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The effect of early leaf removal on whole-canopy gas exchange and vine performance of *Vitis vinifera* L. ‘Sangiovese’

S. PONI, F. BERNIZZONI and S. CIVARDI

Istituto di Frutti-Viticultura, Università Cattolica del Sacro Cuore, Piacenza, Italy

Summary

The physiological effects induced at the whole canopy level by early vine defoliation, which has already proven to be very effective in reducing crop via diminished fruit-set while achieving loose clusters and better must quality, was investigated. Fruiting ‘Sangiovese’ vines grown in large pots were subjected to a pre-bloom defoliation (D) by removing the first six basal leaves from each shoot and compared to non-defoliated control (ND). Vegetative growth and grape yield and composition were assessed along with seasonal canopy net CO₂ exchange rates (NCER) measured via an enclosure method. While confirming that early defoliation sharply reduced fruit set, cluster compactness and yield per shoot, the post-treatment seasonal NCER/vine data were slightly higher in ND vines (13.3 μmol·s⁻¹ vs. 12.2 μmol·s⁻¹ recorded for D canopies). Yet, when these data were given on a per unit of area basis, defoliated vines showed higher rates than ND vines (4.75 μmol·m⁻²·s⁻¹ vs. 4.16 μmol·m⁻²·s⁻¹). Overall, NCER/yield (shoot basis) increased by 38 % in D vines, thus resulting in enhanced carbohydrate content for ripening; this finding accords well with advanced maturation and highly improved must soluble solids concentration. The solid physiological background of this early defoliation technique now warrants further investigation in terms of mechanical viability.

Key words: *Vitis vinifera* L., leaf removal, gas exchange, fruit-set, berry growth.

Introduction

Leaf removal in the fruiting zone, whether manual or mechanical, is a common practice in high vigor, vertically trained vine canopies (SMART 1985, BLEDSOE *et al.* 1988). Usually applied between fruit-set and veraison, it achieves increased light and pesticide penetration to the fruit zone, thus reducing disease incidence. The improved exposure of fruit to direct light increases its temperature, which aids in malic acid degradation (KLEWIER and SMART 1989), improves the sugar-acid ratio (RUFFNER *et al.* 1975) and, especially in white varieties, the aroma potential (REYNOLDS *et al.* 1996). In cool climates, improved cluster exposure can enhance berry color (DOKOOZLIAN and KLEWIER 1996), although other work conducted in warm climates has warned about the negative effects on berry pigmentation

due to over-exposure of the fruiting zone (BERGQVIST *et al.* 2001). While the effects of leaf removal on cluster microclimate and must quality appear to be rather firmly corroborated, uncertainty still exists when trying to assess the effect of leaf removal on whole-canopy CO₂ budget. Here the effects are complicated by the fact that the potential reduction in photosynthesis following leaf removal might not follow a linear pattern, as removed leaves might re-expose to light previously shaded leaves (INTRIERI *et al.* 1997) and, additionally, grapevines have the capacity to compensate for leaf removal by growing replacement foliage and stimulating the existing leaves to assimilate more efficiently. Yet it is difficult to extrapolate the responses observed for single leaves to the entire canopy, although the advent of whole-canopy gas exchange systems has offered the chance to immediately assess the effect of leaf removal on the carbon exchange rate of the whole plant (INTRIERI *et al.* 1997, PETRIE *et al.* 2003). Quite interestingly, PETRIE *et al.* (2003) found that leaf removal from the lower quarter of the canopy during the lag-phase of berry growth caused a significant decrease of whole-vine photosynthesis even on a per-unit leaf area basis, thus suggesting that the lower portion of the canopy contributed more than the upper portion to the whole-vine carbon budget.

Quite recently, PONI *et al.* (2006) have shown that a particularly early defoliation, *i.e.* removal of the first six main basal leaves at pre-bloom, is a powerful tool in controlling excessive cropping, via an effect induced by reduced fruit-set, while achieving looser clusters that are less susceptible to Botrytis infection and improved must composition in both ‘Sangiovese’ and ‘Trebiano romagnolo’. Yet, these authors characterized the seasonal modification of canopy function elicited by leaf removal on a single-leaf basis only. The present study was thus designed to assess the dynamic effects of an early leaf removal on whole-canopy gas exchange and determine how these changes are linked to yield performance and final grape composition.

Materials and Methods

Plant material and experimental layout: This trial was carried out in 2005 near Piacenza (44° 55’ N, 9° 44’ E), Italy, on five-year-old ‘Sangiovese’ grapevines (clone 12T grafted to SO4) grown outside in 120-L pots wrapped with foil to limit root-system overheating. ‘Sangiovese’ was chosen because not only is it the top red cultivar grown in Italy, with current acreage at

about 70,000 ha, and serves as the basis of such prestigious wines as Brunello and Chianti, but it is also characterized by highly compact clusters that are very susceptible to rot. In addition, given its very high bud fruitfulness, 'Sangiovese' easily tends to over-crop, especially when grown at vigorous sites.

Six vines trained to bilateral Guyot, with total cane length of about 1.5 m per vine, were arranged along a single SE-NW (35°) oriented row. Shoots were vertically positioned along catch wires up to a maximum canopy length of 1.8 m. To mimic a field situation, border rows were created with extra vines of the same variety 2 m away from the test row. Vines were protected against hail damage by a white shade net (90 % light transmission) and were irrigated twice a day with micro-drippers to deliver about 6 L of water per day. Pest treatments were applied as per local practices; no sprays against *Botrytis* were performed.

When shoots had reached the stage of "separate clusters" (stage G: BAGGIOLINI 1952), shoot thinning was applied to each vine so as to retain 18 shoots per vine (12 per meter of cane length), and clusters were manually thinned to one inflorescence per shoot. On day 142 (22 May) of the year (DOY), corresponding to stage H ("separate flower buttons": BAGGIOLINI 1952), three vines were assigned in a completely randomized design to a defoliated treatment (D), which consisted of removing the first six basal main leaves of each shoot; the remaining three vines were not defoliated (ND). Concurrently, eight shoots per vine were randomly chosen and tagged for subsequent detailed measurements. All the shoots of each vine were trimmed to 15 main leaves on DOY 159 (8 June, fruit-set stage) to avoid shoot over-hang of the fruiting area and to reproduce a condition frequently met under field conditions.

Fruit-set estimate, vegetative growth, yield and grape composition: Each cluster per tagged shoot was photographed against a dark background with a digital camera held perpendicular to the inflorescence the day before defoliation. A regression between actual flower number (Y) and the number of flowers counted on photo prints (Y) was then established for 30 inflorescences taken from extra vines and the resulting linear relationship ($y = 1.7907x$, $r = 0.94$) was used to estimate initial flower number on tagged inflorescences.

At varying dates before and after defoliation, the lamina length of each main and lateral leaf inserted on four tagged shoots was measured. This allowed estimation of total leaf area per shoot using models relating actual leaf area (y) and squared lamina length (x) for main ($y = 0.9189x$; $R^2 = 0.89$) and lateral ($y = 1.0029x$; $R^2 = 0.93$) leaves. Regressions were built over 30-leaf samplings of each leaf type taken at the end of the season from extra vines. Leaf area removed by defoliation and final total leaf area per shoot were estimated via a leaf area meter (LI-3000A, LICOR Biosciences, Lincoln, Nebraska, USA), with main and lateral contributions being kept separate.

At harvest (31 August, DOY 242), the tagged clusters were individually picked, immediately weighed and the number of berries counted. Cluster compactness was visually estimated using code OIV 204 (OIV 1983), which

ranks as 1: "berries in grouped formation with many visible pedicels" and as 9: "berries out of shape". No rot damage was detected on any of the tagged clusters.

Half of each cluster was crushed and the concentration of total soluble solids (°Brix) was determined using a temperature-compensating refractometer (RX-5000 ATAGO-CO Ltd, Washington, USA). Titratable acidity (TA) was measured by titration with 0.1 N NaOH to a pH 8.2 end point and was expressed as g/L of tartaric acid equivalents. Total anthocyanins and phenolics were determined on the second half of each cluster after Iland (1988). The cluster parts were homogenized at high speed (20000 rpm) with an Ultra-Turrax (Rose Scientific Ltd, Alberta, Canada) homogenizer for 1 min. Two grams of the homogenate were transferred to a pre-tared centrifuge tube, enriched with 10 ml aqueous ethanol (50 %, pH 5.0), capped and mixed periodically for an hour before centrifugation at 3500 rpm for 5 min. A portion of the extract (0.5 ml) was added to 10 ml 1M HCL, mixed and let stand for three hours; the absorbance values were then registered at 520 nm and 280 nm as taken on a Kontron (Tri-M Systems and Engineering Inc., Toronto, Canada) spectrophotometer. Total anthocyanins and phenolics were expressed as mg per berry and per g of fresh berry mass.

Whole-canopy gas exchange: The gas exchange of the six canopies was continuously monitored from DOY 141 (21 May) on a 24-h basis until DOY 218 (August 6) using the fully automated tree-enclosure system adapted to grapevine canopies by PONI *et al.* (1997). The chambers were then dismantled on DOY 219 for canopy maintenance and equipment recalibration and re-assembled on DOY 236 for the last four days of data recording. The system provides automated logs at 10-min intervals of CO₂ vapour pressure concentration at chamber inlets and outlets, thereby allowing calculation of canopy net CO₂ exchange rate (NCER). Reference inlet and outlet CO₂ air streams are switched at two-minute intervals to an EGM4 Infra-Red Gas Analyzer (PP-System, Hoddesdon, UK) by a solenoid valve. The system also features air-feed centrifugal blowers for a maximum flow rate of about 260 l·s⁻¹, and inflated 0.025-mm-thick, transparent polyethylene chambers enclosing the entire canopy. A CR10 data logger and control module (Campbell Scientific) are used for system programming and automated data storage.

The flow rate fed to the chambers was progressively adapted to the increasing leaf area and started at 9 l·s⁻¹ on DOY 141 and gradually raised to 15 l·s⁻¹ on DOY 170: thereafter the flow kept constant for the remaining of the measurement season. Since the polyethylene chambers had a volume of 1.25 ± 0.12 m³, a complete volume air change occurred at intervals varying from about 120 to 80 s (further details of this apparatus can be found in PONI *et al.* 1997). The chambers were equipped with zips which allowed fairly easy access to the canopies for growth measurements without necessitating dismantling; data recorded during chamber openings were discarded. Daily records of photosynthetic active radiation and air temperature were recovered from a weather station placed in close proximity to the vines.

Statistical treatment: Treatment comparison was performed by t-test and by assessing the variation around means as determined by the standard error.

Results

Defoliation at stage H removed about 70 % of pre-treatment shoot leaf area and 57 % of final shoot leaf area (Tab. 1). Seasonal development of leaf area per vine indicated that D vines had higher growth rates immediately after defoliation and trimming; yet from veraison onward, ND vines exhibited stronger lateral formation which contributed to their higher final total leaf area (Fig. 1).

Fruit-set, percent of total berries to total flower number, total berries per cluster, cluster weight and compactness were markedly reduced by leaf removal (Tab. 2). Conversely, berry weight was unaffected. Leaf removal significantly increased must soluble solids and pH and lowered titratable acidity (Tab. 3). Yet, despite a tendency towards higher values in defoliated vines, total anthocyanins did not differ regardless of unit of expression, whereas total phenols were higher in D vines when given on a per g of fresh weight basis.

Shoot efficiency evaluated as total sugar per berry and per unit leaf area was not affected by treatments; nor was the leaf area-to-yield ratio (shoot basis), which nevertheless was slightly higher for the defoliated shoots (Tab. 1). Total sugar per shoot was instead higher in the ND vines.

The measuring season (DOY 141 to 239) was characterized by mostly clear days with one period (DOY 150-154) of un-seasonally cool weather (Fig. 2 A). The net carbon exchange rate (NCER) per vine decreased by over 75 % due to defoliation (2-d average prior to leaf

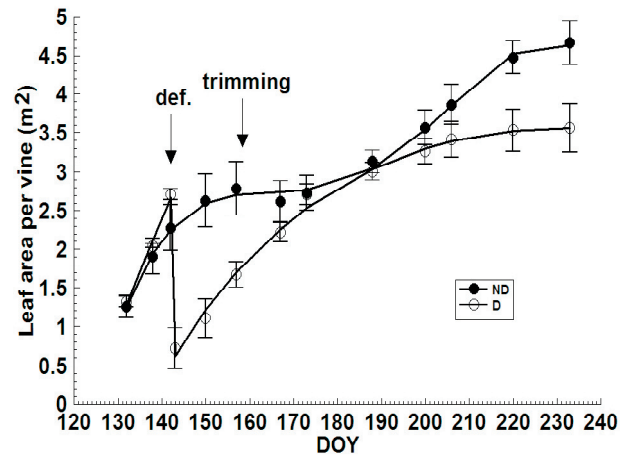


Fig. 1: Seasonal leaf area development per vine determined from single-shoot records ($n = 8$) on control (ND) and defoliated (D) plants. Pre-defoliation linear model for D was: $y = 0.159x - 19.736$, $r = 0.99$; post-defoliation non linear model for D was $y = -293.7 + 3243.9/\ln x - 8849.7/(\ln x)^2$, $R^2 = 0.99$. Non linear model for ND was: $y = -4833.9 - 161.9x + 8.02x^2 - 0.149x^3 + 1447.2x^3$, $R^2 = 0.99$. Vertical bars indicate standard error (SE).

removal versus 2-d average after defoliation) and then started to recover very promptly, reaching values similar to those of ND at trimming. Thereafter, ND and D vines showed similar NCER up to veraison (estimated around DOY 200), beyond which ND vines benefited from a more pronounced lateral re-growth (Fig. 2 B). Post-defoliation grand NCER per vine mean (DOY 143 to DOY 239) was $13.3 \mu\text{mol}\cdot\text{s}^{-1}$ in ND vines vs. $12.2 \mu\text{mol}\cdot\text{s}^{-1}$ recorded in vines subjected to leaf removal ($p < 0.05$). The ratio of NCER per yield (shoot basis) calculated throughout the season was $2.43 \text{ nmol}\cdot\text{s}^{-1}\cdot\text{g}^{-1}$ for ND and $3.31 \text{ nmol}\cdot\text{s}^{-1}\cdot\text{g}^{-1}$

Table 1

Influence of early defoliation on vegetative growth and source-sink balance of 'Sangiovese' grapevines as compared to a non defoliated control. LA = leaf area

Source of variation	Removed LA/shoot (cm ²)	Final LA/shoot (cm ²)	Final main LA/shoot (cm ²)	Final lateral LA/shoot (cm ²)	Total sugar (g)			LA shoot per yield (cm ² ·g ⁻¹)	NCER shoot per yield (nmol·s ⁻¹ ·g ⁻¹)
					per shoot	per berry	per cm ² LA		
Control	0	2693 a	1646 a	1047	58.8 a	0.347	0.0218	8.1	2.43 b
Defoliated	1130	1986 b	1202 b	784	40.6 b	0.394	0.0209	9.6	3.31 a
Significance ^{zy}	-	*	*	ns	*	ns	ns	ns	**

^z Means separated within columns by t test. ^y *, **, ns: Significant at $p \leq 0.05$, 0.01, or not significant, respectively.

Table 2

Influence of early defoliation on fruit set traits and cluster components of 'Sangiovese' grapevines as compared to a non-defoliated control

Source of variation	Flowers per cluster	Fruit set (%)	Total berries per cluster	Cluster weight (g)	Berry weight (g)	Cluster compactness (rating)
Control	435	38.8 a	169 a	334 a	1.98	6.60 a
Defoliated	487	21.0 b	103 b	207 b	2.01	4.25 b
Significance ^{zy}	ns	**	**	**	ns	**

^z Means separated within columns by t test. ^y *, **, ns: Significant at $p \leq 0.05$, 0.01, or not.

Table 3

Influence of early defoliation on standard must quality parameters, total phenols and anthocyanins of 'Sangiovese' grapevines as compared to a non-defoliated control

Source of variation	Soluble solids (°Brix)	pH	TA (g·l ⁻¹)	Total anthocyanins		Total phenolics	
				mg·berry ⁻¹	mg·g ⁻¹	mg·berry ⁻¹	mg·g ⁻¹
Control	17.6 b	3.18 b	7.35 a	1.901	0.905	4.857	2.312 b
Defoliated	19.6 a	3.31 a	5.67 b	2.036	0.993	5.419	2.643 a
Significance ^{zy}	**	**	*	ns	ns	ns	*

^z Means separated within columns by t test. ^y *, **, ns: Significant at $p \leq 0.05$, 0.01, or not significant, respectively.

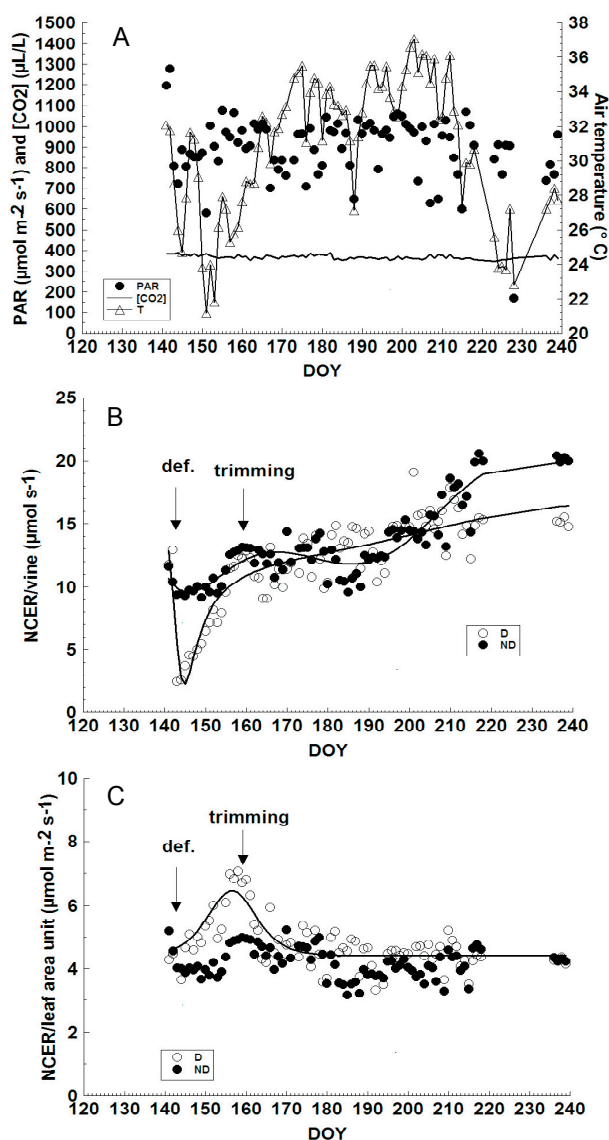


Fig. 2: Climate parameters (A), net carbon exchange rate (NCER) per vine (B) and per unit of leaf area (C) recorded daily throughout the experimental period in ND and D vines. In A, data of Photosynthetic Active Radiation (PAR), air temperature (T) and ambient CO_2 concentration $[\text{CO}_2]$ are daily means averaged at 10-minute intervals from dawn to dusk. In B and C, data are daily means over three vine replicates. In B, data for ND and D vine were fitted by a high precision polynomial order 8 equation giving $R^2 = 0.86$ and 0.76 , respectively. In C, data for D vines were fitted by a logistic dose response curve, $R^2 = 0.65$.

for D ($p < 0.01$) (Tab. 1). When NCER per vine was given on a per unit of leaf area basis data showed that, despite some day-to-day fluctuations, NCER rates measured in control vines were fairly constant over time and mostly varying around $4\text{--}5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Fig. 2 C). NCER per unit leaf area in defoliated vines recovered to pre-treatment levels three days after leaf pulling and progressed steadily to peak around trimming. After trimming, NCER per unit leaf area in D vines declined and stabilized at levels similar to those measured in control for the remainder of the season. The post-defoliation grand mean of NCER per unit of leaf area (DOY 143 to DOY 239) was $4.16 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in ND plants vs. $4.75 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ recorded in D vines ($p < 0.01$).

Discussion

According to pioneering work by COOMBE (1959) and more recent contributions (CASPARI and LANG 1996), our study confirms that a severe source limitation occurring at the onset of flowering can sharply decrease the percentage of berry set. The decrease observed in our trial (a 19 % D fruit-set drop as compared to ND) matches the abrupt 75 % reduction in NCER per vine (Fig. 2 B) and is similar to the fruit set constraint observed in the field on 'Trebiano romagnolo' by PONI *et al.* 2006. Yet, while early leaf removal was strikingly effective in reducing berry number per vine, berry size was unaffected. Although the lack of response in berry size could be simply attributed to physiological berry growth compensation (fewer berries per cluster tend to grow more), it has to be noted that around fruit-set (to be identified with trimming date) the NCER recovery by the D vines was virtually complete (Fig. 2 B), therefore making it unlikely that a severe source limitation was present during the sensitive stage of cell division, which in turn, might lead to a larger reduction of final berry size (HARDIE and CONSIDINE 1976).

Another finding which is basically confirmatory of previous work (PRIOR 2003, PONI *et al.* 2006) is that the yield per shoot reduction induced by defoliation treatments through a fruit-set effect was more or less proportional to the leaf-removal constraint, thereby explaining the similarity between final leaf-to-fruit ratios (Tab. 1). In other words, early leaf removal tunes the vines to a lower level as to vegetative growth and crop potential without significantly altering their ratio. Yet, the non-significant LA per

yield ratios per shoot in Tab. 1 are not a satisfactory explanation for the remarkable differences found at harvest in must composition and indicate that “quality” rather than “amount” of source is the crucial issue. As a matter of fact, when NCER rather than total leaf area is taken into account, it is remarkable that seasonal NCER/vine was reduced in D treatment by 9 % whereas yield per shoot was 38 % less, implying that early defoliation makes more carbohydrates available for fruit ripening.

Although the capacity of photosynthetic compensation in retained grapevine leaves triggered by leaf removal is well-documented (HOFÄCKER 1978, CANDOLFI-VASCONCELOS and KOBLET 1991, PONI and GIACHINO 2000, PETRIE *et al.* 2003), the dynamics of canopy function in this study warrants further analysis. Photosynthetic compensation was triggered very promptly by leaf removal and peaked about 15 d after defoliation. This response along with faster post-defoliation lateral development accounts for the quite rapid NCER recovery on a canopy basis. Then, too, the time trend shown in Fig. 2 C underlies the temporary nature of leaf-assimilation compensation in grapevine leaves, as also shown by CANDOLFI-VASCONCELOS and KOBLET (1991). As found likewise by PONI *et al.* (2006) at the single-leaf level, shoot trimming triggered in the defoliated canopies a much more pronounced decline of canopy-derived assimilation rates per unit leaf area than those observed in the ND vines. It is quite likely that the leaves on the D vines may have suffered from an excessive build-up of assimilates, leading in turn to sub-optimal daily assimilation rates, which might reflect both the previous strong compensation efforts and the decrease in sink demand due to removal of shoot tips and young leaves. The sensitivity of photosynthetic rates in response to leaf removal has also been shown by PETRIE *et al.* (2003), who reported no compensation of canopy-derived assimilation rates in vines defoliated at lag-phase of berry growth versus the non-defoliated two months after treatment. Again, this outcome was explained by very weak re-growth after leaf removal, which presumably represented an insufficient sink demand for stimulation of photosynthesis.

Post-veraison NCERs per unit leaf area recorded in D vines were similar to those recorded in control vines, thereby contradicting expectations for higher rates bound to a relatively younger canopy (undefoliated vines still carry basal leaves that have already started to senesce). Note, however, that whole-canopy derived data inherently takes into account the contribution of the entire population of leaves, including laterals. As shown in Fig. 1 and Tab. 1, lateral development in the present study was fostered in ND vines and, as pointed out by PONI and GIACHINO (2000), the degree of lamina expansion and maturity of lateral leaves is closely related to their assimilation capacity. Therefore, we cannot rule out that such an effect might have offset the likely higher mean assimilation rates reached by main leaves of defoliated vines after veraison.

The enhancement of must quality recorded in D vines has all the features of “advanced” ripening and is primarily the outcome of more carbohydrates available for maturation (Tab. 1). Yet, it cannot be ruled out that improved

cluster exposure in defoliated vines might have exerted some positive effects on sugar accumulation while reducing titratable acidity via an effect on malic acid degradation. Berry pigmentation was not improved in this study by early defoliation and this can accord with unchanged berry size. Then, too, it should be remembered that accumulation of anthocyanins in ‘Sangiovese’ berries is quite sensitive to the extent of cluster exposure (PONI and INTRIERI 1996) and, as already shown for ‘Pinot Noir’ (PRICE *et al.* 1995), ‘Merlot’ (MABROUQ and SINOQUET 1998) and ‘Cabernet Sauvignon’ and ‘Grenache’ (BERGQVIST *et al.* 2001), over-heating due to prolonged exposure to high light may be detrimental to pigment synthesis. This effect might have counter-acted any benefit from advanced ripening in D vines.

The assessment of the physiological effects induced by early leaf removal evaluated on a whole-canopy basis indicates that the post-defoliation CO₂ balance is shifted towards higher assimilates available per unit of crop, thus confirming previous findings derived from single-leaf-based studies. Moreover, reduced cluster compactness induced by early defoliation is conducive to less susceptibility to rot. Given this quite promising physiological background, further work is being undertaken to assess the viability of mechanically applying this technique.

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