EVALUATION OF LOW-ENERGY DEMAND ADAPTIVE MECHANISMS IN SANGIOVESE GRAPEVINE DURING DROUGHT

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Abstract

Aims: The aim of this paper is to evaluate the photoinhibition capability, CO_2 fixation activity and some adaptive mechanisms external to the photosystem II reaction centres in Sangiovese grapevine subjected to drought conditions.

Methods and results: The diurnal time courses of gas-exchange and chlorophyll fluorescence parameters were monitored on free (natural position) and artificially retained (horizontal) leaves in Sangiovese potted vines maintained at 90 % and 40 % of maximum water availability from fruit-set to veraison. Changes in leaf and shoots characteristics were also monitored. Under drought, the inhibition of photosystem II in Sangiovese leaves may be severe and persistent according to leaf position (basal leaves with chlorosis and necrosis) and ability to avoid direct light (medial leaves with a more vertical position followed by lower temperatures and higher CO_2 fixation capability and water use efficiency during the hottest hours of the day).

Conclusion: In the Sangiovese leaves developed under drought, the protective effect of increasing leaf angle with a more vertical position and the energy costs saved by reducing photosynthetic pigments formation, changing leaf optical properties, diminishing xylem and shoot growth and leaf area development and limiting down-regulation of photoassimilation help maintain high physiological efficiency in all the distal leaves.

Significance and impact of study: The results indicate that cultivar Sangiovese exhibit high adaptation to dry conditions.

Key words: leaf orientation, chlorophyll fluorescence, net photosynthesis, stomatal conductance, photosynthetic pigments

Résumé

Objectif : L'objectif de cette recherche est d'évaluer, chez le cépage Sangiovese, la capacité de photo-inhibition, l'activité de fixation du CO_2 et certains mécanismes extérieurs aux centres réactionnels du PSII en conditions de sécheresse.

Méthodes et résultats : Après avoir mis en pot des branches de vigne (cépage Sangiovese) en leur assurant une disponibilité en eau de 90 % et 40 % de la nouaison à la véraison, l'on a laissé certaines feuilles en position naturelle et maintenu artificiellement les autres en position horizontale, pour y monitorer l'évolution diurne des paramètres d'échange de gaz et de fluorescence chlorophyllienne, ainsi que la modification des caractéristiques des feuilles et des pousses. En situation de sécheresse, il peut se produire une inhibition grave et persistante du PSII suivant la position des feuilles (chlorose et nécrose des feuilles basales) et leur capacité d'éviter la lumière directe (feuilles médianes en position plus verticale, températures plus basses, capacité de fixation du CO_2 pendant les heures les plus chaudes de la journée).

Conclusion : Chez les feuilles de Sangiovese qui se sont développées en conditions de sécheresse, l'effet de protection obtenu en augmentant l'angle des feuilles les plus verticales et, par ailleurs, les économies d'énergie découlant de différents facteurs (diminution de la formation de pigments photosynthétiques, modification des propriétés optiques de la feuille, diminution de la croissance du xylème et des pousses, limitation de la régulation négative de photoassimilation) aident à maintenir à un niveau élevé l'efficience physiologique des feuilles distales.

Signification et impact de l'étude : Les résultats montrent que le cépage Sangiovese présente une haute capacité d'adaptation aux conditions de sécheresse.

Mots-clés : orientation des feuilles, fluorescence chlorophyllienne, photosynthèse nette, conductance stomatale, pigments photosynthétiques

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INTRODUCTION

The maintenance of high photosynthetic capacity in the canopy is one of the major aims of grapevine cultivation for ensuring optimal yield and high grape composition. In all places where the grapevine is cultivated without irrigation or in conditions of high thermal and radiative regimes the photoinhibition phenomena, resulting from down-regulation of CO_2 fixation or photosystem II (PSII) damage, drastically reduces canopy efficiency. This type of dysfunction is normally related to high irradiance and temperature, which cause light-induced oxidative stress, and it is greatly amplified by water stress (Powles, 1984). Apart from internal adaptive mechanisms evolved to protect against photoinhibition (Osmond, 1994; Giardi *et al.*, 1996; Medrano *et al.*, 2002), some processes external to the PSII reaction centres, such as leaf movements, may exert an efficient non-radiative energy dissipation (Gamon and Pearcy, 1989). The purpose of this study was to assess the importance of leaf movements and some morphofunctional changes at leaf and shoot level on photoinhibition and gas exchange in water-stressed vines of Sangiovese, a drought-avoidance grapevine cultivar (Silvestroni *et al.*, 2005; Palliotti *et al.*, 2007) which is cultivated on 69,750 ha (10.3 % of the total Italian vineyard acreage), and to verify if these movements and changes play a protective role by increasing heat dissipation and reducing or avoiding down-regulation of photoassimilation.

MATERIALS AND ANALYTICAL AND EXPERIMENTAL METHODS

1. Experimental conditions

The trial was carried out in 2006 using twenty 4-year-old potted (50 l) vines of cv. Sangiovese, clone VCR30 grafted on 1103 Paulsen, clone ISV1 rootstock grown in an outdoor area close to the faculty of Agriculture of the University of Perugia (Umbria region, central Italy). All the pots were filled with a loamy soil of field capacity of 30.2 % [(vol water/vol soil) x 100] and wilting point of 16.7 %. In February, each vine was pruned retaining three spurs with 2 buds each. All shoots were oriented up-right using suitable stakes. Ten vines were maintained at about 90 % of maximum water availability (well-watered vines) and 10 pots received, from fruit-set to veraison, 40 % of maximum water availability (water-stressed vines). During water limitation, all stressed pots were covered with a plastic film to avoid interference due to rainfall and soil water evaporation. At the onset of water stress, the water supply corresponding to each treatment regime was determined every three days in June and every two days in July and August.

2. Gas exchange and chlorophyll fluorescence

After three weeks of water deprivation, the diurnal time courses of net photosynthesis (*Pn*) and stomatal conductance (*gs*) (using a portable open-system infra-red gas analyser, LCA3, Analitical Development Company, Hoddesdon, Hertz, UK), operating in the open mode, chlorophyll fluorescence parameters (with a portable continuous excitation type fluorimeter, Handy-PEA, Hansatech Inst., UK), leaf temperature (with an infrared thermometer, Mod. TM909L9, Assi-control, Italy) and incident photosynthetic photon flux density (PPFD, using a Li-190SB point quantum sensor, Li-Cor, USA) were evaluated on free (natural position) and artificially retained (horizontal) mature leaves in both well-watered and water-stressed vines. The horizontal leaves were retained by sandwiching them between nylon strips and a cross-shaped wood frame. Measurements were taken at three-hour intervals, between 08.00 and 17.00 h. Fifteen mature free and horizontal leaves per treatment were selected and used for physiological measurements. Moreover, between 13.00 and 14.00 h, leaf water potential was measured on three leaves per treatment using a portable Scholander type pressure chamber (model 1000; PMS Instrument Co., USA) and relative water content was determined on twenty leaf discs per treatment as: (FW-DR)/(TW-DW) x 100, where FW is fresh weight, DW is dry weight after 3 days of drying at 80 °C and TW is turgid weight obtained after 24 h in distilled water at 4 °C in the dark. All measurements were taken during the first week of July 2006, after having maintained the leaves in a horizontal position for three consecutive days characterized by clear skies, high air temperature and no rainfall. Fluorescence parameters, such as *Fo* (ground fluorescence), *Fm* (maximum fluorescence) and *Fv* (variable fluorescence, *Fm* - *Fo*) yield, were collected using the method described by Strasser *et al.* (1995) by exposing the leaves to actinic light of 3000 µmol photons m^{-2} s^{-1} after 20 min of dark adaptation. *Fv/Fm* ratio, indicating the maximum quantum yield of PSII (Russel *et al.*, 1995), was calculated automatically by the Handy-PEA fluorimeter, such as Area over fluorescence curve between *Fo* and *Fm*, which indicates the pool size of plastoquinone on the reducing side of PSII.

3. Leaf and shoot characteristics

Just before grape ripening, shoot length and the leaf area per vine, separated into leaves from primary and lateral shoots, from three potted vines per treatment kept out of the trial were measured using an area meter (Hayashi Demco C., mod. AAM-7). The number of laterals per shoot and the mean vine leaf size were also measured.

The following measurements were taken one week before veraison on the same free-to-move leaves from both well-watered and water-stressed vines used for

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physiological traits: 1) chlorophyll a and b, and carotenoid contents on ten leaf discs (1.76 cm^2 each) per treatment according to Lichtenthaler and Wellburn (1983); 2) optical characteristics, i.e. reflectance, transmittance and absorptance, on twenty leaves per treatment, using a proper tripod and LI-190S Quantum Sensor (Li-Licor, Lincoln, USA) (Schultz, 1996a); 3) proline contents on five leaves per treatment according to Bates *et al.* (1973) and Claussen (2005); 4) stomata density and size by impression method using clear nail polish painted on the abaxial leaf surface (the mean stomatal size was calculated from stomata length x width x 0.785, the standard formula for an ellipse); 5) leaf orientation, between 13.00 and 14.00 h on one hundred leaves per treatment, by measuring the angles between the main vein of the leaves relative to the horizon (0°) using a compass protractor. Moreover, shoot and xylem cross-sectional areas and the areas of single xylematic vessel were measured at the middle portion just after leaf fall. Shoot sections about 0.5 mm thick from 5 shoots per treatment were cut using a microtome midway to internodes. Sections were directly observed with a stereomicroscope.

Physiological data are presented as the mean ± standard error (SE), whereas data concerning leaves and shoots were subjected to analysis of variance and differences between water supply level were determined using the t-test or Student-Newman-Keuls test at 0.05 level.

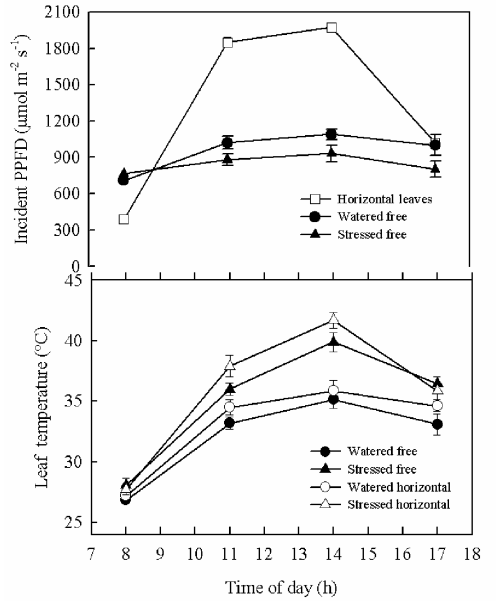


Figure 1 - Diurnal time courses of incident photosynthetic photon flux density (PPFD) and leaf temperature in free and horizontal leaves from well-watered and water-stressed vines.
Each point is the mean of five replicates ± SE.

RESULTS AND DISCUSSION

1. Chlorophyll fluorescence and gas exchange analyses

As found in a mature vineyard of cv. Sangiovese during the summer of 2003 (Silvestroni *et al.*, 2005), during the first week of July 2006 also in water-stressed potted vines of Sangiovese approximately 40 % to 60 % of the basal leaves first became chlorotic followed by necrosis. At the same time, contrary to well-watered vines, a conspicuous down-regulation of PSII activity was found at midday on green basal leaves of water-stressed vines, emphasized by high depression of the *Fv/Fm* ratio with a value of 0.56. The decrease in the *Fv/Fm* yield was due to high values of *Fo* (570 in arbitrary units, AU) and low values of *Fm* (1310 AU) and Area (just 24500 AU). These changes in fluorescence parameters suggest initial PSII photodamage, a diminished non-radiative energy dissipation and a reduced pool size of plastoquinone, respectively (Osmond and Grace, 1995; Strasser *et al.*, 1995). Parallelly, the net photosynthesis and stomatal conductance were also drastically reduced, with values lower than 1 µmol CO_2 m^{-2} s^{-1} and 0.025 mol H_2O m^{-2} s^{-1}, respectively.

During the hottest days of July, at midday the medial leaves from stressed vines were in a significantly more vertical position compared to well-watered vines, precisely +12° with the horizon (table 2), which is in contrast to the majority of basal leaves, which were irreversibly photoinhibited with chlorosis and necrosis. This mechanism affected leaf light interception and leaf temperature, especially during the hottest hours of the day (figure 1), and induced a significant reduction in *Pn*, and gs during the whole day in comparison to medial leaves from well-watered vines, without change the WUEi (intrinsic water use efficiency calculated as *Pn/gs* ratio) (figure 2).

Considering all the treatments, a close, curvilinear correlation between gs and *Pn* ($r^2 = 0.821$) was assessed and according to Escalona *et al.* (1999) and Cifre *et al.* (2005) in free leaves from water-stressed vines the variation of *Pn* appears to be almost fully caused by *gs* changes (stomatal limitations), as indicated by increased WUEi (figures 2 and 3). The high WUEi found on these leaves during the entire day in comparison to horizontal leaves from water-stressed vines seems to reflect an high ability to maintain high stomatal activity under these drought conditions (figures 2 and 3).

Contrary to horizontal leaves from water-stressed vines, where during the hottest hours a severe water stress took place with *gs* lower than 0.05 mol H_2O m^{-2} s^{-1} and non-stomatal limitations to *Pn* become dominant (Cifre *et al.*, 2005), the free leaves from water-stressed vines

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Table 1 - Chlorophyll fluorescence parameters (in arbitrary units) in free and horizontal restrained leaves from well-watered and water-stressed vines at 14.00 h.

Each point is the mean of ten replicates ± SE.

Treatment	*Fo*	*Fm*	*Fv*	*Area*
Watered free	557 ± 11	2878 ± 61	2320 ± 82	63600 ± 4510
Stressed free	599 ± 14	2880 ± 45	2281 ± 51	69720 ± 3620
Watered horizontal	660 ± 18	2450 ± 58	1790 ± 65	31680 ± 2760
Stressed horizontal	666 ± 24	2217 ± 67	1551 ± 74	34745 ± 2450

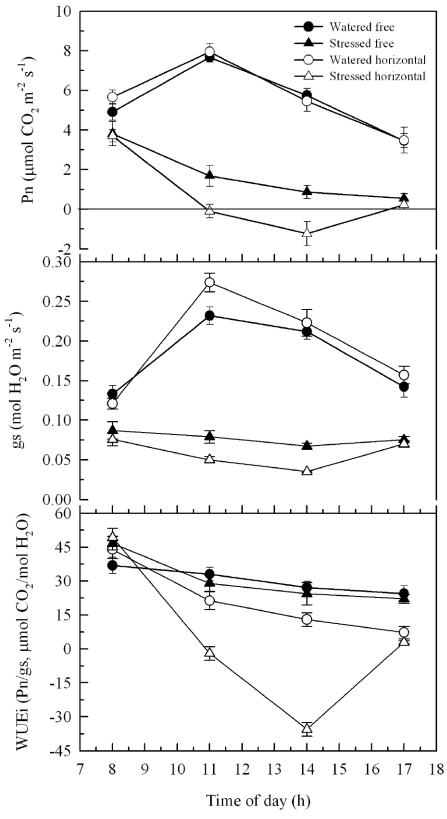


Figure 2 - Diurnal time courses of net photosynthesis (*Pn*), stomatal conductance (*gs*) and intrinsic water use efficiency (WUEi) in free and horizontal leaves from well-watered and water-stressed vines.

Each point is the mean of five replicates ± SE.

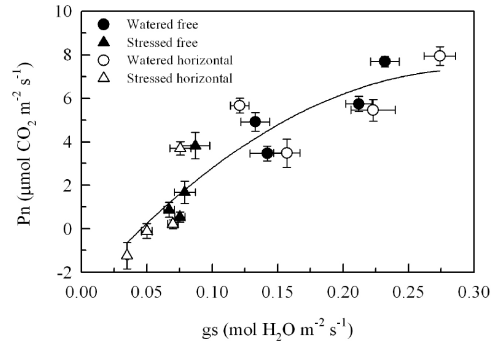


Figure 3 - Relationship between stomatal conductance (*gs*) and net photosynthesis (*Pn*) ($y = -2.87 + 67.9\,x - 113.1\,x^2$, $r^2 = 0.821$) in free and horizontal leaves from well-watered and water-stressed vines of Sangiovese cultivar.

Each point is the mean (n = 5 ± SE) of morning (8.00 and 11.00 h) and afternoon (14.00 and 17.00 h) readings.

were able to maintain good values of *gs* and positive *Pn* activity during the entire day (figures 2 and 3).

As expected, the horizontal leaves from both treatments experienced higher incident PPFD and leaf temperature than the free leaves, especially during the hottest hours of the day (figure 1), and in conditions of low water availability these leaves annulled the CO_2 fixation ability and exerted high respiration activity, up to 1.42 µmol CO_2 m^{-2} s^{-1} (figure2). In the horizontal leaves, the low water availability limits photosynthetic energy conversion and the high incident light enhances photoinhibition (figure 4). In fact, contrary to free leaves, at midday the horizontal leaves showed photoinhibition, with *Fv/Fm* values of 0.73 and 0.69 in well-watered and water-stressed vines, respectively, followed by light recovery during the afternoon. The recovery of the *Fv/Fm* ratio found in the horizontal leaves from the medial position of the shoot, irrespective of water regime, together with the *Fv/Fm* values early in the morning very close to that of free leaves, suggests that down-regulation rather than photodamage occurred.

As found in basal leaves, also in medial leaves maintained in horizontal position the low *Fv/Fm* ratio values are due to a concomitant increase in *Fo* and decrease in *Fm* in comparison to free leaves (table 1). Moreover, in these horizontal leaves the *Fv* and Area parameters were also greatly reduced, suggesting a lower impairment of PSII activity and a reduction in the pool size of plastoquinone, respectively (Strasser *et al.*, 1995). Changes in *Fo* and *Fm* found in « Sangiovese » leaves were similar to those reported by Medrano *et al.* (2002) in water-stressed vines of cv. « Tempranillo ».

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Table 2 - Vine growth and morpho-functional changes in leaves and shoot of Sangiovese grapevine developed after the onset of water stress.

	Well-watered vines	Water-stressed vines	*t-test*
Primary shoot length (cm)	223.0	137.2	*
Lateral shoot length (cm)	12.7	7.8	*
Lateral shoots (n°/vine)	30.1	18.7	*
Leaf area (m^2/vine)	3.68	1.92	*
Areas in lateral shoots (%)	33.7	19.6	*
Leaf size of primary shoots (cm^2)	155.1	112.9	*
Leaf size of laterals (cm^2)	71.4	53.1	*
Leaf angle (° with the horizon)[a]	76	88	*
Stomata size (μm^2)	181.7	134.2	*
Stomatal density (n°/mm^2)	171.1	193.0	*
Area occupied by stomata (%)[b]	3.11	2.59	*
Chlorophyll a (mg/dm^2)	1.16	0.79	*
Chlorophyll b (mg/dm^2)	0.64	0.42	*
Carotenoids (mg/dm^2)	0.52	0.39	*
Proline (μmol g^{-1} fresh weight)	2.26	2.50	*n.s.*
Absorptance (%)	80	70	*
Transmittance (%)	9	21	*
Reflectance (%)	11	9	*n.s.*
Shoot cross-sectional area (mm^2)	37.9	29.3	*
Xylem cross-sectional area (mm^2)	19.1	10.6	*
Vessels diameter (μm)	62.8	23.2	*

As reported by Schultz (1996b) for Grenache cultivar, also in Sangiovese *Fv/Fm* yield was significantly correlated to leaf temperature, and when it become higher than 37-38 °C, a strong reduction of *Fv/Fm* yield occurred and photoinhibition begins (figure 5).

The water status of the leaf was significantly influenced by leaf orientation more than by water regime (figure 6). During the 13.00-14.00 h interval, the horizontal leaves from water-stressed vines showed significantly lower leaf water potential and relative water content, whereas in well-watered conditions leaf orientation had no effect in terms of leaf water potential or relative water content.

2. Leaf and shoot characteristics

The growth of primary and lateral shoots as well as the number of laterals per shoot and per vine from water-stressed vines were significantly reduced in comparison to well-watered vines (table 2). Early water stress caused a significant reduction in leaf area due to fewer leaves per vine and smaller leaf size in both primary and lateral shoots. In the water-stressed vines, mean primary and laterals leaf number per vine were 14 % and 60 % less in comparison to well-watered vines, respectively, and primary and lateral leaves were 28 % and 26 % smaller, respectively (table 2).

Beside an increased lamina inclination, in Sangiovese leaves which developed after the onset of water stress, early and constant water limitation, like that which occurred in water-stressed vines, produced a significant reduction in stomatal size (-26 %) and a significant increase in the stomatal density (+13 %) (table 2). These changes reduce the area occupied by the stomata from 3.11 % to 2.59 %, helping the water preservation. At the same time, the chlorophyll a, b and carotenoid concentration was also significantly reduced, whereas no change occurred in the proline content. As expected from the reduction of photosynthetic pigments concentration, the leaf optical properties were also affected by water availability during leaf development; indeed, significant reduction in absorbance and significant increase of transmittance were found in leaves from water-stressed vines in comparison to homologous leaves from well-watered vines.

In comparison to well-watered vines, early water limitation significantly reduced also the cross-sectional areas of primary shoots and xylem tissue and the mean diameter of xylematic vessels (table 2). These last results suggest that the shoots from water-stressed vines exhibit a reduction of hydraulic conductance and risk of cavitation and embolisms, since vulnerability to cavitation has been shown to be negatively correlated with vessel diameter

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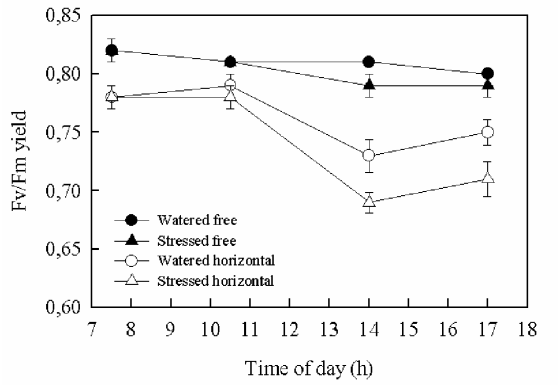


Figure 4 - Diurnal time courses of *Fv/Fm* yield in free and horizontal leaves from well-watered and water-stressed vines.
Each point is the mean of ten replicates ± SE.

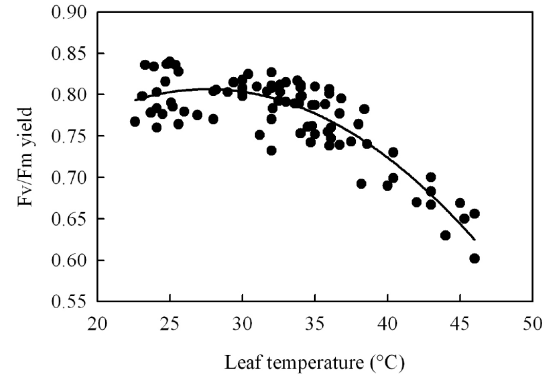


Figure 5 - Relationship between leaf temperature and the *Fv/Fm* yield in Sangiovese vines.

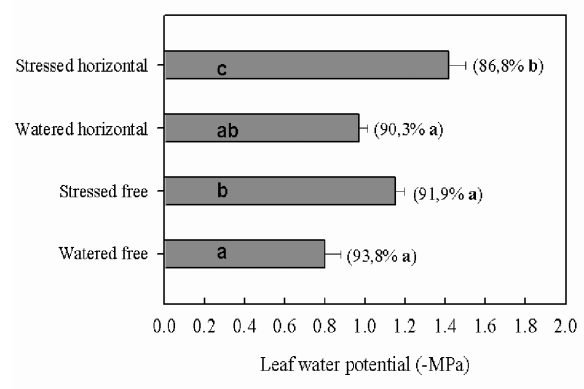


Figure 6 - Leaf water potential and relative water content (values in brackets) measured during 13.00-14.00 h in free and horizontal leaves from well-watered and water-stressed vines.
Different letters show significant differences at P ≤ 0.05 (Student-Newman-Keuls test).

within a species (Schultz and Matthews, 1988; Lo Gullo *et al.*, 1995; Lovisolo and Schubert, 1998; Schultz, 2003).

These results indicate that some adaptive mechanisms external to the PSII reaction centres used by cultivar Sangiovese, which exhibits high adaptation to dry conditions, seem to be mainly those characterized by low energy requirements. The energy costs saved by reducing photosynthetic pigments formation, changing leaf optical properties, limiting total transpiring leaf area, diminishing xylem and shoot growth and leaf area development and limiting both down-regulation of photoassimilation and chronic photoinhibition by leaf movements help maintain high physiological efficiency in all the distal leaves.

In water-stressed vines, the protective effect of increasing leaf angle with a more vertical position led to lower leaf temperatures, which with the combination of the reduction of photosynthetic pigments increased the light-avoiding capability and assured a higher *gs* and *Fv/Fm* yield compared with horizontally fixed leaves. This behaviour leads to a better CO_2 fixation and WUEi ability under these limiting environmental conditions and limits the negative effects on vine yield and grape quality, which can be expected from severe drought conditions, at least like those studied here.

CONCLUSIONS

In drought-avoidance grapevine cultivars, such as Sangiovese, the inhibition of photosystem II may be severe and persistent according to leaf position (basal leaves with chlorosis and necrosis) and ability to avoid direct light (medial leaves by modification in leaf lamina orientation) and increase the light-avoiding capability (by significant changes in several morphofunctional characteristics of leaves and shoots). The results indicate that cv. Sangiovese exhibit high adaptation to dry conditions. The reduction of leaf area by chronic photoinhibition of large amounts of basal leaves, not found in other grapevine cultivars (i.e. Montepulciano and Pignoletto) (Silvestroni *et al.*, 2005; Palliotti *et al.*, 2007), must be considered an important drought-avoidance mechanism, which reduces water loss by transpiration process, enabling the vine to withstand long water limitation periods while keeping the medial leaves with good photosynthetic behaviour.

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