The influence of vine water regime on the leaf gas exchange, berry composition and wine quality of Arvine grapes in Switzerland

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ABSTRACT

Aim: The aim of the present study was to analyze the impact of different water regimes, by means of various levels of irrigation, on the physiological and agronomical behavior of an aromatic white grapevine (cv. Arvine). The consequences of the plant water status were followed through to chemical (aromatic precursors) and sensorial analysis of resulting wines.

Methods and results: Adult vines of Vitis vinifera L. cv. Arvine 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 (ΨPD) and stem (ΨSTEM) water potentials and the carbon isotope composition (δ13C) in the must]. Gas exchange (net photosynthesis AN and transpiration E), stomatal conductance (gs), yield parameters, berry composition at harvest, analysis of potential grape aromatic properties (glycosyl-glucose G-G, precursor 3-mercaptohexanol P 3-MH) and the sensorial quality of wines were analyzed over a period of 8 consecutive years (2009-2016) on the Agroscope experimental vineyard in Leytron under the relatively dry conditions of the Rhône valley, in Wallis, Switzerland.

In non-irrigated vines, the progressively increasing water deficit observed over the season reduced the leaf gas exchange (AN and E) and gs. The intrinsic water use efficiency (WUEi, AN/gs) increased over the season and was greater in vines that had suffered water restriction than in irrigated vines. The rise in WUEi was correlated with an increase in δ13C in the must sugars at harvest. A decrease in plant vigor was observed in the water stressed vines over multiple years. Moderate to high water stress during fruit ripening lowered the contents of total and malic acidity in the musts and the content of yeast available nitrogen (YAN). On the other hand, contents in sugar and the aromatic precursor (P-3MH) in berries were not influenced by the vine water status. Values of G-G in berries increased with rising water stress in non-irrigated vines. Wines from plants subjected to water stress and to yeast available nitrogen deficiency (non-irrigated vines during hot and dry seasons) presented a less distinctive typicity, and developed a lower aromatic expression with a more bitter taste, than wines from non-stressed plants. Overall, and compared with stressed vines, the organoleptic characteristics and quality of Arvine wines coming from vines where no restrictions in water and nitrogen had been suffered during the growing season were better appreciated.

Conclusions: The vine’s physiological behavior (leaf gas exchange, plant vigor) and agronomic parameters (yield, berry composition), together with the quality of white aromatic Arvine wines, were strongly influenced by vine water regimes during the growing season.

Significance and impact of the study: Vine water status and must nitrogen contents are key factors in grape composition and in the sensorial quality of resulting aromatic white wines.

KEYWORDS

water stress, gas exchange, water use efficiency (WUE), carbon isotope composition, berry composition, aromatic compounds, wine quality
INTRODUCTION

The vine water status derives from numerous pedoclimatic factors (soil properties, soil water reserves, mesoclimate (Seguin, 1975), from the rootstock’s genetic characteristics (root density, for example) and grape variety (drought sensitivity), and from cultivation practices (cover crop, leaf-fruit ratio), including irrigation in some cases. Restrictions in water supply during the season may affect plant growth (Chaves et al., 2010), the canopy’s photosynthetic capacity, yield components (floral initiation, the rate of fruit set, berry weight …) and the quality of grapes and wines (van Leeuwen and Seguin, 1994). Stomatal regulation of leaf transpiration provides a short-term response of controlling water losses in vines when edaphic water stress and/or atmospheric demands (water vapor deficit in the air, VPD) rise sharply during the day (Lovisolo et al., 2016). By limiting water flux in the plant (lowered transpiration) and canopy development (decreasing leaf area by leaf fall), the plant is able to maintain its water status and stabilizes the leaf water potential above the threshold required for avoidance of hydraulic rupture (cavitation phenomena with development of air bubbles in vessels) in cases of high water stress (Tyree and Sperry, 1988).

The effects of drought on yield components depend on the timing, the intensity and the duration of water deficit (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, 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; Deluc et al., 2009) which may result in a loss of aromatic compounds and wine quality (Reynolds et al., 2010; Reynard et al., 2011; Verdenal et al., 2012).

| 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 1. Monthly rates of precipitation (mm) at the experimental site in Leytron (Switzerland) during the eight-year study period (2009-2016) and long-term precipitation averages (1981-2010).
The Arvine grape variety, cultivated mainly in the Swiss canton of Wallis, is well appreciated for the character and the complex fruity and floral bouquet of its wines (Spring et al., 2014). This aromatic typicity arises from sulphur compounds of the thiol family and in particular 3-mercapto-hexanol (Fretz et al., 2005), whose aromas are evocative of grapefruit, lemon, rhubarb and exotic fruits. These aromas are linked to glutathione and cysteine (P-3MH) in musts and liberated in volatile form during alcohol fermentation (Tominaga et al., 2000).

In this 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, 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 Arvine 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 Arvine, 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.

|               | 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      |

TABLE 2. Monthly mean temperatures (°C) at the experimental site in Leytron (Switzerland) during the eight-year study period (2009-2016) and long-term temperature averages (1981-2010).
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 (δ13C)

Predawn leaf water (Ψ<sub>PD</sub>) and midday stem water (Ψ<sub>STEM</sub>) potentials were measured using a pressure chamber (Scholander et al., 1965) according to Turner (1988). Ψ<sub>PD</sub> was measured between 0400 and 0500 in the morning, in complete darkness, on eight mature, undamaged and non-senescent leaves. Midday Ψ<sub>STEM</sub> measurements were performed between 1400 and 1500, when evapotranspiration was at a maximum. Midday Ψ<sub>STEM</sub> 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 composition (δ13C) of the must sugars was 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 δ13C values per mille (%), with deviations of the isotope ratio relative to known standards as follows: δ = [(R<sub>sample</sub> − R<sub>standard</sub>) / R<sub>standard</sub>] × 1000, where R is the ratio of heavy to light isotopes (13C/12C). The R<sub>standard</sub> 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<sub>N</sub>) and transpiration (E)], stomatal conductance (g<sub>s</sub>) and mesophyll resistance (r<sub>m</sub>) were measured.

FIGURE 1. Seasonal evolution of the predawn leaf water potential (Ψ<sub>PD</sub>) for different irrigation treatments. Arrows indicate irrigation onset.
Means ± SE for eight leaves. Letters indicate statistical significance at the 5 % level of probability. Arrows indicate start of irrigation. Arvine, Leytron (Switzerland), 2009-2016
on healthy, fully expanded, mature and non-senescent leaves well exposed to direct sunlight (PFD > 1800 μmol m⁻² 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, 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 \( CO_2 \), \( \Gamma \) is the \( CO_2 \) 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, \( A/g_s \)) and instantaneous water use efficiency (WUE inst, \( A/N/E \)) were determined from single leaf gas-exchange measurements that related the net photosynthesis rate (\( A \)) either to the stomatal conductance for water vapor (\( g_s \)), termed WUE (Osmond et al., 1980), or to the leaf transpiration rate (\( E \)), termed WUE inst.

5. 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, 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 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).

6. 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, titrable acidity (g tartaric acid/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. The aromatic potential of the Arvine grape variety was evaluated by the Glycosyl-Glucose (G-G) method, according to Williams et al. (1995), and the precursor 3-mercaptohexanol (P-3MH) was analyzed according to the Luisier et al. (2008) method on musts, after crushing and the addition of sulphites.

FIGURE 2. Relationship between the predawn leaf water potential (\( \Psi_{PD} \), A), the stem xylem water potential (\( \Psi_{STEM} \), 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 ± SE. Arvine, Leytron (Switzerland), 2009-2016.
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).

7. 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蒲 and ΨSTEM 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

Tables 1 and 2 present monthly and annual rainfall and temperatures for the period under study, from 2009 to 2016. The experimental wine-growing area is situated in a relatively dry Alpine region where long-term mean rainfall (1981-2010) is around 600 mm per year. During the study period, rainfall amounts were a little below the long-term average, especially in 2010, 2011 and 2015 when measured precipitation was approximately 100-130 mm less per year. Particularly dry summer periods (August-September) were recorded in 2009, 2010, 2011, 2015 and 2016. The year 2014 was an exception when rainfall was slightly above normal (106 mm) and August (87 mm) than normal (1981-2010). Annual temperatures were greater by about 0.6 to 1.6°C than the long-term means (1981-2010), except for the years 2010 and 2013 when average annual temperatures were equivalent to the long-term figures. In comparison with the 30-year mean figures, particularly high summer temperatures (July-September) were recorded in the region in 2009, 2011, 2012, 2015 and 2016.

2. Plant water status

Seasonal monitoring of vine water status was carried out by means of predawn leaf water potential measurements (Ψ蒲) throughout the study period 2009-2016 (Figure 1). In irrigated vines from bloom to fruit ripening, no water stress was recorded, and values of Ψ蒲 varied between -0.05 and -0.25 MPa throughout the season and according to the year. Non-irrigated vines, however, showed a gradual increase in water stress from the end of July (DOY 2010), with Ψ蒲 values fluctuating between -0.3 and -0.5 MPa, indicative of moderate water stress.

An exception was noted for the year 2014 when any manifestation of water stress was absent for the whole season. Soil-covering associated with no irrigation resulted in moderate to high water stress towards the end of berry ripening (values of Ψ蒲 < -0.5 MPa), especially during the hot, dry summers of 2009, 2011, 2015 and 2016. Water stress remained more moderate during the summers of 2010, 2013 and 2014 due to the cooler temperatures and regular rainfall in July and August, which meant lower water vapor deficits (VPD) and a reduced rate of soil water depletion. The measurement of Ψ蒲 in darkness provides an estimate of vine water status when leaf transpiration is greatly reduced, and thus reflects the soil water availability (edaphic stress) in the wettest part of soil colonized by roots (Améglio et al., 1999). When measured during the hottest hours of the day (solar midday), ΨSTEM allows not only an estimation of edaphic stress, but also of climatic stress resulting from the evaporative demand of the air (i.e. VPD). These two physiological approaches of Ψ蒲 and ΨSTEM provide valuable information concerning the supply of water to vines (Choné et al., 2001, van Leeuwen et al., 2001a; van Leeuwen et al., 2001b; van Leeuwen et al., 2009). Values of Ψ蒲 and of Midday ΨSTEM are notably correlated (R² = 0.85, P < 0.01) throughout the 2009-2016 study period.

A correlation (R² = 0.81, P < 0.01 and R² = 0.80, P < 0.01, respectively) was observed between these two indicators of vine water status, Ψ蒲 et ΨSTEM recorded during the fruit-ripening to harvesting period, and the carbon isotopic composition (δ¹³C) in musts at harvest-time (Figure 2A, B). Values of δ¹³C varied from -23 ‰ (high water stress) to -27 ‰ (no water stress) in irrigated vines, to -27 ‰ (no water stress) in irrigated vines. Measurement of C isotopic composition in musts has the advantage of providing an integral overview of the vine water regime during the phase of sugar accumulation, that is, between the time of fruit-ripening and harvesting (Gaudillère et al., 2002).

3. Physiological behavior in response to progressive water deficit

3.1 Water and gas exchange relationships

Figure 3 shows the impact of the different water regimes, estimated by night-time Ψ蒲 (Figure 3A),
on stomatal conductance $g_s$ (Figure 3B), net photosynthesis $A$ (Figure 3C), transpiration $E$ (Figure 3D), mesophyll resistance $r_m$ (Figure 3G) and water use efficiency WUE (Figure 3 E, F).

Taking the 2015 season as an example, increasing water stress observed in non-irrigated vines was accompanied by a decrease in $g_s$, $A$ and $E$. The values of $g_s$ measured were below 100 mmol m$^{-2}$s$^{-1}$ at the end of the season in non-irrigated vines with covered soils, corresponding to half of the rates observed in well-watered vines (irrigated vines). From the end of July (DOY 2010) net photosynthesis was reduced by 30 to 50% in vines suffering from water restrictions, in comparison with irrigated vines, where levels of almost

FIGURE 3. Changes in the predawn leaf water potential ($\Psi_{pd}$, A), stomatal conductance ($g_s$, B), net photosynthetic rate ($A_{n}$, C), transpiration rate ($E$, D), instantaneous water use efficiency ($WUE_{inst}$, E), intrinsic water use efficiency ($WUE_i$, F) and mesophyll resistance ($r_m$, G), during the 2015 season. Means ± SE for eight leaves. Arvine, Leytron (Switzerland).
5 μmol CO$_2$ m$^{-2}$s$^{-1}$ were reached by the end of the season. In addition, leaf transpiration decreased by nearly a half during grape ripening in vines with plastic-covered soils and no irrigation, compared with the well-watered vines. Under increasing water stress conditions, the plant can respond rapidly by stomatal regulation of gas exchange (photosynthesis and transpiration), a process which has been well described by many studies (Chaves et al., 2007; Chaves et al., 2010, Medrano et al., 2002; Medrano et al., 2003). Effectively, stomatal control of transpiration allows a rapid response to edaphic and atmospheric water deficits, while managing risk of hydraulic rupture in vessels which, in extreme cases, could lead to embolism (Lovisolo et al., 2002, Zufferey et al., 2011).

Under the conditions of moderate to strong water stress of the present study (non-irrigated vines with plastic-covered soils), net photosynthesis dropped off less markedly than $g_s$ during the growing season. Consequently, intrinsic water use efficiency ($\text{WUE}_i$, $\text{A}/g_s$) rose during the growth period, stabilizing at the end of fruit ripening. $\text{WUE}_i$ was higher in vines which were stressed during ripening, compared with well-watered vines. As previously demonstrated by numerous studies in Mediterranean climates (Schultz 1996, Chaves et al., 2007; Pou et al., 2008, Flexas et al., 2007, Tomas et al., 2014), the $\text{WUE}_i$ tends to increase under drought conditions. However, it has been noted that, when water stress becomes very high, there is a reduction in $\text{WUE}_i$ (Prieto et al., 2010), suggesting an increase in mesophyll resistance, as observed in the present study, thus reducing assimilation (Flexas et al., 2007). Moreover, a correlation between $\text{WUE}_i$ and $\delta^{13}$C in grape sugars (results not presented) would confirm findings from other research (de Souza et al., 2005a, de Souza et al., 2005b; Bchir et al., 2016). Non-irrigated vines demonstrated higher $\delta^{13}$C values than irrigated vines without water stress. This result is probably associated with a lower discrimination with regard to $\delta^{13}$C and to enrichment of $\delta^{13}$C in musts, which correlates with an increase in $\text{WUE}_i$. There is generally an enrichment of $\delta^{13}$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 $\delta^{13}$C. Lastly, recent studies (Spangenberg et al., 2017, Spangenberg and Zufferey, 2018; Spangenberg and Zufferey, 2019) have shown 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.

The decline in $g_s$ and in $A_{\text{net}}$ during the growth season was followed by an almost linear decrease in $E$. In this way, the $A_{\text{net}}/E$ ratio, named instantaneous water use efficiency ($\text{WUE}_{\text{inst}}$), diminished over the season (Figure 3E) but remained, nevertheless, practically identical among the different vine water regimes. Stomatal conductance $g_s$ is sensitive not only to water stress but also to environmental factors, such as, for example, the water vapor deficit of the air or VPD (Prieto et al., 2010; Zufferey and Smart, 2012). A rise in VPD generally leads to the progressive closure of stomata but an increase in $E$, resulting finally in a fall in $\text{WUE}_{\text{inst}}$. The rise in VPD tends to diminish $\text{WUE}_{\text{inst}}$ over a wide range of water deficits as a result of decreasing $g_s$ and $A_{\text{net}}$, but not the $\text{WUE}_i$.

| Foliar analysis (% D.M) | N-tester | YAN (mg N/L) |
|------------------------|---------|-------------|
|                        | N       | P           | K           | Ca          | Mg          |
| Irrigated vines        | 2.58a (±0.15) | 0.26a (±0.02) | 1.04a (±0.07) | 4.29a (±0.17) | 0.29a (±0.02) | 524a (±15) | 231a (±14) |
| Non irrigated vines    | 2.46a (±0.17) | 0.25a (±0.02) | 0.97ab (±0.05) | 4.14a (±0.15) | 0.33ab (±0.02) | 509a (±13) | 215ab (±12) |
| Non irrigated vines + plastic covered | 2.35a (±0.16) | 0.22a (±0.03) | 0.84b (±0.07) | 4.10a (±0.12) | 0.36b (±0.02) | 483a (±15) | 189b (±15) |

Letters indicate statistical significance at the 5 % level of probability. Averages 2009-2016, Arvine, Leytron (Switzerland).
Mesophyll resistance \( (r_m) \) increased during the growing season (Figure 3G), whatever the vine water status. Water stress did, nevertheless, accentuate \( r_m \), showing that resistance increased to \( \text{CO}_2 \) transfer from sub-stomatal cavities towards carbon fixation sites or chloroplasts (Flexas et al., 2002). The increase in \( r_m \) coupled with the decrease in \( g_s \) in non-irrigated vines subjected to water stress, leads to a fall in leaf photosynthesis, as was observed in this study.

### 3.2 Mineral supply and pruning weight

The leaf content of N, P, K and Ca had a tendency to diminish with rising water stress, especially in the non-irrigated vines with plastic-covered soils when compared with well-watered vines (Table 3); this tendency was not, however, significantly different in the study period. The leaf content of Mg did however increase with water stress, and in a significant way. These results confirm those obtained from other grape varieties under the same study conditions (Zufferey et al., 2017, 2018). No significant differences in leaf chlorophyll content was found among the different water regimes imposed on vines. The content of yeast available nitrogen in musts (YAN), however, dropped as water stress increased in non-irrigated vines with plastic-covered soils (Table 3, Figure 4).

A relationship between plant water status, measured by \( \Psi_{\text{pd}} \) during the period between fruit-ripening and harvesting, and the YAN \( (R^2 = 0.62, P < 0.01) \) was highlighted: the latter decreased as water stress rose. The reduced availability of soil water and the increased plant water stress caused weakening of leaf transpiration, the process which drives minerals uptake (including nitrogen) at the root level and their subsequent transport through the canopy transpiration flow (Gonzalez-Dugo et al., 2010). Nitrogen mineralization and soil microbial activity are both negatively influenced by the soil drying conditions (Celette and Gary, 2013). Studies, carried out in different wine-growing “terroirs” by Reynard et al. (2011), have also brought to light the major role played by water supply to vines on the nitrogen content in leaves and berries. Verdenal et al. (2012) further observed that water and nitrogen supplies constitute a marker of the « terroir » effect, related to wine quality of Arvine wines, under pedoclimatic conditions of the Swiss canton Wallis.

Plant vigor, estimated by pruning weight in winter, was greatly influenced by the vine water status (Table 4). Water-stressed vines (non-irrigated vines with plastic-covered soil) showed the lowest...
weights of pruned wood, compared with irrigated vines. When compared with well-watered vines (irrigated vines), the loss in pruned wood weight reached 19% on average in the 8 years of study in non-irrigated vines with plastic-covered soil, and 5% in non-irrigated vines (rain fed).

### 3.3 Yield components and must characteristics at harvest

Arvine bud fertility (number of inflorescences per shoot) remained uninfluenced by vine water regimes on average over the 8-year study period (Table 5). Water stresses suffered by non-irrigated vines with plastic-covered soils had no impact on the fruiting of buds. The replenishment of carbon (starch) and nitrogen reserves was most likely to have been sufficient from one year to the next during the study period, in both irrigated and non-irrigated vines (Zufferey et al., 2015).

The yield regulation was carried out identically between the different irrigation treatments, where 5 clusters per plant were removed. In non-irrigated vines with plastic-covered soils, subjected to the highest water restrictions, lower berry weights were observed than from irrigated vines, or non-irrigated vines where water stresses were weak to moderate (Table 5). Finally, vine water status had no impact on cluster weights and yield per m² of soil (and per vine) at harvest time (Table 5). The water stress, which made its appearance relatively late during the ripening period in non-irrigated vines, generally had no major effect on yield (Ojeda et al., 2001; Zufferey et al., 2018), in contrast with early water deficits during the season (before veraison) (Ollat et al., 2002).

Table 6 presents must characteristics at harvest time, such as sugar content, total acidity, tartaric and malic, pH and values of glycosyl-glucose (G-G) and of aromatic precursor (3 mercapto-hexanol, P-3MH). The vine water regime did not exert any major influence on sugar contents, nor on the pH in must. Malic acid content and total

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

|              | Pruning weight (g/vine) |       |
|--------------|-------------------------|-------|
|              | 2009    | 2010    | 2011    | 2012    | 2013    | 2014    | 2015    | 2016    | Mean    |
| Irrigated vines | 643a   | 650a    | 640a    | 696a    | 644a    | 626a    | 540a    | 479a    | 615a    |
|               | (±45)   | (±27)   | (±25)   | (±37)   | (±27)   | (±30)   | (±22)   | (±17)   | (±37)   |
| Non irrigated vines | 555ab | 630a    | 574b    | 647a    | 638a    | 585a    | 546a    | 489a    | 579a    |
|               | (±25)   | (±30)   | (±27)   | (±34)   | (±30)   | (±25)   | (±22)   | (±30)   |          |
| Non irrigated vines + plastic covered | 503b   | 590a    | 407c    | 566b    | 490b    | 453b    | 506a    | 474a    | 500b    |
|               | (±24)   | (±20)   | (±30)   | (±40)   | (±20)   | (±27)   | (±25)   | (±35)   |          |

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

**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).

|           | Bud fertility (inflo/shoot) | Cluster removal (-x clusters per vine) | Berry weight (g) | Cluster weight (g) | Yield (kg/m²) |
|-----------|----------------------------|----------------------------------------|------------------|-------------------|---------------|
| Irrigated vines | 1.8a        | -5.2a                                 | 1.3a             | 240.4a            | 0.93a         |
|            | (±0.05)      | (±0.1)                                | (±0.1)           | (±15)             | (±0.13)       |
| Non irrigated vines | 1.8a        | -5.2a                                 | 1.2a             | 225.2a            | 0.91a         |
|            | (±0.04)      | (±0.2)                                | (±0.1)           | (±20)             | (±0.12)       |
| Non irrigated vines + plastic covered | 1.8a        | -5.2a                                 | 1.0b             | 208.4a            | 0.86a         |
|            | (±0.05)      | (±0.2)                                | (±0.1)           | (±21)             | (±0.10)       |

Letters indicate statistical significance at the 5% level of probability. Averages 2009-2016, Arvine, Leytron (Switzerland).
Acidity in musts were found to be lower from vines where moderate to high water stress had been experienced (non-irrigated vines), compared with well-watered vines (irrigated vines). During the hot and dry years of 2009, 2011 and 2015, the water stress observed in non-irrigated vines with plastic-covered soils led to the yellowing and loss of leaves from the basal zone of shoots: consequently, the microclimate of the cluster zone was modified, and clusters were more exposed to direct sunlight and berry temperatures rose. Such conditions may well have led to the degradation of malic acid in berries and a reduction in total acidity of musts (Ruffner, 1982a; Ruffner, 1982b). Conversely, tartaric acid increased with rising water stresses.

The aromatic potential of the Arvine grape variety was evaluated by global analysis of glycosylate compounds (G-G method) and direct quantification of the precursor 3-mercaptohexanol (P-3MH) in musts. G-G values were higher in non-irrigated vines where a moderate to strong water stress had been experienced, than in irrigated vines. Identical results had been obtained by Dienes-Nagy et al. (2016) in a study over several years and in varying climatic conditions: in hot and dry seasons, the G-G content of musts was higher than in cooler, rainy years. Observation of P-3MH concentration in musts, however, showed no significant differences between irrigated and non-irrigated vines. Furthermore, the quantity of P-3MH in musts may be influenced by the presence of Botrytis cinerea on grapes (Thibon et al., 2011, Spring et al., 2014), this fungus may provoke over-production of P-3MH in this case. During the present trial period, Botrytis cinerea was inexistent, whatever the year or the water regime imposed on vines.

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).

### Table 6. Harvest characteristics: sugar content, pH, titratable acidity (total acidity, tartaric and malic acid), glycosyl glucose (G-G) and aromatic precursor (P-3MH) in must.

|                     | Sugar (g/L) | pH   | Total acidity (g/L) | Tartaric acid (g/L) | Malic acid (g/L) | G-G (mg/L) | P-3MH (mg/L) |
|---------------------|-------------|------|---------------------|---------------------|------------------|------------|--------------|
| Irrigated vines     | 239a        | 3.07a| 10.9a               | 8.1a                | 4.8a             | 41.1a      | 48a          |
|                     | (+11)       | (+0.05) | (+0.4)            | (+0.3)             | (+0.5)           | (+3.1)    | (+4)         |
| Non irrigated vines | 239a        | 3.06a| 10.4a               | 8.3a                | 4.0ab            | 43.6ab     | 47a          |
|                     | (+10)       | (+0.04) | (+0.3)             | (+0.2)             | (+0.4)           | (+2.5)    | (+3)         |
| Non irrigated vines + plastic covered | 237a | 3.04a | 9.7b | 8.7b | 2.9b | 47.8b | 48a |
|                     | (+8)        | (+0.05) | (+0.3)            | (+0.2)             | (+0.6)           | (+2.2)    | (+4)         |

Letters: statistically significant at the 5 % level of probability. Averages 2009-2016, Arvine, Leytron (Switzerland).

The aromatic potential of the Arvine grape variety was evaluated by global analysis of glycosylate compounds (G-G method) and direct quantification of the precursor 3-mercaptobenzaldehyde (P-3MH) in musts. G-G values were higher in non-irrigated vines where a moderate to strong water stress had been experienced, than in irrigated vines. Identical results had been obtained by Dienes-Nagy et al. (2016) in a study over several years and in varying climatic conditions: in hot and dry seasons, the G-G content of musts was higher than in cooler, rainy years. Observation of P-3MH concentration in musts, however, showed no significant differences between irrigated and non-irrigated vines. Furthermore, the quantity of P-3MH in musts may be influenced by the presence of Botrytis cinerea on grapes (Thibon et al., 2011, Spring et al., 2014), this fungus may provoke over-production of P-3MH in this case. During the present trial period, Botrytis cinerea was inexistent, whatever the year or the water regime imposed on vines.

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 5 presents sensorial analysis notes conferred on wines (noted from 1 to 7), carried out a few weeks after bottling, and covering the main wine characteristics: wine bouquet (quality of aromas), structure, bitterness and global appreciation of the wine.

The quality of the Arvine wine bouquet (typicality and finesse of aromas) was judged to be slightly less attractive in wines whose grapes came from non-irrigated vines, where a strong water stress had been experienced, particularly in the years 2010 and 2011, compared with well-watered (irrigated) vines. Taking into consideration the whole period, however, differences were not always significant. Poorer supplies of nitrogen to musts (concentration of yeast available nitrogen in musts below 200 mg/L, Spring et Lorenzini, 2006), which were observed in water-stressed vines, most certainly influenced bouquet appreciations, and also the perception of bitterness and astringency on the palate. Indeed, wines from water-stressed vines and from musts deficient in yeast available nitrogen (non-irrigated vineyards with plastic-covered soils) were distinguished by higher notes of bitterness, in comparison with vines well supplied with water and nitrogen (irrigated vines). These results corroborate the conclusions reached by Verdenal et al., (2012) with regard to the importance of water and nitrogen supplies to Arvine vineyards and their impact on the wine quality from different pedo-climatic conditions. The global appreciation – or hedonic impression – of wines tasted in the present study was judged...
FIGURE 5. Evaluation of wine quality by tasting according to different sensory variables: olfactive (bouquet), gustatory (structure, bitterness) 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. Arvine, Leytron (Switzerland), 2009-2016.
to be superior in wines coming from irrigated vines, well-supplied with nitrogen, as opposed to vines with high water deficits and yeast available nitrogen deficiency in musts. This was especially true for the hot and dry years, such as 2009, 2010 and 2011. Research led by Spring et al., (2014) into the effects of nitrogen supply and the characteristics of Arvine wines, demonstrated that available nitrogen content in musts, below 180-200 mg/L, brought about a decrease in aromatic precursor concentrations in must (P-3MH) and in aromas in wines. The YAN content observed over the years of the present study remained on average above 180 mg/L, including non-irrigated vines with plastic-covered soils. In this study, P-3MH content was equivalent in musts from both irrigated and non-irrigated vines.

In white cultivars, a low to slightly moderate water stress benefits the development of aromatic components (Choné et al., 2006; Reynolds et al., 2010). A severe or sometimes even moderate water stress can have a negative impact on white wine quality, particularly affecting the finesse and the typicality 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).

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