Differential effects of canopy manipulation and shading of *Vitis vinifera* L. cv. Cabernet Sauvignon. Leaf gas exchange, photosynthetic electron transport rate and sugar accumulation in berries

by

F. Iacono[1]), M. Bertamini[1]), A. Scienza[2]) and B. G. Coombe[3])

[1]) Istituto Agrario di S. Michele all'Adige, Italia
[2]) Università degli studi di Milano, Istituto di Coltivazioni Arboree, Milano, Italia
[3]) University of Adelaide, Waite Agricultural Research Institute, Department of Horticulture, Viticulture and Oenology, Adelaide, Australia

S u m m a r y : Partial cluster and leaf removals were performed on *Vitis vinifera* L. cv. Cabernet Sauvignon at veraison during two years to give 4 treatments: control (C), cluster thinning (CT), leaf removal (LR) and cluster thinning + leaf removal (CT+LR). A half of each plot was shaded by a 50 % shading net at veraison (40 % berries coloured).

Shading significantly reduced stomatal conductance but not CO_2 assimilation rate (P_n) and carboxylation efficiency. P_n was decreased by cluster thinning and enhanced by leaf removal. Leaves of CT vines showed a photosynthetic decay 2 days after the treatment while LR leaves presented an afternoon photosynthetic enhancement 3 days after the treatment probably due to a higher photoassimilate requirement of the bunches (sink). Stomatal conductance did not totally contribute to the P_n depression or enhancement. Electron transport rate and maximum Rubisco activity were strongly affected by CT and LR suggesting that photochemical and biochemical processes were affected to a greater extent than physical processes.

Juice sugar concentration was reduced by shading, an effect explained straightforwardly by the lessening of stomatal conductance. CT and LR had large effects on biochemical and photochemical processes but these were in the opposite direction to the expected effects on juice sugar concentration. It is suggested that CT increased sugar concentration because of the low fruit sink load per vine, and that LR decreased sugar concentration because of the low leaf area per vine.

If cluster thinning is to be used by growers to gain increased sugar concentration it is recommended to do it at veraison; the sugar accumulation rate is then high and the adaptation of photosynthetic processes to thinning takes several days.

K e y   w o r d s : Vitis vinifera, source to sink ratio, light, gas exchange, apparent electron transport rate, sugar accumulation, berry.

A b b r e v i a t i o n s   a n d   s y m b o l s : C: control, untreated; CT: cluster thinned; LR: partial leaf removal; P_n: CO_2 assimilation rate [μmol m^{-2}s^{-1}]; g_s: stomatal conductance [mmol m^{-2}s^{-1}]; C_i: interior CO_2 concentration [ppm]; P_n/C_i: Carboxylation efficiency [μmol m^{-2}s^{-1}ppm^{-1}]; Rubisco: ribulose bis-phosphate carboxylase-oxygenase; V_c: maximum rate of Rubisco activity [μmol m^{-2}s^{-1}]; ETR: apparent electron transport rate [μmol m^{-2}s^{-1}].

Introduction

The potential sink strength of a plant organ is mainly determined genetically and can be fully expressed when the supply of assimilate is sufficient to meet the demand and the environmental conditions for the metabolic activity of the sink organs are optimal (Ho 1988). A source limitation to net photosynthesis occurs if the capacity of the reactions that supply photosynthates are inadequate for the demand of the sink tissues. On the other hand, a sink limitation occurs when the rate at which photosynthates are utilized and stored is less than that at which it is supplied to the sink tissues (Baysdorfer and Bassham 1985). Partial defoliation, partial fruit removal, as well as modifications of light and ambient CO_2 and O_2 gases have been utilized to demonstrate sink and source limitations in many different crops.

The presence of fruits stimulates net photosynthesis in grapevines (Chaves 1984; Downton *et al.* 1987; Hunter and Visser 1988; Kaps and Cahoon 1989; Edson *et al.* 1993) and other tree crops (Sams and Flore 1983; Fujii and Kennedy 1985; Schaffer *et al.* 1987; Gucci *et al.* 1991 b). Gucci *et al.* (1991 a) found that net photosynthesis inhibition in defruited sour cherry trees was particularly evident in the afternoon and was not associated with changes in the chlorophyll content. Research concerning canopy microclimate on grapevines indicates that the percentage of effective leaf surface is a major factor determining the productivity of a vine (Koblet 1984; Schneider 1985; Smart *et al.* 1985; Iacono *et al.* 1990, 1992; Bertamini *et al.* 1991).

Presumably, there are mechanisms which adjust the rates of single processes of photosynthesis so that electron transport, carbon fixation, and starch and sucrose synthesis occur at the appropriate rate.

Correspondence to: Dr. F. Iacono, Istituto Agrario di San Michele all'Aldige, Dipartimento Produzione Agricola, Via E. Mach, 1, I-38010 San Michele all'Adige (TN), Italy. Fax: (039) 461650872.

Stomatal conductance is possibly directly affected by fruit removal if fruits act as a water reservoir during certain stages of growth. GUCCI et al. (1991 b) showed that both stomatal and nonstomatal components contributed to the reduction of photosynthesis; diurnal trends of gas exchange parameters showed that there was no decline of interior CO_2 concentration associated with lower net photosynthesis and stomatal conductance.

The role of photorespiration is controversial. LENZ (1979) found an increase in photorespiration following fruit removal in citrus, while FUJII and KENNEDY (1985) found no correlation between photorespiration and fruit load in apple trees.

The aim of the present study was to characterize the short- and long-term responses of mature grapevine plants to source and sink manipulation. We monitored changes in gas exchange and fluorescence in leaves and sugar accumulation in berries to elucidate possible mechanisms (biochemical, physical or photochemical) whereby photosynthetic changes are directly linked to juice quality. Furthermore, since the sugar level in berries at harvest time is a critical factor in cool climate viticulture, technical recommendations are also given.

Materials and methods

Plant material and experimental layout: The details of the vines and design used for this experiment have been described by IACONO et al. (1994). Briefly, plots were established in a Cabernet Sauvignon vineyard at San Michele all'Adige (Trentino, Italy) and four treatments were applied at veraison (40% berries coloured): untreated control (C), thinning clusters with all but the basal clusters removed from all shoots (CT), partial leaf removal where all leaves around the clusters were cut off (LR), and the combination in which both CT and LR were applied together (CT+LR). In addition one of every pair of these 4 treatments was shaded by a 50 % shadecloth from veraison until harvest. These 2 x 4 factorial plots were replicated 4 times. Light incidence (PPFD) at the level of clusters was measured as in IACONO et al. (1994). Sugar concentration in berry juice was determined every 14 d using a 200 g berry sample from each plot.

Gas exchange measurements: P_n, g_s and C_i were measured with an open gas exchange system; the cuvette in which leaves were enclosed had a 30 cm² glass window in the top side (Central Unit CMS 400 by H. Walz, Effeltrich, Germany). All measurements were performed on the 11th leaf from the base of the shoot. Data were recorded as soon as cuvette conditions reached steady-state at 1500 µmol photons m⁻²s⁻¹ (PPFD), 25 °C air temperature, and 60 % relative humidity. The equations of VON CAEMMERER and FARQUHAR (1981) were used to calculate the photosynthetic parameters.

In 1992, gas exchange was measured 7, 14 and 21 d after treatments from 10.00 a.m. to 01.00 p.m. on 2 leaves per plot. In 1993, gas exchange was measured on sun-exposed vines of C, CT, and LR treatments under the same

standard conditions used in 1992. Measurements started the day of bunch and leaf removal and were repeated 1, 2, 3, and 7 d later at three different times of the day (09.00-10.00 a.m., 12.00 a.m. - 01.00 p.m., and 03.00-04.00 p.m.) on two leaves per treatment.

V_c was calculated using equations of SHARKEY (1988) assuming that the rate of mitochondrial respiration was 1 µmol m⁻²s⁻¹ (PAMMENTER et al. 1993). $V_c = (P_n+R_d)(C_i+K')/(C_i-\Gamma^*)$ where R_d is the mitochondrial respiration, K' is the effective Michaelis-Menten constant for CO_2 (46 Pa, according to FARQUHAR et al. 1980), and Γ^* is the compensation point of CO_2 in the absence of respiration.

Fluorescence measurements: For the description of the fluorescence measurements we adopted the nomenclature proposed by VAN KOOTEN and SNEL (1990). A modulation fluorometer (Pam 2000, H. Walz, Effeltrich, Germany) was used supported by the software DA-2000, version 1.0, also by Walz. In 1993, 7 d after the treatments, fluorescence was measured on 3-4 fully expanded leaves per plot on shaded and sun-exposed treatments at noon (12.00 a.m.-01.00 p.m.). Yield of quantum efficiency of photosystem II (PSII) was estimated from fluorescence intensity (measured with a single flash of 0.1 s length at 3400 µmol photons m⁻²s⁻¹) both at steady state (F_s') and when all of the PSII reaction centres are in an energised state (F_m'). From the formula of GENTY et al. (1989), quantum yield = $(F_m'-F_s')/F_m'$. This was then combined with PPFD to estimate ETR by the formula

ETR = Yield·PPFD·0.5·0.8, where Yield = $(F_m'-F_s')/F_m'$, 0.5 adjusts for the transport of 1 electron from 2 quanta absorbed and 0.8 adjusts for 81 % of incident quanta absorption by leaves of cv. Cabernet Sauvignon.

Results

Long-term experiment

Sugar accumulation in berries: CT significantly increased whole plant leaf area/yield ratio whilst LR decreased it. The combination of both treatments (CT+LR) did not modify this parameter (Tab. 1a). At harvest, the fruit with highest sugar concentration was from cluster thinned vines, and the lowest from leaf removed vines (Tab. 1 a). Similar differences were apparent at earlier stages of ripening, i.e. at 14, 28 and 42 d after veraison. Shading lowered sugar concentration, the effects being greatest and significant at 14 d and at harvest (Tab. 1 b). There were no statistically significant interactions in sugar concentrations between treatments at any ripening stage.

Leaf photosynthetic responses to radiation and source to sink ratio modifications: In 1992, P_n and P_n/C_i were significantly reduced by CT, and enhanced by LR, as was P_n/C_i in 1993 (Tab. 2 a). The variation in P_n did not appear to depend on stomatal control. Shading significantly depressed stomatal conductance (g_s) (Tab. 2 b). Interactions between treatments and gas exchange parameters were not significant.

Table 1

Influence of canopy manipulation, shading and year on sink to source relationships and sugar concentration in juice. C: control; CT: cluster thinning; LR: leaf removal

Treatments		[a]WPLA/ Yield (m²/kg)	Sugar at veraison (g/L)	Sugar 14 days after veraison (g/L)	Sugar 28 days after veraison (g/L)	Sugar 42 days after veraison (g/L)	Sugar at harvest (g/L)
a) Canopy Manipulation (CM)	C	1.48 b		146 b	176 ab	182 ab	182 b
	CT	2.34 a	75	155 a	182a	188 a	190 a
	LR	1.01 c		135 c	165 c	168 c	173 c
	CT+LR	1.54 b	82	151.ab	178 ab	178 b	180 b
	[b]P of F ratio	<0.001	0.349	0.001	0.046	0.010	0.006
b) Shading (S)	Not Shaded	1.56	80	151	177	181	186
	Shaded	1.55	78	141.	172	176	176
	P of F ratio	0.641	0.890	0.002	0.395	0.379	0.002
c) Year (Y)	I	1.82	71	148	177	177	182
	II	1.26	82	144	171	180	180
	P of F ratio	<0.001	0.011	0.274	0.214	0.379	0.603

[a]: WPLA/Yield= Whole Plant Leaf Area / Crop per vine
[b]: Probability of F ratio. Mean separation by Duncan's Multiple Range Test

Table 2

Influence of canopy manipulation, shading and day of measurement on gas exchange parameters in 1992: CO_2 assimilation rate (P_n), stomatal conductance (g_s), carboxylation efficiency (P_n/internal CO_2 concentration). Values are averages from the factorial combinations. No interactions between treatments were significant. C, CT, LR: see Tab. 1

Treatments		P_n (μmol m⁻²s⁻¹)	g_s (mmol m⁻²s⁻¹)	P_n/C_i (μmol m⁻²s⁻¹ ppm⁻¹)	P_n/C_i(1993) [b](μmol m⁻²s⁻¹ ppm⁻¹)
a) Canopy Manipulation (CM)	C	14.74 b	228.4	0.072 b	[c]0.059 b
	CT	13.45 c	211.9	0.064 c	0.052 c
	LR	16.47 a	259.4	0.080 a	0.069 a
	CT+LR	14.85 b	242.3	0.071 b	
	[a]P of F ratio	0.010	0.151	0.011	<0001
b) Shading (S)	Not Shaded	15.49	253.6	0.074	
	Shaded	14.27	217.4	0.070	
	P of F ratio	0.055	0.020	0.179	
c) Measurement day (D)	7	16.25 a	270.8 a	0.077	
	14	14.32 b	216.3 b	0.070	
	21	13.92	214.6 b	0.068	
	P of F ratio	0.003	0.003	0.027	

[a]: Probability of F ratio. Mean separation by Duncan's Multiple Range Test
[b]: In 1993 measures were done only on not shaded C, CT, and CT+LR treatments.
[c]: Data are the averages of values recorded the seventh day after treatments

Table 3

Influence of source to sink ratio manipulation on radiation (PPFD) and fluorescence parameters: fluorescence intensities at steady state (F_s) and energized state (F_m'), PS II quantum yield (Yield) and apparent non-cyclic electron transport rate (ETR- see formula in the text). Measurements were made 7 d after treatment. C, CT, LR: see Tab. 1

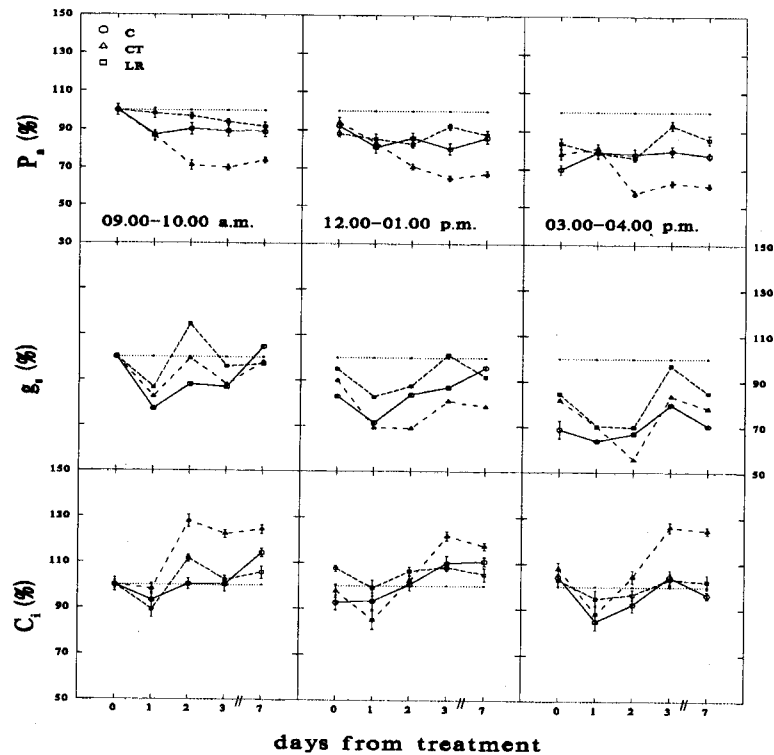| Treatment		PPFD (μmol m⁻²s⁻¹)	F_s' (arbitrary units)	F_m' (arbitrary units)	Yield (arbitarry units)	ETR (μmol m⁻²s⁻¹)
Canopy Manipulation	C	1175 b	0.290 b	0.705 ab	0.589 a	280 b
	CT	1240 ab	0.315 c	0.615 c	0.489 c	245 c
	LR	1310 a	0.260 c	0.725 a	0.641 a	340 a
	CT+LR	1200 b	0.280 b	0.680 b	0.588 b	285 b
	[a]P of F ratio	0.098	<0.001	<0.001	>0.001	<0.001

[a]: Probability of F ratio. Mean separation by Duncans Multiple Range Test

Fig. 1: Short-term trend of CO_2 assimilation rate (P_n), stomatal conductance (g_s) and interior CO_2 (C_i) in 1993 in relation to source to sink ratio manipulation. Values are standardized by considering 100 the average of the values recorded at day 0 and 09.00-10.00 a.m. (Means ± Standard Error). C: control; CT: cluster thinning; LR: leaf removal.

Also quantum yield of PSII (Yield = $(F_m'-F_s')/F_m'$) in the light showed significant differences among treatments. Partial leaf removal slightly increased radiation vs. control vines (Tab. 3). Steady state fluorescence emission (F_s') was depressed by LR and enhanced by CT but the reverse was true for fluorescence emission at energized state (F_m'). Partial leaf removal greatly increased ETR and partial cluster thinning decreased it; these effects were probably due to sun exposure changes.

Short-term experiment

P_n measured over three one-hour periods during morning, mid-day and afternoon, declined during the first day in control and cluster-thinned vines, but thereafter remained steady in control vines while declining further to a low rate on CT vines (Fig 1). The effects of LR were quite different to that of CT: at the 9-10 reading P_n values were always high, but later in the day readings were high only on day 3.

Interior CO_2 concentrations (Fig 1) were, in general, the mirror image of P_n especially after cluster thinning; an exception were the noon and afternoon readings on day 2 when C_i was low, matching a lowered stomatal conductance. Stomatal conductance was also affected by leaf removal, being higher than other treatments at each time of day and on each day, particularly on day 3. The short-term trends of P_n and C_i shown in Fig. 1 accord with the P_n/C_i ratios of Tab. 2 a, i.e. a decrease after CT and an increase after LR.

Since P_n/C_i changes may imply enzymatic modifications in the photosynthetic machinery, we estimated

Rubisco activity (V_c). Fig. 2 shows that V_c decayed significantly after 2 d from CT treatment while control showed only a small decline in the morning and at noon on all days; LR was almost constant both during the day and during the 7 d of measurement.
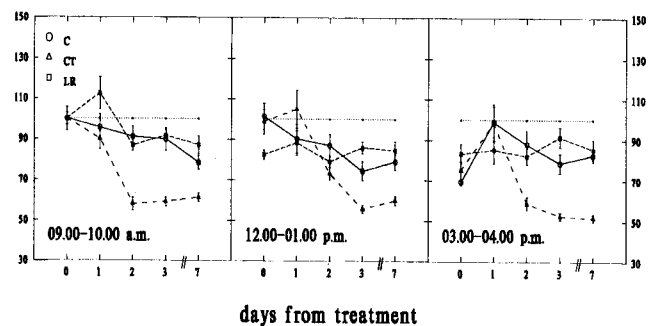
$V_c(\%)$

Fig. 2: Short-term trend of maximum Rubisco activity (V_c) in 1993 in relation to source to sink ratio manipulation throughout the day. Values are standardized by considering 100 the average of the values recorded at day 0 and 09.00-10.00 a.m. (Means ± Standard Error). C, CT, LR: see Fig. 1.

Discussion

The reduction in berry juice sugar concentration following shading at veraison was not associated with appreciable changes in yield or leaf area and can be explained adequately by a decline in stomatal conductance and other similar consequences of lowered radiation incidence. In

contrast, the effects of the other treatments, cluster thinning and partial leaf removal, were much more intricate.

Cluster thinning lowered yield appreciably with no change in leaf area and caused elevated juice sugar concentration within 14 days after treatment, an effect then maintained throughout ripening (Fig. 3). These responses were accompanied by an unchanged stomatal conductance and a reduction in CO_2 assimilation rate, carboxylation efficiency, Rubisco activity and electron transport rate. An explanation for the apparent anomaly of lower assimilation rate and yet higher fruit sugar concentration is found in the calculation of sugar yield per vine. Sugar accumulation in fruit of the whole vine can be approximated by multiplying vine yield by sugar concentration at harvest. These data (not presented) show that differences in sugar per vine were proportional to vine yield (C=4.37; CT=2.91; LR=3.46; CT+LR=2.28 kg/vine) and, therefore, that CT reduced sugar yield by 40% yet photosynthetic processes, though reduced, were sufficient to give an increased juice sugar concentration in the 33 % smaller weight of fruit. The reduction in assimilation rate was apparent in the morning of the second day after cluster thinning and continued through the day. GUCCI et al. (1991 b) found that fruit removal of mature sweet cherry trees resulted in a significant decrease in leaf net photosynthesis and an increase in leaf starch within 24 h. They also reported that starch content of leaves increased by 67 % within 24 h of fruit removal and concluded that, although large starch grains accumulated and more chloroplasts were damaged, the proportion of the observed post-harvest decline in net photosynthesis due to this effect was minor.
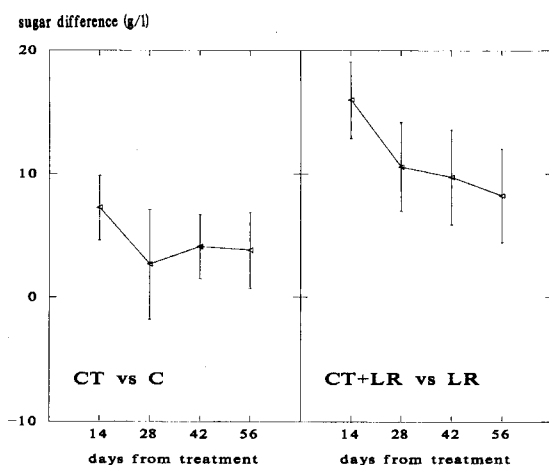

Fig. 3: Berry sugar level differences during berry ripening. (Means ± Standard Error). C, CT, LR: see Fig. 1.

Partial leaf removal had no significant effect on yield but caused lowered juice sugar concentration within 14 d after treatment; this effect was then maintained throughout ripening (Fig. 3). These changes were accompanied by an unchanged stomatal conductance but an increased CO_2 assimilation rate, carboxylation efficiency, Rubisco activity and electron transport rate. As with cluster thinning, an explanation of these effects is found by considering photosynthesis on a whole vine basis. Assimilation rate measurements (P_n) do not equate to photosynthate production

per vine. Firstly, the rate reading is only for a short time and on a small portion of leaf. More important, it does not relate to measures involving whole plant leaf area. The halving of leaf area by the leaf removal treatment (Tab. 1), compared with the 12 % increase in P_n, shows that leaf removal was likely to have reduced total photosynthesis per vine; this would explain the effect of leaf removal in lowering juice sugar concentration despite increased rates in components of photosynthesis (Tab. 2 a). The enhancement of P_n, carboxylation efficiency, Rubisco activity, and electron transport rate became apparent by the third day after treatment, and were evident during the afternoon when photosynthesis is normally depressed; this may be a reflection of the reduced source/sink ratio.

A delay of a few days for the effect of leaf removal to appear in the photosynthetic machinery was also shown by HODGKINSON (1974). He found that maximum fluorescence quantum yield was not elevated above that in control plants until the seventh day after removal. Several possible mechanisms of feedback on electron transport have been proposed including depression of stromal phosphate levels (HORTON 1989; SHARKEY and VANDERVEER 1989) limited ATP supply (PREISS 1984; LAISK et al. 1991), and an increase in non-photochemical quenching linked to a reduction in the maximum Rubisco activity (PAMMENTER et al. 1993). Moreover, WAREING et al. (1968) and VON CAEMMERER and FARQUHAR (1984) found that the photosynthetic enhancement following defoliation may have been due to the combined enhancement of Rubisco activity and ribulose-1,5-biphosphate regeneration rate. CANDOLFI-VASCONCELOS and KOBLET (1991) obtained similar results in grapevines.

Like LAYNE and FLORE (1993) and PAMMENTER et al. (1993), our data suggest that source/sink manipulation affects biochemical and photochemical processes to a greater extent than stomatal conductance. Further, such effects are slow to develop.

Practical considerations

The large but opposite effects of leaf removal and cluster thinning on juice sugar concentration were both evident within 14 d after treatments performed at veraison: thereafter, the differences were maintained as the berries ripened. The same early response, followed by parallel concentration curves, were shown by IACONO et al. (1991) following cluster thinning of several grape varieties.

Obviously veraison is an optimal stage for grape quality enhancement by cluster thinning because sugar accumulation rate is rapid early during the ripening phase and the effect of the time delay required for photosynthesis to adjust is lessened.

Partial leaf removal created source limitations. Even though components of leaf photosynthesis were enhanced by this treatment, both juice sugar concentration and sugar yield per vine were reduced.

These results show the predominating effect of crop yield on assimilate partitioning.

Acknowledgements

References

BAYSDORFER, C.; BASSHAM; J. A.; 1985: Photosynthate supply and utilization in alfalfa. A developmental shift from a source to a sink limitation of photosynthesis. Plant Physiol. **77**, 313-317.

BERTAMINI, M.; IACONO, F.; SCIENZA, A.; 1991: Manipolazione dei rapporti sink-source mediante il diradamento dei grappoli e riflessi sulla qualità (cv. Cabernet S.). Vignevini **18** (10), 41-47.

CANDOLFI-VASCONCELOS, M. C.; KOBLET, W.; 1991: Influence of partial defoliation on gas exchange parameters and chlorophyll content of field-grown grapevines - Mechanisms and limitations of the compensations capacity. Vitis **30**, 129-141.

CHAVES, M. M.; 1984: Photosynthesis and assimilate partitioning in fruiting and non-fruiting grapevine shoots. In: Proc. of the VIth Intern. Congr. on Photosynthesis. Brussels, Belgium. Adv. Photosyn. Res. **4** (2), 145-148.

DOWNTON, W. J. S.; GRANT, W. J. R.; LOVEYS, B. R.; 1987: Diurnal changes in the photosynthesis of field grown grapevines. New Phytol. **105**, 71-80.

EDSON, C. E.; HOWELL, G. S.; FLORE, J. A.; 1993: Influence of crop load on photosynthesis and dry matter partitioning of Seyval grapevines. I. Single leaf and whole vine response pre- and post-harvest. Amer. J. Enol. Viticult. **44**, 139-147.

FARQUHAR, G. D.; VON CAEMMERER, S.; BERRY, J. A.; 1980: A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta **149**, 78-90.

FUJII, T. A.; KENNEDY, R. A.; 1985: Seasonal changes in the photosynthetic rate in apple trees. A comparison between fruiting and non-fruiting trees. Plant Physiol. **78**, 519-524.

GENTY, B.; BRIANTAIS, J. M.; BAKER, N. R.; 1989: The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biophys. Acta **990**, 87-92.

GUCCI, R.; PETRACEK, P. K.; FLORE, J. A.; 1991 a: The effect of fruit harvest on photosynthetic rate, starch content and chloroplast ultrastructure in leaves of Prunus avium L.. Adv. Horticult. Sci. **5**, 19-22.

- -; XILOYANNIS, C.; FLORE, J. A.; 1991 b: Gas exchange parameters, water relations and carbohydrate partitioning in leaves of field grown Prunus domestica following fruit removal. Physiol. Plant. **83**, 497-505.

HO, L. C.; 1988: Metabolism and compartimentation of imported sugars in sink organs in relation to sink strength. Ann. Rev. Plant Physiol. Plant Mol. Biol. **39**, 355-378.

HODGKINSON, K. C.; 1974: Influence of partial defoliation on photosynthesis, photorespiration and transpiration by lucerne leaves of different ages. Austral. J. Plant Physiol. **1**, 561-578.

HORTON, P.; 1989: Interactions between electron transport and carbon assimilation: Regulation of light-harvesting and photochemistry. In: BRIGGS, W. R. (Ed.): Photosynthesis, 393-406. Alan R. Liss, Inc, New York.

HUNTER, J. J.; VISSER, J .H.; 1988: The effect of partial defoliation, leaf position, and developmental stage of Vitis vinifera L. cv. Cabernet Sauvignon. S. Afr. J. Enol. Viticult. **9** (2), 9-15.

IACONO, F.; BERTAMINI, M.; MATTIVI, F.; 1994: Differential effects of canopy manipulation and shading. Note I Composition of grape berries (Vitis vinifera L. cv. Cabernet Sauvignon). Wein-Wiss. **49**, 220-225.

- -; - -; SCIENZA, A.; 1990: The role of pruning, leaf removal and cluster thinning on vegetative and productive response of Vitis vinifera (cv. Cabernet Sauvignon). In: Abstracts of contributed papers at the XXII International Horticultural Congress Firenze (Italy), Aug. 27-Sept. 01. 2. Poster n. 4184.

- -; - -; - -; STEFANINI, M.; 1992: Valutazione dell'efficienza di una forma di allevamento della vite. In: Proceedings of Giornate Scientifiche S.O.I. Ravello (Italy) April 8-10, 310-311.

KAPS, M. L.; CAHOON, G. A.; 1989: Berry thinning and cluster thinning influence vegetative growth, yield, fruit composition and net photosynthesis of Seyval blanc grapevines. J. Amer. Soc. Horticult. Sci. **71**, 167-176.

KOBLET, W.; 1984: Influence of light and temperature on vine performance in cool climates and applications to vineyards management. In: HEATHERBELL, D. A.; LOMBARD, P. B.; BODYFELT, F. W.; PRICE, S. F. (Eds.): Proc. Intern. Symp. on Cool Climate Viticult. Enol., 25-28 June 1984. Oregon, 139-157.

LAYNE, D. R.; FLORE, J. A. 1993: Physiological responses of Prunus cerasus to whole-plant source manipulation. Leaf gas exchange, chlorophyll fluorescence, water relations and carbohydrate concentrations. Physiol. Plant. **88**, 44-51.

LAISK, A.; SIEBKE, K.; GERST, U.; EICHELMANN, H.; OJA, V.; HEBER, U.; 1991: Chlorophyll fluorescence and photosynthesis: The basics. Ann. Rev. Plant Physiol. Plant Mol. Biol. **42**, 313-349.

PAMMENTER, N. W.; LORETO, F.; SHARKEY; T. D.; 1993: End product feedback effects on photosynthetic electron transport. Photosyn. Res. **35**, 5-14.

PREISS, J.; 1984: Starch, sucrose biosynthesis and partition of carbon in plants are regulated by orthophosphate and triose-phosphates. Trends Biol. Sci. **9**, 24-27.

SAMS, C. E.; FLORE, J. A.; 1983: Net photosynthetic rate of sour cherry (Prunus cerasus L. Montmerency) during the growing season with particular reference to fruiting. Photosyn. Res. **4**, 307-316.

SHAFFER, B.; LIU, K.; GOLDSCHMIDT, E. E.; BOYER C. D.; GOREN, R.; 1986: Citrus leaf chlorosis induced by sink removal: starch, nitrogen, and chloroplast ultrastructure. J. Plant Physiol. **124**, 307-319.

SHARKEY, T. D.; 1988: Estimating the rate of photorespiration in leaves. Physiol. Plant. **73**, 147-152.

- -; VANDERVEER, P. J.; 1989: Stromal phosphate concentration is low during feedback limited photosynthesis. Plant Physiol. **91**, 679-684.

SCHNEIDER, C.; 1985: Influence de la suppression des entre-coeurs de souches de vigne sur le microclimat lumineux et la recolte. Conn. Vigne Vin **1**, 17-30.

SMART, R. E.; ROBINSON, J. B.; DUE, G. R.; BRIEN C. J.; 1985: Canopy microclimate modification for the cultivar Shiraz. 1. Definition of canopy microclimate. Vitis **24**, 119-128.

VAN KOOTEN, O.; SNEL, J. F. H.; 1990: The use of chlorophyll fluorescence nomenclature in plant stress physiology. Photosyn. Res. **25**, 147-150.

VON CAEMMERER, S.; FARQUHAR, G. D.; 1981: Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta **153**, 376-387.

- -; - -; 1984: Effects of partial defoliation, changes of irradiance during growth, short term water stress and growth at enhanced $p(CO_2)$ on the photosynthetic capacity of leaves of Phaesolus vulgaris L.. Planta **160**, 320-329.

WAREING, P. F.; KHALIFA, M. M.; TREHARNE, K. J.; 1968: Rate-limiting processes in photosynthesis at saturating light intensities. Nature **220**, 453-457.