Influence of partial defoliation on gas exchange parameters and chlorophyll content of field-grown grapevines — Mechanisms and limitations of the compensation capacity

by

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Einfluß einer Teilentblätterung auf Gaswechsel und Chlorophyllgehalt von Freilandreben — Mechanismen und Grenzen der Kompensationskapazität

Z u s a m m e n f a s s u n g : Diese Studie befaßte sich mit der Untersuchung der Kompensationsmechanismen der Rebe bei Entblätterungsstreß. Untersucht wurde an Freilandreben der Einfluß einer Teilentblätterung auf den Gaswechsel und Chlorophyllgehalt der Rebblätter. 16jährige traubentragende Reben und 2jährige nicht tragende Topfreben wurden verglichen. Die Entblätterung geschah eine Woche nach der Vollblüte. Drei unterschiedliche Varianten des Entfernens der Hauptblätter (Stehenlassen von 3, 6 bzw. 12 Hauptblättern) wurden mit zwei Varianten des Entfernens der Geizblätter (mit bzw. ohne Geizblätter) kombiniert. Gaswechsel und Chlorophyllgehalt wurden vom Zeitpunkt der Entblätterung bis zur Ernte am 11. Hauptblatt gemessen.

Der Einfluß einer Entblätterung auf den Gaswechsel war sowohl an jungen Freiland-Topfreben wie an Ertragsreben sehr ähnlich.

Die Pflanzen mit weniger Hauptblättern hatten eine höhere photosynthetische Leistung und einen höheren Chlorophyllgehalt je Flächeneinheit als die Kontrollpflanzen, jedoch nur bis zum Reifebeginn. Diese Leistungssteigerung von teilweise entblätterten Reben konnte jedoch den Blattflächenverlust nur zum Teil kompensieren. Das Entfernen von Geizblättern resultierte in einer Erhöhung der photosynthetischen Leistung der Hauptblätter während der Reifeperiode. Die Pflanzen ohne Geizblätter hatten eine höhere Wassernutzungseffizienz. Der Chlorophyllgehalt war bei entblätterten Reben generell höher.

Die Erhöhung der photosynthetischen Leistung als Folge einer teilweisen Entblätterung war hauptsächlich das Resultat einer erhöhten Mesophyll-, aber auch einer verbesserten stomatären Leitfähigkeit. Ein weiterer Kompensationsmechanismus bestand in der Verzögerung der Seneszenz der Blätter und des Blattfalles.

K e y   w o r d s : leaf, defoliation, photosynthesis, transpiration, chlorophyll, age, stress, compensation.

Introduction

Canopy management practices are very important to promote a suitable microclimate not only for fruit growth and maturation but also to avoid the propagation of fungal diseases. These practices reduce the assimilating leaf area. Pests, diseases and unfavourable weather conditions can also greatly reduce leaf area. In a previous paper (CANDOLFI-VASCONCELOS and KOBLET 1990) we studied how defoliation stress affects fruit yield and quality as well as bud fertility and starch reserves in the wood. We found that grapevines have a strong capacity of compensation by increasing leaf area and we had evidence of an increment of the physiological efficiency of the leaves on defoliated plants. We also saw that plants bearing only main leaves compensated for the absence

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of laterals by delaying leaf senescence and abscission. HOFÄCKER (1978), working with green cuttings of Riesling × Silvaner and established potted Riesling plants under controlled environment, found that photosynthesis, stomatal conductance and chlorophyll content increased with increased level of defoliation. HUNTER and VISSER (1988 and 1989), working practically simultaneously with us in South Africa, report similar findings for mature field-grown Cabernet Sauvignon.

The aim of our experiments was to study the possibilities and limitations of the compensation capacity related to leaf removal in Pinot noir grapevines. We investigated the influence of removing main or lateral leaves on gas exchange parameters and chlorophyll in order to find mechanisms contributing to this increment of the physiological efficiency of the remaining leaves.

In this work we also compared the gas exchange response of two plant systems to defoliation: mature 16 years old field-grown plants and 2 years old potted plants grown under field conditions. The grapevine, like other woody perennials, has a long juvenile period during which the growth is only vegetative. It is very difficult to obtain young fruit bearing Pinot noir experimental plants. Working with young potted plants is nonetheless a much simpler approach to use in physiological studies. To find out if mature plants can be simulated by using young potted plants, we tested whether these two plant systems reacted the same way when they received the same defoliation treatments.

Materials and methods

1. Plant material

Mature plants: Field-grown 16 years old Pinot noir grafted on Grézot 1, planted on a deep gravelly loam soil were used in this investigation. The plants were trained to double Guyot (cane pruning) with a spacing of 2.2 m × 1.2 m. All the weak and non-fruiting shoots were removed on May 26, leaving an average of 14 shoots per plant.

Potted plants: 2 years old Pinot noir grafted on 5C Teleki were planted on April 18, 1988, in 5 l pots containing sandy loam soil covered with a 5 cm layer of peat-moss to prevent excessive evaporation. The pots were buried in an open field and kept well watered. On May 25, the plants were thinned to 1 shoot per plant. These young plants had no fruit.

2. Defoliation treatments

The experiment included 6 defoliation treatments. Each treatment consisted of 5 single-plant replications for the mature and 8 for the potted vines in a randomized complete block design. Defoliation was accomplished on June 29, 1988, about 1 week after full bloom, on the mature plants and on July 13, at the 16-leaf stage for the potted plants which corresponds to the same phenological stage as for the mature plants. Just before defoliation, all the plants were topped to 12 nodes per shoot. The defoliation treatments were:

12: All the main leaves were retained
6: The upper 6 main leaves were retained
3: The upper 3 main leaves were retained

In half of the plants from these 3 groups lateral shoots were removed periodically as they emerged. On the other half, laterals were allowed to grow:

LR: Laterals removed
LP: Laterals present

The resulting experimental design was a 3 by 2 factorial, with 3 levels of defoliation (3, 6 or all 12 main leaves retained) and 2 levels of laterals (all retained or all removed).

3. Gas exchange measurements

Net CO_2 assimilation rate (A), transpiration rate (E), stomatal conductance to CO_2 transfer (g_s), mesophyll or intracellular conductance to CO_2 transfer (g_m) and intercellular CO_2 partial pressure (C_i) were measured on the 11th main leaf (from the base) of 1 shoot per plant. For this purpose we used a portable LCA-2 system (Analytical Development and Co. Ltd, Hoddesdon, Herts, England). This apparatus consists of four units: an infra-red gas analyzer model LCA-2, a Parkinson leaf chamber (PLC-B for broad leaf), a data-logger (DL2) and an air supply unit with an incorporated mass flow meter (ASUM). The instrument operates as an open system. Air flow rate was adjusted to 200 ml · min^{-1}. A value of 0.3 m^2 · s · mol^{-1} was obtained for the boundary layer resistance using PARKINSON's method (1984). All measurements were carried out between 9:00 and 11:00 a.m. (10.00—12:00 a.m. light saving time), at photosynthetic flux densities above 1000 µmol · m^{-2} · s^{-1} and cloudless sky. The air temperature ranged between 26 and 31 °C. The measurement period started just before the defoliation treatments were accomplished and proceeded until fruit harvest.

Except for g_m and water use efficiency (WUE), all the calculations were performed using the built-in equations of the program version 5.1 of the datalogger DL2 (Analytical Development and Co. Ltd., Hoddesdon, Herts, England).

g_m was calculated using the calculated values supplied by the data logger for C_i and A and assuming that CO_2 partial pressure at the site of carboxilation (C_c) is zero:

$$A = \frac{C_i - C_c}{r_m}; \quad g_m = \frac{1}{r_m}$$

By assuming $C_c = 0$, the carboxilation resistance is implicitly included in the estimate of r_m (JARVIS 1971).

Water use efficiency was calculated as the quotient between the photosynthetic and transpiration rates (WUE = A/E).

4. Data collected and analytical procedures

The chlorophyll content was determined only for the potted vines on 4 occasions during the same period as for the gas exchange measurements, using 4 other groups of plants treated exactly the same way. For these measurements 5 leaf discs (8 mm in diameter) were taken from the 11th leaf of 8 plants per treatment on each date, using a cork borer. Chlorophyll was extracted with the method described by HISCOX and ISRAELSTAM (1979). Chlorophyll contents and chlorophyll a/b ratio were computed using the equations of ARNON (1949).

Leaf area was measured on the same plants with an area-meter (model LI-3100 from Li-cor, Inc., Lincoln, Nebraska, USA).

5. Statistical analysis

The WIDAS statistical package (Wissenschaftliches Integriertes Daten-Auswertungs-System, Data General Corporation) was used for statistical analysis of data. Results were subjected to a two-way analysis of variance (number of main leaves left × presence or absence of lateral shoots). Duncan's multiple range test was used to compare means.

Results

It is evident that the onset of the ripening process including sugar accumulation in the berries is an important physiological event having not only an influence on the
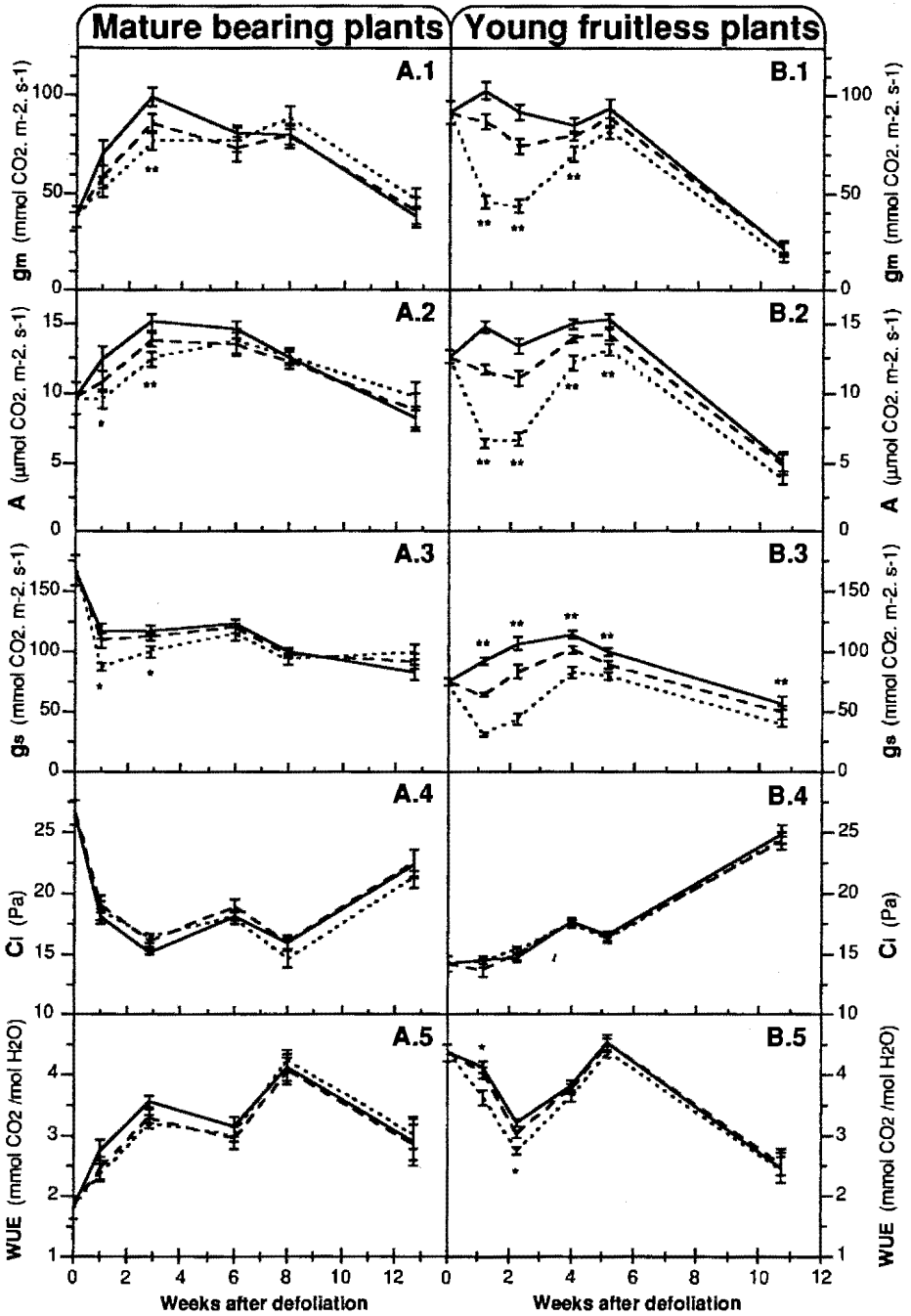
Fig. 1: Effect of removing main leaves on mature, fruit bearing plants (A.1—A.5) and young fruitless potted plants (B.1—B.5) on mesophyll conductance (g_m) (A.1 and B.1), net CO_2 assimilation rate (A) (A.2 and B.2), stomatal conductance to CO_2 transfer (g_s) (A.3 and B.3), intercellular CO_2 partial pres-

fruit itself but also on leaf factors related to photosynthesis (Fig. 1, A.1—A.5 and 2, A.1—A.5). For convenience, the measuring season was divided into two distinct periods which reflected major changes in gas exchange parameters. For mature plants, period I was the time interval between defoliation treatment (1 week after full bloom) and veraison (7 weeks after treatment); period II, from veraison to fruit maturity, corresponds to the ripening period. For young potted plants, period I elapses during the first 5 weeks following defoliation treatment and period II lasts from this date until 12 weeks after treatment.

1. Influence of removing main leaves

Fig. 1 shows the main effect of removing main leaves on gas exchange parameters of mature plants bearing fruits (A.1—A.5) and young fruitless potted plants (B.1—B.5). It is obvious that most of the responses to main leaf removal are confined to period I or pre-veraison.

During period I, photosynthetic rate (Fig. 1, A.2 and B.2), mesophyll conductance (g_m) (A.1 and B.1) and stomatal conductance (g_s) (A.3 and B.3) were higher for either mature or young potted plants with fewer main leaves. There was no treatment effect on the intercellular CO_2 partial pressure (C_i) and water use efficiency (WUE) for the mature plants. Young potted plants showed during period I, in response to defoliation, higher efficiency of carbon fixation per unit of water loss (A.4 and B.4).

During period II, no treatment effect could be detected on mature plants in any of the parameters studied (Fig. 1, A.1—A.5). Young potted plants showed higher values of A and g_s on treatments 3 and 6 as compared to treatment 12 during the same period (B.2 and B.3, respectively). No treatment effect was observed on g_m (B.1), C_i (B.4) and WUE (B.5) on young vines during period II.

Fig. 3 shows the effect of removing main leaves on total chlorophyll content, chlorophyll a/b ratio, and total leaf area on young potted plants. During period I, chlorophyll increased with increasing level of leaf removal (1). Chlorophyll a/b ratio showed a peak in the 2nd week after treatment and was higher for plants with a reduced number of main leaves (2). During the 2nd period, chlorophyll content was higher in leaves of defoliated plants and decreased continuously in all treatments (1). There was no treatment effect on the chlorophyll a/b ratio during this period (2).

Just after treatment, the remaining leaf area of plants with reduced main leaf number was 30 % for treatment 3 and 60 % for treatment 6 related to the control plants. Leaf area increased for all treatments, attaining a maximum at the end of period I (Fig. 3, 3). Leaf abscission caused a decrease in the total leaf area during period II for all treatments but was particularly hastened on plants having more main leaves (3).

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sure (C_i) (A.4 and B.4), and water use efficiency (WUE) (A.5 and B.5) of the 11th main leaf (from the base). Full lines: plants with 3 main leaves left; dashed lines: plants with 6 main leaves left; dotted lines: plants with all 12 main leaves left. Vertical bars: standard error; * and **: differences significant at the 5 % and the 1 % level of probability.

Einfluß der Entfernung von Hauptblättern an Ertragsreben (A.1—A.5) sowie an 2jährigen nicht tragenden Topfreben (B.1—B.5) auf Mesophyll-Leitfähigkeit (g_m) (A.1 und B.1), Nettoassimilationsrate (A) (A.2 und B.2), stomatäre Leitfähigkeit für CO_2 (g_s) (A.3 und B.3), interzellulären CO_2-Partialdruck (C_i) (A.4 und B.4) und Wassernutzungseffizienz WUE (A.5 und B.5) des 11. Hauptblattes. Ausgezogene Kurven: Reben mit 3 Hauptblättern; gestrichelte Kurven: Reben mit 6 Hauptblättern; gepunktete Kurven: Reben mit allen 12 Hauptblättern. Senkrechte Balken: Standardfehler; * und **: signifikante Unterschiede bei 5 % und 1 % Signifikanzniveau.
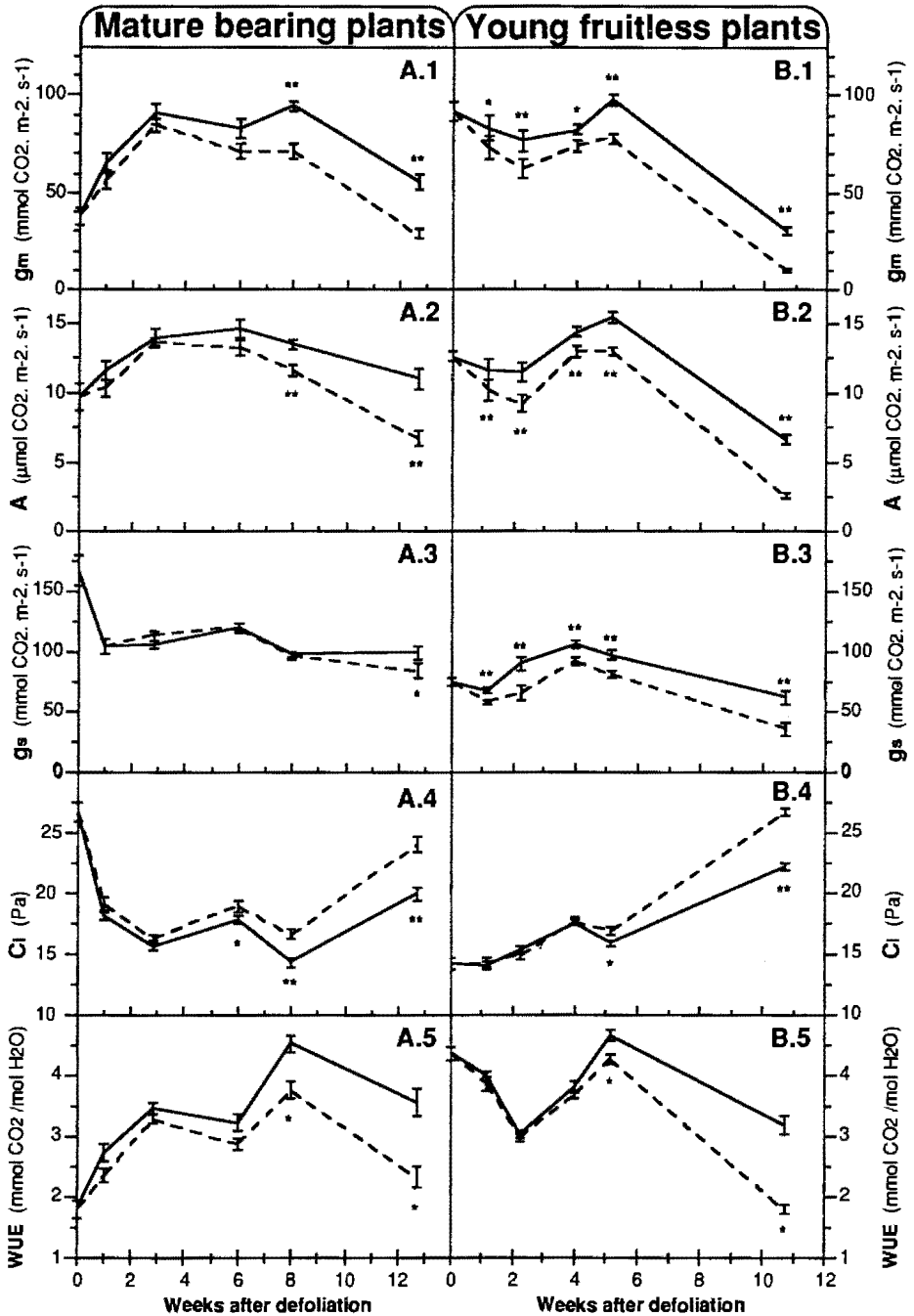
Fig. 2: Effect of removing lateral laves on mature, fruit bearing plants (A.1—A.5) and young fruitless potted plants (B.1—B.5) on mesophyll conductance (g_m) (A.1 and B.1), net CO_2 assimilation rate (A) (A.2 and B.2), stomatal conductance to CO_2 transfer (g_s) (A.3 and B.3), intercellular CO_2 partial pres-

2. Influence of removing lateral leaves

The main effect of removing lateral leaves on gas exchange processes of mature fruit bearing and young potted vines is plotted in Fig. 2. In contrast to the responses to main leaf removal, responses to lateral leaf removal were more pronounced during period II.

During period I, practically no treatment effect could be detected in mature grape-vines (Fig. 2, A.1—A.5). In contrast, young potted vines showed higher mesophyll con-ductance, photosynthesis, and stomatal conductance in plants with no lateral shoots (LR) (B.1, B.2 and B.3).

During period II, both plant systems showed higher g_m, A, g_s, and WUE in plants whose lateral shoots had been removed (Fig. 2, A.1—A.3, A.5 and B.1—B.3, B.5). Mature and young potted plants showed lower C_i in plants without lateral shoots (A.4 and B.4).

Fig. 4 shows the response of removing lateral shoots on total chlorophyll content, chlorophyll a/b ratio of the remaining main leaves and total leaf area of young potted plants. During period I, chlorophyll content increased for both plants with and without laterals (1). Chlorophyll a/b ratio was higher for LP plants, but after the 3rd week post-treatment the tendency was inverted (2). During the 2nd period, LR plants had higher levels of chlorophyll and also higher chlorophyll a/b ratios as compared to LP plants (1 and 2).

During the first 5 weeks post-treatment, total leaf area remained constant for LR plants and increased more than 2-fold for LP plants (Fig. 4, 3). Total leaf area decreased during period II due to leaf abscission on LP plants, but LR plants managed to main-tain a constant leaf area by delaying leaf abscission (3).

Discussion

There are numerous reports that demand for assimilates by sinks can determine photosynthetic supply (NEALES and INCOLL 1968; KRIEDEMANN et al. 1976; KRIEDEMANN 1977; HOFÄCKER 1978; GIFFORD and EVANS 1981; KAPS and CAHOON 1989). During period I, the increment of the photosynthetic rate was the more marked as the level of main leaf removal increased, suggesting a compensatory response to defoliation (Fig. 1, A.2 and B.2).

The leaf selected from each plant for measurements throughout the season was one of the youngest main leaves of the canopy by the time of the defoliation treatment, but had already reached 85 % of its final size. When the defoliation treatments were accomplished these upper leaves, being close to the apex, were exporting assimilates to the growing shoot tip (HALE and WEAVER 1962; KOBLET 1969; QUINLAN and WEAVER 1970). The removal of the shoot tip represented the elimination of an important sink. This explains the different assimilation patterns observed immediately after the treatment

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sure (C_i) (A.4 and B.4), and water use efficiency (WUE) (A.5 and B.5) of the 11th main leaf (from the base). Full lines: treatment LR, plants without lateral shoots; dashed lines: treatment LP, plants with lateral shoots. Vertical bars: standard error; * and **: differences significant at the 5 % and the 1 % level of probability.

Einfluß der Entfernung von Geizblättern an Ertragsreben (A.1—A.5) sowie and 2jährigen nicht tra-genden Topfreben (B.1—B.5) auf Mesophyll-Leitfähigkeit (g_m) (A.1 und B.1), Nettoassimilationsrate (A) (A.2 und B.2), stomatäre Leitfähigkeit für CO_2 (g_s) (A.3 und B.3), interzellulären CO_2-Partial-druck (C_i) (A.4 und B.4) und Wassernutzungseffizienz (WUE) (A.5 und B.5) des 11. Hauptblattes. Ausgezogene Kurven: Behandlung LR (Reben ohne Geiztriebe); gestrichelte Kurven: Behandlung LP (Reben mit Geiztrieben). Senkrechte Balken: Standardfehler; * und **: signifikante Unter-schiede bei 5 % und 1 % Signifikanzniveau.

on plants with reduced number of main leaves and control plants. For the former, it meant a lesser decrease of the source to sink relationship since there was not only elimination of mature leaves (source) but also the growing leaves (sink). In consequence,
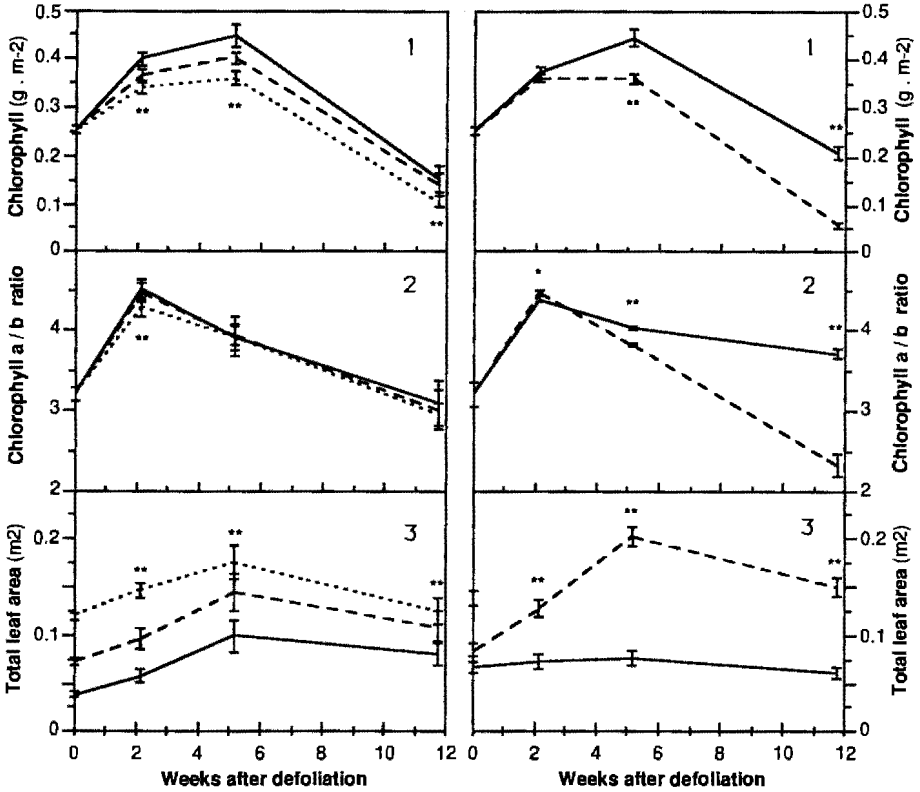

Fig. 3 (left): Effect of removing main leaves from young fruitless potted plants on total chlorophyll content (1) and chlorophyll a/b ratio (2) of the 11th main leaf (from the base) and total leaf area of the plant (3). Full lines: plants with 3 main leaves left; dashed lines: plants with 6 main leaves left; dotted lines: plants with all 12 main leaves left. Vertical bars: standard error; * and **: differences significant at the 5 % and the 1 % level of probability.

Fig. 4 (right): Effect of removing lateral leaves from young fruitless potted plants on total chlorophyll content (1) and chlorophyll a/b ratio (2) of the 11th main leaf (from the base) and total leaf area of the plant (3). Full lines: treatment LR, plants without lateral shoots; dashed lines: treatment LP, plants with lateral shoots. Vertical bars: standard error; * and **: significant at the 5 % and the 1 % level of probability.

Abb. 3 (links): Einfluß der Entfernung von Hauptblättern bei 2jährigen nicht tragenden Topfreben auf den Gesamtchlorophyllgehalt (1) und das Verhältnis Chlorophyll a/b des 11. Hauptblattes sowie auf die Gesamtblattfläche der Pflanze (3). Ausgezogene Kurven: Reben mit 3 Hauptblättern; gestrichelte Kurven: Reben mit 6 Hauptblättern; gepunktete Kurven: Reben mit allen 12 Hauptblättern. Senkrechte Balken: Standardfehler; * und **: signifikante Unterschiede bei 5 % und 1 % Signifikanzniveau.

Abb. 4 (rechts): Einfluß der Entfernung von Geizblättern bei 2jährigen nicht tragenden Topfreben auf den Gesamtchlorophyllgehalt (1) und das Verhältnis Chlorophyll a/b (2) des 11. Hauptblattes sowie auf die Gesamtblattfläche der Pflanze (3). Ausgezogene Kurven: Behandlung LR (Reben ohne Geiztriebe); gestrichelte Kurven: Behandlung LP (Reben mit Geiztrieben). Senkrechte Balken: Standardfehler; * und **: signifikante Unterschiede bei 5 % und 1 % Signifikanzniveau.

there was an increment of A. For the latter, it represented an increment on the source/sink ratio and led to a slight reduction of A. The effect of topping on the young potted fruitless grapevines (Fig. 1, B.2) was much more pronounced. It caused a 50 % decrease of the assimilating rate of treatment 12 and a decrease of approximately 10 % of treatment 6. This shows the comparatively greater importance of the vegetative shoot tip as a sink in the carbohydrate budget of plants bearing no fruit. This is in agreement with the data obtained by CHAVES (1984).

The general increase of the CO_2 uptake rate registered during the first 3—5 weeks after defoliation might be the response to increased sink size: during this period there was a rapid increment in dry weight of roots, trunk, main and lateral shoots (results not shown). This rapid growth slowed down after the 5th week and simultaneously the photosynthetic rate decreased.

The decrease in the CO_2 uptake rate of the measured main leaves during the period post-veraison indicates that these leaves were already undergoing senescence. Younger and therefore photosynthetically more active leaves (KRIEDEMANN 1968 and 1977; KRIEDEMANN et al. 1970; ALLEWELDT et al. 1982) must then replace these older leaves to assure fruit maturation and replenishment of the parent vine reserves. During fruit ripening, lateral leaves being the youngest of the canopy, are most probably the largest contributors to the canopy's photosynthesis. CANDOLFI-VASCONCELOS and KOBLET (1990) concluded that lateral leaves play the main role during the ripening phase and SCHULTZ (1989) showed that lateral leaves have in fact higher rates of photosynthesis than main leaves during this period which gives support to our hypothesis.

With the beginning of the lateral shoots growth new vegetative sinks appear and shift the assimilating rates to higher values (Figs. 1 and 2). Young potted plants and mature bearing plants showed an increment of the lateral shoot production as the main leaf area decreased (data not shown). In previous studies we observed the same behavior on completely defoliated plants (CANDOLFI-VASCONCELOS and KOBLET 1990). An interesting feature of defoliated plants was the higher rate of organogenesis. In fact, on the plants where lateral shoots were removed periodically, plants with fewer main leaves always yielded higher dry masses of lateral shoots between two consecutive removals (data not shown). Plants whose lateral shoots were periodically removed were always in a less favorable situation: they were repeatedly investing nutrients in the production of lateral shoots that would never contribute to the canopy's photosynthesis. According to HALE and WEAVER (1962), lateral shoots are no longer sinks as soon as they have 2 mature leaves. KOBLET (1969) states that lateral leaves become exporters of assimilates when they reach 75 % of their final size. They export assimilates not only to their own apex in support of their own growth but also to the main shoot. Plants whose lateral shoots were allowed to grow, were therefore correctly investing assimilates in the expansion of the assimilating surface. From veraison to fruit ripening, plants without lateral leaves maintained higher rates of photosynthesis because they could not count on the laterals' contribution.

Defoliated plants showed various compensatory responses to defoliation stress. Observed compensatory mechanisms were the increase of chlorophyll content, the increase of stomatal and mesophyll conductance which allowed an increase of the photosynthetic activity.

The CO_2 influx to the reaction sites inside the chloroplasts is controlled by conductances to CO_2 transfer in the gaseous and liquid phase (SESTAK 1981). Defoliated plants showed higher stomatal conductance which confirms the results obtained by HOFÄCKER (1978) and HUNTER and VISSER (1988). According to DOWNTON et al. (1988), C_i calculated from gas exchange measurements can be overestimated if part of the stomata are closed due to water stress which can lead to erroneous conclusions of non-

stomatal limitation of photosynthesis. Our experimental plants were kept well watered and the measurement period was chosen to minimize midday stomatal closure. The increment registered for g_s of defoliated plants could be due either to stomata opened wider or to more stomata opened per unit of surface, increasing the functional leaf area. If the latter is true, the calculated value for C_i is probably underestimated. The dependence of the CO_2 assimilation on the stomatal control was found to be much more important in young potted plants than in mature plants. In fact, young plants showed a strong parallelism between the photosynthesis and stomatal conductance curves (Figs. 1 and 2). All the same, it has to be stated that stomatal control was not dominant for either of the two plant systems. This can be concluded from the fact that the intercellular CO_2 partial pressure varied in opposite direction as did photosynthetic rate (FARQUHAR and SHARKEY 1982). It follows that the most important change must have been in the mesophyll cells.

The main component of the mesophyll conductance is the carboxylating efficiency (BJORKMAN 1981; RAVEN and GLIDEWELL 1981; FARQUHAR and VON CAEMMERER 1982), at least in the temperature range registered during the measurements (MACHLER *et al.* 1990). Both mature fruiting plants and young fruitless plants showed a high degree of mesophyll control over the photosynthesis, as judged by the similarity of the curves of these parameters. Increase of the photosynthetic activity as response to defoliation was achieved by enhancing the carboxylating efficiency and increasing stomatal conductance. These results are consistent with those presented by KRIEDEMANN in 1977.

The transpiration rate of mature plants, except for the first 3 weeks following treatment, showed no response either to main leaves' or lateral shoots' removal. In contrast, young potted plants either with no laterals or with reduced number of main leaves, showed always higher rates of transpiration than the LP plants after treatment. Nevertheless, increase of the rate of carbon gain was almost always higher than that of water loss, resulting in increased water use efficiency. This was particularly evident on mature and young plants without lateral shoots during period II (Fig. 1, B.5, and Fig. 2, B.5). Young potted plants with reduced main leaf area showed also a higher WUE during period I (Fig. 1, B.5). HUNTER and VISSER (1988) also reported increased transpiration and water use efficiency with increased level of defoliation.

The use of potted plants as simpler approach to test gas exchange response to defoliation stress cannot be considered an unrealistic design. Despite of differences between the two plant systems (plant age, presence of fruit, rootstock, roots environmental conditions), we obtained very similar treatment responses in both mature bearing grapevines and young potted plants. Potted plants showed however a higher sensitivity of the leaf stomata. This could be due to the restricted soil volume available to root growth which could affect water relations.

Total chlorophyll content increased with increasing level of defoliation which was another compensatory mechanism to defoliation. Similar results are reported by HOFÄCKER (1978) and HUNTER and VISSER (1989). Chlorophyll a and b contents were higher in plants with fewer main leaves and in plants without lateral shoots. Chlorophyll a/b ratio increased during the first 2 weeks after defoliation because chlorophyll a showed the steepest increment during this initial period and chlorophyll b exhibited a delayed response, showing the highest increment rate between the 2nd and 5th week post-defoliation. Plants bearing no lateral shoots showed higher chlorophyll a/b ratios, particularly after midseason, indicating that even if they possessed more chlorophyll a and b than LP plants they were not utilizing their light harvesting pigments as efficiently as plants with lateral shoots. Lower chlorophyll a/b reflects, according to BJORKMAN (1981), increased proportion of the light-harvesting chlorophyll-a,b-protein (LHchl) complex to the total chlorophyll complement of the chloroplast. The LHchl

complex contains all the chlorophyll b and is primarily associated with photosystem II (PS II) and, therefore, lower chlorophyll a/b also reflects a higher PS II/PS I ratio. Curiously, the increments observed in chlorophyll content led to increased chlorophyll a/b ratio indicating that higher efficiency of light capturing is needed when the chlorophyll level is low. Plants with reduced leaf area showed a slower rate of chlorophyll degradation and a delay in the rate of leaf abscission during period II, indicating a delay of leaf senescence, which confirms the results obtained in our previous experiments (CANDOLFI-VASCONCELOS and KOBLET 1990).

Compensation to a decrease of the main leaves area was only observed during pre-veraison. However, the largest differences in the assimilation rates observed in the mature fruiting plants between defoliated and control plants did not exceed 30 % for treatment 3 and 14 % for treatment 6. Young potted plants having 3 and 6 main leaves left attained photosynthetic rates 66 and 42 % higher than the control, respectively. Anyway, these increments were not high enough to enable full compensation because the assimilating leaf area was reduced up to 70 %.

Compensation to removal of lateral leaves became more pronounced during fruit ripening. During period II, fruit-bearing and fruitless plants with no laterals had 20—45 % higher photosynthetic rates (Fig. 2, A.2 and B.2) and managed to keep up to 260 % higher levels of chlorophyll (Fig. 4, 1) as compared to the control. The fact that these differences are more pronounced during period II, when the photosynthetic rate and chlorophyll content already started to decline, indicates that main leaves are able to delay senescence if they do not have the support of the lateral leaves, whose photosynthetic performance is reported to be higher than that of main leaves during the ripening phase (SCHULTZ 1989).

Conclusions

1. Compensation by increasing the photosynthetic performance as a response to main leaves removal was only partial and confined to the pre-veraison period.

2. In contrast, removal of lateral shoots resulted in the maintenance of higher assimilation rates on the remaining main leaves towards the end of the season.

3. Main leaves' photosynthesis had a limited importance during fruit maturation. Most likely the lateral leaves assumed the primary role.

4. The observed compensation mechanisms related to leaf removal were:
— Increase of the photosynthetic rate
— Increase of the mesophyll conductance
— Increase of the stomatal conductance
— Increase of the water use efficiency
— Increase of the chlorophyll content
— Delay of the leaf senescence and abscission

5. Increase of the photosynthetic activity as response to defoliation was achieved mainly by enhancing the mesophyll conductance but also by increasing the stomatal conductance.

6. Young potted plants and mature field-grown plants showed very similar responses to defoliation treatments.

Summary

In order to study the compensation mechanisms related to leaf removal, gas exchange response to defoliation as well as chlorophyll content were investigated in

field-grown Pinot noir grapevines. Mature 16 years old bearing plants and 2 years old fruitless potted plants were compared. Defoliation treatments were performed 1 week after full bloom. Besides topping, three levels of main leaf removal (3, 6 or all 12 main leaves retained) were combined with two levels of laterals (all retained or all removed). The single leaf measurements (on the 11th main leaf from the base) were carried out from treatment time to fruit maturity.

Young potted plants and mature field-grown plants showed very similar responses to defoliation treatments.

Plants with fewer main leaves showed higher photosynthetic rates and chlorophyll content per unit leaf area than the control plants, but only during the pre-veraison period. Yet, compensation was only partial because the increments registered in the gas exchange performance were insufficient to overcome the shortage of leaf area. Removal of lateral leaves resulted in the maintenance of higher assimilation rates of the remaining main leaves during fruit maturation. Plants without lateral leaves showed an increment in water use efficiency. Chlorophyll content was always higher for defoliated plants.

Increase of the photosynthetic activity as response to defoliation was achieved mainly by enhancing the mesophyll conductance, but also by an increase of the stomatal conductance. Another compensation mechanism observed was a delay in leaf senescence and abscission.

Acknowledgements

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