

Effects of canopy manipulations on whole-vine photosynthesis: Results from pot and field experiments

by

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S u m m a r y : A two-year study was conducted with potted and field-grown grapevines to examine the effects of canopy restriction and leaf removal on total vine assimilation (TVA). TVA was measured using a flow-through gas exchange system equipped with flexible plastic chambers enclosing the entire canopy. Canopy restriction was applied to potted bush-shaped (BS) and field-grown spur-pruned cordon (SPC) vines on trellises to force the foliage into the smallest canopy volume. Leaf removal was performed on free cordon (FC) and SPC-trained vines at different dates to eliminate internal leaves shaded to varying extent. Canopy restriction reduced TVA more severely in the BS canopies than in the trellised SPC vines. Leaf removal elicited varying responses depending upon canopy shape, initial canopy density and leaf/fruit ratio. The FC vine showed no decrease in TVA after 27 % of its total leaf area had been removed, suggesting the occurrence of active photosynthetic compensation. TVA decreased with defoliation in the SPC vine, although the effect was mostly due to the leaf removal applied earlier in the season. In the FC vine a regression of total leaf area versus TVA showed maximum TVA at 6.0–6.5 m² of leaf area per meter of canopy. In SPC vines this relationship indicated a linear increase of TVA with leaf area and the lack of a saturation threshold under our experimental conditions. Sugar accumulation in the grapes of SPC vines correlated closely to the ratios leaf area/fruit and TVA/yield.

K e y w o r d s : *Vitis vinifera* L., canopy density, leaf removal, leaf/fruit ratio, gas exchange.

Introduction

Canopy structure and leaf distribution in grapevine are primarily affected by training system and pruning. More specifically, summer pruning leads to marked changes in canopy characteristics. For example shoot topping applied to mature vines typically brings about variations in canopy light interception, canopy age, leaf and cluster microclimate, and source/sink ratio. The effect of shoot topping, as well as of any other canopy manipulation (e.g. shoot positioning, leaf removal), thus depends upon the complex interaction of these factors, which ultimately influences the whole-canopy photosynthesis. Since extrapolating from traditional, single-leaf gas exchange measurements seems inadequate given the size and complexity of the experimental unit, the question arises as to how whole-canopy photosynthesis can be reliably quantified. Modelling might be a useful tool since it enables the well established single-leaf responses to be scaled up to the entire canopy. Unfortunately, the models for grapevine growth postulated to date (SMART 1974; GUTIERREZ *et al.* 1985; CRESPIAN *et al.* 1987; WERMELINGER *et al.* 1991) do not include, or only partially consider, leaf gas exchange as the controlling process. A more focused approach has recently been reported by SCHULTZ (1993, 1995), who developed a model based on single-leaf gas exchange to account for the dynamics encountered in the field. The model is able to satisfactorily simulate the daily courses of leaf photosynthesis for the entire season and accounts for adaptive responses to low light conditions and changes in temperature, although expansion of the model into a whole-canopy level still needs to be tested.

As an alternative to the modelling approach, the photosynthesis of whole-grapevine canopies can be directly meas-

ured by a home-built gas exchange system equipped with a chamber large enough to enclose the vine's shoot system (PONI *et al.* 1997). Given the size of the experimental unit to be measured, the potential complexity of the apparatus and the absence of commercially-available models, data originating from such systems have seldom appeared in literature (KATERJI *et al.* 1994) and most of them refer to experiments with small potted vines (EDSON *et al.* 1995; MILLER *et al.* 1996). The present study reports two-year data of total CO₂ assimilation per vine measured on both potted and field-grown plants before and after manipulations that varied canopy shape and thickness and removed, at various stages, fully and partially shaded leaves from the canopy interior.

Material and methods

G a s e x c h a n g e s y s t e m : The gas exchange system for measurements of total vine assimilation (TVA) includes an air-fed centrifugal blower for high flow rates, two flexible, transparent polyethylene chambers which enclose the entire canopy, a portable infrared gas analyzer and a data logger for system programming, data storing and processing. The details of the components and overall operation of the system for simultaneous, automated measurements of gas exchange of potted grapevine canopies are reported in PONI *et al.* (1997).

P o t s t u d i e s : In 1995, three-year-old, non-fruiting Chardonnay grapevines (*Vitis vinifera* L.) grown outside in 45 l pots containing a medium of 2.5:1.5:1 peat, sand and soil (v:v:v) were used (Fig. 1 A). Two vines were selected for uniformity of shoot number (13–14 per vine) and all clusters

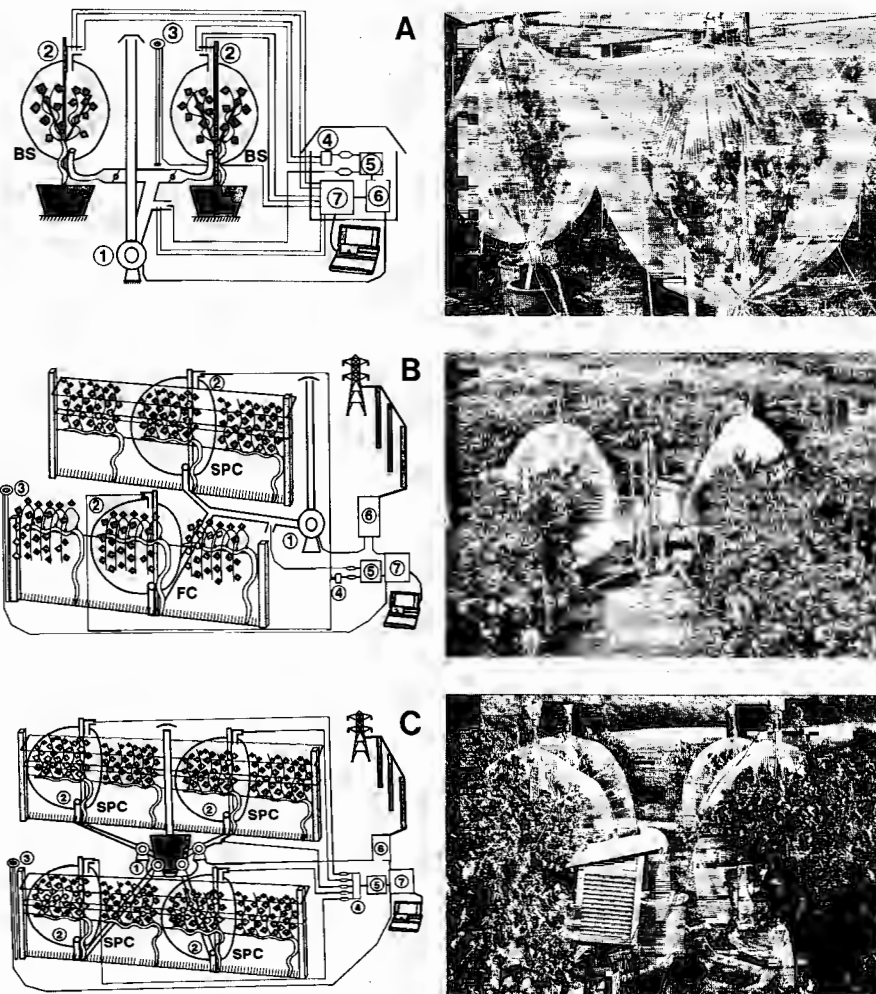


Fig. 1: Schematic and actual configuration of the automated chamber system set up for potted (A) and field-grown free cordon (FC) (B) and spur-pruned cordon (SPC) (C) trained vines. Main components are: 1) blower; 2) polyethylene chambers; 3) cosine corrected quantum sensor; 4) solenoid; 5) ADC-LCA 1 infrared gas analyzer; 6) power pack; and 7) Campbell CR10 measurement and control module. In A, the dotted lines refer to the CO_2 pathways, whereas solid lines indicate inlet and outlet sampling for RH and air temperature.

were removed at pre-bloom. Both canopies reached their maximum size by mid-June (1.4 and 1.8 m^2 leaf area, respectively) and were trained to a bush-like shape (BS) resembling, on a smaller scale, the geometry of gobelet-trained vines in the field. The vines were watered daily throughout the experimental period and pest control was applied on a calendar based schedule.

In a first series of measurements performed on June 25, the whole-canopy light response curve for one of the two vines was compared to the light response curve of single, mid-shoot, healthy leaves sampled from the same vine. Canopy light conditioning was performed by layering a series of black net shelters over the polyethylene chamber. Six levels with decreasing light intensity were thus created, and each level was allowed to equilibrate at least for 20 min. Filters made of the same material were used for single-leaf light conditioning. Single-leaf assimilation was measured by a standard ADC-LCA 1 portable gas exchange system. Data are reported as CO_2 assimilation per unit leaf area (A ,

$\mu\text{mol m}^{-2} \text{s}^{-1}$) calculated either from single-leaf or whole-canopy measurements.

A second experiment was started on June 27 with a three-day automated recording of gas exchange on both bush-shaped canopies. On June 30 the chambers were temporarily removed to apply the canopy restrictions in order to simulate the effects induced in actual trellises by hand or mechanical shoot positioning and tying. Restriction consisted of tying the shoots at two canopy levels (medium and high) to reduce the mean canopy diameter by about 50%. Whole-vine gas exchange monitoring of the modified canopies then continued until July 3. On July 2, a light response curve for one of the restricted canopy types (the same previously measured under the bush-shape) was evaluated and compared to those obtained from single leaves and unrestricted canopies measured in the first experiment.

At the end of the experiment all the leaves of both canopies were stripped and their area was measured with a LICOR 3000 meter. Total vine assimilation (TVA, $\mu\text{mol s}^{-1}$) was

calculated from air flows and CO₂ differential automatically recorded for each vine every 3 min. Specific assimilation per vine (SVA, $\mu\text{mol m}^{-2} \text{s}^{-1}$) was then derived from the ratio of TVA to total leaf area (LA, m²).

Field studies: A first set of experiments was performed in 1995 using the gas exchange system in the above described configuration. Chamber size was increased to accommodate the bigger field-grown canopies (Fig. 1 B) and air flow was adjusted to 30-35 l s⁻¹ to provide adequate air movement, to limit overheating and to prevent the inlet-outlet CO₂ differential to drop below a threshold of about -40 $\mu\text{l l}^{-1}$.

Measurements were taken on two mature vines, cv. Sangiovese (*Vitis vinifera* L.) grafted to SO 4, and either trained to free cordon (FC) and spur-pruned cordon (SPC) canopy systems on two adjacent NS-oriented rows spaced 2.5 apart (Fig. 2). Between-vine spacing was 1.5 m for both systems and bud load was 12-15 per meter of cordon length. As there were no support wires, the FC vines featured the free-growing shoots and a broad, open canopy typical for such a system, whereas the SPC shoot growth was directed upward by paired catch wires established at 0.35 and 0.80 m above the cordon, which was 1.20 m from the ground. The distance between wires was 0.30 cm for the bottom pair and 0.40 cm for the top pair.

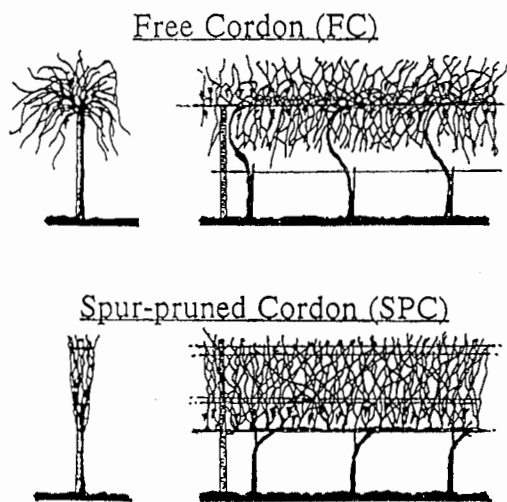


Fig. 2: Schematic configuration of canopy structure of the free cordon (FC) and the spur-pruned cordon (SPC) vines used in the 1995 and 1996 field experiments.

The system began operating on August 20, when both canopies had already completed growth, and daily gas exchange was recorded until September 27. Within this period, the chambers were dismantled three times, for intervals varying from 2 to 4 d, to remove leaves. Internal leaves exhibiting a decreasing level of shading were removed from the two vines on August 31 and September 7 and 13. The degree of light exposure of these internal leaves was visually assessed three times during the day (10 a.m., noon, 2 p.m.). Each time the leaves in the shade were marked with a white dot. Internal leaves found to be shaded at all three times during the day were classified as 'fully shaded' and removed first; those found to be shaded two times a day were defined as 'mostly

shaded' and were removed at the second date; the internal leaves found to be shaded just once were classified as 'slightly shaded' and removed last.

The area of all removed leaves was measured after each defoliation; at harvest (September 25) all remaining leaves per vine were stripped and their area was recorded as well. Yield per vine was registered and the leaf/fruit ratios were calculated.

In 1996 a second set of canopy manipulation experiments was carried out with NS-oriented, SPC-trained vines in the same field plot. The system configuration was upgraded to perform simultaneous, automated recordings of gas exchange of 4 vines in two adjacent rows (Fig. 1 C). The air flow was further increased (55-65 l s⁻¹ depending on vine size) to achieve better temperature control inside the chamber and to limit the inlet-outlet CO₂ difference to a maximum of -25 $\mu\text{l l}^{-1}$.

When the canopies had almost completed growth, a series of measurements was conducted to assess the effect of increased canopy compactness on SPC vines. The system was started on July 23 for a two-day recording of gas exchange of the 'untouched' vines. The chambers were removed at sunset of July 26 to perform a temporary canopy restriction on both row panels, and then immediately reassembled. The distance between the two pairs of catch wires was reduced by metal twists to increase foliage compactness so as to simulate the action of commercial tying machines. Gas exchange recording on the constrained vines continued until sunset of July 30, when the chambers were removed again to release the wires.

The same SPC vines were also used for a defoliation experiment beginning on August 1 with the automated recording of gas exchange on the 'untouched' vines. The chambers were removed on August 12 and the internal leaves were marked with dots according to their light exposure as in the 1995 experiment. The same day, after completion of the leaf exposure assessment, all the leaves classified as 'fully' or 'mostly shaded' were removed from each vine. Gas exchange measurements on the defoliated vines were then conducted from August 13 to 18 before all the internal, slightly shaded leaves were removed (August 19). Gas exchange recording then continued for two consecutive days before the final dismantling of the system.

The area of the removed leaves was measured at the two stages. Total node number per vine was recorded at leaf fall and total leaf area calculated by multiplying node number by mean leaf area from the leaf removal data. The course of ripening was followed by taking samples of 30 berries from each vine from August 12 until harvest on September 25, to determine fresh weight and °Brix. Yield of individual vines was also recorded at harvest and the leaf/fruit ratio per vine was calculated. TVA and SVA were calculated as in the 1995 experiments.

Results and Discussion

Light response curves and effects of canopy restriction (1995 experiments): The

photosynthetic light response curve of potted BS canopies increased more gradually than that of individual leaves. The light-saturated, single-leaf assimilation was almost two times the rate of whole-canopy assimilation (Fig. 3). This was presumably caused by the variation in leaf angle and location within the canopy, as only some of the leaves were exposed to saturating light intensity at any given time. Although the whole-canopy mean leaf assimilation is not strictly net leaf photosynthesis as it also includes the respiration of non-photosynthetic organs, the comparison of specific assimilation rates provides a useful tool for assessing the overall foliage efficiency for a given canopy type. It is clear that a maximum efficiency is reached when the light response curve for a given training system approximates most closely the optimum trend calculated from single leaves.

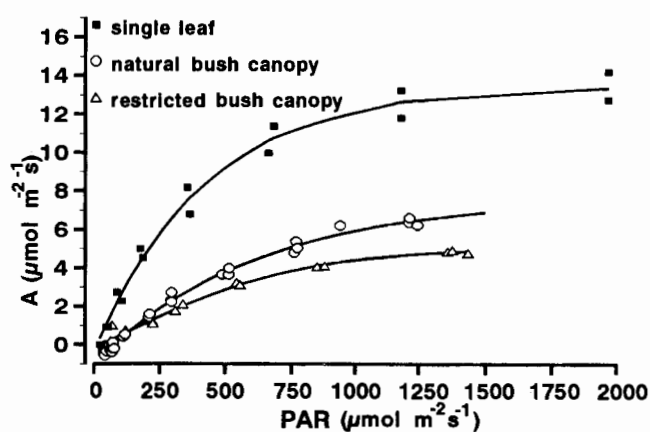


Fig. 3: Photosynthetic light response curve for single leaves and whole canopies having a natural (unrestricted) and a restricted bush shape (1995 experiment). Regression equations for assimilation are: $y = -2.99 + 3.12 / (1 + \exp(-(x+1258.15)/411.01))$, $R^2 = 0.98$ (single-leaf); $y = 7.69 - 8.71 \exp(-x/619.8)$, $R^2 = 0.99$ (bush); and $y = -4.12 + 9.2 / (1 + \exp(-(x-101.64)/346.17))$, $R^2 = 0.99$ (restricted).

The gas exchange system proved to be sufficiently sensitive to detect the limiting effect brought about by canopy confinement. Between 10:00 and 16:00 (PAR above saturation level) potted vines with restricted canopy had a mean TVA rate of $7.9 \mu\text{mol s}^{-1}$ which was significantly lower than the rate measured before canopy manipulation ($10.9 \mu\text{mol s}^{-1}$). This indicates that the reduction in canopy dimensions resulted in a limitation of overall foliage efficiency (Fig. 4).

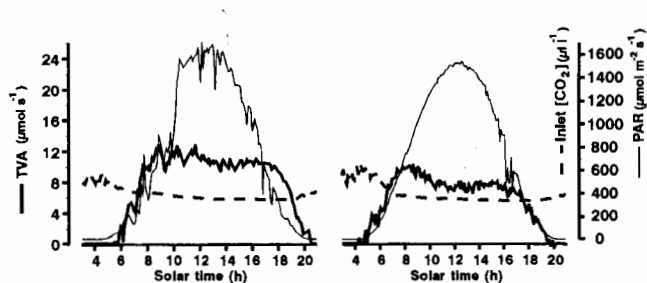


Fig. 4: Diurnal trends of PAR, inlet CO_2 , and total vine assimilation (TVA) measured on a natural bush shaped (BS) (left) and a restricted BS canopy (right) during two consecutive mostly clear days (1995 experiment). Each plot consists of data averaged over two vines. Mean TVA between 10:00 and 16:00 were 10.9 and $7.9 \mu\text{mol s}^{-1}$ for natural BS and restricted BS, respectively. Means differ as per t-test, $p \leq 0.05$.

The unrestricted and the restricted canopy types also differed in the photosynthetic light response, in that the latter had lower A rates at PAR levels above $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 3). It is thus assumed that the behavior of these two canopy types will be rather similar on overcast days with a high fraction of diffuse light, whereas on clear, sunny days the unrestricted canopy will reach a higher photosynthetic rate.

Effects of canopy restriction (1996 experiment): The effect of canopy restriction of field-grown vines could be evaluated only 3 d after the treatment due to cloudiness on days 1 and 2. Canopy confinement induced a significant limitation of mean TVA as compared to the pre-restriction values when evaluated between 10 a.m. and 4 p.m. (Fig. 5). Throughout this interval, the PAR levels generally exceeded the saturation threshold (ca. $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) except for two short periods when radiation dropped to about $600 \mu\text{mol m}^{-2} \text{s}^{-1}$, which caused a temporary reduction of TVA. Therefore, the post-restriction mean TVA is considered to be inherently affected by variations in incoming radiation.

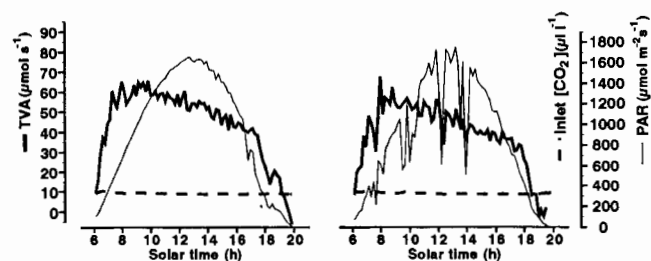


Fig. 5: Diurnal trends of PAR, inlet CO_2 and TVA measured in 1996 on field spur-pruned cordon (SPC) vines 1 d before (left) and 3 d after canopy restriction (right). Each plot consists of data averaged over 4 vines. Mean TVA between 10:00 and 16:00 were 53.0 and $45.3 \mu\text{mol s}^{-1}$ for pre- and post restriction, respectively. Means differ as per t-test, $p \leq 0.05$. TVA: see Fig. 4.

Leaf removal (1995 experiment): The data are reported only for the FC vine since the SPC vine was affected by a sudden outbreak of *Empoasca vitis*, which took place concurrently with leaf removal and caused reddening of the leaf margins. This effect overlapped with the response to leaf removal, making it impossible to separate one from the other.

The total amount of leaf area removed from the FC vine was 3.43 m^2 (27.3 % of pre-defoliation) for a final leaf/fruit ratio of $12.1 \text{ cm}^2 \text{ g}^{-1}$ (Tab. 1). The TVA and SVA plots are reported as percentage of the mean rate during the pre-defoliation measurement interval (Fig. 6). For the sake of clarity, leaf area per vine before and after each leaf removal is indicated as well. Interestingly, the trends showed that TVA did not drop below initial levels despite removing up to 27 % of total leaf area from the canopy interior. A related effect is the increase in SVA.

The nature of photosynthetic compensation for the loss of leaf area needs to be considered carefully. The data of the present study confirm previous findings by WILLIAMS *et al.* (1987), who removed ca. 30 % of total leaf area from the canopy interior and had no variations on fruit ripening char-

Table 1

Defoliation. Total and removed leaf area and leaf/fruit ratios of free-cordon (FC) trained vine during the 1995 experiment

Treatments	Leaf area (m ²)	Leaf area removed (m ²)	Leaf/fruit ratio ^a (%)	Leaf/fruit ratio ^a (cm ² g ⁻¹)
Not defoliated	12.54	0	0	16.62
1 st leaf removal	11.18	1.36	10.9	14.81
2 nd leaf removal	9.49	3.06	24.4	12.57
3 rd leaf removal	9.11	3.43	27.3	12.07

^a At harvest, yield was 7.6 kg.

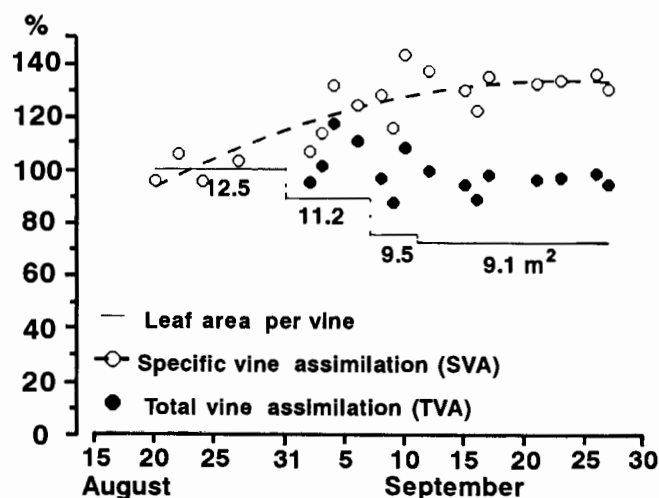


Fig. 6: Seasonal variation of TVA and specific assimilation per vine (SVA) in the FC canopy as affected by leaf removal (1995 experiment). Data are percentage of mean values recorded before defoliation. The significant regression equation for TVA on time is: $y = 32.9 + 3.7x - 0.034x^2$, $R^2 = 0.75$. TVA, FC: see Fig. 4 and Fig. 2, resp.

acteristics. Since it is unlikely that in the present study the initial removal of internal, mostly shaded leaves caused a significant change in the light exposure of the remaining external leaves, the most obvious assumption is that increased SVA simply reflects the fact that the removed leaves were at or close to the compensation point of photosynthesis. This was also confirmed by the permanently shaded individual FC leaves, which showed no net assimilation (not reported). However, leaves removed on the second and third dates were only partially shaded and probably able to provide a positive carbon balance throughout the day. Furthermore, the FC-canopy had a constant assimilation over a one-month time span, thereby offsetting the inherent adverse effect of canopy aging. These phenomena suggest that active photosynthetic compensation may have occurred in the retained leaves, which may have benefitted from decreased source strength (see Tab. 1 for decreasing leaf/fruit ratios).

The different levels of total leaf area caused by progressive leaf removals in the FC canopy made it possible to study its relation to TVA and SVA (Fig. 7). Although the TVA response to leaf area values lower than 8 m² could not be studied due to the small number of vine replicates (Fig. 7, left), it is noticeable that TVA in FC did not decrease be

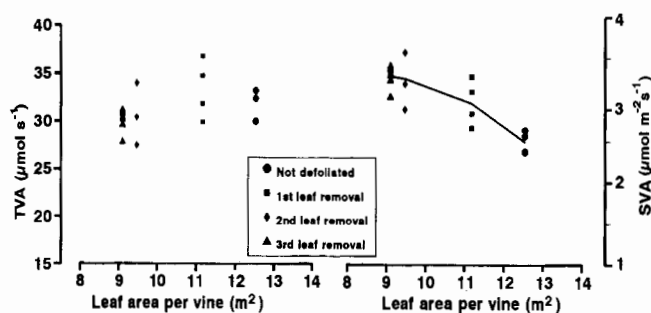


Fig. 7: Total (left) and specific (right: $y = 3.67 - 0.000163x^{3.49}$, $R^2 = 0.74$) assimilation per vine in relation to total leaf area before and after defoliation in the FC canopy (1995 expt.). Points are means obtained from 10:00 to 12:00 on different days. FC: see Fig. 2

tween the interval of the maximum pre-defoliation leaf area (12 m², or 8 m² per m of row length) and the minimum after the last defoliation (about 9 m², or 6 m² per m of row length). The decrease of SVA beyond this threshold (Fig. 7, right) reveals that in our FC canopy a total leaf development of 9 m² may optimize trellis fill and minimize internal shading, and that a rise in leaf area beyond this limit aggravates mutual shading.

Leaf removal (1996 experiment): The total leaf area of the 4 SPC-trained vines ranged from 5.8 to 10.6 m² before defoliation (Tab. 2). The percentage of leaf area removed at each date was similar among vines, thereby maintaining the initial relative differences. The final leaf/fruit ratios per vine ranged from 5.2 to 8.3 cm² g⁻¹.

The TVA response to progressive leaf removal was evaluated from the data recorded during the clear days within each measurement period. TVA significantly decreased after leaf removal and SVA was not affected (Fig. 8). These results suggest that, although leaves were classified with the same method used for FC in 1995, portions of the leaves judged to be fully or mostly shaded contributed more to photosynthesis in the SPC than in the FC-trained vines. A possible explanation is that leaves assigned to the same light exposure regime at given times may actually experience a different light microclimate for the rest of the day as a consequence of canopy shape and shoot orientation. For example, leaves classified as fully or mostly shaded in the FC canopy are likely to remain in this status longer during the day since the downward growing FC canopy (Fig. 2) allows the formation of a wide, external leaf layer which casts permanent shade over the underlying layers. The situation might be different in a vertical SPC canopy, where leaves belonging to the same category are more likely to be reached by light spots (KRIEDEMANN *et al.* 1973). This might be facilitated by the improved trellis design, which shows an enlargement of canopy width from bottom to top, thereby enabling more light penetration to the inner layers.

Although the relationship in Fig. 8 fits a negative logarithmic model, the position of the individual data points shows that the second leaf removal did not affect the TVA rates, indicating the occurrence of an offset mechanism. It seems that such a mechanism in the SPC trained vines is regulated by both initial canopy density and the leaf/fruit ratio. The second defoliation lowered the leaf/fruit ratio to 5-8 cm² g⁻¹,

Table 2

Leaf area per vine (total and removed), leaf/fruit ratios and yield at harvest of spur-pruned cordon (SPC) trained vines during the 1996 defoliation experiment

Vine	Treatments	Leaf area (m ²)	Leaf area removed (m ²)	(%)	Leaf/fruit ratio (cm ² g ⁻¹)	Yield (kg)
1	Not defoliated	8.82	0	0	11.31	7.8
	1 st leaf removal	7.38	1.44	16.3	9.46	
	2 nd leaf removal	6.46	2.36	26.8	8.28	
2	Not defoliated	5.83	0	0	10.60	5.5
	1 st leaf removal	5.09	0.74	12.7	9.25	
	2 nd leaf removal	4.53	1.30	22.3	8.24	
3	Not defoliated	10.56	0	0	7.09	14.9
	1 st leaf removal	8.99	1.57	14.9	6.03	
	2 nd leaf removal	7.71	2.86	27.1	5.17	
4	Not defoliated	8.75	0	0	7.74	11.3
	1 st leaf removal	7.40	1.35	15.4	6.55	
	2 nd leaf removal	6.62	2.13	24.3	5.86	
Mean ± SE	Not defoliated	8.49 ± 0.85	0	0	9.18 ± 0.90	9.9 ± 1.8
	1 st leaf removal	7.21 ± 0.69	1.27 ± 0.16	14.8 ± 0.7	7.82 ± 0.77	
	2 nd leaf removal	6.33 ± 0.57	2.16 ± 0.28	25.1 ± 1.0	6.89 ± 0.70	

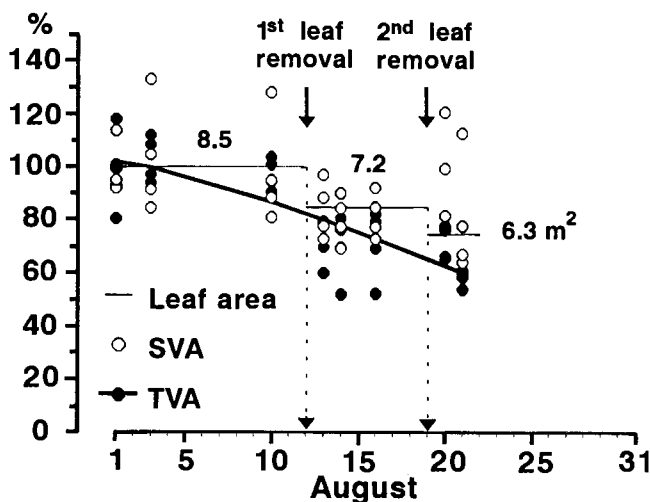


Fig. 8: Relative changes of TVA and SVA in SPC-trained vines as affected by leaf removal (1996 experiment). Data are means of 4 vines and are given as percentage of mean values recorded before defoliation. Significant regression equation for TVA on time is: $y = 101.9 - 0.654x \ln x$, $R^2 = 0.63$. SPC, TVA, SVA: see Figs. 2, 4 and 6, resp.

values reported as source-limiting in grapevine (KLEWER and WEAVER 1971). Thus, higher leaf photosynthetic rates may have been induced as a result of decreased source strength (Tab. 2).

The plot of TVA versus leaf area per vine indicated a positive linear relationship (Fig. 9, left), suggesting that a canopy filling of about 10 m² per vine was still insufficient to reach maximum TVA in the tested trellis. This response is quite different from that reported for the FC vine and indicates that optimal canopy filling varies as a function of canopy shape.

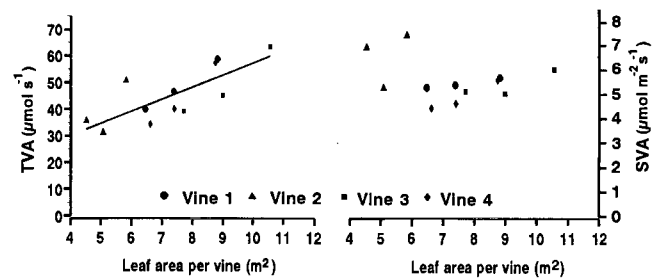


Fig. 9: TVA and SVA versus total leaf area and after defoliation performed on the SPC-trained vines (1996 experiment). Each data point represents the mean of the 4 vines calculated for each period between 10:00 and 12:00. Significant regression equation for TVA on total leaf area per vine is: $y = 12.01 + 4.54x$, $R^2 = 0.60$. SPC, TVA, SVA: see Figs. 2, 4 and 6, resp.

Sugar accumulation closely reflected the source-sink balance in each vine. Ripening was delayed in vine 3, which had the highest crop and the lowest leaf/fruit ratio (Tab. 2). Sugar accumulation also slowed down in vine 4 after the second leaf removal, which caused the leaf/fruit ratio to drop below the threshold of 6 cm² g⁻¹. Overall, the ratios set by the second leaf removal were highly correlated to final °Brix (Fig. 10 a), confirming the validity of this indicator to predict ripening development (MAY *et al.* 1969; KLEWER and WEAVER 1971). Leaf/fruit ratios calculated on total leaf area per vine are an arguable expression of the actual carbohydrate supply. This supply is in fact a function of the amount of effective leaf area, which in turn is affected primarily by leaf health and exposure. The present study also tested the ratio TVA/yield as an indicator of carbohydrate supply to clusters. The negative exponential regression fitting the data ($R^2 = 0.77$) showed a good relationship between final °Brix

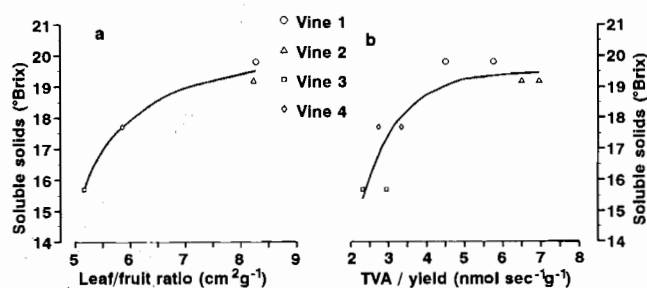


Fig. 10: Soluble solids (°Brix) in relation to (a) the leaf/fruit ratio recorded in 1996 after the two defoliations on the SPC vines ($y = 2.65 + 22.27/(1 + \exp(-(x-3.86)/0.85))$, $R^2 = 0.98$) and to (b) the TVA/yield ratio measured between 10:00 and 12:00 on 2 days after the second leaf removal ($y = 19.49 - 41.74\exp^{-x}$, $R^2 = 0.78$). SPC, TVA: see Figs. 2 and 4, resp.

and late-season TVA/yield (Fig. 10 b). It is remarkable that no change in °Brix occurred as TVA/yield increased from about 4.5 to 7.0 nmol s⁻¹g⁻¹.

From a physiological standpoint, this type of response implies that beyond a given TVA/yield ratio sink demand places a limitation on berry capacity to accumulate sugars. None of our data makes it possible to partition this effect according to factors such as a decrease in sink activity, diversion toward other vine parts (trunk and roots), limitation due to an excessive built-up of carbohydrates in the source. More practically, the fit in Fig. 10 b suggests that the SPC-trained vines can tolerate a certain source limitation before sugar concentration is affected.

Conclusions

The whole-canopy photosynthesis can be directly and objectively measured by the system presented in this paper, which can easily be adapted to varying canopy sizes and which is sufficiently sensitive to detect even small differences in gas exchange. For a given canopy type, the comparison of light response curves for specific assimilation rates determined on both single leaves sampled within the same canopy and on the whole canopy itself can estimate the importance of factors which inherently limit leaf function in a canopy, such as shading, aging and pest incidence.

The canopy restriction experiments showed that open, sparsely foliated canopies are likely to be more affected by techniques which squeeze the foliage within a more limited canopy volume. The constraint caused by catch wires inherently limits photosynthesis in vertical hedgerow canopies such as SPC. Under these circumstances, the additional effects of more severe canopy restriction might be less pronounced and more difficult to detect.

The defoliation studies suggest that some photosynthetic compensation may occur as a result of the removal of leaves at various shading levels. This effect was clear in the FC-trained vine, whereas the SPC vines generally showed less compensation capacity, which is also related to the initial amount of leaf area and leaf-to-fruit ratio. Canopy

shape was an important factor of variability in the response to leaf removal as was the leaf area level which also assures the maximum TVA. The ultimate goal would be to define a threshold for each given canopy type (e.g. upright canopies with catch wires, free growing canopies with no supporting wires). Our findings suggest that a canopy filling of about 6 m² per m of cordon in FC may be close to the optimum leaf density. The threshold for optimal leaf density in SPC could not be established since the TVA continued to increase with increasing leaf area.

Acknowledgements

The authors are grateful to EMILIA COLUCCI and M. TREVISI for their valuable assistance in assembling the pot and field experiments.

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Received February 21, 1997