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DIURNAL DYNAMICS OF STOMATAL CONDUCTANCE AND LEAF TEMPERATURE OF GRAPEVINES (*Vitis vinifera* L.) IN RESPONSE TO DAILY CLIMATIC VARIABLES

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Abstract. Few studies examined the stomatal conductance (gs) characteristics of grapevines with an emphasis on daily climatic responses. In the present study, diurnal measurements on leaf temperature and gs of three grapevine cultivars (Alphonse Lavallée, Crimson Seedless and Italia) were carried out. The leaf temperature values for the cultivars at 08:30 were 25.0 ±1°C and it increased to a maximum value between 12:00 and 14:50 p.m. After an almost steady course, it decreased along with the decrease in ambient temperature. The gs values increased from morning (08:30 a.m.) to mid-morning (10:30 a.m.) for all the cultivars. After reaching a peak level at mid-morning, the gs decreased gradually from the mid-morning throughout the afternoon. In the morning, the highest and the least gs values were obtained from Italia (232 mmol H_2O m^{-2} s^{-1}) and Crimson Seedless (149.6 mmol H_2O m^{-2} s^{-1}) cultivars. At around 10:30, the gs for Italia, Crimson Seedless and Alphonse Lavallée were at the highest levels with their valus 287.7, 262.1 and 242.0 mmol H_2O m^{-2} s^{-1}, respectively. The last measurements on gs at around 16:10 varied from to 96.7 (Italia) to 112.0 mmol H_2O m^{-2} s^{-1} (Alphonse Lavallée). During the daily time course, the *g*s depended mainly on irradiance. T_{leaf} showed a strong relationship with T_{air} for all the cultivars. There was a strong, but negative correlation between leaf temperature and air humidity for all the cultivars.

Key words: stomatal conductance, leaf temperature, sunlight, *V. vinifera*

INTRODUCTION

Reliable knowledge on the plant response to fluctuating ambient climatic conditions may help in performing the practical applications in plant management, such as growth and yield variability [Massonnet et al. 2007], as the assimilate production is controlled

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by the tree architecture and leaf function [Flore and Lakso 1989], both modulated by environmental interactions.

In plants, the water pathway from the stem to leaf evaporation sites is essential for maintaining leaf water balance, allowing stomata to stay open, and resulting in carbon capture. While there have been advances in understanding the mechanics of stomatal opening and closing in various plant species [Beyschlag and Ryel 1992, Jones 1998, Massonnet et al. 2007, Aliniaeifard and Meeteren 2014], the corresponding physiological mechanisms remain incompletely understood. Stomatal behavior is a complex phenomenon involving feedback controls which interact with a wide range of environmental stimuli [Zweifel et al. 2007], such as light, temperature and water status of the leaves [Johnson et al. 2009]. All the responses to various stimuli are integrated into a system of regulation of stomatal conductance (gs), allowing for harvesting as much carbon as possible.

Water deficit, due to limitations of soil available water, usually impacts on leaf gs. Plants have developed certain acclimation strategies to react rapidly in a changing, restrictive environment. Amongst the strategies, stomatal regulation plays a key role in plant response to water stress, because the stomatal regulation causes rapid variation in water use efficiency [Kaiser and Kappen 2000]. Thus, there has been increasing interest in studying the stomatal behaviors of various plant species. Chouzouri and Schultz [2005] showed that there was a good correlation between drought tolerance and the decrease in gs, as soil water availability became restricted. Detailed investigations on various plant species such as apple, apricot, grape, olive and peach, cultivated under arid environmental condition revealed that the plant species represent different physiological strategies in stomatal response to environmental variables [Larsen et al. 1989, Johnson et al. 2009]. Previously, the importance of investigations on the peach palm physiology has been emphasized [Clement et al. 1988], and Mora-Urpí et al. [1997] had identified several important issues for future research on peach palms, including the relationship among environmental and physiological variables, growth, and yield. However, there is still insufficient knowledge about the stomatal regulation and leaf temperature in grapevines, except for few studies [Chouzouri and Schultz 2005, Rogiers et al. 2011].

The vast majority of studies on the investigation of leaf stomatal behaviors have been conducted on the comparison of drought-stressed or non-stressed plants [Paranychianakis et al. 2004, Zufferey et al. 2011], while interestingly a few studies have measured the diurnal dynamics [Düring and Loveys 1996] and/or environment-dependent response of stoma [Zweifel et al. 2007].

The main aims of this study were (a) to investigate the daily changes of stomatal conductance (gas exchange) in grapevines, (b) to reveal the possible genotypic differences between certain internationally important grape cultivars, and (c) to scrutinize the relationships between environmental variables with stomatal conductance and the leaf temperature.

MATERIALS AND METHODS

Study design. The study was established on three year old grapevines in an experimental glasshouse. The grapevine cultivars Alphonse Lavallée, Crimson Seedless and

Italia (Ideal) in equal vegetative growth were individually cultivated in 40 l (solid volume) pots (35 cm diameter, 35 m height) on Richter 99 (*Vitis berlandieri* × *Vitis rupestris*) rootstock. The pots contained sterile peat (1.034% N, 0.94% P_2O_5, 0.64% K_2O, pH 5.88, Klassman®) and perlite (0–3 mm in diameter) mixture in equal volume. In winter pruning, four shoots per each vine were maintained. Lateral shoots emerging from the active summer shoots were removed daily, allowing only the main shoots to elongate in order to ensure valid measurements. The shoots were tied with thread to wires established 2.5 m above the pots to let the plants grow on a fence in an upright position, thus ensuring equal benefit from the sunlight [Sabir 2013].

Night and day temperatures during the vegetative development period were around 20 ±3 and 30 ±4°C, respectively. To achieve a concrete irrigation, two soil moisture sensors (Irrometer company, Riverside, CA) were installed 30 cm depths to continuously monitor changes in soil-water content (http://www.irrometer.com). The irrometer readings were taken every day to maintain the soil moisture at the field capacity level according to the manufacturer's guideline. To ensure the uniformity of irrigation, the water was transported directly into the pots by micro irrigation systems consisted of individual spaghetti tubes.

Measurements. The stomatal conductance (gs) and leaf temperatures (T_{leaf}) measurements were made on twelve leaves (6^{th} leaf of each main shoot) from twelve individual vines about every 55 ±20 min from 08:30 to 16:10 h. Fully expanded but not senescent sunlit leaves at the outer canopy were chosen for measurement [Johnson et al. 2009]. As previously described by Düring and Loveys [1996] and Stavrinides et al. [2010], gs was measured near the central vein of the leaf blade with a steady state porometer (SC-1 Leaf Porometer) [Zufferey et al. 2011] and was expressed as mmol H_2O m^{-2} s^{-1}. The same area of the leaves were measured [Miranda et al. 2013], because instantaneous gs can be non-uniform over such a large leaf. T_{leaf} was measured concomitantly with a fine-wire thermocouple (located in the LI-1600 chamber). Instantaneous air temperature, air humidity (using mobile data logger EBRO EBI 20) and light intensity (using light meter Lutron LX-105) inside the experimental glasshouse were recorded at the time when the leaf temperature was recorded [Hirayama et al. 2006]. The recordings were read with the software Winlog-Basic.

Statistical analysis. Data were subjected to analysis of variance (ANOVA) and mean values were compared by the Tukey test ($P < 0.05$) when a significant difference was detected in physiological variables due to time of day or season. Regression analyses were performed to reveal the relationships between environmental variables with stomatal conductance and leaf temperature.

RESULTS AND DISCUSSION

Climate parameters. Diurnal course of average air temperature (T_{air}), air relative humidity (RH) and solar radiation inside the experimental glasshouse, averaged over the three consecutive day time period of measurement, is shown in Fig. 1. T_{air} increased rapidly during the day, reaching a maximum around early afternoon. Contrary to the increase of air temperature that attains an average maximum of about 33.8°C at

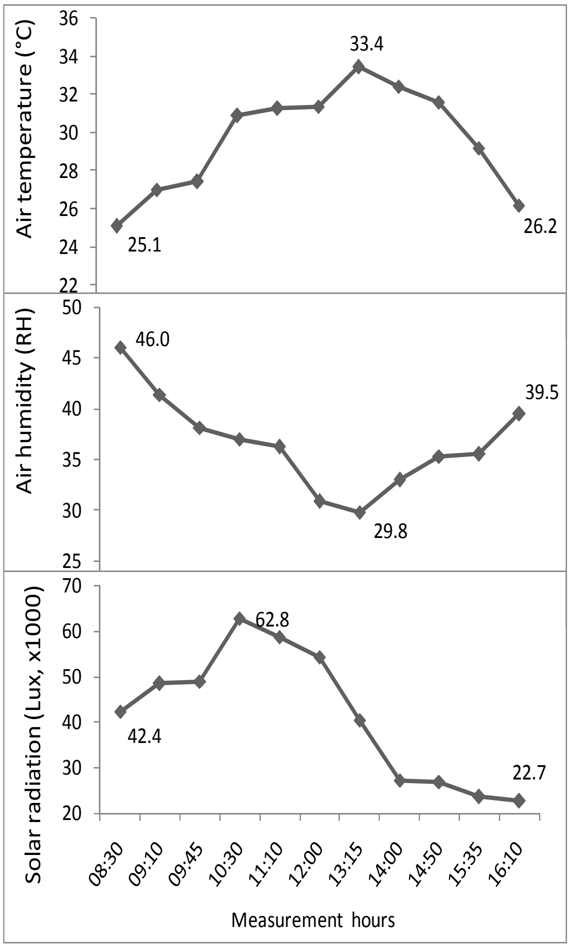

Fig. 1. Diurnal course of average air temperature (T_{air}) (A), air relative humidity (B) and solar radiation (C) inside the experimental glasshouse. The data were collected over the three clear days. The mean values are plotted against hour of the day

13:15 p.m., the RH which was 46.0% at 08:30 a.m., diminished constantly and reached the minimum level 29.8%. Light intensity inside the glasshouse was 42400 lux at 08:0 a.m. It peaked at around 10:30 a.m. (62800 lux), and gradually decreased to a minimum level of 22700 lux at 16:10 pm. Hunter and Bunnardot [2011] studied the climatic requirements grapevines using the mean hourly temperature, wind speed and relative humidity data of five seasons. They have concluded that the climatic requirements for optimum photosynthetic activity were defined as follows; temperature 25°C to 30°C, windspeed <4 m/s, relative humidity 60 to 70%. In the present study, the average T_{air} in the experimental glasshouse was slightly higher than the suggested optimum values of the mentioned study. Conversely, the diurnal RH inside the glasshouse was quite lower than the suggested ranges. Therefore, general climatic conditions during the investigations were similar to those of Mediterranean climate zone where the viticulture is widespread.

Diurnal dynamics of leaf temperature among the cultivars. Diurnal dynamics of leaf temperature among the grapevine cultivars are depicted in Fig. 2 (A, B and C). In Alphonse Lavallée cultivar, the leaf temperature value at 08:30 was 24.2°C and it incre-

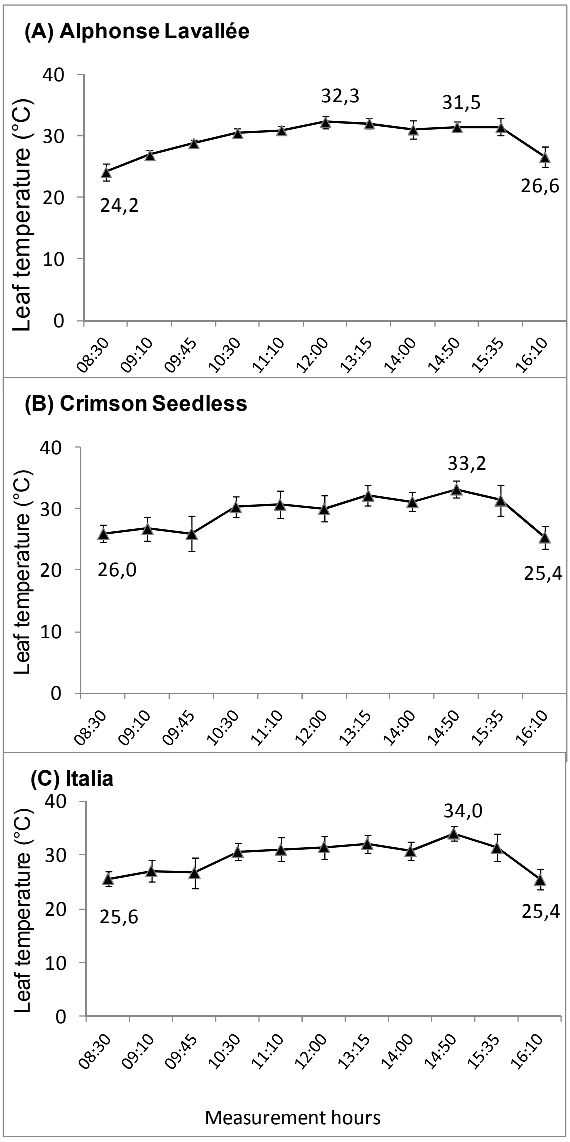

Fig. 2. Diurnal course of average leaf temperatures (T_{leaf}) of Alphonse Lavallée (A), Crimson Seedless (B) and Italia (C) cultivars. The data were collected over the three clear days. The mean values are plotted against hour of the day, with the error bars representing the 95% confidence interval

ased gradually to a maximum value (32.3°C) at around 12:00 when ambient temperature reached 31.4°C and RH dropped to 30.9%. After an almost steady course, it sharply decreased to 26.6°C at around 16:10 pm. Diurnal leaf temperature values of Crimson Seedless and Italia cultivars were quite similar to that of Alphonse Lavallée, except for slight fluctuations around 09:45 am and 14:00 pm. Actually, such a similar fluctuation was also detected in solar radiation course at the same time. These findings may possibly indicate that Crimson Seedless and Italia have higher sensitivities to solar radiation than Alphonse Lavallée. In spite of the mentioned differences, considering the overall values across the studied cultivars, the range of T_{leaf} was between the threshold values for optimum photosynthesis (25–30°C) suggested by Greer [2012] for grapevine. Midday leaf temperature values of the cultivars in the present study are higher than those measured by Rogiers et al. [2009]. According to their results, leaf temperature was highest for Shiraz and Sauvignon Blanc (27.8°C) and lowest for Pinot noir (25°C) and Semillon (25.3°C) when ambient temperature reached 27.8°C and RH dropped to 31%. However might it be surprising, Düring and Loveys [1996] found that the leaf temperature of 10-year-old field-grown Sultana vines raised to a maximum 37°C in the early afternoon. As previously stated by Marguerti et al. [2012], the leaf temperature, transpiration rate and acclimation of grapevines are directly influenced by the rootstock. Therefore, such a high differences in T_{leaf} among the studies may be arisen from different effects of rootstocks on transpiration rates and cooling of the scion as well as certain climatic disparities.

Diurnal dynamics of stomatal conductance among the cultivars. As illustrated in Fig. 3A, B and C, the gs values increased progressively from morning (08:30) to mid-morning (10:30) for all the cultivars. After reaching a peak level at mid-morning, the gs decreased gradually throughout the afternoon. The general diurnal course of gas-exchange followed the pattern mentioned by Düring and Loveys [1996] and Zufferey et al. [2011] for different grapevines, Ribeiro et al. [2009] orange, and Tucci et al. [2010] for peach palm cultivated under different ecological conditions. The *g*s values in this study never reached a steady-state during daily time courses. This was similar to the findings of Rayment et al. [2000] where the gs rarely followed a steady course. In the morning, the highest and the least gs values were obtained from Italia (232 mmol H_2O m^{-2} s^{-1}) and Crimson Seedless (149.6 mmol H_2O m^{-2} s^{-1}) cultivars. At around 10:30, the gs for Italia, Crimson Seedless and Alphonse Lavallée were at the highest levels with their values 287.7, 262.1 and 242.0 mmol H_2O m^{-2} s^{-1}, respectively. These values are well-adjusted to the findings of Zsófi et al. [2014] who investigated a gs range between 197 and 269 mmol $m^{-2}s^{-1}$ for the Hungarian grapevine cultivar Kékfrankos. In the final measurements of the present study, at around 16:10 p.m., the gs values were at minimum levels, ranging from 96.7 mmol H_2O m^{-2} s^{-1} (Italia) to 112 mmol H_2O m^{-2} s^{-1} (Alphonse Lavallée) when solar irradiation was around 227 000 lux.

In Crimson Seedless, after a midday depression at around 13:30 pm, a slight recovery of gs in the afternoon at around 14:50 was observed, indicating the more sensitive response of this cultivar since there were no recovery response in other grape cultivars. Beyschlag et al. [1992] found that evergreen *Arbutus unedo* L. and *Quercus sober* L. leaves were fully infiltratable in the early morning and in the late afternoon. This corresponds to midday depression with a recovery of transpiration and photosynthesis in the

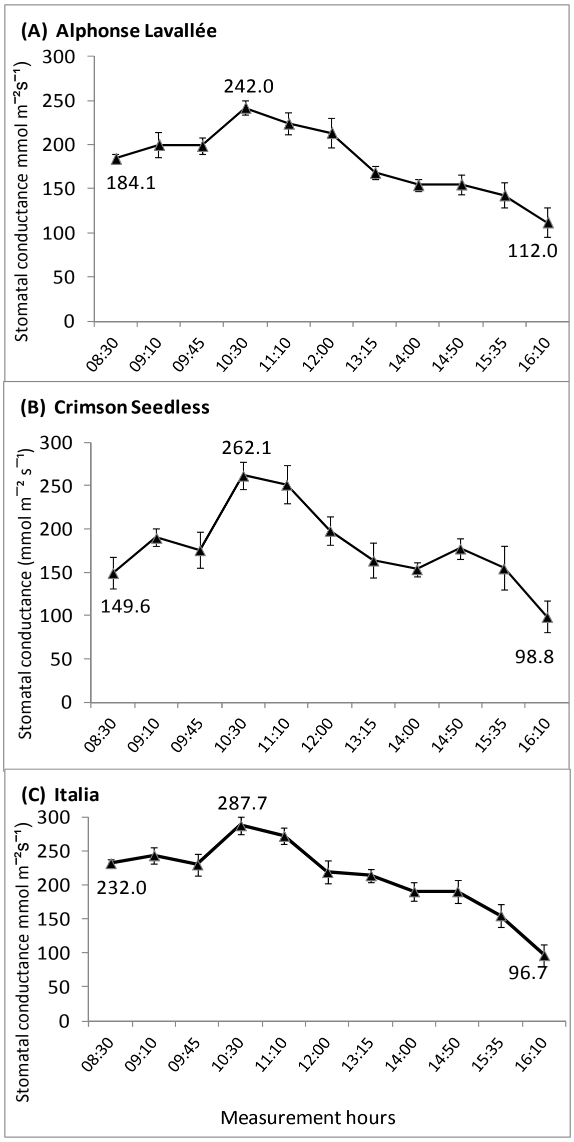

Fig. 3. Diurnal course of average stomatal conductances (*g*s) of Alphonse Lavallée (A), Crimson Seedless (B) and Italia (C) cultivars. The data were collected over the three clear days. The mean values ±SE are plotted against hour of the day, with the error bars representing the 95% confidence interval

late afternoon. In our investigations, stomatal conductances of all the grapevine cultivars were also high in the morning but did not recover in the afternoon, except for a rise in Crimson Seedless at around 14:50 pm. As previously stated by various researchers, this kind of differences between grape varieties in their stomatal responses to environmental variables can be attributed to a number of differences in morphological and physiological characteristics of their leaves [Winkel and Rambal 1990, Gibberd et al. 2001, Rogiers et al. 2011]. It is well-established that the stomatal conductance in plant species depend upon conditions such as solar irradiance, leaf temperature, relative humidity, soil and plant water status. In addition to grapevine cultivars, the genotypic variation in stomatal conductance is not unusual as is present in other plant species such as sunflower [Virgona et al. 1990], wheat [Condon et al. 1990], spruce [Grossnickle and Fan 1998], apple Massonnet et al. [2007] and arabidopsis [Aliniaeifard and Meeteren 2014]. It is generally suggested that the cultivars with a prevailing stomatal limitation generally appear more water-conserving and consequently exhibit a higher water use efficiency than cultivars with limitation by the photosynthetic machinery [Jones 1985].

Overall findings across the cultivars revealed that, the *g*s depended mainly on irradiance during the daily time course, as stated previously by Grossnickle and Fan [1998] who studied on genetic variation in summer gas exchange patterns of interior spruce (*Picea glauca* × *Picea engelmannii*). Porometer and lightmeter measurement obviously indicated that the maximal *g*s was reached after the maximal irradiance. Such a hysteresis of *g*s to irradiance has also been described previously by Vialet-Chabrand et al. [2013]. The lack of increase of T_{leaf} during diurnal course mainly between 09:10–10:30, where the highest solar radiation and increasing T_{air} was observed is connected with an increase of gs (also transpiration rate) which plays an important role in cooling leaves. The diurnal course of stomatal conductance of across the grapevines followed just opposite pattern of air humidity. A number of possible causes of the such a reverse, but tight, relation can be put forward. To illustrate, this suite of responses may describe a pattern in which the stomata functions primarily to regulate water loss, as already mentioned by Mooney et al. [1983] who studied the stomatal response of shrubby plants to humidity.

Relationships between environmental variables with stomatal conductance and leaf temperature. Regression analysis (r, the Pearson correlation coefficient) results are presented in Table 1. Correlations of gs and leaf temperature with air temperature, air humidity and solar radiation in grapevine cultivars are depicted in Fig. 4, 5 and 6.

Table 1. Regression table with significance levels

		Air temperature	Air humidity	Solar radiation
Alphonse Lavallée	stomatal conductance	0.169^{ns}	0.104^{ns}	0.959^{**}
	leaf temperature	0.909^{**}	-0.922^{**}	0.054^{ns}
Crimson Seedless	stomatal conductance	0.359^{*}	-0.236^{ns}	0.819^{**}
	leaf temperature	0.793^{**}	-0.681^{**}	0.132^{ns}
Italia	stomatal conductance	0.214^{ns}	0.060^{ns}	0.879^{**}
	leaf temperature	0.871^{**}	-0.754^{**}	-0.026^{ns}

Significant values are indicated with * for P < 0.05 and with ** for P < 0.01 level, ns: not significant

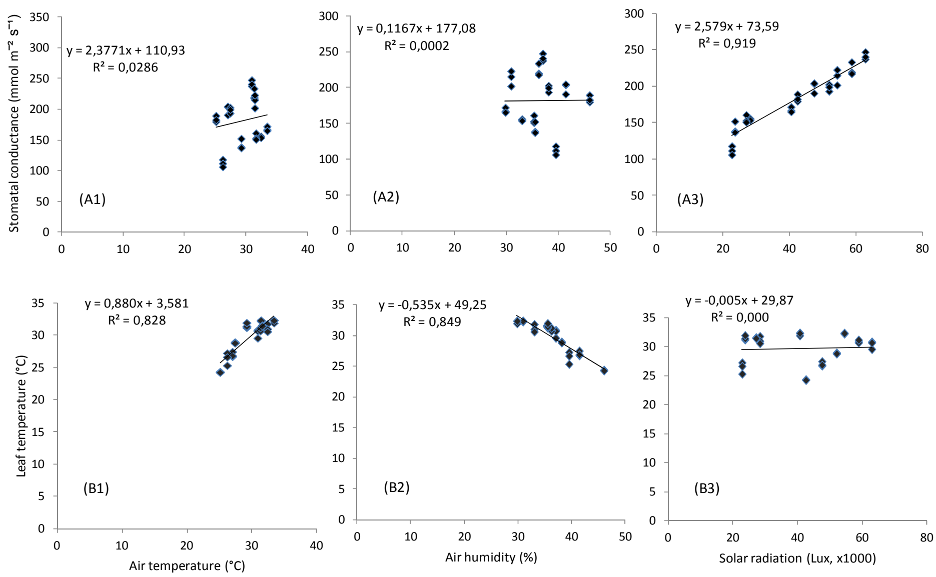

Fig. 4. Correlations of stomatal conductance (A1, 2, 3) and leaf temperature (B1, 2, 3) with air temperature, air humidity and solar radiation in Alphonse Lavallée grapevines

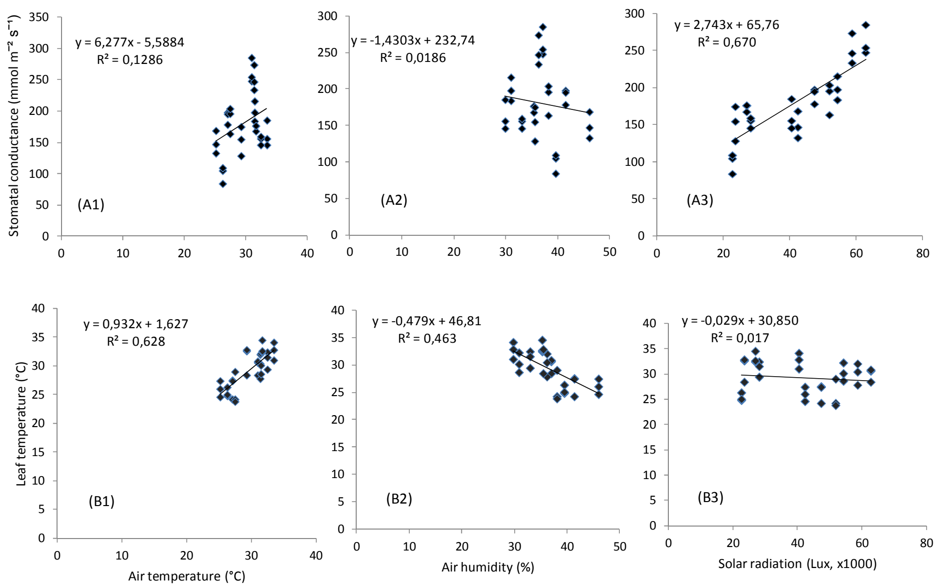

Fig. 5. Correlations of stomatal conductance and leaf temperature with air temperature, air humidity and solar radiation in Crimson Seedless grapevines

The gs responses of Alphonse Lavallée and Italia to T_{air} were insignificant while there was a significant positive correlation (P < 0.05) between gs and T_{air} in Crimson Seedless ($R^2 = 0.128$). The gs insignificantly responded to air humidity across the cultivars. However, the gs better correlated with solar radiation for all the cultivars ($R^2 = 0.919$, 0.670 and 0.773 for Alphonse Lavallée, Crimson Seedless and Italia, respectively) than with the other measured parameters. This indicate the significant effect of the sunlight on stomatal control as previously stated by Marschner [1995] and Dalmolin et al. [2012].

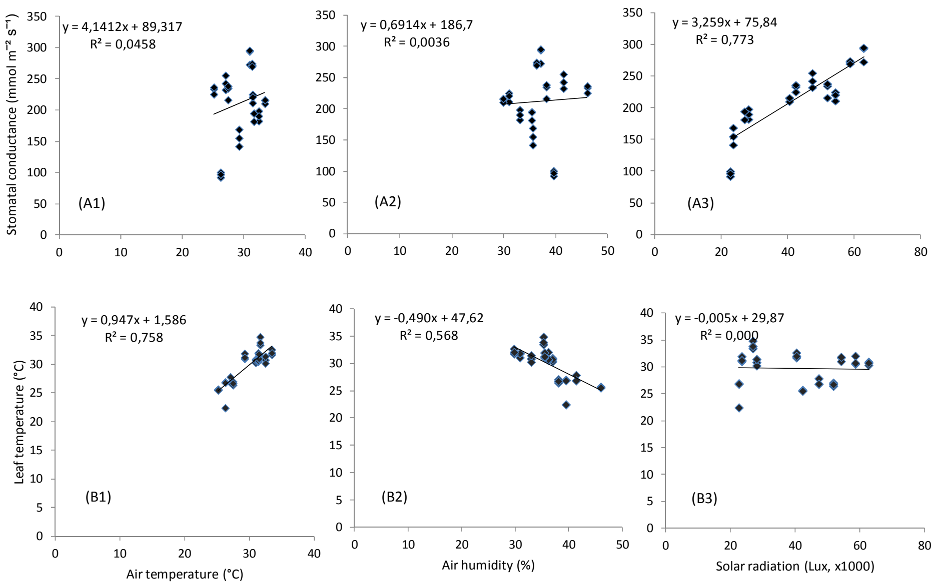

Fig. 6. Correlations of stomatal conductance and leaf temperature with air temperature, air humidity and solar radiation in Italia grapevines

T_{leaf} showed a strong relationship (P < 0.01) with T_{air} for all the cultivars ($R^2 = 0.828$, 0.628 and 0.758 for Alphonse Lavallée, Crimson Seedless and Italia, respectively). On the other hand, there was a strong (P < 0.01), but negative correlation between leaf temperature and air humidity for all the cultivars ($R^2 = 0.849$, 0.663 and 0.568 for Alphonse Lavallée, Crimson Seedless and Italia, respectively). Leaf temperature response of the cultivars to solar radiation was insignificant.

CONCLUSION

Considerigng the present and previous findings on grapevines, it possible to conclude that (a) the increase of stomatal conductance in the early morning was mainly due to the increase of light intensity, (b) the stomatal conductance can change with short term changes of solar radiation, (c) the stomatal response of different grapevine genotypes were quite different, although the diurnal leaf temperatures of the cultivars were very similar, (d) daily stomatal conductance courses of Alphonse Lavallée and Italia were more stable than that of Crimson Seedless and therefore the latter cultivar might be more sensitive to environmental variables.

The description of environmental plasticity of different grape cultivars is of particular interest for horticulture in order to reveal the potential adaptation of a cultivar to a given climate and therefore the need of finely tuning cultural practices when the environmental conditions are restricting for productivity. In order to understand the behavior of the grapevine within a particular terroir and to facilitate future terroir selection and zoning, these concepts must be studied in concert. Further examination of a large range of grape cultivars can yield valuable knowledge and further value.

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DOBOWA DYNAMIKA PRZEWODNOŚCI SZPARKOWEJ I TEMPERATURY LIŚCI WINOROŚLI (*Vitis vinifera* L.) W REAKCJI NA DZIENNE ZMIENNE KLIMATYCZNE

Streszczenie. Istnieje niewiele badań, które zajmowały się cechami przewodności szparkowej (gs) winorośli z akcentem na dzienne zmienne klimatyczne. W niniejszym badaniu przeprowadzono pomiary temperatury liści oraz gs trzech odmian winorośli (Alphonse Lavallée, Crimson Seedless i Italia). Temperatura liści u tych odmian o godzinie 8.30 wynosiła 25,0 ±1°C i zwiększała się do maksymalnej wartości między 12.00 a 14.50. Po okresie prawie wyrównanych wartości temperatura spadała wraz ze spadkiem temperatury otoczenia. Wartości gs rosły w godzinach porannych (8.30–10.30) dla wszystkich odmian. Po osiągnięciu poziomu szczytowego, gs stopniowo zmniejszała się począwszy od godzin rannych przez całe popołudnie. Największe i najmniejsze wartości gs rano osiągnięto u odmian Italia (232 mmol H_2O m^{-2} s^{-1}) i Crimson Seedless (149,6 mmol H_2O m^{-2} s^{-1}). Około 10.30 wartości gs dla Italia, Crimson Seedless oraz Alphonse Lavallée były największe i wynosiły, odpowiednio, 287,7; 262;1 i 242,0 mmol H_2O m^{-2} s^{-1}. Ostatni pomiar gs około 16.10 wskazywał od 96,7 (Italia) do 112,0 mmol H_2O m^{-2} s^{-1} (Alphonse Lavallée). Podczas dnia gs zależał głównie od napromieniowania. $T_{liść}$ wykazywał silny związek a $T_{powietrze}$ dla wszystkich odmian.

Słowa kluczowe: przewodność szparkowa, temperatura liści, światło słoneczne, *V. vinifera*

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