

Influence of leaf ageing, leaf area and crop load on photosynthesis, stomatal conductance and senescence of grapevine (*Vitis vinifera* L. cv. Pinot noir) leaves

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Summary

Treatments varying the leaf area (source) to crop load (sink) balance of pot-grown Pinot noir vines caused differences in the photosynthesis (Pn) rates of the fourth leaf, 48 h after they were applied. Stomatal conductance was only affected by leaf removal, not by the presence or absence of crop. The vines with and without crop were subject to a range of leaf removal treatments. All treatments retained leaves at nodes 1–4 from the shoot base and then had 100 % (control), 66 %, 33 %, or 0 % leaves retained from node 5 to the apex of the shoot. Leaf removal elevated the Pn rate of the fourth leaf, but there was no difference in Pn rate between vines with or without crop pre-veraison. From veraison on the photosynthetic rate of vines with crop and 100 % leaves retained increased. Similar, high Pn rate was also observed for vines without crop and 0 % leaves retained. The lower Pn rate of vines with crop pre-veraison suggests that there is potential to increase vine productivity in this period. The Pn rate of vines without crop, 100 % and 66 % leaves retained declined from 15 d after treatment. Average Pn of all treatments over the 4 measurements prior to harvest was positively correlated with the vine leaf area (source) to total vine dry weight (sink) ratio. Leaves of vines with a high source:sink ratio (without crop, 100, 66 or 33 % leaves retained) senesced *i.e.* decreased in chlorophyll content more rapidly than leaves of the low source to sink ratio treatments. Results indicate that the decline in grapevine leaf Pn, previously associated with advanced leaf age is actually caused by a progressive increase in leaf area to fruit weight (source:sink) ratio, as leaves emerge on the developing vine.

Key words: source:sink ratio, leaf area, leaf age, crop load, photosynthesis, stomatal conductance, fruit maturity.

Introduction

Pn of a grapevine leaf may be influenced by ambient factors and leaf age (KRIEDEMANN 1968; KRIEDEMANN *et al.* 1970; LIU *et al.* 1978; ALLEWELDT *et al.* 1982; WILLIAMS and SMITH 1985; PONI *et al.* 1994). When the source or

sink size is manipulated by defoliation (HOFÄCKER 1978; HUNTER and VISSER 1988), topping (KAPS and CAHOON 1989), or girdling (KRIEDEMANN and LENZ 1972; HOFÄCKER 1978), the leaves usually respond by increasing their photosynthetic rate as the relative source:sink ratio decreases. The presence of fruit stimulates the Pn rate of individual leaves (HOFÄCKER 1978; CHAVES 1984; DOWNTON *et al.* 1987; KAPS and CAHOON 1989). KRIEDEMANN *et al.* (1970) and PONI *et al.* (1994) concluded that Pn reaches a maximum 30 d after unfolding, and then declines as leaves age. However SCHULTZ (1996) has reported that the leaves opposite the cluster maintain the highest Pn rates until the month prior to harvest. Cropping has also been associated with higher late season Pn in peach (CHARMERS *et al.* 1975; DE JONG 1986) and apple (PALMER *et al.* 1997). This suggests that the higher demand for photosynthates associated with fruit ripening has the potential to maintain or increase grapevine Pn. It also suggests that the Pn decline attributed to leaf ageing may in part be caused by the increasing leaf area during the season, *i.e.* an increase in the source:sink ratio. This provides a cultural challenge to viticulturists, suggesting that once an adequate leaf area has been developed early in the season, the vine has greater capacity to fix CO₂ than it can utilise. Under these circumstances the vine could be considered to be sink-limited. However, post-veraison the demand for photosynthates may be greater than the total vine Pn, and under these circumstances the vine could be considered to be source-limited.

To achieve optimal yields of ripe fruit, without excessive vegetative growth, vines have to be manipulated to optimise supply and demand at the different stages of development. To investigate these factors, an experiment was undertaken to determine whether varying the source:sink ratio of fruiting, cutting grown grapevines would influence the leaf ageing response and rate of leaf Pn over a growing season.

Material and Methods

Rooted, fruiting grapevines (*Vitis vinifera* L, cv. Pinot noir), were grown from 6-node cuttings using the method described by MULLINS and RAJASEKARAN (1981). After 5 weeks, vines were selected for uniformity and planted into 1-l pots containing a 80:20 bark:sand mix, 5 kg m⁻³ of 9 month 16:3.5:10 slow release Osmocote® fertiliser and

4 kg·m⁻³ dolomite were added. Vines were placed in a shaded (87 % light transmittance) glasshouse (day/night temperatures 24/15 °C) in the Lincoln University nursery complex. Fine sand was put over the potting mix to allow an even spread of water. Water was supplied, twice daily, by trickle irrigation until drainage occurred. Twelve weeks after being potted, fertigation (Wuxal® 9:4:6), was applied weekly to supplement the Osmocote®. The vines were grown in pots for 7 weeks before they were blocked according to the stage of inflorescence development, and a single shoot was trained vertically.

Two crop loads (presence (+) / absence (-) of fruit) and 4 leaf treatments were imposed (2x4 factorial) on the vines, with 6 replicates of each combination. The basal 4 leaves were retained and subsequent leaves were either: a) left intact - control (100 % retained); b) one in three removed (66 % retained); c) two in three removed (33 % retained); d) all leaves removed (0 % retained).

At the start of the experiment, vines had 7-9 fully expanded leaves and the berries were pea size (growth stage 31, EICHHORN and LORENZ 1977). Once the treatments were imposed, subsequent leaves were removed from the shoot as they appeared.

Photosynthesis and stomatal conductance measurement: Leaf Pn and stomatal conductance measurements were made using a portable system (Li-Cor 6400, Li-Cor Inc. Lincoln, NE, USA), in a similar position on the fourth leaf of each vine at approximately weekly intervals. Measurements of 'potential Pn' were made under a saturating light intensity of 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and optimum leaf temperature of 28 °C.

Harvest measurements: Vines were harvested 70 d from the initial treatment. Leaf area was measured using a leaf area meter (Li-Cor, model 3100, Lincoln, NE, USA). Drying was conducted in an oven at 70 °C, for approximately 3 d, until no further loss of moisture could be detected. Separate dry weights were taken from the leaves, shoots, washed roots and the berries (after freezing). Further details on vine dry weights are presented in PETRIE *et al.* (1999)

Leaf chlorophyll concentration: The leaf chlorophyll content was measured non-destructively on the fourth leaf using a Minolta-502 dual wavelength chlorophyll (SPAD) meter (Minolta Co. Ltd, Osaka, Japan). An average figure was calculated from a single measurement on each side of the main vein, at the distal part of the leaf. The relationship between the Minolta-502 output and chlorophyll content was calculated using mean SPAD values and chlorophyll extracted from 1 cm² leaf disks at 6 positions on 20 leaves (chlorophyll concentration ($\mu\text{g}\cdot\text{mm}^{-2}$) = $-0.41 + 0.086 \text{ SPAD}$ (arbitrary units); $r^2 = 0.87$). Dimethyl sulphoxide was used to extract the chlorophyll, and the chlorophyll concentration was calculated from absorbance measurements (ARNON 1949; HISCOX and ISRAELSTAM 1978).

Statistical analysis: ANOVA and Fishers Protected Least Significant Difference (LSD) tests were used to compare all treatments. ANOVA and regression analysis was conducted using Minitab version 9.2 (Minitab

Inc., 3081 Enterprise Drive, State College, PA). LSD were conducted as per OTT (1992).

Results

Photosynthesis and stomatal conductance: Net Pn was influenced by crop load, leaf removal and, where appropriate, the stage of development of the fruit (Fig. 1). 48 h after starting the treatments, the Pn rate of the fourth leaf of the leaf removal vines, was significantly greater than the control. Prior to veraison the highest level of leaf removal resulted in Pn of approximately 12.5 $\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. There were no significant differences between the (+) crop and (-) crop treatments within a leaf removal treatment. Between veraison and harvest the rate of Pn of all vines with fruit were similar, regardless of leaf treatment, and in turn similar to that of the full leaf removal, (-) crop treatment. To confirm the significance of measurements over the whole experiment, ANOVA was used to analyse the effect of crop load and leaf removal on the pre- and post-veraison (designated as 35 d after leaf removal) Pn rate. The post-harvest Pn measurements were excluded. The leaf removal - crop load - veraison interaction was significant ($p=0.038$), indicating that leaf removal treatments were having different effects on the photosynthetic rates of the (+) and (-) crop treatments before and after veraison.

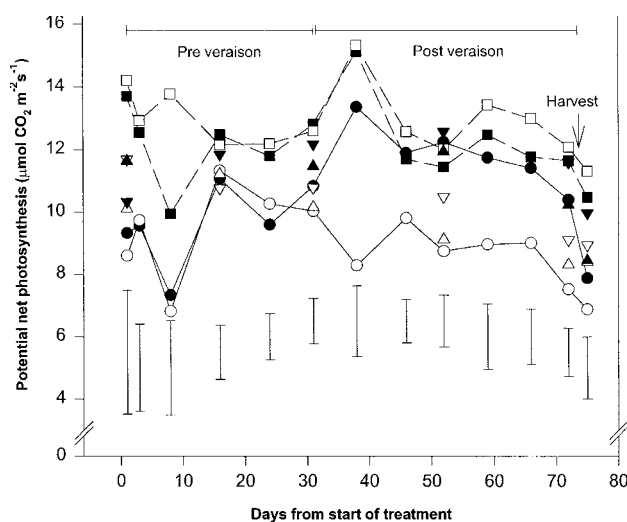


Fig. 1: Influence of leaf removal and crop load on net photosynthesis. The values are means of 6 plants. Bars represent 5 % LSD over all treatments. Intermediate treatments have been omitted for clarity. —○— (+) Crop, 100 % leaf retained. —△— (+) Crop, 66 % leaf retained above the fourth leaf. —□— (+) Crop, 33 % leaf retained above the fourth leaf. —●— (-) Crop, 100 % leaf retained. —▲— (-) Crop, 66 % leaf retained above the fourth leaf. —■— (-) Crop, 33 % leaf retained above the fourth leaf.

From day 15 of the experiment the Pn of the 100 % and 66 % leaf retention, (-) crop treatments began to decline; this continued during the course of the experiment. Harvesting the (+) crop vines caused decline in Pn to that of the

(-) crop vines, particularly in the 100 % and 66 % leaf retention treatments, indicating the sensitivity of Pn to leaf area:crop load ratio. This relationship was further amplified by the reduction in Pn associated with higher source:sink ratio (leaf area/total vine dry weight ($\text{cm}^2 \cdot \text{g}^{-1}$); Fig. 2).

Like Pn, stomatal conductance was significantly in-

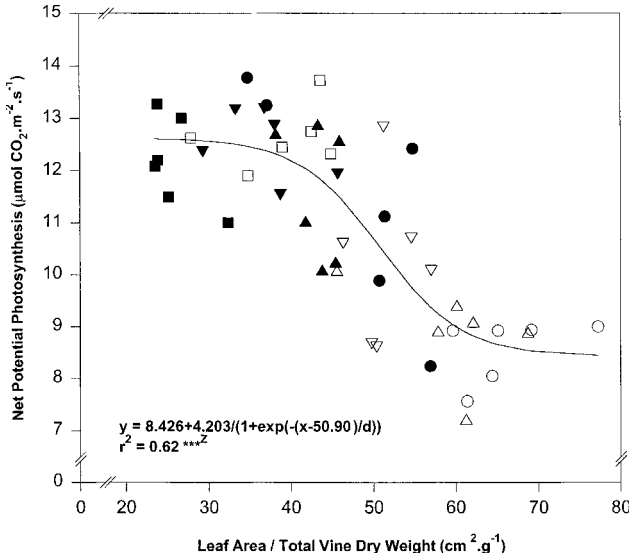


Fig. 2: The relationship between leaf area (cm^2) per total vine dry weight (g) and net photosynthesis. l, s, t, □, m, ●, △, ○ : see Fig. 1. ^zP values significant at 5 % (*), 1 % (**), and 0.1 % (***) or not significant (ns).

creased by leaf removal on 10 of the 13 dates measurements were taken (Fig. 3), but was unaffected by crop load (data not shown).

At harvest the 0 % leaf retained, (+) crop treatment caused a 84 % reduction in leaf area compared to the 100 % leaf retention (+) crop. The 100 % leaf retention (-) crop had a 34 % larger leaf area than the 100 % leaf retention (+) crop (Table).

Leaf chlorophyll concentration: Leaf chlorophyll measurements (SPAD) were well correlated with the leaf chlorophyll concentration. When crop was present leaf chlorophyll concentration was maintained throughout the experiment, and leaf removal resulted in an increase in, or retention of chlorophyll, which also occurred for the full leaf removal (-) crop treatment (Fig. 4). The source:sink relationship had a marked affect on the rate of senescence of the fourth leaf, which senesced more rapidly when high source:sink ratios were maintained (i.e. (-) crop and 100 % and 66 % leaves retained; Fig. 4).

Discussion

Photosynthesis: KRIEDEMANN *et al.* (1970) and more recently PONI *et al.* (1994) have reported that grapevine leaf Pn slowly declines, from 30 d after unfolding, as the leaves age and new leaves further up the shoots and on laterals reach a maximum rate of Pn. In those studies, vines had adequate leaf area to meet photosynthetic demand. Our results demonstrate that limiting the leaf area, and thus in-

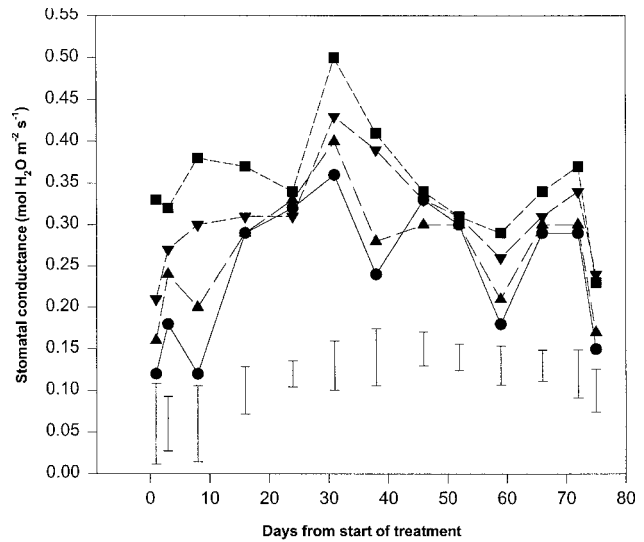


Fig. 3: Influence of leaf removal on stomatal conductance. There was no effect of crop on stomatal conductance values. Therefore the values are means of 12 plants. Bars represent 5 % LSD over all treatments. —□— 100 % leaf retained. —●— 66 % leaf retained. —▲— 33 % leaf retained. —□— 0 % leaf retained. For details see Fig. 1.

Table

The effect of leaf removal on vine leaf area, relative to (+) crop 100 % leaves retained treatment

| | (+) Crop | (-) Crop |
|-----------------------------------|----------|----------|
| 100 % Leaves Retained | 100 % b | 134 % a |
| 66 % Leaves Retained ^y | 84 % c | 99 % b |
| 33 % Leaves Retained ^y | 47 % e | 67 % d |
| 0 % Leaves Retained ^y | 16 % f | 19 % f |

Percentages separated using Fishers LSD test (5%).

^y Leaf retention treatments were imposed from above the fourth leaf.

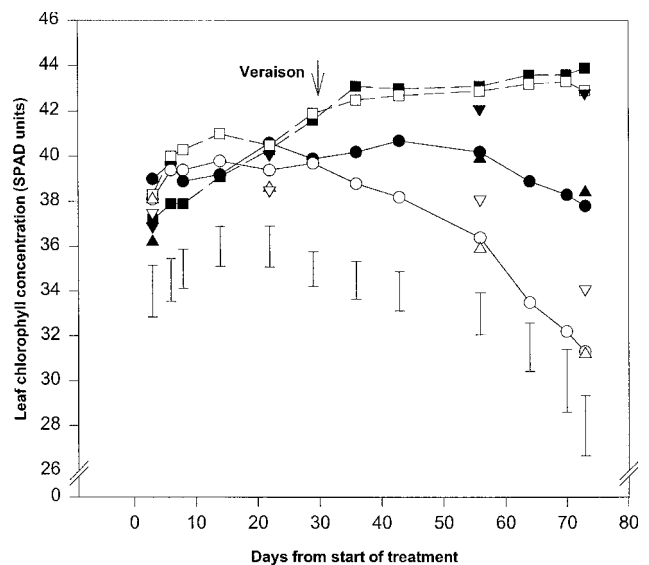


Fig. 4: Influence of leaf removal and crop load on leaf chlorophyll concentration. The values are means of six plants. Bars represent 5 % LSD over all treatments. Intermediate treatments have been omitted for clarity. For details see Fig. 1.

creasing the relative sink size, caused the photosynthetic rate of the basal leaves to be maintained throughout the experiment (Fig. 1). This also highlights the effect veraison has on the relative source:sink balance within the vine. Prior to veraison, fully leafed (+) crop and (-) crop treatments behaved in a similar way, however at veraison the demand for photosynthates increased causing the photosynthetic rates of all the (+) crop treatments to rise to a similar maximum. Previous experiments using defoliation treatment showed increased Pn rates in pot-grown fruiting Müller-Thurgau and Riesling vines (HOFÄCKER 1978). Similar to our study defoliation had no effect on Pn post-veraison in field-grown mature vines (CANDOLFI-VASCONCELOS and KOBLET 1991).

It appeared that leaf area (source size) was limiting the photosynthetic capacity of the (+) crop treatments, as they rose to the same maximum rate. We speculate that if the leaf area in our control treatments were in excess of that required to ripen fruit, then the Pn of the vine leaves would have been depressed. In a field situation the increase in Pn at veraison may not be as dramatic as shown here, as a leaf area more than adequate to ripen the fruit may be available. The effect of an excess leaf area was demonstrated by CANDOLFI-VASCONCELOS and KOBLET (1991) who recorded a decrease in Pn when lateral leaves were allowed to develop on mature vines. Conversely, the photosynthetic rate of the (-) crop 33 %, 66 % and 100 % leaf retained vines (and the (+) crop vines prior to veraison) was lower than for the other treatments (Fig. 1). The (-) crop vines also had a similar total dry weight to the (+) crop vines at each of the leaf removal treatments (100 % leaf retained, 65 g; 66 % leaf retained, 57 g; 33 % leaf retained, 41 g; 0 % leaf retained, 18 g; PETRIE *et al.* 1999). This suggests that inadequate demand for photosynthates limited the photosynthetic capacity of these vines. The end product inhibition of Pn is caused by a build up of carbohydrates in the leaves (FLORE and LAKSO 1989; FOYER and GALTIER 1996), which occurs when they cannot be utilised by the growing tissues as quickly as they are produced.

MILLER *et al.* (1997) used the ratio of leaf area to total dry weight as an estimate of a vine's source:sink relationships. This ratio is applicable to (+) and (-) crop vines as the dry matter produced by the vine can be partitioned into vegetative or reproductive organs, but the total dry matter does not change. In our experiment a negative correlation between leaf area to dry weight ratio and net potential Pn (averaged over the 4 measurements prior to harvest) occurred (Fig. 2). This relationship demonstrates photosynthetic compensation, which buffered the differences in leaf area between the (+) and (-) crop treatments (Table), and allowed them to produce similar dry weights (PETRIE *et al.* 1999). The leaves of the (+) crop treatments responded to the smaller source size by fixing more dry matter per unit surface area (photosynthesis at a higher rate), which in turn suggests that fully foliated treatments were at times sink-rather than source-limited.

The relationship between vine leaf area/dry weight and Pn was characterised by a sigmoid curve (Fig. 2). The Pn of the source-limited vines ((+) crop and/or low leaf retention) reached a maximum at the upper plateau of the

curve, at approximately $12.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. These leaves may have had their Pn limited by biochemical factors in the photosynthetic apparatus. Leaves of the sink-limited ((-) crop, 100 % and 66 % leaf retention) vines appeared to have a maximum Pn rate of approximately $8.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Demand placed by other sinks for carbohydrates, especially respiration, may have prevented the Pn rate dropping any further.

EDSON *et al.* (1993) found very little relationship between whole vine Pn or dry weight measurements and single leaf Pn measurements made on potted vines. They concluded that single leaf measurements assess localised changes in the metabolic balance of the vine, suggesting that these measurements will not provide a good indication of overall vine performance. MILLER *et al.* (1997) have also compared single leaf and whole vine Pn as a function of vine dry weight. They found a far stronger relationship between whole vine Pn and dry weight than single leaf Pn and dry weight. By including the effect of source:sink ratio (leaf area to total dry weight), we found a far better relationship with single leaf Pn over the (+) and (-) crop and leaf removal treatments (Fig. 2). This would not be expected based on the proposals made by EDSON *et al.* (1993). However our vines were far younger and smaller than those of EDSON *et al.* (1993), so localised changes in the metabolic balance may effect the whole plant. The photosynthetic rate of a whole vine grown using the technique of MULLINS and RAJASEKARAN (1981) may be able to be more accurately estimated from a single leaf than from larger plants, but more research is required to confirm this.

The photosynthetic rate of the (+) crop, 100 and 66 % leaf retained vines decreased after harvest, to levels similar to the (-) crop treatments (Fig. 1), demonstrating the crop demand response on vine Pn. A similar depression in Pn caused by the removal of fruit was recorded by HOFÄCKER (1978) and EDSON *et al.* (1993). The period post-harvest is an important time for vines to recharge their carbohydrate reserves (WILLIAMS 1995). The decrease in photosynthetic rate, post-harvest, suggests that the vine's ability to accumulate reserves during this period are limited by the demand for photosynthates. This represents an inefficiency in carbohydrate production. If the vines maintained their photosynthetic rate, and could partition these photosynthates into reserves, then the next year's potential for growth and yield would increase.

Stomatal conductance: Stomatal conductance and leaf chlorophyll concentration were investigated as possible mechanisms used by the vine to compensate for decreased leaf area and increased photosynthate demand. The (+) and (-) crop treatments recorded similar stomatal conductance both, pre- and post-veraison on (+) crop vines (data not shown). However, at higher levels of leaf removal, the stomatal conductance of the vines increased, and this contributed in part to greater photosynthetic rates (Fig. 3). A similar increase in stomatal conductance was also recorded by HOFÄCKER (1978), HUNTER and VISSER (1988), CANDOLFI-VASCONCELOS and KOBLET (1991) and in response to defoliation. Increases in the photosynthetic rates of the exposed part of the canopy or leaves in response to partial shading have been reported by NABI (1998)

and PEPIN *et al.* (in press). Shading caused stomatal conductance- and Pn-related transpiration in the treated portion of the canopy to decrease. At the same time, there was an almost immediate increase in stomatal conductance and Pn on the exposed part of the canopy. In contrast, when the transpiration rate of the shaded part of the canopy was maintained by decreasing the vapour pressure, no change in the Pn rate of the exposed portion of the seedling occurred (PEPIN *et al.* in press). They concluded that the short-term change in photosynthetic rate in response to a change in effective leaf area was controlled by hydraulic signals. Leaf removal potentially caused a similar effect in the experiments described here, as defoliation would have reduced transpiration, increasing water availability to the remaining leaves and allowing stomatal conductance to increase. Pot-grown vines have been shown to have a greater variability of stomatal conductance than field-grown vines. This is possibly because the restricted soil volume available for root growth affects their water relations (CANDOLFI-VASCONCELOS and KOBLET 1991). A disruption in water relations may have led to the inconsistency in the effect of leaf removal on stomatal conductance.

It is unlikely that stomatal conductance had complete control over Pn as no change occurred when the photosynthetic rates of the (+) crop vines increased at veraison. Similar conclusions were made by CANDOLFI-VASCONCELOS and KOBLET (1991). This meant that other factors, possibly linked to an accumulation of assimilates in the leaves, were responsible for the decrease in leaf Pn of the (-) crop vines, as proposed by FOYER and GALTIER (1996). Starch content of the leaves was not measured, but the specific leaf weight was unaffected by any treatment (data not shown).

Leaf chlorophyll concentration: While leaf chlorophyll concentration followed a similar pattern to photosynthetic rate, there was no direct correlation between chlorophyll concentration and photosynthetic rate at any date sampled or over all the sample dates (data not shown). The full leaf, (+) crop treatment maintained leaf chlorophyll concentration throughout the course of the experiment. Leaf removal caused an increase in the chlorophyll concentrations of the leaves and this was more apparent in the (+) crop treatments (Fig. 4). Similar effects of leaf removal on leaf chlorophyll content and concentration have been observed by other authors (HOFÄCKER 1978, CANDOLFI-VASCONCELOS and KOBLET 1991).

Pn responded more rapidly than leaf chlorophyll concentration to the (+) crop and leaf removal treatments and to changes in berry development. This was particularly obvious post-harvest where a rapid decrease in Pn of the (+) crop vines was observed, with no associated reduction in chlorophyll concentration. This makes it unlikely that chlorophyll concentration had a direct effect on Pn unless leaf senescence has commenced. Data presented here indicate that high source:sink relationships in grapevines may lead to early senescence. It also suggests that the developing canopy and progressive increase in source:sink ratio may contribute to the decline in leaf Pn from 30 d after unfolding.

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Received September 21, 1999