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Distribution of leaf photosynthesis and transpiration within grapevine canopies under different drought conditions

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Summary

The effects of seasonal drought on the distribution of leaf area, photosynthesis and transpiration within the canopy were evaluated for two Spanish grapevine cultivars. Both varieties were cultivated according to their typical training system.

At early stages of drought, reduction of photosynthesis and transpiration was only observed in sun-exposed leaves. As drought intensified, even less sun-exposed leaves were affected. Severe drought reduced photosynthesis and transpiration in all locations of the canopy except for most shaded leaves in the inner part. However, those leaves were almost unproductive, and seemed to be insensitive to variation of both light intensity and drought. Leaf area was also reduced by drought, but the distribution of these reductions within the canopy differed between cultivars, possibly reflecting differences in the training system.

Leaves from all locations of the canopy except those in the central part showed a similar radiation use efficiency, suggesting that the observed variation in photosynthesis within the canopy was mostly related to different light interception, while other factors such as different leaf age should play only a minor role. Photosynthetic radiation use efficiency strongly depended on both, pre-dawn leaf water potential and light-saturated stomatal conductance. The interest of these results for modeling purposes is discussed.

Key words: *Vitis vinifera*, canopy photosynthesis, canopy location, leaf area, light use efficiency, water use efficiency, drought.

Introduction

The effects of drought on leaf photosynthesis have been extensively studied (Chaves 1991, Lawlor 1995). In drought-stressed grapevines, fully expanded sun-exposed leaves usually show large variation in photosynthesis both on a seasonal and a diurnal basis (Chaves *et al.* 1987, Escalona *et al.* 1999, Flexas *et al.* 1999).

However, variation in photosynthesis also depends on leaf orientation, training system (Intrieri *et al.* 1997, Schultz *et al.* 1999 a), crop load (Edson *et al.* 1993, Miller *et al.* 1997, Petrie *et al.* 2000), and leaf aging (Poni *et al.* 1994, Escalona *et al.* 1999). Therefore, a large variability of the photosynthetic rate also occurs within a grapevine canopy, even though field data reflecting the actual extent of such variation at the whole canopy level are scarce (Petrie *et al.* 2000, Poni *et al.* 2000).

Environmental effects on transpiration and photosynthesis are often derived from single-leaf measurements leading to assumptions on whole-canopy responses (Smart 1974). Measurements of photosynthesis and transpiration in different canopy locations can be more accurate to extrapolate the whole plant carbon gain, assuming a similar contribution by leaves within a certain canopy location and determining the total leaf area of each location (Zufferey and Murisier 1997, Zufferey *et al.* 2000).

Variation of light interception by each canopy location depends on the total leaf area as well as on its distribution within the different canopy locations (Carbonneau 1983, Sommer *et al.* 1993). Soil water deficit decreases total leaf area, especially if it starts at the beginning of the growing season when vegetative growth is maximal (Schultz and Matthews 1988, Winkel and Rambal 1993). Different exposure to incident light of various canopy locations as well as variation of leaf photosynthesis throughout the canopy may lead to important differences in the reduction of photosynthesis due to drought. However, the effects of drought on variation of photosynthesis within the canopy have not yet been studied. This is certainly important for estimating the effects of different environmental conditions and cultural practices on total plant photosynthesis, as well as on the contribution of each part of the canopy to total carbon assimilation.

Material and Methods

Plant material and treatments: The experiment was conducted in a commercial vineyard (Ca´n Ribas, Mallorca, Spain) during 1997 and 1999. In 1997 the grapevines used were 20 years old grafted on Richter 110 and planted in rows (distance between rows: 2.5 m, distance between plants: 1.4 m). The rows were SE-NW oriented. Two cultivars of *Vitis vinifera* were studied: Tempranillo (T), widely grown in Spain, and Manto Negro (MN), a Majorcan variety with a longer growth period and usually showing higher yield stability under drought. Bud break, bloom, veraison and date of ripeness were, on average of the two years, 13th April, 11th May, 12th July and 28th August, respectively, for T, and 21th April, 22th May, 27th July and 10th September for MN. The training systems were those traditionally used in Mallorca for each cultivar: a bilateral cordon for T (two wires at 0.7 and 1.1 m, respectively) and the traditional gobelet for MN (4 arms, 0.5 m high). The different training systems used for the two cultivars limit the scope of analyzing inter-cultivar or training system differences. Thus,

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the present work was focused to evaluate the carbon and water balances of these two cultivars with their typical training systems.

Eight different zones within the canopy, corresponding to different leaf locations, were considered (see Fig 1). Locations 1, 2 and 3 were southeast and locations 5, 6 and 7 northwest oriented. Canopy bottom leaves corresponded to locations 1 and 7, middle leaves to locations 2 and 6 and locations 3 and 5 corresponded to leaves in the upper lateral parts of the canopy. Location 4 corresponded to the top of the canopy, and consisted of leaves in a nearly horizontal position. Finally, location 8 included leaves of the inner part of the canopy, covered by at least one location of leaves, and shaded for most of the day except for occasional sunflecks. This division of the canopy in 8 locations is identical to that proposed by Zufferey and Murisier (1997).

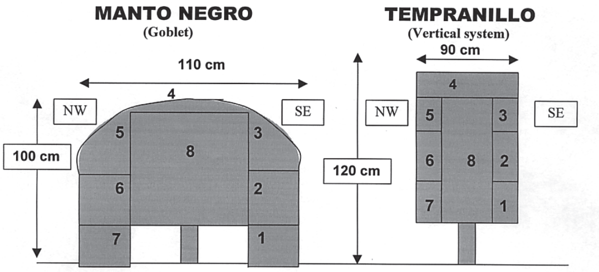

Fig. 1: Schematic distribution of the canopy locations for the cvs Manto Negro and Tempranillo.

The vineyard was traditionally managed without any irrigation until 1992 when irrigation treatments were started. Five rows per cultivar (70 vines per row) were maintained without irrigation (only rainfall) and 5 rows were irrigated from June to August. Irrigation was adjusted to account for about 30 % of ETP (measured with an evaporimeter pan) and applied twice a week by a drip system (one dripper per plant). In case of occasional rainfall the precipitation was subtracted from the calculated amount of irrigation water. Sampling was always done in the central row of 5 adjacent rows with the same treatment to minimize any border effect.

Climatic conditions were recorded by a weather station (Delta-T Devices, U.K.) located inside the vineyard. Total soil water availability (SWA) during the season was calculated from soil characteristics and the recorded precipitation. Considering at 2 m soil depth, 25 % of stones, a field capacity of 26 % v/v and a wilting point of 13 % v/v, the maximum water storage capacity of 1 m^2 of soil surface was 120 l. The total SWA during the growing season (April to September) was calculated by adding summer rainfall and irrigation to SWA in early spring, which was assumed to be at field capacity.

Vine water status and yield: Pre-dawn leaf water potential (Ψ_{pd}) was measured with an Scholander chamber (Soil Moisture Equipment Corp., USA) three times during summer at 'pea size', veraison and ripeness) in 1997 and 1999. Readings were randomly taken from leaves of the location 3 (Fig. 1). Yield of 6 vines per treatment was determined at harvest.

Diurnal changes of leaf gas exchange: Net CO_2 assimilation (A) and transpiration (E) were measured in 1997 and 1999, using a portable gas exchange analyzer (Li-6400, Li-Cor Inc., Nebraska, USA). For each of the 8 canopy zones, measurements were made on 6 leaves randomly chosen on different plants along the row, in their natural position, at three sampling times: early July ('pea size'), end of July (veraison) and mid-August (ripeness). For each sampling measurements were taken at 6, 9, 12, 15, 18, and 20 h local time. Total daily carbon assimilation and water consumption by each canopy location were calculated by integrating the daily time variations of net photosynthesis and transpiration, respectively.

At the first sampling in June measurements were made on both, irrigated and non-irrigated plants. On the second and third samplings, only non-irrigated plants were measured. Based on our previous results (Escalona *et al.* 1999, Flexas *et al.* 2002), irrigated plants usually maintain similar rates on the second and third sampling dates. Nevertheless, this assumption was tested measuring both irrigated and non-irrigated on locations 3 and 5. Rates of photosynthesis differed by <15 % between sampling dates.

Total vine leaf area and specific leaf weight: All leaves of each location of the canopy were collected from 6 different plants per cultivar and treatment immediately after harvest. Leaves were taken to the laboratory and processed as follows: for each location, fresh weight, leaf area (AM-100 Leaf Area Meter ADC Herts, UK) and specific leaf weight (SLW) of 10 leaves were determined separately. All remaining leaves of each location were dried. The total leaf area of a location was estimated by dividing the total dry weight of the location by the mean SLW of the 10 leaves. Measurements were made in 1997 and 1999.

Calculation of the photosynthetic active radiation-use-efficiency: PAR-use-efficiency was calculated as the slope of the relationship between daily photosynthesis and total daily PAR intercepted at different locations of the canopy.

Statistical analyses: Means ± SE of 4-8 replicates were calculated for each parameter and treatment. One-way ANOVA, using treatment as a factor, was used to test the significance of the treatment effects on the studied parameters. Means were separated at $p<0.05$ according to Duncan test (SPSS 9.01 for Windows, SPSS Inc.). Correlations between different parameters were calculated from mean values, its significance was determined according to the Pearson test for linear regression.

Results and Discussion

Environmental conditions, soil water availability and plant water status: Environmental conditions were typical for Mediterranean summers, with considerable year-to-year variation. Irradiance, temperature and evapotranspiration (up to 160 l m^{-2} $month^{-1}$) were maximum in mid-July (veraison). During the two years of this study, almost no rainfall occurred from June to September. These climatic conditions created low seasonal soil water availability (SWA) in non-irrigated plants (less than 300 l m^{-2} in both years, see Tab. 1). Irrigation improved SWA significantly (Tab. 1).

Table 1

Annual rainfall and estimated soil water availability (SWA) during the growing seasons 1997 and 1999

Year	Total rainfall (l m^{-2})	SWA Non-irrigated (l m^{-2})	SWA Irrigated (l m^{-2})
1997	530.6	286.4	397.0
1999	427.7	232.5	367.7

Pre-dawn leaf water potential (Ψ_{pd}) decreased in non-irrigated plants during the growing season (Tab. 2). Maximum values of ca. -0.01 MPa were found in June. At the end of August, Ψ_{pd} dropped to -0.2 to -0.4 MPa, depending on the year (Tab. 2). In irrigated plants, Ψ_{pd} was maintained high through the growing season. Differences in water availability and plant water status were reflected by significantly lower yields at the end of the season in non-irrigated plants (Tab. 2). Although Ψ_{pd} was generally lower in 1997, in 1999 drought effects were more severe (see, for instance, yield values in Tab. 2). This was due to a lower average SWA (Tab. 1) and to very low air humidity (high vapour pressure deficit) in June and early July (not shown).

Light interception, photosynthesis, transpiration and leaf area distribution in different canopy locations under progressive drought: As expected from the orientation of the rows, diurnal light interception trends were clearly different among canopy positions (Fig. 2). The daily patterns of irradiance for the 8 canopy locations were remarkably similar to those shown by Zufferey and Murisier (1997) for Chasselas in Switzerland, despite slightly different row orientations (N-S in their study, NW-SE in the present study) and training systems (Guyot *versus* bilateral cordon or gobelet). Total daily light interception ranged from 4 mol PPFD d^{-1} (location 8) to 45 mol PPFD d^{-1} on top of the canopy (location 4).

Diurnal patterns of photosynthesis and transpiration showed coincident behavior with important variations among canopy locations in all treatments and sampling times (*e.g.* Fig. 2). Both photosynthesis and transpiration of SE-oriented leaves (locations 1, 2 and 3) reached their maximum at noon with a sharp decrease thereafter. By contrast, photosynthesis and transpiration of NW-oriented leaves (locations 5, 6 and 7) progressively increased during the morning, reaching maximum values late in the afternoon. Top leaves (location 4) showed sustained maximum rates during most of the day. Inner leaves (location 8) had very low rates during the whole day. These variations were largely due to differences in daily patterns and amounts of incident light, as already described by Intrieri *et al.* (1997) and Schultz *et al.* (1999 a). However, leaves from location 8 seemed to be less responsive to light than leaves from any other location. For instance, early in the morning net photosynthesis in location 6 was about three times that of location 8 at midday at similar light intensity (Fig. 2). Recently Palliotti and Cartechini (2001) have demonstrated that diffuse light largely contributes to increased photosynthesis in grapevine leaves. This may not be the case for leaves from location 8, which have mostly developed under diffuse light conditions.

As drought developed, there was a marked reduction of maximum photosynthetic rates, as previously reported by Kriedemann and Smart (1971), Liu *et al.* (1978), Chaves *et al.* (1987), Schultz (1996) and Escalona *et al.* (1999). This reduction was observed in all canopy locations except location 8. Moreover, the time of the day at which maximum rates were reached was advanced as was described by Chaves *et al.* (1987) and Flexas *et al.* (1999).

The differences in maximum daily photosynthetic rates between leaves of different canopy locations are reflected by the daily carbon uptake (Fig. 3). Similar values were obtained in the two years for each location, with maximum values of up to 7 g C m^{-2} d^{-1} corresponding to top leaves (location 4). Average daily carbon uptake decreased progressively towards the lower parts of the canopy (Fig. 3). As expected, daily carbon assimilation of inner leaves was lowest. Similar results were observed for daily transpiration (not shown).

Drought induced significant reduction of daily-based photosynthesis (Fig. 3) and transpiration (not shown) in all canopy locations except for location 8. For instance, the

Table 2

Predawn leaf water potential (Ψ_{pd}) at pea size (1) of berries, veraison (2) and ripeness (3) and grape yield at harvest. All values are averages ± standard error of 6 measurements on 6 plants randomly chosen. Irrigated (I) and non-irrigated (NI) plants of Manto Negro (MN) and Tempranillo (T)

Factor	Year	Sampling time	MN		T	
			I	NI	I	NI
Ψ_{pd}	1997	1	-0.05±0.01	-0.13±0.02	-0.06±0.01	-0.18±0.02
		2	-0.09±0.01	-0.53±0.06	-0.15±0.02	-0.31±0.05
		3	-0.13±0.01	-0.45±0.01	-0.16±0.02	-0.43±0.04
	1999	1	-0.03±0.01	-0.15±0.02	-0.10±0.03	-0.09±0.02
		2	-0.08±0.02	-0.18±0.03	-0.15±0.05	-0.24±0.04
		3	-0.04±0.01	-0.18±0.05	-0.03±0.01	-0.32±0.04
Grape yield (kg plant^{-1})	1997		2.42±0.14	1.80±0.17	3.97±0.53	3.25±0.21
	1999		3.29±0.69	2.27±0.37	6.00±0.59	2.37±0.35

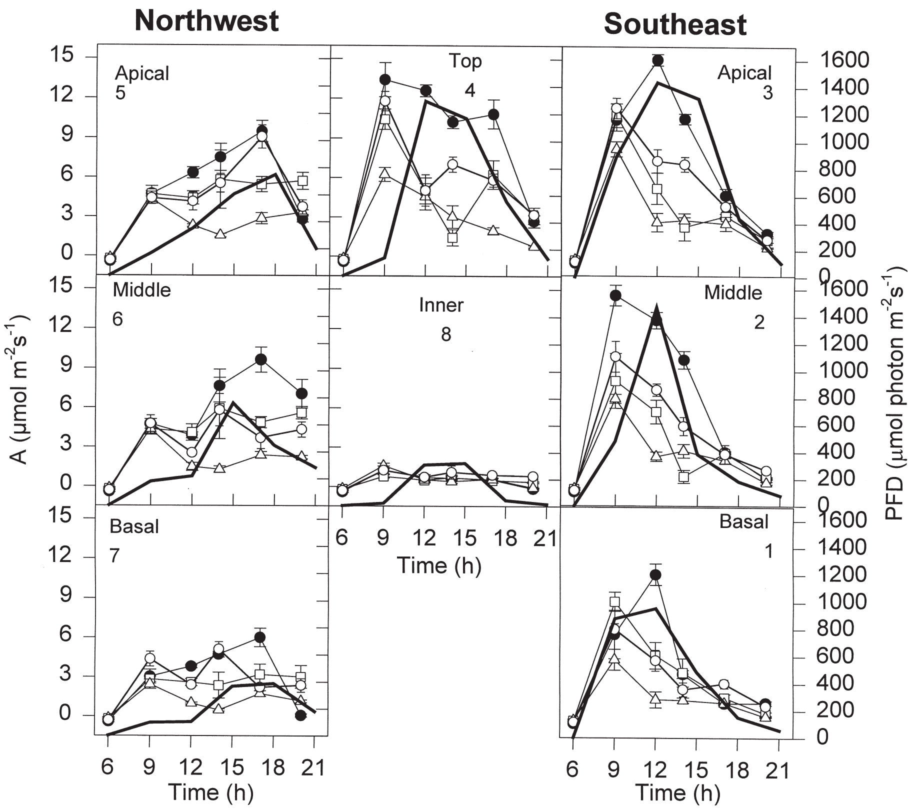

Fig. 2: Diurnal changes of photosynthesis in leaves of different canopy locations of Manto Negro in summer 1999. Means ± S.E. of 6 replicates are shown for irrigated plants at 'pea size' (full symbols) and non-irrigated plants measured at 'pea size' (empty circles), veraison (empty squares), and ripeness (empty triangles). Thick lines represent incident photosynthetically active radiation (PAR) at the leaves of each canopy location in early July. The position of figures 1-8 corresponds to that shown in Fig. 1.

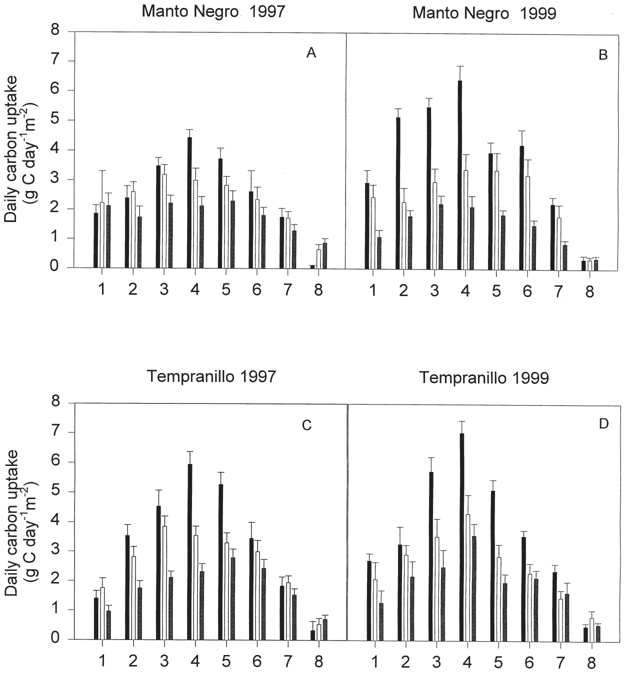

Fig. 3: Daily carbon uptake of different canopy locations at pea size (black bars), veraison (empty bars), and ripeness (dark grey bars) of Manto Negro (**A** and **B**) and Tempranillo (**C** and **D**) berries. Data are means ± S.E. of 6 replicates.

daily carbon assimilation of top leaves (location 4) dropped from 6.7 to 2.0 g C m^{-2} d^{-1} during the period studied. Transpiration values dropped from about 6 l m^{-2} d^{-1} to less than 2 l m^{-2} d^{-1}. By contrast, the daily carbon assimilation of inner leaves (location 8) ranged from 0.2 to 0.9 g C m^{-2} d^{-1}, regardless of water availability.

The reduction of photosynthesis differed among canopy locations depending on the severity of drought (Tabs 3 and 4). In July 1997, under mild drought conditions, photosynthesis was substantially reduced only in locations 4 and 5 in both cultivars (Tabs 3 and 4). Location 3 was only slightly affected reflecting the fact that these leaves only received high light during the morning, when the leaf water status was still high (Chaves *et al.* 1987, Flexas *et al.* 1999). In August 1997, when stress was more severe, drought-induced photosynthetic reductions were highest in the most sun-exposed location (4) and decreased progressively towards less exposed locations, being smallest at locations 1 and 7 (Tabs 3 and 4). Leaves from location 8 had very low assimilation values, even when irrigated, without significant variation due to drought. In 1999, the driest year, drought-induced photosynthetic reductions tended to become similar in all canopy locations but location 8 (Tabs 3 and 4). These results can be explained by the well-known variations of the photosynthetic light-response curve during progressive drought, as light-saturated photosynthesis decreases more distinctly and at earlier degrees of drought than light-limited photosynthesis (Escalona *et al.* 1999). Therefore, at mild and moderate drought, photosynthesis of leaves from the most exposed locations is proportionally more depressed than that from the most shaded locations. At severe drought, however, leaves of all locations indicate

Table 3

Relative changes of daily carbon uptake due to drought as compared to irrigated vines per canopy location for Manto Negro during 1997 and 1999 at two times (S1, veraison; and S2, ripeness). Statistical differences respect to irrigated plants are indicated (ns, non-significant; *, significant at $P < 0.05$)

Location	1997		1999	
	% S1	% S2	% S1	% S2
1	-19.70 ns	-14.36 ns	16.45 ns	62.85 *
2	-8.97 ns	27.14 *	55.66 *	65.05 *
3	8.26 ns	36.11 *	49.93 *	59.49 *
4	32.48 *	52.06 *	47.21 *	66.74 *
5	24.06 *	38.22 *	14.94 ns	53.25 *
6	10.09 ns	31.00 *	24.28 *	64.53 *
7	1.90 ns	26.40 *	19.80 ns	61.44 *
8	-593 *	-833 *	0.31 ns	-10.00 ns

Table 4

Relative changes of daily carbon uptake due to drought as compared to irrigated vines per canopy location for Tempranillo during 1997 and 1999 at two times (S1, veraison; and S2, ripeness). Statistical differences respect to irrigated plants are indicated (ns, non-significant; *, significant at $P < 0.05$)

Location	1997		1999	
	% S1	% S2	% S1	% S2
1	-25.77 ns	31.04 *	23.43 *	52.98 *
2	20.30 ns	50.64 *	10.58 ns	33.52 *
3	14.97 ns	53.55 *	38.33 *	56.47 *
4	40.32 *	61.09 *	38.70 *	49.23 *
5	37.34 *	46.98 *	43.96 *	61.36 *
6	13.27 ns	29.80 *	35.62 *	40.23 *
7	-6.39 ns	16.86 ns	38.69 *	30.97 *
8	-66.9 ns	-121.3 *	-67.42 ns	-10.89 ns

a similar degree of depression due to a strong reduction of the photosynthetic quantum efficiency (Flexas *et al.* 1998; Escalona *et al.* 1999). Similar trends were observed for transpiration (not shown).

Total leaf area of irrigated plants ranged from 5 to 8 m^2 in MN (Tab. 5) and from 4 to 6 m^2 in T at harvest time (Tab. 6). The distribution of leaf area among the different canopy locations was not homogeneous. In MN, all canopy locations except location 8 had a leaf area between 0.4 to 0.7 m^2. In T, more differences were observed between locations. The upper locations (3, 4 and 5) had a higher leaf area (0.5 to 0.7 m^2) than basal locations (1, 2, 6 and 7). These differences in leaf area distribution between the two cultivars are likely to be due to the different training and pruning systems used (Poni *et al.* 1996). Moreover, as T ripens earlier, more senescent leaves were observed in the lower part of the canopy at the moment of leaf area estimation. The internal location 8 comprised up to 20-50 % of the total leaf area in both cultivars, despite the different training systems. Schultz (1995) obtained similar results comparing two different training systems.

Generally drought affected total leaf area in many cultivars (see Tabs 5 and 6; Schultz and Matthews 1988, Winkel and Rambal 1993). On average however, drought-induced leaf area reduction was larger in MN than in T. This may be related to the longer growth period of MN and its sustained until the end of July. Vegetative growth of Tempranillo, by contrast, stopped in early July, which would cause significant drought-induced reductions of total leaf area only if severe drought would occur early in the season. The distribution of drought-induced leaf area reduction within the canopy was also different, probably due to the different training systems. While in MN leaf area was equally reduced in all canopy locations, in T the effects were more marked in the most sun-exposed locations (Tab. 6).

It is remarkable that in 1997, despite strong reductions of photosynthesis due to drought (Tab. 4), the maintenance of a high leaf area in T (Tab. 6) corresponded with the maintenance of similar grape yield in irrigated and non-irrigated plants (Tab. 2). This suggests a dominant role of canopy

Table 5

Total leaf area per canopy location (m^2) at harvest for irrigated (I) and non-irrigated (NI) Manto Negro plants, in 1997 and 1999. Values are means of 4 plants ± standard error. Relative changes of total leaf area due to drought as compared to irrigated vines. Different letters indicate statistically significant differences ($P<0.05$) in total leaf area between treatments and years

Location	1997			1999		
	I	NI	% Change	I	NI	% Change
1	0.41±0.14	0.38±0.10	7.32	0.48±0.14	0.08±0.02	83.33
2	0.67±0.13	0.32±0.06	52.24	0.62±0.10	0.21±0.03	66.13
3	0.47±0.12	0.20±0.03	57.45	0.53±0.11	0.24±0.03	54.72
4	0.55±0.10	0.35±0.08	36.36	0.80±0.06	0.23±0.07	71.25
5	0.56±0.09	0.32±0.08	42.86	0.46±0.06	0.23±0.03	50.00
6	0.58±0.08	0.42±0.09	27.59	0.51±0.12	0.24±0.04	52.94
7	0.73±0.19	0.40±0.09	45.21	0.55±0.17	0.10±0.02	81.82
8	3.80±1.05	2.43±0.61	36.05	2.22±0.51	1.14±0.45	48.65
Whole plant	7.77±1.88^a	4.81±1.14^b	38.10	5.99±0.85^c	2.47±0.68^d	58.76

Table 6

Total leaf area per canopy location (m^2) at harvest for irrigated (I) and non-irrigated (NI) Tempranillo plants, in 1997 and 1999. Values are means of 4 plants ± standard error. Relative changes of total leaf area due to drought as compared to irrigated vines. Different letters indicate statistically significant differences (P<0.05) in total leaf area between treatments and years

Location		1997			1999	
	I	NI	% Change	I	NI	% Change
1	0.20±0.05	0.23±0.06	-15.00	0.29±0.11	0.25±0.10	13.79
2	0.26±0.05	0.39±0.04	-50.00	0.62±0.07	0.30±0.10	51.61
3	0.57±0.05	0.38±0.07	33.33	0.53±0.14	0.19±0.05	64.15
4	0.50±0.11	0.61±0.15	-22.00	0.46±0.09	0.35±0.15	23.91
5	0.34±0.06	0.40±0.08	-17.65	0.56±0.12	0.29±0.07	48.21
6	0.37±0.07	0.41±0.10	-10.81	0.74±0.19	0.38±0.10	48.65
7	0.38±0.09	0.19±0.04	50.00	0.25±0.10	0.22±0.09	12.00
8	1.58±0.28	1.52±0.53	3.80	1.34±0.20	0.63±0.16	52.99
Total	4.20±0.77^a	4.12±1.09^a	1.90	4.79±1.00^b	2.60±0.82^c	45.72

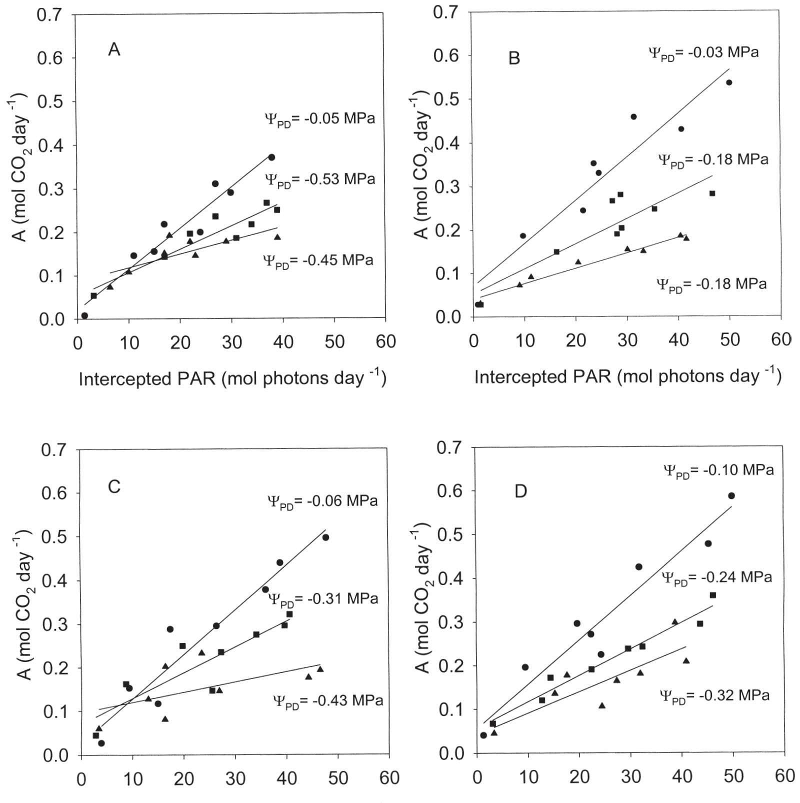

Fig. 4: Relationship between daily photosynthesis and PAR intercepted by the plant in different locations of the canopy in MN in 1997 (**A**, slopes: 9.4 x 10^{-3}, 5.4 x 10^{-3}, 3.1 x 10^{-3}; r^2: 0.93, 0.87, 0.60 at 'pea size', veraison and ripeness, respectively) and 1999 (**B**, slopes: 9.8 x 10^{-3}, 5.8 x 10^{-3}, 3.5 x 10^{-3}; r^2: 0.92, 0.79, 0.97 at 'pea size', veraison and ripeness, respectively); T in 1997 (**C**, slopes: 10.1 x 10^{-3}, 5.9 x 10^{-3}, 2.3 x 10^{-3}; r^2: 0.92, 0.78, 0.33 at 'pea size', veraison and ripeness, respectively) and 1999 (**D**, slopes: 10.1 x 10^{-3}, 6.0 x 10^{-3}, 4.9 x 10^{-3}; r^2: 0.93, 0.96, 0.69 at 'pea size', veraison and ripeness, respectively). Circles, 'pea size'; squares, veraison; triangles, ripeness.

light interception for leaf photosynthesis in total carbon gain, even if photosynthesis is reduced by drought, as previously suggested (Katerji *et al.* 1994).

Modulation of canopy light-use-efficiency under drought and the significance for canopy photosynthesis models: The above mentioned results suggested a dominant role of light interception to explain variations of photosynthesis variations within grapevine canopies. Fig. 4 shows the relationship between daily-integrated leaf CO$_2$ assimilation and daily-integrated light interception for different treatments and sampling times (each point represents one of each canopy location). It is clear that, in spite of the above described different proportional reductions of photosynthesis under drought, rates of photosynthesis of all canopy locations dropped in a linear relationship, with the exception of location 8; this is perhaps due to the insensitivity of these leaves to both irradiance and drought. It has been suggested that different leaf ages may also contribute to changes in CO_2 assimilation between canopy locations (Poni *et al.* 1994, Zufferey *et al.* 2000). In the present study all the measurements were performed from veraison to harvest. Thus, there were probably more senescent leaves in the basal portion of the canopy than in the upper one. However, the close correlation between CO_2 assimilation and incoming irradiance when all canopy locations were included suggests that the effect of leaf age was only of minor importance, at least under our experimental conditions.

The slopes of the relationships between the daily integrated CO_2 assimilation and daily integrated incoming irradiance relationships (Fig. 4) are used to estimate the photosynthetically active radiation (PAR)-use-efficiency. For both cultivars and years, irrigated plants present a PAR-use-efficiency of around 1%. This is relatively high, considering that values of 5 % have been recorded only in the tropical C_4 forage crop *Pennisetum purpureum*, and that most of the highly productive C_3 and C_4 crops (wheat, barley, maize, potato, sugar beet, rice) showed values of 1-1.5 % (Cooper 1976). This is similar to values observed for grapevines in the present study, although here we do not take into account losses due to whole-plant respiration. Drought resulted in a significant and progressive decrease of these high PAR-use-efficiencies down to values of 0.2 % in severly stressed situations (Fig. 4). Moreover, a highly significant correlation was observed between radiation-use-efficiency and either pre-dawn leaf water potential or light-saturated maximum stomatal conductance (Fig. 5), both measured on leaves from location 3. These two parameters have been demonstrated to be the most representative with regard to the severity of drought in grapevine (Flexas *et al.* 2002).

The present results can be useful to test and develop total canopy models of photosynthesis under drought conditions. The strength and linearity of the relationships between canopy photosynthesis and light interception (Fig. 4) is in contrast with results of Kull and Kruijt (1998) for two deciduous tree species (*Populus* and *Corylus*). It allows the use of 'big leaf' models of canopy photosynthesis to estimate whole canopy carbon gain in grapevines (Sellers *et al.* 1992; Kull and Jarvis 1995). These models are based on extension of leaf photosynthesis/conductance models, such as the 'Ball-Berry' model (Ball *et al.* 1987). Although the 'Ball-Berry' model has been applied successfully in grapevine canopies under certain conditions (Schultz *et al.* 1999 b), it often fails to correctly estimate canopy photosynthesis under severe drought conditions like those in our experiments (Moriana *et al.* 2002, Reichstein *et al.* 2002). This is in agreement with the fact that non-stomatal limitation to photosynthesis occurs under severe drought (Flexas *et al.* 2002), which limits the validity of these models (Reichstein *et al.* 2002). However, the strength of the relationships between radiation-use-efficiency and either pre-dawn leaf water potential or light-saturated maximum stomatal conductance (Fig. 5) provides empirical relationships to constrain those models.

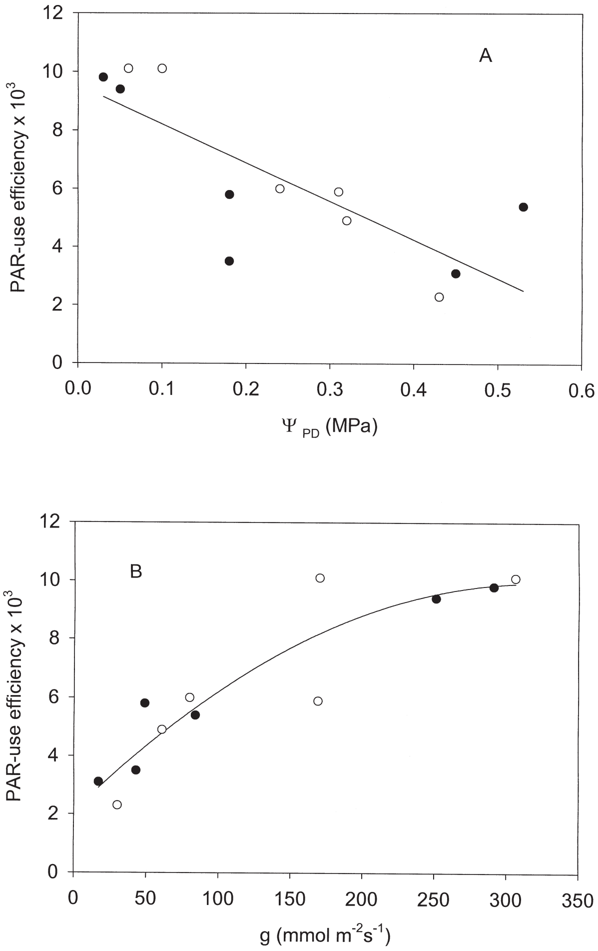

Fig. 5: Relationship between PAR-use-efficiency (*i.e.*, the slope of the relationships in Fig. 4) and (**A**) predawn leaf water potential, and (**B**) light-saturated maximum stomatal conductance (g). Data from 1997 and 1999, and from Manto Negro (full symbols) and Tempranillo (empty symbols) are plotted together.

Apart from problems at severe drought, application of most canopy conductance and/or photosynthesis models is tedious because they include a high number of factors, such as light and leaf area distributions, vapor pressure deficit, CO_2 concentration at the leaf, leaf or air temperature, etc. (Sellers *et al.* 1992; Schultz 1995; Schultz *et al.* 1999 a) as well as model simulations for a number of canopy locations that may thereafter be integrated (Schultz *et al.* 1999 a). The results presented here suggest that a reasonable estimation of whole-canopy grapevine photosynthesis could be obtained under different drought conditions by simple estimation of pre-dawn leaf water potential and/or light-saturated stomatal conductance, as well as estimations of total canopy light interception. Since the latter can easily be estimated by geometrical approaches (Riou *et al.* 1989, 1994), this would strongly simplify estimation of grapevine canopy photosynthesis at different degrees of drought. This possibility may be tested in the near future.

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