Journal of Stress Physiology & Biochemistry, Vol. 8 No. 4 2012, pp. 302-321 ISSN 1997-0838

ORIGINAL ARTICLE

Physiological behaviors and recovery responses of four galician grapevine (*Vitis vinifera* L.) cultivars under water stress

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Received October 12, 2012

Gas exchange parameters and chlorophyll fluorescence of four pot grown Galician grapevines (*Vitis vinifera* L. cv. Albariño, Brancellao, Godello and Treixadura) were examined under different levels of water stress in greenhouse. After extreme stress, gas exchange recovery responses were evaluated. Average Ψ_{PD} for control and stressed plants were -0.4MPa and -1.45MPa respectively. All varieties showed gradual declining of all gas exchange parameters (gs, E and *A*) with increasing of stress periods. Under stressed conditions, Albariño and Godello showed higher CO_2 assimilation rate. At the end of stress period leaf defoliation was found in Albariño and Brancellao. Gas exchange recovery was higher for both Godello and Treixadura. A better response of auxiliary bud recovery was present in Albariño than in Brancellao. Close correlations between water stress and gas exchange parameters were found and it varies on genotype. Albariño, Godello and Treixadura followed same diurnal patterns of gas exchange rate for control and stressed plant respectively. Diurnal pattern of CO_2 assimilation rate of all tested varieties followed gs and E. Only Brancellao showed treatment effect on mid-day Fv/Fm. Among four varieties photoinhibition was only found in Brancellao. At stressed condition physiological responses of grapevines were genotype depended.

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Key words: Vitis vinifera L.; water stress; CO2 assimilation rate; chlorophyll fluorescence.

Abbreviation: A, CO2 assimilation rate; gs, stomatal conductance; E, leaf transpiration; ΨPD, predawn leaf water potential; MPa, mega pascal; PPFD, photosynthetic photon flux density; C, control treatment; S, stress treatment; and R, recovery treatment. F, minimum fluorescence of dark adapted samples; Fm, maximum fluorescence of dark adapted samples; Fv=Fm-F, variable fluorescence yield; Fv/Fm, maximum quantum yield of photosystem-II.

Water stress is a physiological reaction of a plant to insufficient water supply. In agricultural context, water stress is one of the most principal environmental factor limiting plant physiology as well as productivity (Schulze, 1986). Geographically large proportion of grapevines are being cultivated in mediterranean regions with frequent seasonal drought, high temperatures, leaf-to-air vapor pressure deficit and high levels of irradiance (Patakas and Noitsakis, 2001; Patakas *et al.,* 2002). Albariño, Brancellao, Godello and Treixadura are four Galician grapevine cultivars very important for wine production in Spain. In recent year due to dramatic climate change productivity of these cultivars are becoming low. Water stress affects physiological activities of grapevine and depending on the timing and stress level; it regulates the growth rate, and the development of the shoots, leaves and fruit (Chaves *et al.,* 2010; Chone *et al.,* 2001a; Matthews and Anderson, 1989; Medrano et al., 2003; Serrano et al., 2010). At leaf, water stress can play negative role in photosynthesis because of stomatal closure and metabolic imbalance (Escalona *et al.,* 1999; Flexas *et al.,* 1998, 2002a; Flexas, 1999). So, studying grapevine physiology is an important tool to understand the water stress level and how stress may influence grape physiology which ultimately affects grape yield and quality.

According to the severity of water stress grapevine changes their physiological responses in-order to cope up with adverse conditions. Stomatal regulation is one of the major adaptive responses to water stress which in turn regulate transpiration and prevents leaf water potentials decreasing and make it steady to activate the hydraulic conductivity system. It also affects CO_2 assimilation rate (Flexas *et al.,* 1998). Consequently, stomata have a dual role of balancing transpiration and carbon dioxide exchange to prevent excessive water loss, whilst maintaining adequate carbon dioxide levels to support photosynthetic activity to maintain healthy vine function and reproduction (Cowan and Farquhar, 1977).

Depending on stress level plants react differently. In mild water stress there might be a leaf expansion effect but has not effect on photosynthesis rate (Hsiao, 1973) but some studies concluded that mild water stress might cause canopy reduction as well as amount of photosynthetically active radiation intercept and photosynthesis (Chaves *et al.,* 2010; Petrie *et al.,* 2003; Poni *et al.,* 2003). On the other hand severe water stress might causes leaf chlorosis, defoliation, vine cell desiccation and cell death, reduce fruit production, reduction in berry size, berry drying, delay of sugar accumulation in fruit, reduction of fruit coloration (Coggan, 2002; Selker and Baer, 2002). Water stress may also have less obvious or indirect effects on fruit yield and quality. For example, reducing berry size increases the skin to juice ratio, which may increase the concentration of anthocyanins and phenolics in the must and red wine (Hardie and Considine, 1976; Koundouras *et al.,* 2006; Matthews and Anderson, 1988; 1989; Van Leeuwen and Seguin, 1994).

In case of red wine production some extend of water stress is favorable for grape quality (Ribereau-Gayon *et al.,* 1998) because of accumulation of sugar content dependent on water availability in the field (Tregoat *et al.,* 2002; Serrano *et al.,* 2010). Sometimes plants facing drought stress could carry out some adaptive processes which lead plants to experience with adverse climatic condition and also help to establish a new stable physiological condition, through which plants could survive in stressed conditions (Larcher, 1987).

Ideally water stress could be measured by monitoring one or more physiological responses of a vine such as leaf water potential, CO_2 assimilation, stomatal conductance, leaf transpiration and chlorophyll fluorescence. Among them stomatal conductance as well as CO_2 assimilation provide direct information associated with water loss (Monteith, 1995; Maroco *et al.,* 1997). Between soil based and plant based measurements of water stress plant based measurement is preferred because of leaf water potential, stomatal conductance and chlorophyll fluorescence could be estimated directly and clearly through leaf measurements (Pellegrino *et al.,* 2005). Measurement of gas exchanges of single leaves could suggest the whole plant water status under drought condition (Smart, 1974) and gas exchange analysis is very common and efficient tool to measure CO_2 assimilation, stomatal conductance and transpiration as well (Long *et al.,* 1996).

Different grapevine cultivars might have different response to water stress because stomatal conductance and photosynthesis to stressed conditions vary from genotype to genotype (Kriedemann and Smart, 1969; Tardieu and Simonneau, 1998) and the severity of water stress (Flexas *et al.,* 1999). Different cultivars have different effects on stomatal sensitivity to drought and grape quality which also depends on soil and environmental conditions (Flexas *et al.,* 2002c). In vascular plant like grapevine, water potential in a particular time represents the plant water status on that time. Leaf water potential is also a good indicator of plant water status under stressed condition (Hsiao, 1973; Rana *et al.,* 2004). The most common tool for measuring water potential is the pressure chamber (Scholander *et al.,* 1965; Slavik, 1974).

In recent times chlorophyll fluorescence measurement became one of the powerful tools to plant physiological studies. Without measuring chlorophyll fluorescence, measurement of photosynthetic activities is incomplete because by measuring chlorophyll fluorescence yield photochemical efficiency can be estimated clearly (Maxwell and Johnson, 2000). As water stress increases, the biochemical limitation of the photosynthetic process does not allow achievement of the potential rate for CO_2 assimilation, despite CO_2 saturation (Lawlor and Cornic, 2002). So, photosynthesis becomes limited due to irreversible damage to the photosystems (Havaux *et al.,* 1986). In dark adapted condition, decreasing of Fv/Fm and increasing of Fo represents leaf photo inhibitory damage due to water stress (Erpon *et al.,* 1992).

In artificial condition gas exchange parameters of stressed plants gives doubtful and complex results compared with field conditions (Flexas *et al.,* 2002b) because these values are regulated by high temperature and irradiance associated with water stress (Correia *et al.,* 1999; Ort *et al.,* 1994). Alternatively it is easy to achieve accurate stress level in potted grapevine in control conditions (Escalona *et al.,* 1999) because in an open field water deficit might be achieved very slowly (Flexas *et al.,* 1998; Loveys and During, 1984).

The objectives of this study were to see different physiological responses (E, gs and *A*) as well as recovery responses of four Galician grapevine varieties under different levels of water stress conditions.

MATERIALS AND METHODS

Plant material establishment

32 dormant grapevines (*Vitis vinifera* L.) from Galician (Spanish) varieties (Treixadura, Albariño and Brancellao grafted on 110-R and Godello/SO_4 rootstocks) were used for this study. Plants were planted in 5L plastic pots using light textured soil without fertilizer and placed in greenhouse 5 month before starting treatment. 10 gm of organic fertilizer named "Compo Abono Arbolesfrutales" containing "9%N, 5%P_2O_5, 13% K_2O, 4% MgO and 56% Organic materials" was applied to each pot. Additionally all potted plants received 0.1L of full Hoagland solution (Hoagland and Arnon, 1950) to enhance growth. Lateral buds, shoots, leaves and

young flowers were removed in order to get homogeneity among the plants. Before applying treatments plants were irrigated at the interval of two days. Inside the greenhouse temperature was recorded with 'HOBO Pro Series Temp, RH (C) 1998 ONSET'.

Drought establishment in different phases of study

Plants were allowed to grow under favorable conditions and then pots were watered sufficiently up to water saturation. After 24 hours of water draining total weight of pots was measured which indicate 100% water content into the pots. To minimize the direct soil water evaporation 2 cm perlite was extended over each pot (Escalona *et al.,* 2002). Measurements were taken on 7-8 different days of the stressed period. Total experiment was carried out with three phases. Diurnal gas exchange was measured only for second and third phase of our experiment.

First phase of stress treatment was conducted on four cultivars initiated on 4 May, 2012. Plants were allowed to face 11 days of stress period. **Second phase** of stress treatment was conducted on two cultivars (Treixadura and Godello). Water withholding was started on 23 May, 2012 and plants were allowed to face 11 days of stress period. Diurnal time course of gas exchange parameters were measured at 7 different times (8:00h, 10:00h, 12:00h, 14:00h, 16:00h, 18:00h and 20:00h) on 6th day of the stressed period. **Third phase** of stressed treatment was carried out with Albariño cultivar grown in peat and perlite (50%+ 50%). On 19 June 2012, irrigation was stopped and allowed 6 days to face stressed condition. Predawn leaf water potential and gas exchange were measured on 6 consecutive days. Diurnal pattern of gas exchange were measured at 7 different times (9:00h, 11:00h, 13:00h, 15:00h, 17:00h, 19:00h and 21:00h) of two different days (1st and 5th) of the stressed period.

Recovery response measurement: At the end of stress period for above three phages plants were irrigated 80% and recovery measurements were taken on the next afternoon.

Experiments were conducted according to randomize block design. Two block per variety and four plants per block were designed (2X4).

Gas exchange measurement

Gas exchange parameters (*A*, gs and E) were measured with portable gas analyzer IRGA (Lc-Pro$^+$, ADC, UK). For all three phages data were taken between 12:00h–13:00h of 7-8 consecutive days of total stressed period. Leaf chamber temperature was fixed to 28ºC with 'Peltier heat module' and CO_2 concentration was fixed to 550µmolm^{-2}S^{-1} by using CO_2 cartridge. Photon flux density PFD was set at 1200µmolm^{-2}S^{-1} with 'LCpro lamp'. Measurements were taken for each plant, on mature, undamaged leaves that had grown fully exposed to the sun. Eight full expanded leaves of same age and same location per treatments were examined and were then averaged.

Water potentiality measurement

Predawn leaf water potential (Ψ_{PD}) was measured only second and third phage of treatment with a Scholander pressure chamber (Soil Moisture Equipment Crop., Santa Barbara, UK) at 06:00h before sunrise on 1 to 5 consecutive days from beginning to the end of stressed period for each variety.

Chlorophyll fluorescence measurement

According to Roiloa and Retuerto, (2006) chlorophyll fluorescence healthy and exposed leaf was measured with pulse-amplitude-modulated fluorometer (PAM-2000, Walz, Effeltrich, Germany).

F, Fv and Fm parameters were measured after 30 min of dark adaptation with the Dark Leaf Clip DLC-8 in which the fiber optics are positioned at right angle with respect to the leaf surface at a distance of 7 mm).The Fv/Fm ratio, indicating the maximum quantum yield of photosystem-II (PSII) was calculated automatically by the MINI PAM. Measurements were applied around solar noon when differences are maximal (Palliotti *et al.,* 2008; Roiloa and Retuerto, 2006).

Statistical analysis

Statistical analysis was carried out with the SPSS statistical computer package (IBM SPSS for Windows, Version Release 19.0). Statistically differences in Ψ_{PD}, E, gs *A* and Fo/Fm were analyzed by GLM procedure and factor level was established according to factor significance and interactions. Studies of instantaneous comparisons were carried out by analysis of variance (ANOVA). Significant effect of means was identified with Tukey-test at 0.05 probabilities.

RESULTS

Temperature:

During the whole experiment period inside the greenhouse average temperature was 18.5^0C. The maximum (43.9^0 C) and minimum (2.89^0 C) temperature were recorded during the study period.

First phage

Gas-exchange: As expected, among the four grapevine cultivars there were highly significant differences in gas exchange parameters between stress and control plants. But within the cultivars, in Albariño and Brancellao there were not significant differences in gs (Fig.1). Carbon-dioxide assimilation rate (*A*) was highly significant for three varieties (Treixadura, Godello and Brancellao) but not for Albariño (Fig.1). There was no significant difference of E in Brancellao. Among the stressed plants of four cultivars except gs there were significant differences in leaf transpiration E ($P<0.012$) and CO_2 assimilation rate ($P<0.01$). In our study, among stressed plants Albariño showed maximum stomatal conductance (gs=0.09 mmolm^{-2}s^{-1}) and Godello showed maximum CO_2 assimilation rate (*A*=5.55µ molm^{-2}s^{-1}) (Tab.1).

Daily evaluation of gas exchange parameters:

In the first study, Albariño showed rapid decline of *A* from 3th to 8th day (8.53µmolm^{-2}s^{-1} to 2.97 µmolm^{-2}s^{-1}) of stress period. But from 8th day (*A*=2.97 µmolm^{-2}s^{-1}) to 11th day (*A*=2.85 µmolm^{-2}s^{-1}) declining rate of *A* was very slow. At 3rd day, *A* of **Treixadura** was 6.38 µmolm^{-2}s^{-1} and it rapidly declined to 3.83 µmolm^{-2}s^{-1} at 4th day of stress period. From 4th to 10th (*A*=3.07µmolm^{-2}s^{-1}) day of stress period declining rate of *A* was very slow. **For Godello** there was no rapid declining of *A* till 8th day of stress period. At the beginning (3th day) *A* was 6.95 µmolm^{-2}s^{-1} and at 8th day it declined to 6.04 µmolm^{-2}s^{-1}. Although at 11th day *A* declined to 1.79 µmolm^{-2}s^{-1} but throughout the stressed period Godello showed higher stability in decreasing photosynthesis. Till 10th day there was lower *A* for **Brancellao** but it showed good steady in *A* declining rate (Fig.2b).

Brancellao, Godello and Treixadura showed almost same stomatal conductance (gs) along the stress period. But for Albariño stomatal conductance was not steady under stress conditions (Fig.2a). The evolution of E, along the time was similar in all cultivars tested (Fig.2c).

Correlations

Figure 3 Shows the relationships between; E and gs; gs and *A* for four water stressed grapevine cultivars. Strong correlation between gs and *A* was found in Treixadura (r^2=0.86), Brancellao (r^2=0.66) and Godello (r^2=0.28). Alternatively for Albariño, *A* was weakly correlated with gs (r^2=0.0002). There was strong correlation between gs and E for Treixadura and Brancellao. On the other hand correlation coefficient between E and gs of Godello was r^2=0.03. Under stressed condition only Albariño negatively correlate between E and gs (r^2=0.09) (Fig.3c).

Leaf Defoliation: At the end of stressed period leaf chlorosis and defoliation was noticed in Albariño and Brancellao. After 5-7 days of extreme water stress, Albariño and Brancellao plants were almost defoliated and rest of leaves were dried. Leaf drying and fall were started from the base of shoots. After 10- 15 day of re-watering plants of both varieties started to recover auxiliary buds burst.

Recovery: Godello and Treixadura showed higher recovery response of E, gs and *A.* Albariño and Brancellao showed comparatively lower and same recovery responses. (Fig. 4).

Second experiment

Water potential

There were significant differences of predawn leaf water potential (Ψ_{PD}) of two varieties (Godello and Treixadura) at different levels of soil water content. At control and mild water stressed conditions, the plants of both varieties showed same Ψ_{PD} while at extreme water stress (Tab.2).

Gas exchange

Between two varieties (Godello and Treixadura) gs, *A* and E were significantly different in all treatments (control, stressed and recovery). Within the variety, gas exchange parameters (gs, *A* and E) of control plants were significantly different from both stressed and recovery plants.

There was no significant difference of *A* between stressed and recovery plants for Treixadura while it was statistically difference for Godello (Fig.5). There was no significant difference of gs between stressed and recovery treatment for both cultivars. In case of leaf transpiration (E), Godello showed significant difference in all treatments but not for Treixadura (Fig.5).

Gas exchange pattern at different days after water withholding

Both Godello and Treixadura exhibited same gas exchange pattern with increasing of water stress during the whole stressed period. At stressed condition Godello showed higher gas exchange parameters (gs, *A* and E) (gs=0.084 mmolm^{-2}s^{-}1; *A*= 7.95 µmol m^{-2}s^{-}1) (Fig.6).

Correlations: Both Godello and Treixadura showed strong correlation between predawn leaf water potential (Ψ_{PD}) and either stomatal conductance (gs) or CO_2 assimilation (*A*) (Fig.7) There were high correlation between gs and *A*; E and gs.

Diurnal pattern of leaf gas exchange parameters

Control and stressed plants of both Godello and Treixadura showed same diurnal time course of gs, *A* and E respectively.

gs: Maximum gs values for control plants were recorded at 12:00h and afterward both varieties started to decline gs. For stressed plants maximum and minimum gs were observed at 10:00h and 16:00h respectively. After 16:00h both of varieties recovered gs while Godello showed higher recovery response of gs than Treixadura (Fig.8a).

***A*:** Control plants of both varieties showed maximum CO_2 assimilation rate (A) between 10:00 to 12:00h while stressed plants at 8:00h to 10:00h.

For Godello, maximum *A* (4.6µmolm^{-2}s^{-1}) of stressed plants was found at 10:00h afterward it started to decline. Godello started to recover *A* after 14:00h (Fig. 8b). Stressed plants of Treixadura showed maximum *A* (4.2 µmolm^{-2}s^{-1}) between 8:00h to 10:00h and minimum *A* (0.26 µmolm^{-2}s^{-1}) at 18:00h. Afterward it also started to recover the *A* value (Fig. 8b).

E: For control plants of both cultivars maximum and minimum E was shown at 12:00h and 20:00h respectively while maximum and minimum E of stressed plants were recorded at 10:00h and 16:00h respectively. Afterward both varieties started to recover E. Godello showed higher recovery response of E than that of Treixadura (Fig.8c).

Third experiment

All the gas exchange parameters of Albariño were strongly followed by leaf water potential (Ψ_{PD}) at different days of stress period (Tab.3). At the 2nd day of stress period gs was increased rapidly as Ψ_{PD} increased very small amount and afterward it declined rapidly with declining of water potential (Fig.9a). Albariño showed higher recovery response of Ψ_{PD} and average recovery of Ψ_{PD} was (-0.022MPa) which is same as control plants (-0.021) (Fig.9).

Diurnal pattern of gas exchange

At the beginning (1st day) of stress period both of control and stressed plants of Albariño showed higher gas exchange at 11:00h and afterward started to decline slowly along the day. There was a good steady state of declining of all parameters. No recovery was noticed along the 1st day of stress period (Fig.10a).

But at extreme stress period (6th day), gas exchange parameters were higher in the early morning (9:00h) and afterward started to decline rapidly. Although gs and E had started to recover slowly from 17:00h but *A* was continued to decline along the day (Fig.10b).

Correlations

All the gas exchange parameters of Albariño strongly correlated with Ψ_{PD}. (Fig.11a). There was strong positive correlation of *A* with gs (r^2=0.43), gs and E (r^2=0.48). (Fig.11b).

Chlorophyll fluorescence

Among the cultivars there were significant differences of Fv/Fm at different treatments. In this case Brancellao and Treixadura showed clear differences of total Fv/Fm but Albariño and Godello behaved intermediate of two cultivars (Fig.12A).

In dark adapted conditions, Brancellao only showed significant difference of Fv/F (P=0.03) among the treatments. Albariño, Godello and Treixadura have no significant differences among control, stress and recovery plants (Fig. 13a) .In the same treatment no significant difference of Fv/Fm was found among the four varieties (Fig.13b).Among the three treatments there were significant differences of qP at Brancellao for dark adapted condition (Tab.4).

Table 1 Comparison of E, gs and *A* of four grapevine varieties at stressed condition. Values are mean of each parameter of the whole stressed period ± SE of mean.

Variety	E(molm^{-2}s^{-1})	gs(m molm^{-2}s^{-1})	*A*(µmolm^{-2}s^{-1})
Treixadura-S	0.48±0.04	0.03±0.002	3.49±0.28
Godello-S	0.70±0.08	0.05±0.005	5.55±0.55
Albariño-S	0.99±0.09	0.09±0.01	4.33±0.26
Brancellao-S	0.70±0.07	0.03±0.002	2.09±0.30

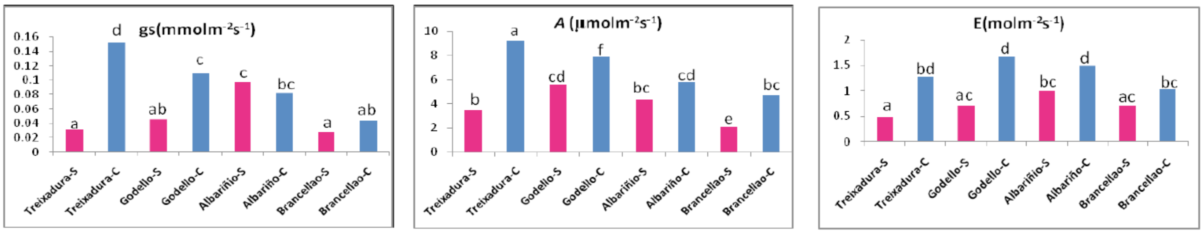

Figure 1. Total gas exchange parameters of four grapevine cultivars during first experiment (S and C indicate stress and control conditions). Different letters indicate statistically significant differences according to Tukey's test (P<0.05).

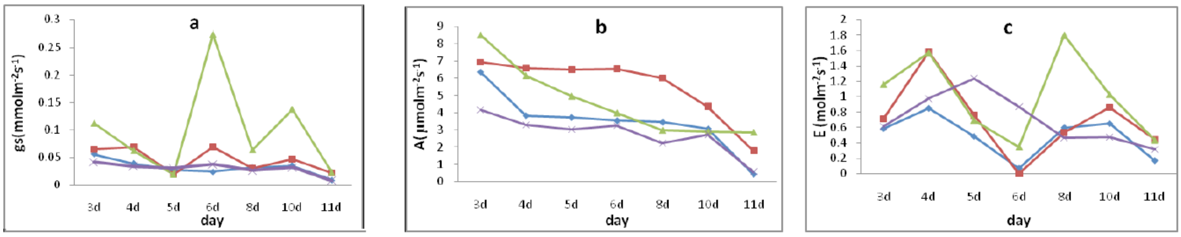

Figure 2. Daily evaluation of physiological parameters of four cultivars along the stress period. (**a**=Stomatal Conductance; **b**=Carbondioxide assimilation rate; **c**=Leaf transpiration).Values are mean of individual parameters along each day.

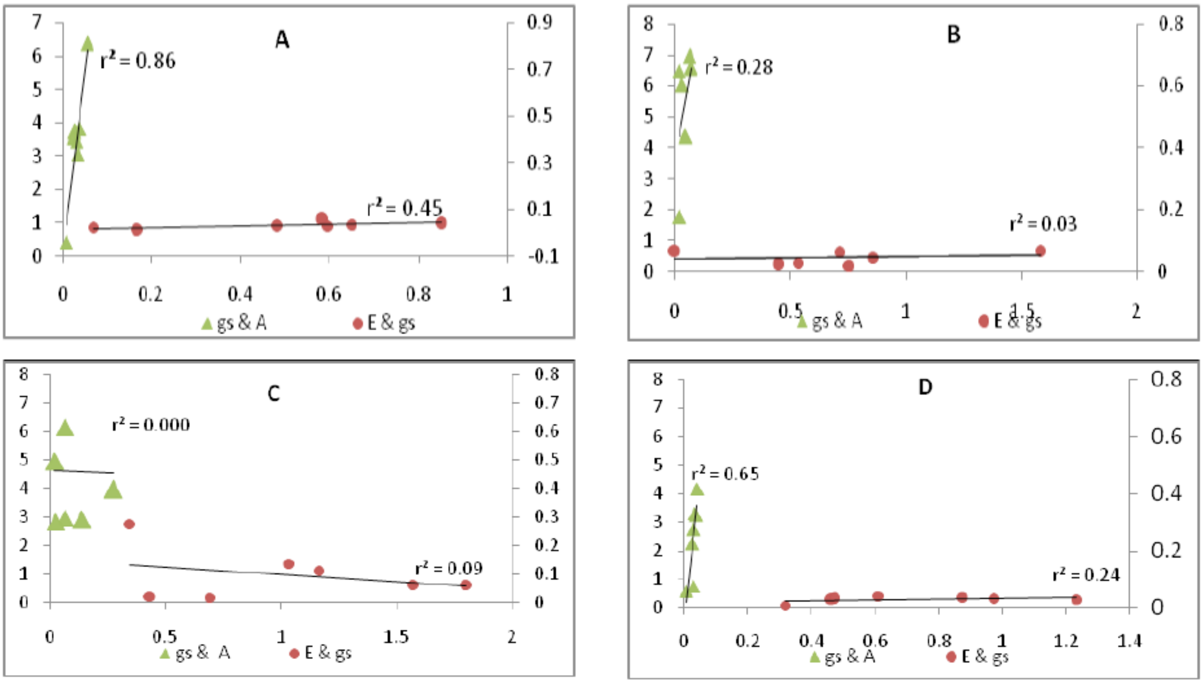

Figure 3. Correlation of gas exchange parameters of four grapevine varieties in stressed condition. (Values are mean of all parameters. A= Treixadura; B=Godello; C=Albariño and D=Brancellao).

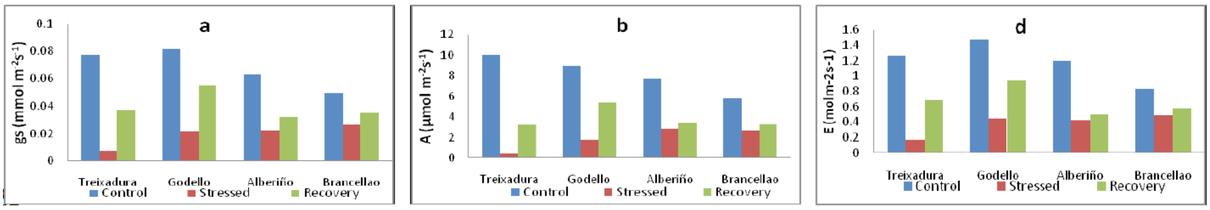

Figure 4. Comparisons of gs, *A* and E of four grapevine varieties under control, stressed and recovery conditions. (a), Stomatal conductance, (b), CO_2 assimilation rate; (c), Leaf transpiration. Values are means of every individual parameter.

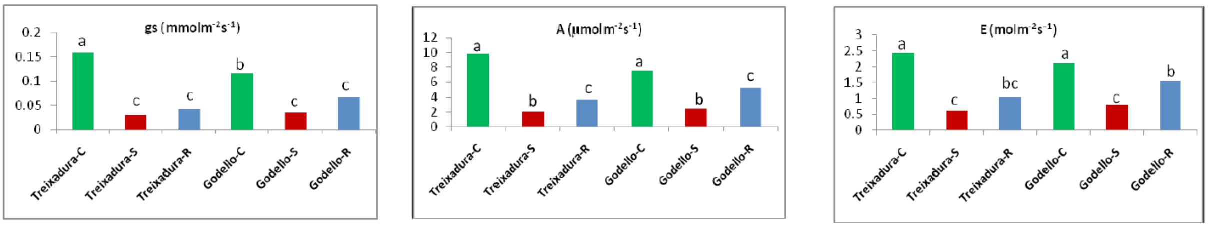

Figure 5. Mean data of gas exchange parameters of two grapevine varieties (Treixadura and Godello) at different level of water treatments. Different letters were plotted according to Tukey's test (P<0.05).

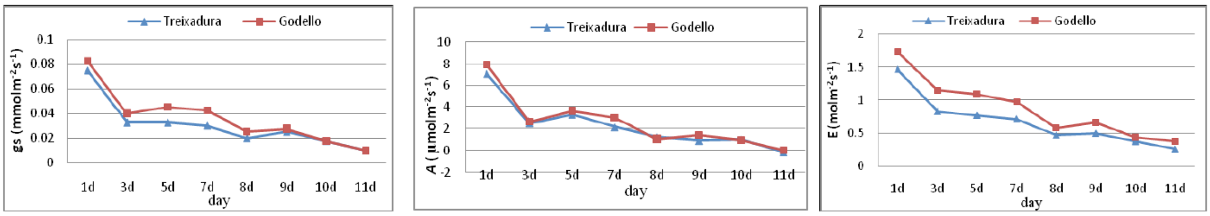

Figure 6. Daily evolution of gas exchange parameters of two cultivars (Godello and Treixaura) along the stress period. Values are mean of individual parameters.

Table 2 Predawn leaf water potential Ψ_{PD} (MPa) at different water stress treatment between two grapevine varieties (Treixadura and Godello). Values are mean±SE of mean of Ψ_{PD}. Different letter indicates significant difference according to Tukey's test

Variety	Control	Mild stress	Extreme stress	Recovery
Treixadura	-0.4±0.03a	-0.6±0.03b	-1.5±0.03c	-0.9±0.05d
Godello	-0.4±0.25a	-0.6±0.05b	-1.4±0.05c	-0.8±0.07d

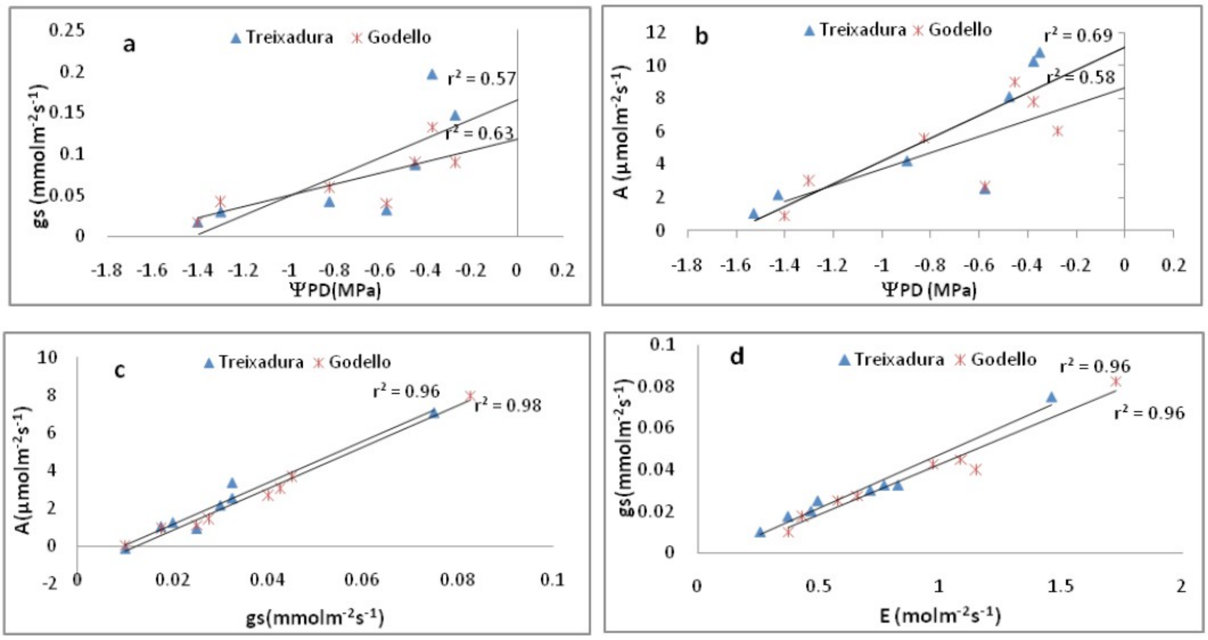

Figure 7. Correlation of Ψ_{PD} with gas exchange parameters and gas exchange parameters themselves. (a), correlation between of predawn leaf water potential (Ψ_{PD}) and Stomatal conductance (gs). (b), leaf water potential (Ψ_{PD}) and CO_2 assimilation rate (A). (c), stomatal conductance (gs) and CO_2 assimilation (A). (d), leaf transpiration (E) and stomatal conductance (gs).

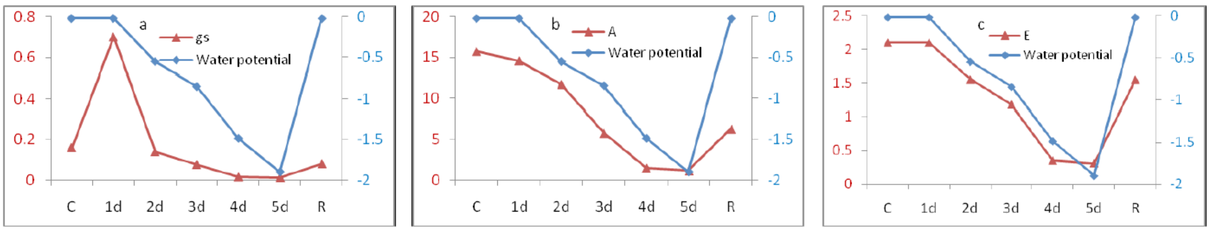

Figure 8. Diurnal time course of gas exchange parameters of two varieties (Godello and Treixadura). (a)stomatal conductance(gs); (b) CO_2 assimilation rate(*A*); (c) leaf transpiration Values are mean of individual parameters.

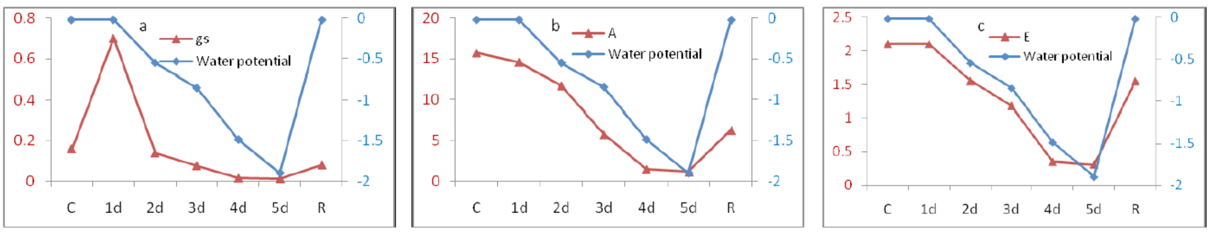

Figure 9. Daily evolution of gas exchange parameters of Albariño cultivars along the stress period (3rd experiment).Values are mean of individual parameters at different days. ('d' indicate day of stressed period , 'C and R' indicate control and recovery plants respectively).

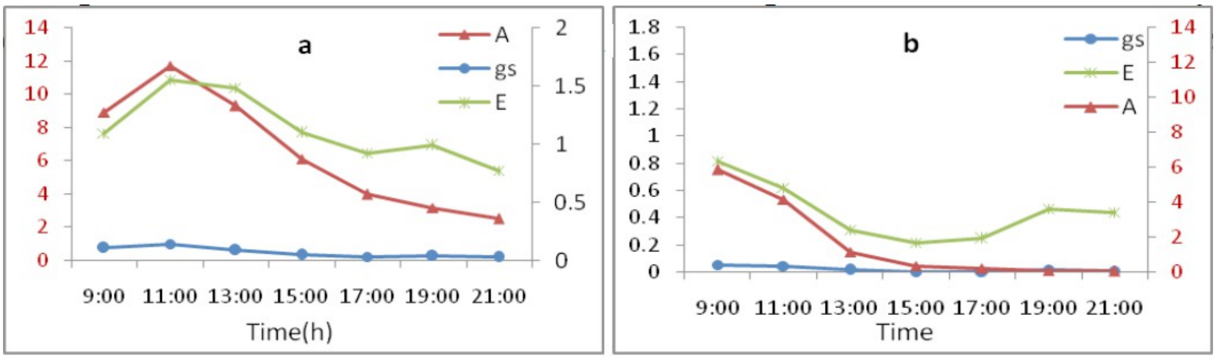

Figure 10. Diurnal pattern of *A*, gs and E of Albariño at (a), 1st day and (b), 6th day of stressed period. Values are mean of every parameter at different time. Primary X axis of 'a' and secondary X-axis of 'b' indicate *A* values.

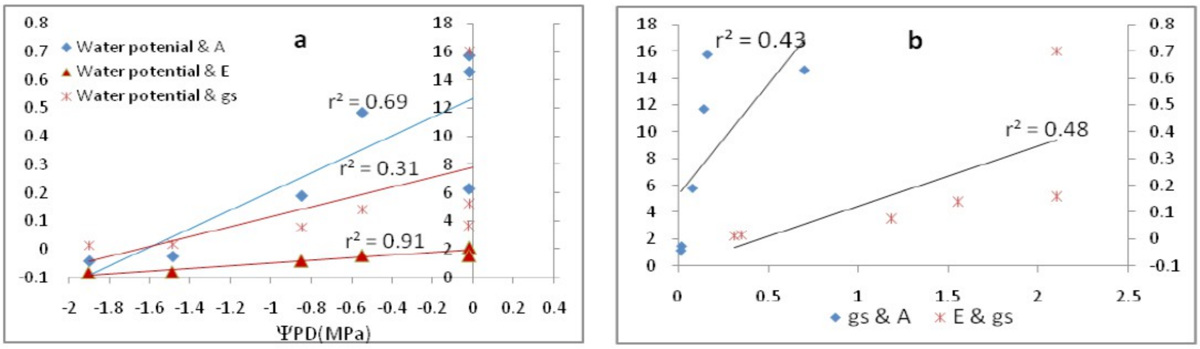

Figure 11. Correlations of (a), between Ψ_{PD} and gas exchange parameters. (b), within gas exchange parameters. Values are mean of every parameters of Albariño grapevine variety.

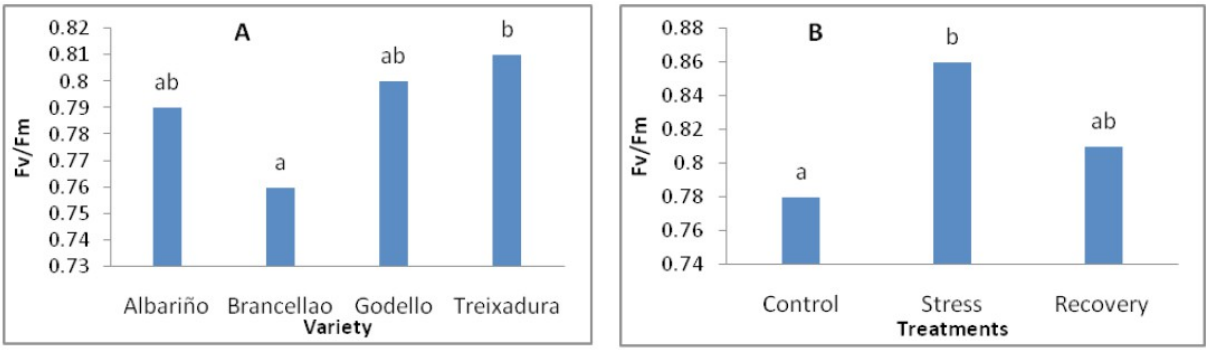

Figure 12. Fv/Fm comparison of four grapevine varieties in dark adapted condition. (A), yield comparison among the varieties. Data were analyzed with Tukey`s-test (P<0.05).

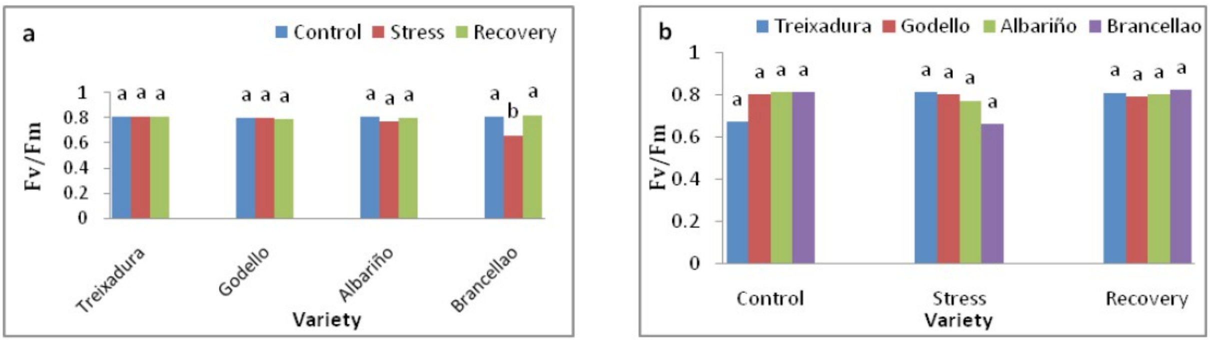

Figure 13. Mean Comparison of fluorescence yield of four cultivars at different water levels. Data have been analyzed according to Tukey's test (P<0.05). Here values are mean of total yields.

Table 3 Gas exchange parameter of Albariño at different days of stress period (3rd experiment). Values are mean±SE of mean of third experiment.('d' indicate day of stressed period , 'C and R' indicate control and recovery plants respectively).

Treatments	Ψ_{PD} (MPa)	E ($molm^{-2}s^{-1}$)	gs ($mmolm^{-2}s^{-1}$)	*A* ($\mu molm^{-2}s^{-1}$)
C	-0.021	2.1±0.14	0.17±0.02	15.76±0.73
1d	-0.02	2.10±0.10	0.7±0.01	14.60±0.86
2d	-0.55	1.55±0.19	0.14±0.03	11.69±0.99
3d	-0.85	1.18±0.24	0.08±0.02	5.78±0.55
4d	-1.49	0.35±0.16	0.02±0.07	1.47±0.72
5d	-1.90	0.31±0.10	0.013±0.01	1.14±0.56
R	-0.022	1.55±0.14	0.08±0.01	6.28±0.68

Table 4 Chlorophyll fluorescence yield of four grapevine varieties under dark adapted conditions at 14.00 h. Data are mean± SE. In each column different letters were plotted according to Tukey-test at 5% level..

Treatments	Treixadura Fv/Fm	Godello Fv/Fm	Albariño Fv/Fm	Brancellao Fv/Fm
Control	0.67±0.14^{a}	0.80±0.01^{a}	0.81±0.01^{a}	0.81±0.01^{a}
Stress	0.81±0.01^{a}	0.80.01^{a}	0.77±0.04^{a}	0.66±0.04^{b}
Recovery	0.80±0.01^{a}	0.79±0.004^{a}	0.80±0.01^{a}	0.82±0.01^{a}

DISCUSSION

In our experiments, we achieved to apply equal level of water stress to individual treatments. Ψ_{PD} in control plants was -0.4MPa which was gradually declined to -0.6 MPa at mild and to -1.5 MPa at extreme water stress. These results agree with Escalona *et al.* (2002) who conducted a research with pot grown Tempranillo grapevine variety.

Gas exchange

In all studies, there were higher stomatal conductance (gs) and CO_2 assimilation rate (*A*) at control plants and it declined at stressed plants except Albariño. In the first study Albariño showed higher gs at stressed plant than that of control plants although CO_2 assimilation rate (*A*) was higher at control plants (Fig.2). There was high fluctuation in gs and E values during the stressed period. Albariño and Brancellao showed lower and same gas exchange recovery pattern. Among four only two cultivars exhibited leaf chlorosis and defoliation. Albariño showed higher recovery response than Brancellao. Same results were found in one study of Bahar *et al.* (2011) where they reported that leaf of pot grown grapevine cultivars (Chardonnay, Merlot and Cabernet-Sauvignon) were dried and defoliate after 12th -15th days of stressed period and about 7-10 days after re-watering recovering of auxiliary buds were started at top of shoot. **In our first study,** Albariño showed abnormal results of gas exchange parameters and behaved far difference from rest of three varieties. We had not proper explanation for these abnormalities. Instrumental problem, weather or plant itself might be reason for these results. Finally we designed third experiment only for Albariño cultivar.

In the second study, CO_2 assimilation of Godello and Treixadura was accordance with the values of gs and E. Leaves of Godello and Treixadura were green and normal. After extreme stress Godello showed a more rapid recovery response of *A* than Treixadura. From this result it could be said that, Godello could survive more efficiently at soil with low water contain and it is more adapted to emergence irrigation strategies. This variety would have also aptitude to be cultivated in area with shallow or light soils and uncertain rain distribution.

In third study, daily evaluation of gas exchange parameters were strongly followed by stress period. No abnormal results of Albariño like first experiment were seen in third study. Recovery responses of gas exchange parameters were higher than first experiment. So, from third study it could be say that there might be instrumental problems or adverse weather in the first experiment which disturbed physiological activities of Albariño. Because due to severe water stress and elevated temperature leaf transpiration becomes excessive and leaf defoliation help plant to balance its demand for water from root system (Kriedemann, 1968). El-ansary and Okamoto (2007) reported that, due to water stress, one of the major responses of plant is stomatal closure, and declining of gs and *A* is associated with increasing of water stress.

In our studies shoot growth of control plants in all cultivars were higher than stressed plants. These results agree with Lovisolo *et al.* (1998) they worked with container grown grapevine (Freisa) and found that shoot growth rate was higher on irrigated than stressed plants. Among the cultivars only Treixadura showed leaf bending at the mid-day. Same results were reported in one study of Serrano *et al.* (2010) they proposed that declining of PPFD incident ultimately by leaf orientation change of stressed plants could results in lower leaf temperature. This result is also supported by Johnes (2007) reported that if leaf orientation occur after stomatal closure then it might cool the leaf.

Daily evalution of physiological parameters along the stress period

In general, all cultivars of our first study showed slow declining of *A* started from 3^{rd} day while it declined rapidly between 8^{th} to 10^{th} days of stressed period. Same findings were reported by Bahar et al. (2011) who found minimum values of *A* at 6^{th} and 9^{th} days of stressed period. Yamane et al. (2009) conducted a research of water stress in grapevine variety (Aki Queen); they applied water stress on girdled and un-girdled plants. In both cases they found lower CO_2 assimilation at 4^{th} and 5^{th} day of stress period. **In the second study,** at different days of water stress both of Godello and Treixadura behaved same pattern of gs, *A* and E. Both varieties showed decline of gs, E and *A* as the stress period increased. **In the third study,** Albariño also showed a gradually decline of all the gas exchange parameters with the duration of the stress period. These results agree with Flexas *et al.* (2002b) they reported that, as water stress increased, stomatal closure appeared and it limits CO_2 assimilation. In another study with *Malagouzia* grapevine cultivar Patakas *et al.* (2005) found gradual declining of *A* and gs with increasing of stress period.

Correlation

Among the cultivars there were close relationship between different gas exchange parameters. **In our first study,** higher correlation of gs and *A* were found in Treixadura (r^2=0.86) and Brancellao (r^2=0.66) while Godello (r^2=0.28) moderately and Albariño weakly (r^2=0.0002) correlate between gs and *A* during the stressed period. Only Albariño showed negative correlation between E and gs (Fig.4). **In second study,** both Godello and Treixadura plants showed strong correlations between gs and *A*, E and gs, (Fig.8). **In third study,** Albariño closely correlate between *A* and gs, E and gs (Fig.12a), while in the first experiment there was negative correlation between E and gs (Fig.4C). Our results supported by the work of Flexas *et al.* (2002) they worked with 22 pot grown grapevine varieties and found high correlation of gs and *A* during stressed period. In another study Chaves (1991) have mentioned that, high correlation of gs (and, thereby, E) and *A* are well documented.

Diurnal gas exchange pattern

Diurnal time course of leaf gas exchange were measured in second and third studies only. It is expected that there will be different diurnal gas exchange pattern for different level of stress. Among three cultivars, stressed and control plants showed maximum gas exchange values at 10:00h and 12:00h of a sunny day respectively. Stress plants of Godello and Treixadura cultivars followed the same diurnal pattern and recovery of *A*, gs and E. At the mid day depression CO2 was lowest for tested varieties (Fig.9). **In third study,** there were clear differences of diurnal gas exchange pattern at two different days of stress period. At 1st day of stress period diurnal time course of gas exchange parameters were higher at mid morning (11:00h) but at 5th day of stress period higher gas exchange were recorded at early of the morning (9:00h) afterward started to decline. Same result has been reported by Serrano et al. (2010) they also conducted research with potted Grapevine (Chardonnay) and found different values of gs, *A* and E between control and stressed plants. They also reported the maximum gs, *A* and E of control and stressed plants at mid-day and mid-morning respectively. This result is also executed by Chaumont *et al.* (1994); Correia *et al.* (1990) and Flexas *et al.* (1999) who have also reported that, gradual declining in *A* of stressed plants is associated to declining of gs.

Chlorophyll fluorescence

Only Brancellao showed treatments effect on mid-day Fv/Fm at dark adapted condition. On the other hand there was no treatments effect on mid-day Fv/Fm in dark adapted conditions for Treixadura, Godello and Albariño cultivars. In our study the lowest value of Fv/Fm (0.66) was found in stressed plants of Brancellao. According to Osmond and Grace (1995) Fv/Fm values lower than 0.7 found as a consequence of the increase in F_o and the decrease in Fm, which indicate clear damage to the PSII reaction centers. Except this value the mean values of Fv/Fm of control, stress and recovery plant of the four varieties were between 0.77-0.81. Flexas *et al.* (1999) found predawn Fv/Fm between 0.80 to 0.82 for Tempranillo cultivar and suggested no permanent photoinhibition.

In above studies, individual varieties showed different physiological responses of gas exchange to different treatments. These results agree with several authors, Kriedemann and Smart (1969); Tardieu and Simonneau (1998) reported that photosynthetic responses of grapevine vary from genotype to genotype, and also severity of drought (Flexas *et al.,* 1999). Flexas *et al.* (2002c) also reported that, under water stress condition different cultivar have different responses to stomatal conductance.

All the cultivars showed difference in shoot growth, gas exchange parameters and recovery responses. There are not available reports concerning our research with these grapevine cultivars. Albariño is a coastal region cultivar, it might be reason for high sensibility and abnormal physiological behaviors to water stress. Further research in field condition and molecular level is recommended to find-out more authentic conclusions. Brief descriptions of physiological behaviors of four different cultivars are as follows-

Albariño: With increasing of water stress, Albariño gradually decreased leaf transpiration (E) and CO_2 assimilation rate (*A*). E and *A* were highly correlate with Ψ_{PD}. Correlation between gs and *A* was low. Albariño has very good recovering ability to gas exchange and also to Ψ_{PD}. At extreme stress leaf defoliation was observed but no mid-day photoinhibition was found at stressed condition.

Brancellao: At the beginning (mild stress) of the stressed period, Brancellao increased E and maintained a steady state of *A* but at the end of stress period E and *A* were declined very fast. There was a good correlation between gs and *A*. It also showed good recovery responses for gas exchange parameters. At extreme stress leaf defoliation and mid-day photoinhibition was found in stressed plants.

Godello: Stressed plants of Godello caused a decrease in *A* associated with E along the stress period. E and *A* were highly correlated with Ψ_{PD} .CO_2 assimilation (*A*) was also highly correlate with E and gs. At the end (extreme stress) of stressed period it showed more steady state of gas exchange parameters than other varieties. It showed highest gas exchange recovery. No leaf defoliation and mid-day photoinhibition was found at stressed condition.

Treixadura: Gas exchange parameter values of Treixadura fell down as stress increased. *A* was highly correlate with E and gs. After irrigation Treixadura recover Ψ_{PD} very fast but recovery response of gas exchange parameters were not as good as for the rest of varieties. At extreme stress no leaf defoliation and mid-day photoinhibition was found at stress conditions.

According to Tardeu and Simonneau (1998) in our results Albariño and Brancellao exhibited some extent of isohydric response to water stress while Godello and Treixadura behaved some extent of anisohydric properties.

ACKNOWLEDGEMENTS

After giving thanks to almighty I gratefully acknowledge Dr. Prof. Julian Garcia Berrios my honorable thesis supervisor and Dr. Prof. Cristina Cabaleiro Sobrino for their endless help and cooperation. Special thanks to Dr. Prof. Nieves Muñoz, for her advice and help on statistical analysis of data. I want to thank Dr. Prof. Ruben Retuerto and Dr. Prof. Sergio Roiloa for their kind cooperation to use their instrument (MINI PAM). Special thanks to Md. Fahmid Islam and K.M. Taufiqur Rahman for their cooperation during paper writing. Finally I wish to acknowledge authority of "Erasmus Mundus, Expert-2" which gave me opportunity to do my M.Sc. at Universidade De Santiago De Compostela, Spain.

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