blocks of ten vines each.

3. Measurements of plant water status and relative carbon isotope composition ($\delta^{13}\text{C}$)

Predawn leaf water (Ψ_{PD}) and midday stem water (Ψ_{STEM}) potentials 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. Midday Ψ_{STEM} values were determined for eight leaves bagged with a plastic sheet and covered with aluminum foil to stop transpiration at least one hour before the measurement (Fulton *et al.*, 2001).

The stable carbon isotope compositions ($\delta^{13}\text{C}$) of the must sugars and leaf sugars (leaf carbon isotope signature) were determined at harvest at the Stable Isotopes 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) DeltaV mass spectrometer. The stable isotope composition was reported as $\delta^{13}\text{C}$ values per mille (‰), with deviations of the isotope ratio relative to known standards as follows: $\delta = [(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}] \times 1000$, where R is the ratio of heavy to light isotopes (¹³C/¹²C). The R_{standard} value for ¹³C in Vienna Pee Dee Belemnite limestone is 0.0112372 (Deléens *et al.*, 1994).

4. Leaf gas exchange measurements

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 $\mu\text{mol m}^{-2}\text{s}^{-1}$) from June to mid-October. Eight leaves per irrigation treatment were measured in the morning (1000) on days with clear skies. Gas exchange was measured using a portable photosynthesis system (LI-6400, LICOR Inc., Lincoln, NE, USA). R_m was calculated as $r_m = (C_i - \Gamma) / A$, where C_i is the intercellular partial pressure of CO₂, Γ is the CO₂ compensation point (corresponding to 50 ppm for adult leaves with a leaf temperature between 20-25°C, Schultz, 1996), and A is net photosynthesis. The 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 the stomatal conductance for water vapor (gs), termed WUE_i (Osmond *et al.*, 1980), or to the leaf transpiration rate (E), termed WUE_{inst} .

5. Xylem embolism assessment

Xylem embolism, induced by the presence of air bubbles in vessels, was measured using the method introduced by Sperry and Pockman (1993) and established by Cochard *et al.* (2000). The principle of the XYL'EM device (Xylem Embolism Meter, Bronkhorst Instructec, Montigny-les-Cormeilles, France) is to accurately measure the water flow (F; mmol s⁻¹) entering the petiole of a cut leaf 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, the petioles of the apical zone of these shoots 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 the perfusion liquid for all measurements. To measure the maximum conductance (K_{max}), the petioles were then flushed twice over a period of 2 min with water pressurized at 0.15 MPa. The percentage loss of conductivity (PLC), known as the vulnerability to cavitation or embolism, was calculated as $1 - (K_{\text{init}} / K_{\text{max}})$. The shoot Ψ_{STEM} was monitored at regular intervals throughout the day and immediately before petiole sampling. The XYL'EM was interfaced with a computer to automatically log the data. 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 used to determine vulnerability to cavitation, expressed as Ψ_{PLC50} , and the xylem water potential inducing a 50% loss in hydraulic conductivity. Ψ_{PLC50} was estimated by fitting a sigmoid PLC curve

to the 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 and berry mineral nutrition, pruning weight measurements

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, oven-dried, ground and analyzed. The leaf chlorophyll index was measured using an N-tester apparatus (Yara, Nanterre, France) on adult leaves situated at the middle of shoots. Yeast available nitrogen (YAN) was estimated by NIR spectroscopy (WineScan®, FOSS NIRSystems, USA). This method quantifies the N-compounds of juice available to yeasts during fermentation. YAN corresponds to the concentration of ammonium ions and primary amino acids, excluding proline. In winter, the total weight of the pruned vine shoots was recorded (six shoots per vine), representing ten plants per replicate and 40 plants per treatment.

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

Bud fertility (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 the clusters at harvest to be estimated. The fruit

composition parameters at harvest included soluble solids 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 in an identical fashion for all irrigation treatments by the same winemaker. Wine composition was assessed at bottling by using infrared spectroscopy. A sensory analysis was conducted two months after bottling by a panel of 12 experienced tasters. The panelists rated the intensities with 16 sensory attributes, including wine appearance, bouquet and palate. Wines were evaluated on an unstructured line scale from 1 (no perception) to 7 (very intense perception).

8. Statistical analysis

The significance of each treatment was evaluated with analysis of variance ($P < 0.05$) followed by a single-comparison Newman–Keuls test using XLSTAT 2011.2.04 (Addinsoft, Paris, France). The 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 were statistically analyzed using the SigmaStat program package.

Results and discussion

1. Climatic conditions

There were large fluctuations in annual average rainfall and temperature throughout the study period from 2009 to 2016 (Tables 1, 2). Generally, the annual precipitation rates were slightly below the long-term average (1981-2010) of 600 mm: the

Table 1. Monthly rates of precipitation (mm) at the experimental site in Leytron (CH) during the eight-year study period (2009-2016) and long-term precipitation averages (1981-2010)

	2009	2010	2011	2012	2013	2014	2015	2016	Long-term
January	109	11	22	57	21	42	55	110	51
February	28	29	7	0	59	79	11	104	47
March	23	27	14	5	29	5	63	19	42
April	37	8	5	51	45	29	12	38	35
May	25	120	43	52	83	34	123	76	49
June	40	15	40	37	24	17	34	45	54
July	87	73	69	51	52	106	35	46	58
August	16	45	22	65	30	87	78	27	57
September	18	22	42	52	45	15	14	14	44
October	11	14	34	39	67	30	29	32	52
November	68	36	2	53	95	44	42	75	52
December	108	70	168	152	17	42	4	0	64
Year	570	470	468	614	567	530	500	586	603

Table 2. Monthly mean temperatures (°C) at the experimental site in Leytron (CH) during the eight-year study period (2009-2016) and long-term temperature averages (1981-2010)

	2009	2010	2011	2012	2013	2014	2015	2016	Long-term
January	-2,7	-1.5	0.2	1.5	1.0	2.6	1.4	2.2	-0.1
February	1.0	1.5	2.9	-1.7	0.0	4.2	1.3	4.4	1.8
March	5.9	6.1	7.9	9.1	5.2	8.4	7.9	6.6	6.5
April	12.4	11.8	14.2	10.9	10.9	12.8	12.2	11.3	10.4
May	16.4	14.0	17.0	16.1	12.5	15.6	15.6	14.7	14.9
June	18.4	18.9	18.8	20.0	18.1	20.1	20.6	18.7	18.1
July	20.5	21.8	18.6	20.3	21.6	19.3	24.0	21.5	20.1
August	21.6	18.5	21.0	21.3	20.2	18.4	20.9	21.0	19.2
September	16.8	14.8	17.8	15.8	16.3	16.9	14.9	18.4	15.2
October	10.3	10.3	10.4	11.5	12.7	13.0	10.5	10.1	10.3
November	6.7	5.5	5.2	6.4	3.8	8.1	5.9	5.8	4.3
December	1.0	-0.6	1.9	0.6	0.4	2.7	2.2	-0.7	0.6
Year	10.7	10.1	11.3	11.0	10.1	11.7	11.5	11.2	10.1

lowest rainfall measurements were noted for the years 2010, 2011 and 2015, when annual rainfall was 100 to 130 mm lower than the 30-year mean. In addition, relatively dry periods in the months of August and September were observed in 2009, 2010, 2011, 2015 and 2016. The year 2014 was marked by unusually high summer rainfall levels. The annual temperatures were 0.6 to 1.6°C higher than the 30-year average, with the exception of the years 2010 and 2013, when the annual temperatures were identical to those recorded for the period of 1981-2010. The summer temperatures (July-September) were particularly hot in 2009, 2011, 2012, 2015 and 2016, relative to the long-term values.

2. Plant water status

The seasonal courses of Ψ_{PD} , recorded in the growing seasons from 2009 to 2016, highlighted the variations in the vine water regime as a function of year and irrigation level (irrigated and non-irrigated vines, Figure 1). No water stress was observed in the vines that had been watered from bloom to veraison, for which values of Ψ_{PD} oscillated between -0.05 and -0.25 MPa. The non-irrigated vines showed Ψ_{PD} values that became increasingly negative from the end of July (DOY 2010). These values reached -0.3 to -0.5 MPa during the fruit-ripening period, reflecting the presence of moderate water stress. Only in 2014, when there was heavy summer rainfall, was no water stress recorded. In the non-irrigated vines with soil covered by a plastic waterproof sheet, severe water stress (values of $\Psi_{PD} < -0.5$ MPa) was observed at the end of the growing season, especially during the hot, dry summers of 2009, 2011, 2015 and

2016. The water stress remained moderate in 2010, 2013 and 2014, due to cooler summer temperatures and the occasional heavy rainfall event (Tables 1, 2), which resulted in lower ETP values and less depletion of soil water resources.

The Ψ_{PD} and Ψ_{STEM} values recorded between veraison and harvest correlated well ($R^2 = 0.92$, $P < 0.01$ and $R^2 = 0.90$, $P < 0.01$, respectively) with the $\delta^{13}C$ values in the musts at harvest (Figure 2). The $\delta^{13}C$ values varied from -22.5 ‰ (high water stress) in the non-irrigated vines to -27.0 ‰ (no water stress) in the irrigated vines. A correlation between Ψ_{PD} and Ψ_{STEM} ($R^2 = 0.90$, $P < 0.01$) recorded at solar midday was also found, with a vapor pressure deficit (VPD) of approximately 2.5 to 3.5 kPa during the eight-year study period (results not presented).

The different physiological indicators used in this study (Ψ_{PD} , Ψ_{STEM} and $\delta^{13}C$) gave a good picture of the vine water regime during the growing season, as has been previously shown in earlier studies (Choné *et al.*, 2001; van Leeuwen *et al.*, 2009). These indicators often correlate well among each other (van Leeuwen *et al.*, 2001a, b). The Ψ_{PD} and the Ψ_{STEM} data enable the evolution of the plant water status to be followed throughout the growing season. On the other hand, $\delta^{13}C$, which is analyzed in must sugars at harvest, presents an integrative approach to the water regime that prevailed during the sugar-accumulating phase in berries, that is, from the onset of fruit ripening (veraison) to harvest (Gaudillère *et al.*, 2002). The ^{13}C values in must sugars can be used as an indicator of soil water availability in the vineyard (de Souza *et al.*, 2005a, b).

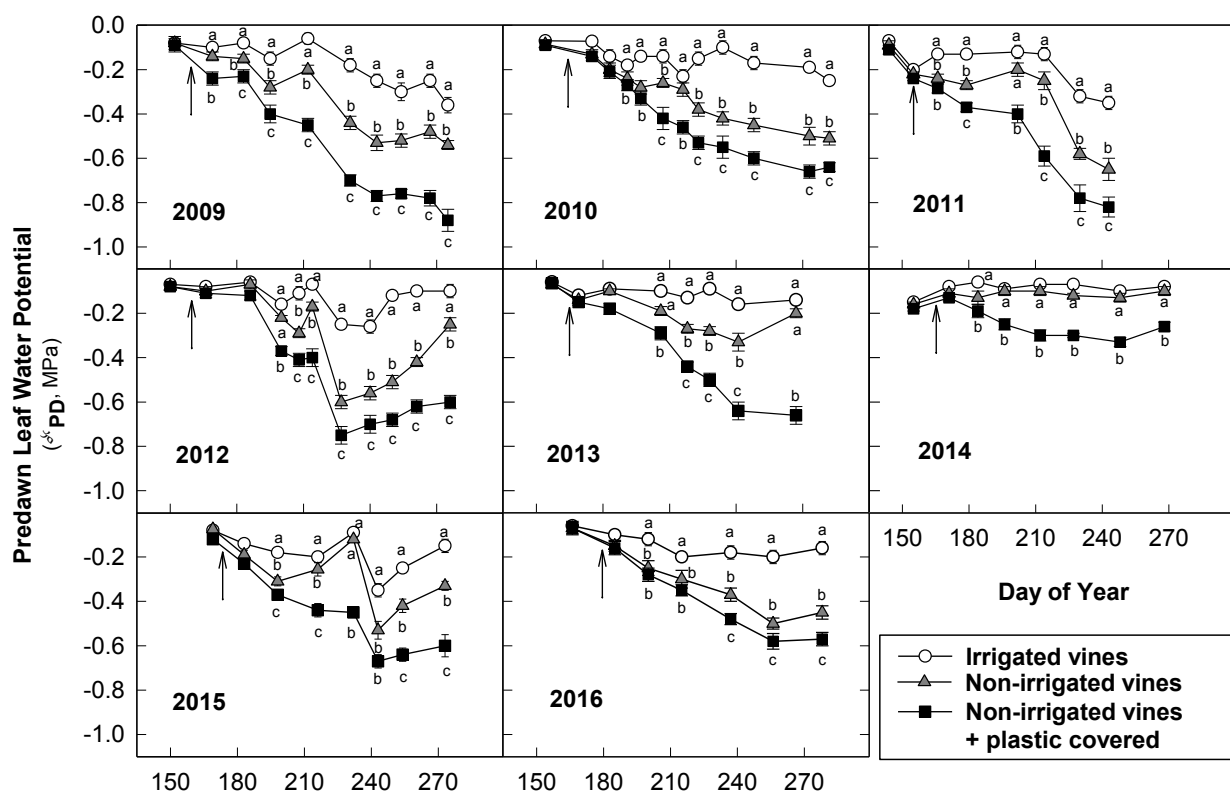


Figure 1. Seasonal evolution of the predawn leaf water potential (Ψ_{PD}) for different irrigation treatments. Arrows indicate irrigation onset.

Means \pm SE for eight leaves. Letters indicate statistical significance at the 5% level of probability. Chasselas (Switzerland), 2009-2016.

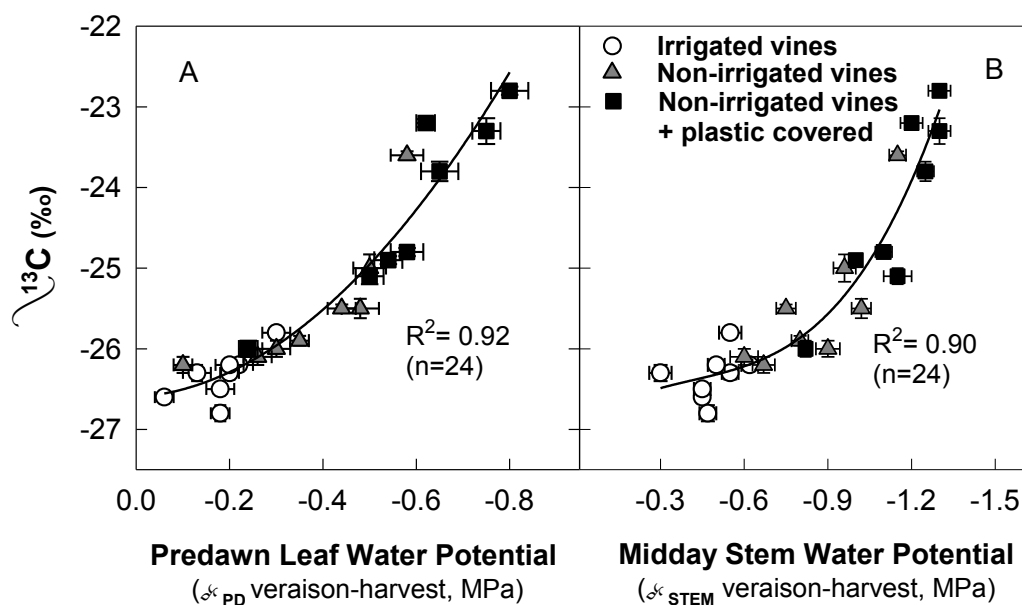


Figure 2. Relationship between the predawn leaf water potential (Ψ_{PD} , A), the stem xylem water potential (Ψ_{STEM} , B) measured during the period of veraison-harvest and the relative C isotope composition ($\delta^{13}C$) in must sugars at harvest for different irrigation treatments.

Means \pm SE. Chasselas, Leytron (Switzerland), 2009-2016.

3. Physiological behavior in response to progressive water deficit

a. Water and gas exchange relationships

The different water regimes, measured by the Ψ_{PD} of the irrigated and non-irrigated vines (Figure 3 A), led to consequences affecting leaf gas exchange, especially net photosynthesis (Figure 3 C), transpiration (Figure 3 D), stomatal conductance g_s (Figure 3 B), mesophyll resistance (Figure 3 G) and water use efficiency WUE (Figures 3 E-F). A reduction in g_s , A and E during the growing season of 2009 was measured (presented as an example) in response to increasing restrictions on soil water availability. In the non-irrigated vines, where the soils were covered by an impermeable plastic sheet, g_s reached very low levels during the season, which corresponded to a residual conductance g_{res} close to $30 \text{ mmol m}^{-2}\text{s}^{-1}$. Compared to that of irrigated vines, the net photosynthesis of non-irrigated vines dropped by 40 to 50% from the end of July (DOY 2010), reaching levels of approximately $5 \text{ Amol CO}_2 \text{ m}^{-2}\text{s}^{-1}$. In the summer, the transpiration rates of the non-irrigated vines dropped sharply in response to moderate to severe water stress, decreasing from 6 to $1.5 \text{ mmol H}_2\text{O m}^{-2}\text{s}^{-1}$ at the end of the season. The leaf senescence observed in September also partly explains the progressive reduction in gas exchange (A et E) during fruit ripening. The leaf stomatal conductance and gas exchange values had a good correlation with the plant water status (Ψ_{PD} values) in the period from bloom to the mid-ripening of the berries; correlation coefficients up to 0.88 ($P < 0.01$) for A, 0.90 ($P < 0.01$) for E and 0.92 ($P < 0.01$) for g_s were recorded (results not presented in the present article).

The stomatal control of photosynthesis and transpiration in periods of progressively developing water stress has been widely documented by various studies (Chaves *et al.*, 2007; 2010). The gradual closure of stomata indeed offers a rapid and effective response to soil water deficits and to increases in VPD, where the latter coincides with the drying of the soil. Stomatal regulation constitutes a short-term adaptation, enabling plants to save water by reducing leaf transpiration and simultaneously limiting the risk of vessel embolism phenomena and the rupture/failure of the hydraulic conductivity in the plant's vascular system (Lovisolo *et al.*, 2002).

The instantaneous water use efficiency (WUE_{inst}), which expresses the ratio between photosynthesis A and transpiration E, tended to increase during the growing season and was identical in both the irrigated

and non-irrigated vines (Figure 3 E). Intrinsic water use efficiency (WUE_i), on the other hand, which is calculated by the A/g_s ratio, was higher in the non-irrigated vines than in the irrigated vines (Figure 3 F). Under the conditions of the present study, as water stress increased, a greater decrease in g_s than in photosynthesis was observed, leading to a higher WUE_i in the non-irrigated vines than in the irrigated vines. Some studies, however, have shown that, in very severe drought situations, WUE_i can decrease (Prieto *et al.*, 2010), suggesting an increase in mesophyll limitations (increase in r_m), which, in turn, lowers the rates of photosynthesis (Flexas *et al.*, 2007). Furthermore, a correlation between the WUE_i and $\delta^{13}\text{C}$ in the berry sugars was observed over the eight-year study period (Figure 4), thus confirming previous observations (Medrano *et al.*, 2005; Zufferey *et al.*, 2017). The increase in WUE_i was linked to that of $\delta^{13}\text{C}$ in the must sugars. Non-irrigated vines presented higher $\delta^{13}\text{C}$ values (less negative), probably associated with a weaker discrimination against ^{13}C and ^{13}C enrichment in must sugars. The latter has been correlated with a rise in the WUE_i of non-irrigated vines compared to well-watered vines. In addition, differences in leaf and fruit isotope signatures were observed (results not presented) under conditions of water stress (Bchir *et al.*, 2016): the $\delta^{13}\text{C}$ in leaves reflects not only the leaf ratio of C_i/C_a and the WUE of the current growing season but also the C assimilated in the previous year and its allocation during spring growth. There is generally an enrichment of ^{13}C in berries compared to leaves due to the import of carbon assimilates from the leaves after the onset of ripening, when water stress is high (stomata closed), thus supplying carbon assimilates enriched in ^{13}C . Lastly, a recent study (Spangenberg *et al.*, 2017) showed that the analysis of carbon isotopes, undertaken in the solid residues and volatile organic components of wine, constitutes a very effective tool for estimating variations in the water status of plants and soils in different vineyards.

Among all treatments, the mesophyll resistance (r_m) was greatest at the end of the season in the non-irrigated vines with sheet-protected soils (Figure 3G). Water stress increases the resistance to the transfer of CO_2 from leaf substomatal cavities to the chloroplasts, where CO_2 fixation sites and photosynthetic enzymes are situated (Flexas *et al.*, 2002). The rise in r_m associated with the decrease in g_s under water stress lowers the availability of CO_2 in the chloroplasts and, consequently, the rate of photosynthesis in the leaves, as observed in the present study.

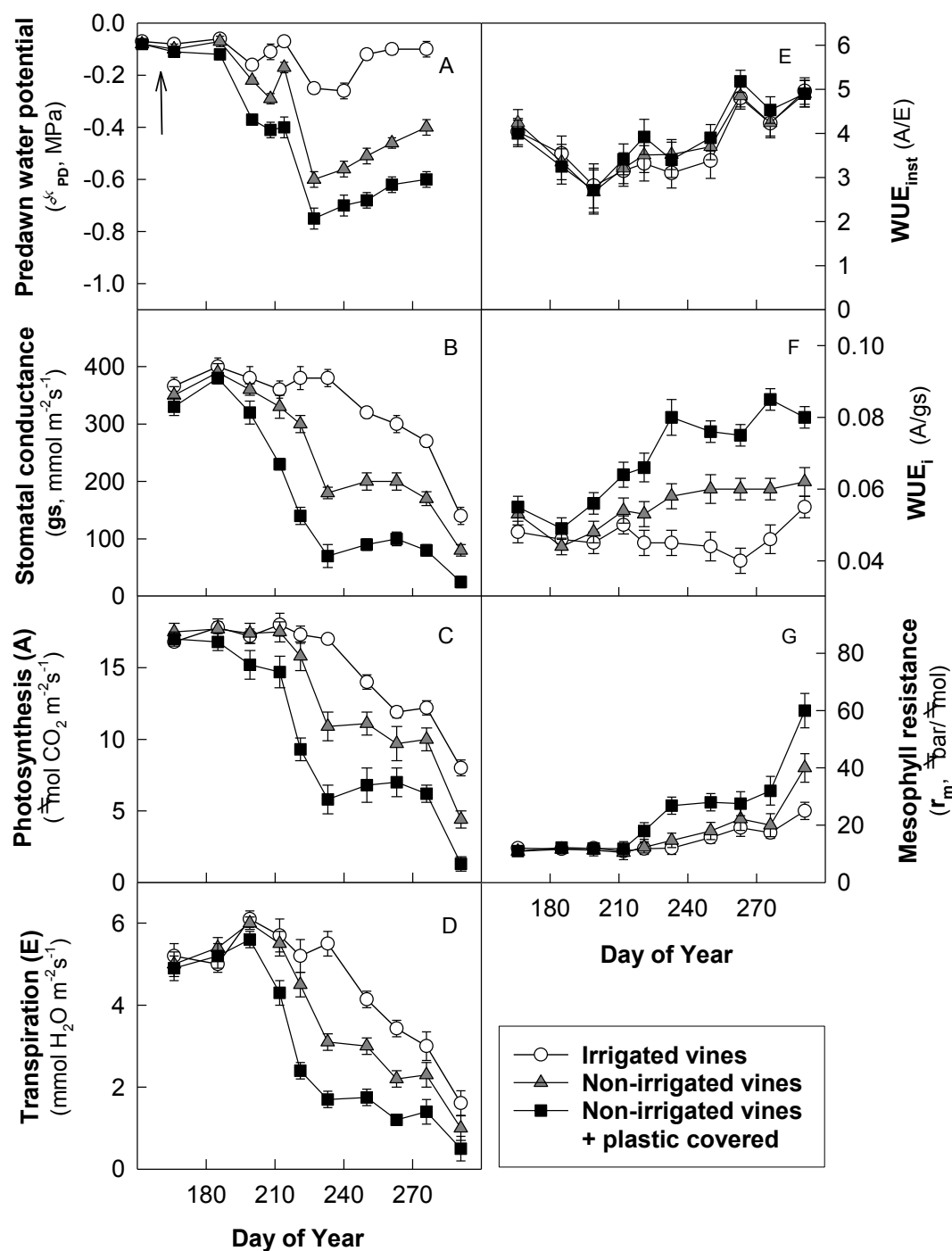


Figure 3. Changes in the predawn leaf water potential (Ψ_{PD} , A), stem water potential (Ψ_{STEM} , B), stomatal conductance (gs, C), mesophyll resistance (r_m , D), photosynthetic rate (A, E), intrinsic water use efficiency (WUE_i , F), transpiration rate (E, G) and instantaneous water use efficiency (WUE_{inst} , H) during the 2009 season.

Means \pm SE for eight leaves. Chasselas, Leytron (Switzerland).

B. Cavitation vulnerability

A curve representing cavitation vulnerability in leaf petioles was established by relating the PLC with Ψ_{STEM} (Figure 5). PLC increased progressively with water stress, reaching approximately 30%, with a

Ψ_{STEM} value of -1.0 MPa. The 50% threshold of PLC was observed at Ψ_{STEM} values of -1.25 MPa. In non-irrigated vines with plastic-covered soils, values close to 70-80% PLC were noted when water stress levels were very high ($\Psi_{STEM} < -1.5$ MPa). In the watered

vines, with Ψ_{STEM} values remaining above -0.8 MPa (weak water stress), no cavitation or very low cavitation values (below 10%) were recorded. The rain-fed vines presented an intermediary situation. An earlier study (Zufferey *et al.*, 2011) demonstrated the sensitivity of cv. Chasselas to embolism under very high water stress conditions during the growing season, as was the case for the non-irrigated vines in the present work. The progressive stomatal control of transpiration, followed by the reduction of hydraulic conductivity in protective « fuse » organs, such as petioles, allows the Ψ_{leaf} value to remain above a critical threshold, which, up to a certain point, prevents hydraulic rupture and embolism. The petiole hydraulic conductivity in the non-irrigated vines indeed decreased progressively as water stress intensified over the season (results not presented). The hypothesis that hydraulic and chemical signals significantly contribute to differences in preservation or water stress behaviors among vine varieties appears increasingly likely, especially in isohydric and anisohydric plants (Tardieu and Simonneau, 1998; Pantin *et al.*, 2013). In particular, the stomatal and hydraulic conductances of the Chasselas cultivar seem to be sensitive to soil water availability and, therefore, to Ψ_{PD} , compared to the Pinot noir vine grown in the same experimental plot in Leytron (Switzerland); the latter appears to be more sensitive to VPD variations (Spring, 1997; Zufferey *et al.*, 2017). Based on the perception of water stress by leaves and roots, different grapevine varieties react differently to water deficits. Some recent studies have attempted to better comprehend the relationships between the stomatal regulation of gas exchange,

hydraulic conductivity in roots and shoots, aquaporin expression levels and hormonal signals (mainly ABA, Stoll *et al.*, 2000) under water stress conditions (Coupel-Ledru *et al.*, 2017). Hydraulic segmentation, whereby the risk of hydraulic rupture is shared among plant organs, may also play an important part in the sensitivity of plants to embolism phenomena during drought. The greater hydraulic resistance measured in shoots than in petioles (Lovisolo *et al.*, 2007) and the anatomical characteristics of vessels (Pagay *et al.*, 2016) may, in addition, contribute to preventing the spread of embolism by reducing cavitation vulnerability in the perennial structure of plants.

c. Mineral supply and pruning weight

Table 3 presents the analysis of leaf mineral content (N, P, K, Ca and Mg) and the chlorophyll index values (N-tester) at veraison and the available nitrogen in the must (YAN) at harvest. The leaf nitrogen content tends to decrease with increasing water stress: leaf N levels were the lowest in non-irrigated vines with plastic-covered soil. No significant difference in the leaf P, K, Ca and Mg contents of the irrigated and non-irrigated vines was observed. Identical results were obtained from the Pinot noir grape variety under the same study conditions (Zufferey *et al.*, 2017). The leaf chlorophyll index remained similar in all irrigation treatments. YAN levels decreased as water stress increased, particularly in non-irrigated vines with plastic-covered soil (Table 3, Figure 6). In water-stressed vines, the reduction in the canopy transpiration flow due to progressive soil drying

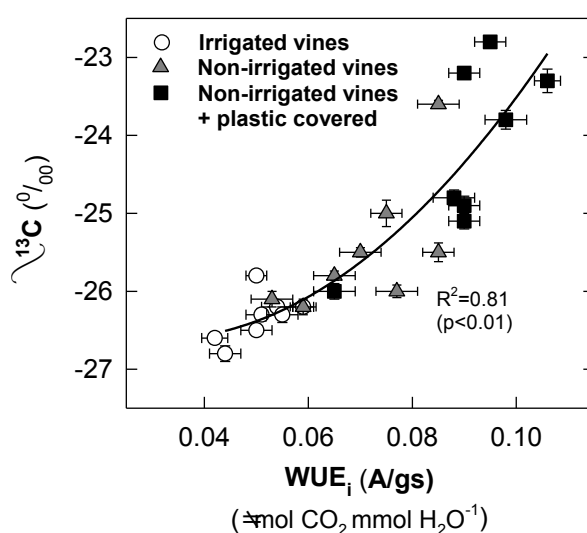


Figure 4. Relationship between the intrinsic water use efficiency (WUE_i) and the relative C isotope composition ($\delta^{13}C$) in must sugars at harvest for different irrigation treatments.
Means \pm SE. Chasselas, Leytron (Switzerland), 2009-2016.

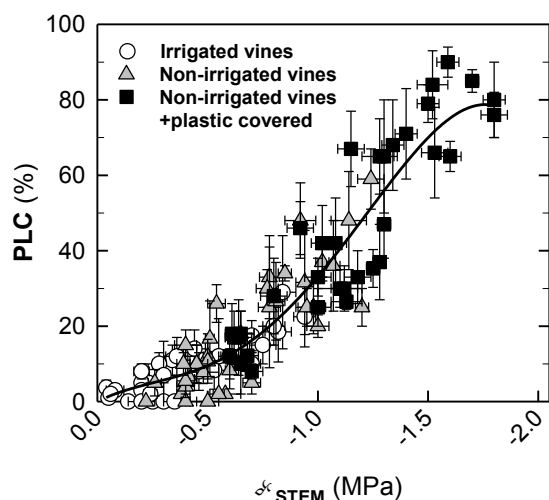


Figure 5. Vulnerability to cavitation (PLC, percent loss of conductivity) versus stem water potential (Ψ_{STEM}) for grapevine leaf petioles measured *in situ* for different irrigation treatments.
Chasselas, Leytron (Switzerland), 2012-2015.

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 the must at harvest.
Letters indicate statistical significance at the 5% level of probability. Averages 2009-2016, Leytron (Switzerland).

	Foliar analysis (% D.M.)					N-tester	YAN (mg N/L)
	N	P	K	Ca	Mg		
Irrigated vines	2.38a	0.25a	1.10a	4.07a	0.31a	586a	170a
Non-irrigated vines	2.32a	0.23a	1.11a	4.05a	0.31a	585a	155ab
Non-irrigated vines + plastic covered	2.11b	0.19a	0.95a	3.91a	0.33a	551a	122b

(non-irrigated vines) and the leaf fall over the growing season reduces the soil mineral uptake, especially the uptake of nitrogen, as noted by Gonzalez-Dugo *et al.* (2010). Nitrogen mineralization and soil microbial activity are also negatively influenced by soil drying conditions (Celette and Gary, 2013). Studies from Reynard *et al.* (2011), which were carried out in different wine-growing “terroirs”, additionally highlighted the depressive effect of water deficit, whether climatic and/or edaphic, on the nitrogen content in leaves and berries.

Plant vigor, estimated by pruning weight, was influenced by the water supply to vines (Table 4). Pruning weights were found to be lower in the non-irrigated vines with plastic-covered soils suffering drought in hot summers (years 2011, 2015, 2016) than in the irrigated vines. An intermediate situation was observed for the rain-fed vines. Compared with the irrigated vines, a pruning weight decrease of nearly 20% was observed in the non-irrigated vines with plastic-covered soils, and a decrease of 2% was observed in the non-irrigated vines (rain fed).

d. Yield components and must characteristics at harvest

Table 5 outlines the results of bud fertility, berry weight, cluster weight, cluster removal and yield observations. No significant differences were found between the yield components studied. Berry and cluster weights only had slightly lower values (significant difference at $P = 0.10$) in the non-irrigated vines with plastic-covered soils that had suffered drought. Any differences in yields were limited by maintaining the same number of clusters per vine (removal of seven clusters per vine) in both the irrigated and non-irrigated vines. A reduction of approximately 10% in yield was observed in the vines that experienced the greatest water stress, compared with the irrigated and rain-fed vines. Moreover, in most of the dry years, water stress appeared after the onset of fruit ripening (veraison), often towards the end of the ripening period; the impact of water stress on yield occurring late during the season is generally less important than that of water stress occurring early in the season (Ojeda *et*

Table 4. Pruning weight (g/vine) per year and the 2009-2016 mean.

Letters indicate statistical significance at the 5% level of probability. Averages 2009-2016, Leytron (Switzerland).

	Pruning weight (g/vine)								Mean 2009-2016
	2009	2010	2011	2012	2013	2014	2015	2016	
Irrigated vines	646a	650a	690a	889a	686a	581a	686a	679a	689a
Non-irrigated vines	638a	635a	570b	834a	713a	610a	714a	704a	677a
Non-irrigated vines + plastic covered	618a	596a	460c	608b	550b	561a	571b	497b	557b

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 indicate statistical significance at the 5% level of probability. Averages 2009-2016, Leytron (Switzerland).

	Bud fertility (inflo/shoot)	Cluster removal (-x clusters per vine)	Berry weight (g)	Cluster weight (g)	Yield (kg/m ²)
Irrigated vines	2.1a	-7a	1.3a	172a	1.52a
Non-irrigated vines	2.1a	-7a	1.2a	165a	1.47a
Non-irrigated vines + plastic covered	2.0a	-7a	1.1a	158a	1.35a

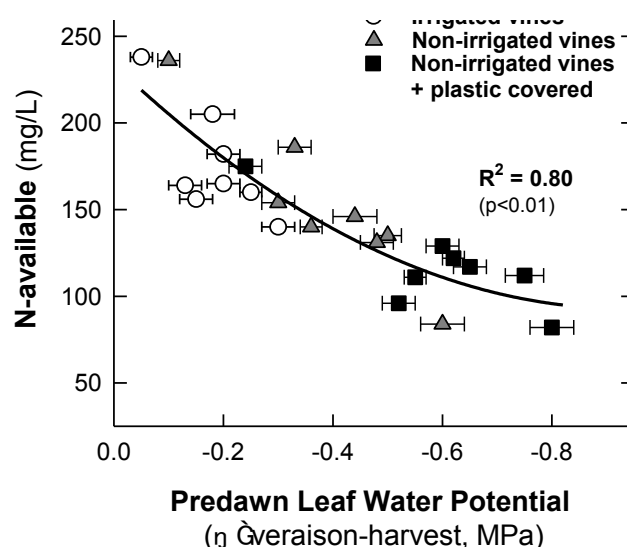


Figure 6. Relationship between the predawn water potential (Ψ_{PD}) and the yeast available nitrogen (YAN) in the must at harvest for different irrigation treatments.

Means \pm SE. Chasselas, Leytron (Switzerland), 2009-2016.

al., 2001; Ollat *et al.*, 2002). Bud fertility was not influenced by the vine water status over the eight-year study period: this result leads us to believe that the carbon and nitrogen reserves in both the irrigated and non-irrigated vines were well reconstituted (restored) from year to year (Zufferey *et al.*, 2015).

The must sugar content increased with water deficits (Table 6). The highest sugar levels were observed in the non-irrigated, plastic-covered vines under moderate to high water stress. It has been well documented that a moderate, progressive restriction

of the water supply beginning at the ripening period increases sugar accumulation in berries (van Leeuwen *et al.*, 2009) by preventing vegetative growth in secondary shoots. As the water deficit suppresses growth, carbon synthesized in the leaves is reallocated to the berries, probably due to the direct effect of ABA signaling the end of berry ripening (Deluc *et al.*, 2009). In the present study, the total acidity and malic acid contents were lower in the must from non-irrigated vines than in the must from well-watered vines. The decrease in total acidity and

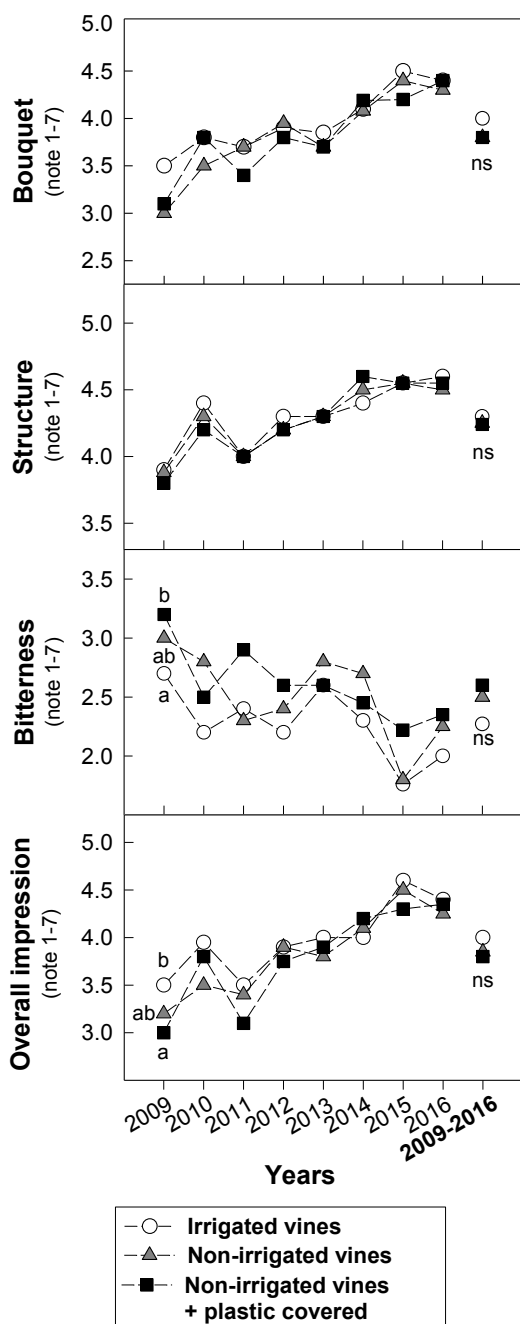


Figure 7. Evaluation of wine quality by tasting according to different sensory variables: olfactive (bouquet), gustatory (structure, tannin quality) and overall impression for the different irrigation treatments.

The notation scale ranges from 1 (poor) to 7 (high). Letters indicate statistical significance at the 5% level of probability. Chasselas, Leytron (Switzerland), 2009-2016.

the malic acid degradation appear to be linked to the berry microclimate (berries exposed to direct sunlight) in non-irrigated, water-stressed plants, due to the leaf fall in the cluster zone. No significant differences were noted for pH and tartaric acid as a

function of plant water status, which is in agreement with other observations (McCarthy, 2000). In wines, values of pH, total acidity and tartaric acid were very similar among the different irrigation treatments, and no significant differences were observed (results not presented).

4. Wine tasting

Figure 7 presents the results of the wine tasting, which occurred several weeks after bottling, for major wine characteristics: wine bouquet (sharpness and quality of aromas), wine structure, wine bitterness, and global appreciation of the wine. Globally, the vine water regime had little influence on the quality and organoleptic characteristics of the Chasselas wines, with the exception of the hot, dry year in 2009, when the quality of wine from the irrigated vines, which had not experienced water stress, was more appreciated. Bitterness was generally more noticeable in wine from non-irrigated vines that had experienced drought than in wine from well-watered vines. No significant difference was recorded for the bouquet and wine structure during the study period, whether from irrigated or non-irrigated vines. Concerning the global appreciation of wines (hedonic impression), those obtained from the irrigated vines were appreciated slightly more than those obtained from the non-irrigated vines. This was due to the perception of less bitterness in the wines from well-watered vineyards than in the wines from non-irrigated vineyards. Progressive and moderate water stress, beginning at fruit ripening, favors the enrichment of sugars, anthocyanins and phenol compounds in the berries of red cultivars (Kennedy *et al.*, 2002; van Leeuwen *et al.*, 2009; Zufferey *et al.*, 2017). On the other hand, in white cultivars, a low to slightly moderate water stress benefits the development of aromatic components (Reynolds *et al.*, 2010). A severe or sometimes even moderate water stress can have a negative impact on white wine quality, particularly affecting the sharpness of aromas and the perception of bitterness (van Leeuwen and Vivin, 2008; Spring and Zufferey, 2011). Furthermore, high water stress is often accompanied by a reduction in the available nitrogen content of must. According to the vineyard, year, vintage, and grape variety, this reduction may impair the aromatic expression (Tominaga *et al.*, 2000), the quality and the characteristics of white wines (Peyrot des Gachons *et al.*, 2005; Reynard *et al.*, 2011).

Acknowledgments: The authors wish to express their warm gratitude to the viticulture and the wine

Table 6. Harvest characteristics: sugar content, pH and titratable acidity (total acidity, tartaric and malic acid) in must.

Letters indicate statistical significance at the 5% level of probability. Averages 2009-2016, Leytron (Switzerland).

	Sugars (g/L)	pH	Total acidity (g/L)	Tartaric acid (g/L)	Malic acid (g/L)
Irrigated vines	230a	3.20a	8.5a	6.5a	3.9a
Non-irrigated vines	240ab	3.22a	7.8b	6.3a	3.3ab
Non-irrigated vines + plastic covered	246b	3.19a	7.6b	6.4a	2.9b

technology and analysis teams for their excellent work and invaluable collaboration.

References

- Bchir A., Escalona J.M., Gallé A., Hernandez-Montes E., Tortosa I., Braham M. and Medrano H., 2016. Carbon isotope discrimination ($\delta^{13}\text{C}$) as an indicator of vine water status and water use efficiency (WUE): looking for the most representative sample and sampling time. *Agric. Water Manage.* **167**, 11-20. doi: 10.1016/j.agwat.2015.12.018
- Bell S-J. and Henschke P.A., 2005. Implications of nitrogen nutrition for grapes, fermentation and wine. *Aust. J. Grape Wine Res.* **11**, 242-295. doi: 10.1111/j.1755-0238.2005.tb00028.x
- Celette F. and Gary C., 2013. Dynamics of water and nitrogen stress along the grapevine cycle as affected by cover cropping. *Eur. J. Agron.* **45**, 142-152. doi: 10.1016/j.eja.2012.10.001
- Chaves M.M., Santos T.P., Souza C.R., Ortuño M.F., Rodrigues M.L., Lopes C.M., Maroco J.P. and Pereira J.S., 2007. Deficit irrigation in grapevine improves water-use efficiency while controlling vigour and production quality. *Ann. Appl. Biol.* **150**, 237-252. doi: 10.1111/j.1744-7348.2006.00123.x
- Chaves M.M., Zarrouk O., Francisco R., Costa J.M., Santos T., Regalado A.P., Rodrigues M.L. and Lopes C.M., 2010. Grapevine under deficit irrigation: hints from physiological and molecular data. *Ann. Bot.* **105**, 661-676. doi: 10.1093/aob/mcq030
- Choné X., van Leeuwen C., Dubourdiou D. and Gaudillère J.-P., 2001. Stem water potential is a sensitive indicator of grapevine water status. *Ann. Bot.* **87**, 477-483. doi: 10.1006/anbo.2000.1361
- Choné X., Lavigne-Cruège V., Tominaga T., van Leeuwen C., Castagnede C., Saucier C. and Dubourdiou D., 2006. Effect of vine nitrogen status on grape aromatic potential: flavor precursors (S-cysteine conjugates), glutathione and phenolic content in *Vitis vinifera* L. cv. Sauvignon blanc grape juice. *J. Int. Sci. Vigne Vin* **40**, 1-6. doi: 10.20870/oeno-one.2006.40.1.880
- Cochard H., Bodet C., Ameglio T. and Cruziat P., 2000. Cryo-scanning electron microscopy observations of vessel content during transpiration in walnut petioles: facts or artifacts? *Plant Physiol.* **124**, 1191-1202. doi: 10.1104/pp.124.3.1191
- CoupeL-Ledru A., Tyerman S., Masclef D., Lebon E., Christophe A., Edwards E.J. and Simonneau T., 2017. Abscisic acid down-regulates hydraulic conductance of grapevine leaves in isohydric genotypes only. *Plant Physiol.* **175**, 1121-1134. doi: 10.1104/pp.17.00698
- Deléens E., Cliquet J.-B. and Prioul J.-L., 1994. Use of ^{13}C and ^{15}N plant label near natural abundance for monitoring carbon and nitrogen partitioning. *Aust. J. Plant Physiol.* **21**, 133-146. doi: 10.1071/PP9940133
- Deloire A., Carbonneau A., Wang Z. and Ojeda H., 2004. Vine and water: a short review. *J. Int. Sci. Vigne Vin* **38**, 1-13. doi: 10.20870/oeno-one.2004.38.1.932
- Deluc L.G., Quilici D.R., Decendit A., Grimplet J., Wheatley M.D., Schlauch K.A., Mérillon J.M., Cushman J.C. and Cramer G.R., 2009. Water deficit alters differentially metabolic pathways affecting important flavor and quality traits in grape berries of Cabernet Sauvignon and Chardonnay. *BMC Genomics* **10**, 212. doi: 10.1186/1471-2164-10-212
- de Souza C.R., Maroco J.P., dos Santos T.P., Rodrigues M.L., Lopes C.M., Pereira J.S. and Chaves M.M., 2005a. Impact of deficit irrigation on water use efficiency and carbon isotope composition ($\delta^{13}\text{C}$) of field-grown grapevines under Mediterranean climate. *J. Exp. Bot.* **56**, 2163-2172. doi: 10.1093/jxb/eri216
- de Souza C.R., Maroco J.P., dos Santos T.P., Rodrigues M.L., Lopes C.M., Pereira J.S. and Chaves M.M., 2005b. Grape berry metabolism in field-grown grapevines exposed to different irrigation strategies. *Vitis* **44**, 103-109.
- Dry P.R., Loveys B.R. and Düring H., 2000a. Partial drying of the rootzone of grape. I. Transient changes in shoot growth and gas exchange. *Vitis* **39**, 3-7.
- Dry P.R., Loveys B.R. and Düring H., 2000b. Partial drying of the rootzone of grape. II. Changes in the pattern of root development. *Vitis* **39**, 9-12.
- Flexas J., Bota J., Escalona J.M., Sampol B. and Medrano H., 2002. Effects of drought on photosynthesis in grapevines under field conditions: an evaluation of stomatal and mesophyll limitations. *Funct. Plant Biol.* **29**, 461-471. doi: 10.1071/PP01119
- Flexas J., Diaz-Espejo A., Galmes J., Kaldenhoff R., Medrano H. and Ribas-Carbo M., 2007. Rapid variations of mesophyll conductance in response to changes in CO_2 concentration around leaves. *Plant*

- Cell Environ.* **30**, 1284-1298. doi: 10.1111/j.1365-3040.2007.01700.x
- Fulton A., Buchner R., Olson B., Schwankl L., Gilles C., Bertagna N., Walton J. and Shackel K., 2001. Rapid equilibration of leaf and stem water potential under field conditions in almonds, walnuts and prunes. *HortTechnology* **11**, 609-615.
- Gaudillère J.-P., van Leeuwen C. and Ollat N., 2002. Carbon isotope composition of sugars in grapevine, an integrated indicator of vineyard water status. *J. Exp. Bot.* **53**, 757-763. doi: 10.1093/jexbot/53.369.757
- Gonzalez-Dugo V., Durand J.-L. and Gastal F., 2010. Water deficit and nitrogen nutrition of crops. A review. *Agron. Sustain. Dev.* **30**, 529-544. doi: 10.1051/agro/2009059
- Kennedy J.A., Matthews M.A. and Waterhouse A.L., 2002. Effect of maturity and vine water status on grape skin and wine flavonoids. *Am. J. Enol. Vitic.* **53**, 268-274.
- Lacroux F., Tregoat O., van Leeuwen C., Pons A., Tominaga T., Lavigne-Cruège V. and Dubourdieu D., 2008. Effect of foliar nitrogen and sulphur application on aromatic expression of *Vitis vinifera* L. cv. Sauvignon blanc. *J. Int. Sci. Vigne Vin* **42**, 125-132. doi: 10.20870/oeno-one.2008.42.3.816
- Lovisolò C., Hartung W. and Schubert A., 2002. Whole-plant hydraulic conductance and root-to-shoot flow of abscisic acid are independently affected by water stress in grapevines. *Funct. Plant Biol.* **29**, 1349-1356. doi: 10.1071/FP02079
- Lovisolò C., Secchi F., Nardini A., Salleo S., Buffa R. and Schubert A., 2007. Expression of PIP1 and PIP2 aquaporins is enhanced in olive dwarf genotypes and is related to root and leaf hydraulic conductance. *Physiol. Plant.* **130**, 543-551. doi: 10.1111/j.1399-3054.2007.00902.x
- Lovisolò C., Lavoie-Lamoureux A., Tramontini S. and Ferrandino A., 2016. Grapevine adaptations to water stress: new perspectives about soil/plant interactions. *Theor. Exp. Plant Physiol.* **28**, 53-66. doi: 10.1007/s40626-016-0057-7
- McCarthy M.G., 2000. Developmental variation in sensitivity of *Vitis vinifera* L. (Shiraz) berries to soil water deficit. *Aust. J. Grape Wine Res.* **6**, 136-140. doi: 10.1111/j.1755-0238.2000.tb00172.x
- Medrano H., Bota H., Escalona J.M., Ribas-Carbo M. and Flexas J., 2005. Variability of intrinsic water use efficiency in Mediterranean grapevines. Proceedings of the XIV GESCO Symposium, Geisenheim, Germany, Vol. II., pp 513-520.
- Ojeda H., Deloire A. and Carbonneau A., 2001. Influence of water deficits on grape berry growth. *Vitis* **40**, 141-145.
- Ollat N., Diakou-Verdin P., Carde J.P., Barrieu F., Gaudillère J.P. and Moing A., 2002. Grape berry development: a review. *J. Int. Sci. Vigne Vin* **36**, 109-131. doi: 10.20870/oeno-one.2002.36.3.970
- Osmond C.B., Björkman O. and Anderson D.J., 1980. Physiological Processes in Plant Ecology (Springer-Verlag: Berlin). doi: 10.1007/978-3-642-67637-6
- Pagay V., Zufferey V. and Lakso A., 2016. The influence of water stress on grapevine (*Vitis vinifera* L.) shoots in a cool, humid climate: growth, gas exchange and hydraulics. *Funct. Plant Biol.* **43**, 827-837. doi: 10.1071/FP16017
- Pantin F., Renaud J., Barbier F., Vavasseur A., Le Thiec D., Rose C., Bariac T., Casson S., McLachlan D.H., Hetherington A.M., Muller B. and Simonneau T., 2013. Developmental priming of stomatal sensitivity to abscisic acid by leaf microclimate. *Curr. Biol.* **23**, 1805-1811. doi: 10.1016/j.cub.2013.07.050
- Peyrot des Gachons C.P., van Leeuwen C., Tominaga T., Soyer J.P., Gaudillère J.P. and Dubourdieu D., 2005. Influence of water and nitrogen deficit on fruit ripening and aroma potential of *Vitis vinifera* L. cv Sauvignon blanc in field conditions. *J. Sci. Food Agric.* **85**, 73-85. doi: 10.1002/jsfa.1919
- Prieto J.A., Lebon E. and Ojeda H., 2010. Stomatal behavior of different grapevine cultivars in response to soil water status and air water vapor pressure deficit. *J. Int. Sci. Vigne Vin* **44**, 9-20. doi: 10.20870/oeno-one.2010.44.1.1459
- Reynard J.-S., Zufferey V., Nicol G.C. and Murisier F., 2011. Soil parameters impact the vine-fruit-wine continuum by altering vine nitrogen status. *J. Int. Sci. Vigne Vin* **45**, 211-221. doi: 10.20870/oeno-one.2011.45.4.1502
- Reynolds A., De Savigny C. and Willwerth J., 2010. Riesling terroir in Ontario vineyards. The roles of soil texture, vine size and vine water status. *Prog. Agric. Vitic.* **127**, 212-222.
- Scholander P.F., Hammel H.T., Bradstreet E.D. and Hemmingsen E.A., 1965. Sap pressure in vascular plants. *Science* **148**, 339-346. doi: 10.1126/science.148.3668.339
- Schultz H.R., 1996. Water relations and photosynthetic responses of two grapevine cultivars of different geographical origin during water stress. *Acta Hort.* **427**, 251-266. doi: 10.17660/ActaHortic.1996.427.30
- Seguin G., 1975. Alimentation en eau de la vigne et composition chimique des moûts dans les Grands Crus du Médoc. Phénomènes de régulation. *Conn. Vigne Vin* **9**, 23-34. doi: 10.20870/oeno-one.1975.9.1.1675
- Spangenberg J.E., Vogiatzaki M. and Zufferey V., 2017. Gas chromatography and isotope ratio mass spectrometry of Pinot noir wine volatile compounds ($\delta^{13}\text{C}$) and solid residues ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) for the reassessment of vineyard water-status. *J. Chromatogr. A* **1571**, 142-155. doi: 10.1016/j.chroma.2017.08.038

- Sperry J.S. and Pockman W.T., 1993. Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis*. *Plant Cell Environ.* **16**, 279-287. doi: 10.1111/j.1365-3040.1993.tb00870.x
- Spring J.-L., 1997. Comportement physiologique des cépages Chasselas, Sylvaner, Gamay et Pinot noir dans les conditions sèches du Valais central. *Rev. Suisse Vitic. Arboric. Hortic.* **29**, 265-271.
- Spring J.-L. and Zufferey V., 2011. Irrigation : comportement de la vigne et qualité des vins de cépages blancs dans le Valais central. *Rev. Suisse Vitic. Arboric. Hortic.* **43**, 162-173.
- Stoll M., Loveys B. and Dry P., 2000. Hormonal changes induced by partial rootzone drying of irrigated grapevine. *J. Exp. Bot.* **51**, 1627-1634. doi: 10.1093/jxb/51.350.1627
- Tardieu F. and Simonneau T., 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. *J. Exp. Bot.* **49**, 419-432. doi: 10.1093/jxb/49.Special_Issue.419
- Tominaga T., Baltenweck-Guyot R., Peyrot des Gachons C.P. and Dubourdieu D., 2000. Contribution of volatile thiols to the aromas of white wines made from several *Vitis vinifera* grape varieties. *Am. J. Enol. Vitic.* **51**, 178-181.
- Turner N.C., 1988. Measurement of plant water status by the pressure chamber technique. *Irrig. Sci.* **9**, 289-308. doi: 10.1007/BF00296704
- Tyree M.T. and Sperry J.S., 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. *Plant Physiol.* **88**, 574-580. doi: 10.1104/pp.88.3.574
- Van Leeuwen C. and Seguin G., 1994. Incidences de l'alimentation en eau de la vigne, appréciée par l'état hydrique du feuillage, sur le développement de l'appareil végétatif et la maturation du raisin (*Vitis vinifera* variété Cabernet franc, Saint-Emilion, 1990). *J. Int. Sci. Vigne Vin* **28**, 81-110. doi: 10.20870/oenone.1994.28.2.1152
- van Leeuwen C. and Vivin P., 2008. Alimentation hydrique de la vigne et qualité des raisins. *Innov. Agron.* **2**, 159-167.
- van Leeuwen C., Choné X., Trégoat O. and Gaudillère J.P., 2001a. The use of physiological indicators to assess vine water uptake and to manage vineyard irrigation. *Aust. Grapegrow. Winemak.* **449**, 18-24.
- van Leeuwen C., Gaudillère J.-P. and Trégoat O., 2001b. L'évaluation du régime hydrique de la vigne à partir du rapport isotopique ¹³C/¹²C. *J. Int. Sci. Vigne Vin* **35**, 195-205. doi: 10.20870/oenone.2001.35.4.984
- van Leeuwen C., Trégoat O., Choné X., Bois B., Pernet D. and Gaudillère J.-P., 2009. Vine water status is a key factor in grape ripening and vintage quality for red Bordeaux wine. How can it be assessed for vineyard management purposes? *J. Int. Sci. Vigne Vin* **43**, 121-134. doi: 10.20870/oenone.2009.43.3.798
- Zufferey V., Cochard H., Ameglio T., Spring J.-L. and Viret O., 2011. Diurnal cycles of embolism formation and repair in petioles of grapevine (*Vitis vinifera* cv. Chasselas). *J. Exp. Bot.* **62**, 3885-3894. doi: 10.1093/jxb/err081
- Zufferey V., Murisier F., Belcher S., Lorenzini F., Vivin P., Spring J.-L. and Viret O., 2015. Nitrogen and carbohydrate reserves in the grapevine (*Vitis vinifera* L. 'Chasselas'): the influence of the leaf to fruit ratio. *Vitis* **54**, 183-188. doi: 10.5073/vitis.2015.54.183-188
- Zufferey V., Spring J.-L., Verdenal T., Dienes-Nagy A., Belcher S., Lorenzini F., Koestel C., Rösti J., Gindro K., Spangenberg J. and Viret O., 2017. Influence of water stress on plant hydraulics, gas exchange, berry composition and quality of Pinot noir wines in Switzerland. *OENO One* **51**, 17-27. doi: 10.20870/oenone.2017.51.1.1314