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Yield, fruit quality, bud fertility and starch reserves of the wood as a function of leaf removal in *Vitis vinifera* — Evidence of compensation and stress recovering

by

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Einfluß unterschiedlicher Entblätterung auf Ertrag, Traubenqualität, Knospenfruchtbarkeit und Stärkegehalt des Holzes von *Vitis vinifera* sowie Kompensations- und Erholungsvermögen

Zusammenfassung: An Ertragsreben wurde der Einfluß des Entfernens von Hauptblättern oder Geiztrieben auf Gesamtblattfläche, Traubenertrag und -qualität sowie Stärkegehalt des Holzes studiert. Die Bedeutung von Haupt- und Geizblättern sowie des Zeitpunktes der Entblätterung auf das Verrieseln wurde untersucht. Ziel der Studie war, Kompensationsmechanismen und -limiten der Rebe unter Streßbedingungen kennenzulernen, wie sie durch eine Entblätterung verursacht werden. Ferner sollte die Erholung der Pflanze nach längerer Streßeinwirkung erforscht werden.

Wurden die Hauptblätter entfernt (L = nur Geizblätter), so bildeten die Pflanzen mehr Geiztriebe mit einer größeren Anzahl Blätter. Dies führte nach dem ersten Streßjahr zu einer ungefähr gleichen Gesamtblattfläche wie bei den Kontrollpflanzen. Nach einem weiteren Streßjahr jedoch hatten die L-Pflanzen zwar weiterhin mehr Geizblätter, allerdings von geringerer Größe. Hieraus resultierte eine im Vergleich zur Kontrolle verringerte Gesamtblattfläche. Pflanzen nur mit Hauptblättern (M) kompensierten das Fehlen der Geiztriebe mit verzögerter Blattalterung und späterem Blattfall. Auch hier ergab sich nach dem zweiten Streßjahr eine geringere Blattgröße.

Der Traubenertrag der L-Pflanzen wurde im 1. Jahr durch die Blattentfernung kaum negativ beeinflußt, aber im 2. Jahr war er 50 % niedriger als in der Kontrolle. Bei den M-Pflanzen ergab sich in beiden Jahren kein verringerter Ertrag. Der Zuckergehalt der Trauben war in den L-Pflanzen im 1. Streßjahr leicht erhöht, nicht aber im 2. Jahr. Diese Reben hatten während beider Jahre eine bessere Beerenfarbe.

Die Blattfläche vom Zeitpunkt der Blüte bis 2—3 Wochen danach ist für den Traubenertrag entscheidend. Eine Entblätterung zu diesem Zeitpunkt verursachte nicht nur ein Verrieseln, sondern im folgenden Jahr zusätzlich eine reduzierte Knospenfruchtbarkeit. Die Zuckereinlagerung in den Trauben hängt von der assimilierenden Blattfläche während der Reifeperiode ab. Der Stärkegehalt im Holz war nach 2 Streßjahren erheblich reduziert. Es ergaben sich schwach positive Korrelationen zwischen Zuckergehalt des Mostes und Stärkegehalt des Holzes.

Die Zuckereinlagerung in die Traube und das Auffüllen der Stärkereserven im Holz ging bereits in der auf eine Streßbehandlung folgenden Saison normal vonstatten. Ein normaler Ertrag war 1 Jahr nach einem längeren Entblätterungsstreß jedoch noch nicht möglich, da die Bildung der Infloreszenzen bekanntlich während dieser Zeit (in unserem Fall die Streßperiode) einsetzt. Erst im 2. Jahr kam es zu einer vollständigen Erholung der Pflanze.

Key words: leaf, shoot, defoliation, bud, fertility, fruit set, berry, yield, must quality, wood, starch, stress, compensation.

Introduction

Pests, diseases and unfavorable weather conditions can strongly reduce the functional leaf area of the grapevines. Mechanical defoliation applied to promote a better

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microclimate of dense canopies also contributes to reduce the leaf surface. However, the repercussions of defoliation on quantity and quality of the fruit do not follow a linear pattern because grapevines have a strong capacity of compensation for the loss of leaf area by increasing the lateral shoots' production (KLIEWER 1970; KLIEWER and FULLER 1973; WOLF *et al.* 1986; HUNTER and VISSER 1988; REYNOLDS and WARDLE 1989), and also by increasing the leaf efficiency in terms of carbon fixation (BUTTROSE 1966; KLIEWER 1970; KLIEWER and FULLER 1973; HOFÄCKER 1978; HUNTER and VISSER 1988; REYNOLDS and WARDLE 1989). Here we present the results of our own investigations about the compensation capacity for stress induced by defoliation, its mechanisms and limitations. In a first step, the roles of main leaves and lateral leaves during the season are compared. Then, the possibility of the lateral shoots to assume the missing main leaves' functions in assuring a normal crop is investigated. The level of carbohydrate reserves after defoliation stress is also studied.

Incidence and severity of *Botrytis* bunch rot are reduced significantly when the leaves around grape clusters are removed (BONIFACE and DUMARTIN 1977; WOLF *et al.* 1986; KOBLET 1988; ENGLISH *et al.* 1989). This management practice is more efficient if carried out early in the season (KOBLET 1969) but it can reduce the fruit yield. On the other hand, if leaf removal is accomplished later, there are no consequences for the final yield. Between bloom and a short time after, the grapevines are susceptible to flower or berry abscission. If the supply of organic nutrients is not sufficient, berry drop due to a reduced assimilating surface can account for considerable crop loss. The sensitive period for berry shedding is examined in this study.

Another aim of this investigation is to verify if the plants stressed over a long period by defoliation can completely recover after the stress is released.

Material and methods

Defoliation trials were carried out from 1985 to 1987 in two vineyards at the Swiss Federal Research Station for Fruit-Growing, Viticulture and Horticulture in Wädenswil, Switzerland.

Experiment I: Influence of removing main leaves or lateral shoots on yield components, fruit quality and starch reserves in the wood — Evidence of compensation capacity

1. Experimental design and plant material

In 1985, mature grapevines of *Vitis vinifera* L. cv. Pinot noir, clone M1/17 on 5C rootstock, were used in this investigation. The plants were trained to double Guyot (cane pruning), with a spacing of 2.2 m × 1.2 m. The experiment included 4 defoliation treatments, replicated 5 times, each replicate being a single vine. All the non-fruiting shoots were removed at the end of June. Defoliation was accomplished on August 8, about 6 weeks after full bloom. The 4 treatments were:

- C — Control: shoot tip, all leaves and later shoots retained
- CT — Control topped: topped to 16 nodes per shoot, all leaves and laterals retained
- L — Lateral leaves: topped to 16 nodes, all main leaves removed
- M — Main leaves: topped to 16 nodes, all lateral shoots removed at weekly intervals from this date onward

Mature grapevines of Pinot noir, clone 2/45 on G-1 rootstock, can pruned, were used in 1986. Defoliation treatments CT, L, M, each replicated 12 times, were carried out on July 8, 1 week after full bloom.

In 1987, half of the plants from each treatment group of the previous year's experiment were defoliated 1 week after full bloom (15.7.87). The other half was defoliated 6 weeks after full bloom (10.8.87). The treatments were applied to the same plants as in the previous year.

2. Harvest and data collected

The crop was harvested on October 23, 17 and 28 in 1985, 1986 and 1987, respectively. 2 d before fruit harvesting, the leaves of all vines under treatment were picked and the fresh weight, leaf color, leaf area and dry weight of all leaf laminae were recorded. The main leaves and lateral leaves from each vine were kept separately in plastic bags with suitable identification and were stored in a cold room at 1 °C until measurement. During leaf harvesting, the number of main leaves, lateral leaves and also the number of lateral shoots arising from each main shoot was recorded. Leaf color was scored using a 5 point scale as follows: 0 = completely yellow; 1 = 0—25 % green; 2 = 25—50 % green; 3 = 50—75 % green; 4 = 75—100 % green. Leaf area was measured with an area-meter (model LI-3100 from Li-cor, Inc., Lincoln, Nebraska, USA). Immediately after, the leaves were dried at 65 °C in an oven and dry weight was noted. Just prior to fruit harvest, 100 berries from each vine were choosen randomly to determine mean berry weight. Afterwards they were used for color determination. Number of clusters per plant was registered. Number of berries per plant was calculated dividing crop weight by mean berry weight. Each vine was harvested individually, and after weighing the crop was crushed to determine soluble solids and acidity. For starch analysis, slices of wood were taken during pruning in the 1st week of February, 1988. The 5th internode from 4 mature canes was sampled from each plant. Using a sharp curve chisel and a hammer, a portion of trunk wood was equally sampled, leaving a small wound of no consequence for the plant. The samples were oven-dried at 65 °C and frozen until analysis.

3. Analytical procedures

3.1. Must quality

Total soluble solids were evaluated with a density meter (model DMA 46 provided by Anton Paar KG, Graz, Austria), total acidity was determined using an automatic end point titration unit (Dosimat 665, Impulsomat 614, Digital pH-meter 632, from Metrohm AG, Herisau, Switzerland) on samples collected from each vine.

3.2. Fruit coloration

For the anthocyanin analysis, skins from 100 g samples of berries from each plant were extracted with methanol acidified with 1 % hydrochloric acid. The berries were manually crushed, the skins were placed in 150 ml flasks with 70 ml of acidified methanol and shaken during 4 h at ambient temperature. The extraction was repeated twice, first with 40 ml methanol during 3 h and then with 30 ml methanol during 3 h. The extracts were mixed together and the absorbency was measured at 530 nm, using a spectrophotometer, after appropriate dilution (1 : 50). Skin coloration results are given as percentage of the highest value of optical density observed.

3.3. Carbohydrate analysis

Wood samples were pulverized and 200 mg dust were used for the extraction. Soluble sugars were extracted twice with 8 ml of 70 % ethanol at 60 °C for 30 min each. After evaporation and suitable dilution, the sugar content was measured by the anthrone method as described by Scott and Melvin (1953). Starch was then extracted twice with 8 ml of 1 M perchloric acid, 1 h each time at 60 °C and was measured after dilution by the same method. Absorbency readings were made at 620 nm with a spectrophotometer. Glucose was used as standard for both soluble sugars and starch. This method had previously been tested to ascertain that no structural carbohydrates would be extracted and to determine which of the solutions (0.5 M NaOH and 1 M perchloric acid) would be more adequate for starch extraction. After the ethanol extraction, samples of ground wood and cotton wool (98 % cellulose), were extracted both with 0.5 M NaOH and 1 M perchloric acid. There were no carbohydrates extracted from the cotton wool samples neither with the NaOH nor with the perchloric acid solution. Starch extraction from the wood samples by the acid solution proved to be much more efficient than by the alkaline solution. For this reason, perchloric acid was used in the routine analyses.

Experiment II: Influence of time of defoliation on berry drop, yield, fruit quality and bud fertility

1. Plant material and experimental design

Mature grapevines of Pinot noir, clone 2/45 on G-1 rootstock, trained and pruned as in the previous experiments, were used in this trial. At full bloom in 1988, 4 marked inflorescences from 25 plants were enclosed in gauze bags. On the same day (June 21) all the plants were topped to 12 nodes per shoot. They were divided into 5 treatment groups replicated 5 times each as follows:

C — Control
T1 — All main leaves removed at full bloom
T2 — All main leaves removed 2 weeks after full bloom
T3 — All main leaves removed 4 weeks after full bloom
T4 — All main leaves removed 6 weeks after full bloom

2. Harvest, data collected and analytical procedures

The gauze bags were emptied at weekly intervals until August 24. The number of fruit caps, flowers and fruitlets were then counted. Plants were harvested on October 18. Cluster number, yield per plant, berry number, berries per cluster, fruit coloration, soluble solids and acidity of the juice were determined and recorded using the same methods as described in Experiment I.

3. Bud fertility

The following winter, 1 shoot per plant was used to test bud fruitfulness. During pruning on the 1st week of February, the shoots were cut into single node portions and placed into water. For this purpose, a metal box (45 cm × 25 cm × 10 cm) was filled with water and activated charcoal was added to prevent water deterioration. The nodes were held in place by a hardware screen of 11.5 mm mesh size placed on top of the box. Incubation was carried out at a temperature of 25 °C. When the inflorescences were sufficiently visible, the number of clusters per node and number of sprouted buds were recorded.

Experiment III: Evidence of recovering capacity after defoliation stress

1. Plant material and experimental design

The plants used in Experiment I in 1986 and 1987 were followed in the next 2 seasons to test if they would recover completely after 2 years of defoliation stress. They were all treated as the control plants (CT), i.e., besides topping, no other defoliation treatment was performed.

2. Harvest, data collected and analytical procedures

At harvesting time in October 1988 and 1989, cluster number, yield per plant, berry number, berries per cluster, fruit coloration, soluble solids and acidity of the juice were determined and registered using the corresponding methods already described in Experiment I. During pruning in the 1st week of February 1989, pruning weight was recorded and samples from the trunk and from the 5th internode of 1 and 2 years old canes were taken from each vine for starch analysis.

Table 1

Influence of removing main leaves or lateral shoots on number, size, surface, and specific weight of main and lateral leaves at vintage time of the 1st stressing season (1985 and 1986) · C: control; CT: control topped; L: only lateral leaves left; M: only main leaves left

Einfluß des Entfernens von Hauptblättern oder Geiztrieben auf die Gesamtblattfläche der Rebe, Hauptblattfläche und Blattzahl je Trieb, Hauptblattgröße und spezifisches Gewicht, Geizblattfläche je Haupttrieb, Zahl der Blätter je Geize, Geiztriebe je Haupttrieb, Geizblattfläche und spezifisches Gewicht bei der Weinlese nach dem 1. Streßjahr (1985 und 1986) · C: Kontrolle; CT: Kontrolle gekappt; L: nur Geiztriebe stehen gelassen; M: nur Hauptblätter stehen gelassen

	C	CT	L	M	SE[1])
1985					
Total leaf area per vine (m^2)	5.54 a[2])	3.98 ab	4.00 ab	2.51 b	0.66
Main leaves area per shoot (m^2)	0.34 a	0.20 b	—	0.22 b	0.02
No. of main leaves per shoot	26 a	15 b	—	15 b	1.0
Main leaves size (cm^2)	132.3 a	137.3 a	—	154.2 a	7.7
Lateral leaf area per main shoot	0.23 ab	0.15 a	0.45 b	—	0.07
No. of leaves per lateral shoot	4 a	4 a	8 b	—	0.5
No. of laterals per main shoot	12 a	7 b	11 a	—	1.3
Lateral leaves size (cm^2)	47.9 a	44.9 a	50.8 a	—	3.9
1986					
Total leaf area per vine (m^2)	—	5.77 a	4.80 a	2.98 b	0.34
Main leaves area per shoot (m^2)	—	0.14 a	—	0.22 b	0.01
No. of main leaves per shoot	—	8 a	—	13 b	0.4
Main leaves size (cm^2)	—	172.5 a	—	170.0 a	5.4
Main leaves S.L.wt[3]) ($mg\ cm^{-2}$)	—	4.9 a	—	5.6 b	0.1
Lateral leaf area per main shoot	—	0.30 a	0.36 a	—	0.03
No. of leaves per lateral shoot	—	7 a	7 a	—	0.3
No. of laterals per main shoot	—	7 a	9 b	—	0.3
Lateral leaves size (cm^2)	—	61.1 a	60.1 a	—	2.5
Lateral leaves S.L.wt[3]) ($mg\ cm^{-2}$)	—	4.2 a	3.6 b	—	0.1

[1]) Standard error of the mean.

[2]) Mean separation by Duncan's multiple range test. Means followed by the same letter within rows do not differ significantly at 5 % level.

[3]) Specific leaf dry weight.

Statistical analysis

Statistical analysis of data was performed utilizing the WIDAS statistical package (Wissenschaftliches Integriertes Daten-Auswertungs-System, copyright Data General Corporation). Results were subjected to a factorial one way (treatment) or two way (treatment × time of treatment) analysis of variance with previous data transformation (square root transformation for counts or arc sine transformation for proportions) whenever required. Duncan's multiple range test was used to compare means. Linear regression, followed by analysis of variance and F-test, was used to test relationships between some of the measured variables.

Results and discussion

I. Influence of removing main leaves or lateral shoots on yield components, fruit quality and starch reserves in the wood — Evidence of compensation capacity

Leaf area

In 1985, treatment L produced a 3 times larger lateral leaf area than the control topped plants, which resulted in larger total leaf surface (Table 1). This was achieved by a stronger production of lateral shoots with a greater number of leaves. In 1986, the same tendencies were observed but the differences were not as remarkable as in the previous year. This ability to increase lateral leaf surface with increasing defoliation had also been observed by WEAVER (1963), KLIEWER (1970) and REYNOLDS and WARDLE (1989). After 2 stressing seasons, the L plants still produced more lateral leaves but they were smaller in average size (Table 2). Therefore, the lateral leaf area was inferior to that of the control plants. The same constraint on the leaf growth was observed in 1987 for M plants: they produced leaves of smaller average size than the control plants (Table 2). This could be due to an insufficient accumulation of reserves required for the initial growth as a consequence of the previous year defoliation.

On plants bearing only main leaves, all the developing lateral shoots were periodically removed and, unable to increase the leaf surface, these plants had to adopt another strategy to compensate for the absence of lateral leaves: they delayed leaf senescence and abscission. This phenomenon is particularly evident in 1986 (Fig. 1). Canopies from M plants remained green until vintage time, in contrast to CT plants which were not only yellowish but had already lost part of their leaves. It is apparent that the process of leaf senescence was somehow restrained in M plants. This overcharged leaves managed to remain physiologically younger and probably more actively assimilating. Therefore, it is evident that defoliation causes an increase of leaf efficiency of the remaining leaves to compensate the stress of reducing the source to sink ratio. MAY *et al.* (1969), BUTTROSE (1966), KLIEWER (1970), KLIEWER and FULLER (1973), HOFÄCKER (1978), REYNOLDS and WARDLE (1989) arrived at the same conclusion.

Main leaves from defoliated plants had a higher specific leaf weight (Tables 1 and 2). This is difficult to explain because leaf carbohydrate content was not measured, but the visual impression was that the main leaves from M plants were thicker and greener. The higher specific weight should not be interpreted as accumulation of surplus carbohydrates in the leaves but as a consequence of a different physiological age: most of the main leaves of the control plants were already senescent and so the translocation of proteins out of the leaves associated with senescence (DALE 1982) might explain this phenomenon.

Table 2

Influence of removing main leaves or lateral shoots at 2 different times on number, size, surface, and specific weight of main and lateral leaves at vintage time of plants stressed over 2 seasons (1987) · CT: control topped; L: only lateral leaves left; M: only main leaves left; T1: treated 1 week after bloom; T2: treated 6 weeks after bloom

Einfluß des Entfernens von Hauptblättern oder Geiztrieben zu 2 verschiedenen Zeitpunkten auf die Gesamtblattfläche je Rebe, Hauptblattfläche und Blattzahl je Trieb, Hauptblattgröße und spezifisches Gewicht, Geizblattfläche je Haupttrieb, Zahl der Blätter je Geize, Geiztriebe je Haupttrieb, Geizblattfläche und spezifisches Gewicht bei der Weinlese nach 2 Streßjahren (1987) · CT: Kontrolle gekappt; L: nur Geiztriebe stehen gelassen; M: nur Hauptblätter stehen gelassen; T1: Blattentnahmen 1 Woche nach der Blüte; T2: Blattentnahmen 6 Wochen nach der Blüte

	CT	L	M	SE[1])	T1	T2	SE	Interaction
1987								
Total leaf area per vine (m^2)	6.51 a[2])	3.20 b	2.12 c	0.32	4.12 a	3.78 a	0.26	*[3])
Main leaves area per shoot (m^2)	0.24 a	—	0.19 b	0.01	0.22 a	0.21 a	0.01	NS
No. of main leaves per shoot	14 a	—	14 a	0.3	15 a	14 a	0.3	NS
Main leaves size (cm^2)	167.8 a	—	134.3 b	7.1	151.4 a	150.7 a	7.1	NS
Main leaves S.L.wt[4]) ($mg\ cm^{-2}$)	5.4 a	—	5.8 b	0.1	5.6 a	5.6 a	0.1	NS
Lateral leaf area per main shoot	0.38 a	0.29 a	—	0.04	0.35 a	0.31 a	0.04	NS
No. of leaves per lateral shoot	9 a	8 a	—	0.4	9 a	9 a	0.6	NS
No. of laterals per main shoot	7 a	8 a	—	0.4	8 a	7 a	0.4	NS
Lateral leaves size (cm^2)	52.4 a	43.1 b	—	2.4	49.3 a	46.2 a	2.4	*
Lateral leaves S.L.wt[4]) ($mg\ cm^{-2}$)	4.2 a	4.2 a	—	0.2	4.4 a	4.1 a	0.2	NS

[1]) Standard error of the mean.
[2]) Mean separation by Duncan's multiple range test at 5 % level. Means followed by the same letter within row sections do not differ significantly.
[3]) NS, *, non-significant or significant at 5 % level, respectively.
[4]) Specific leaf dry weight.

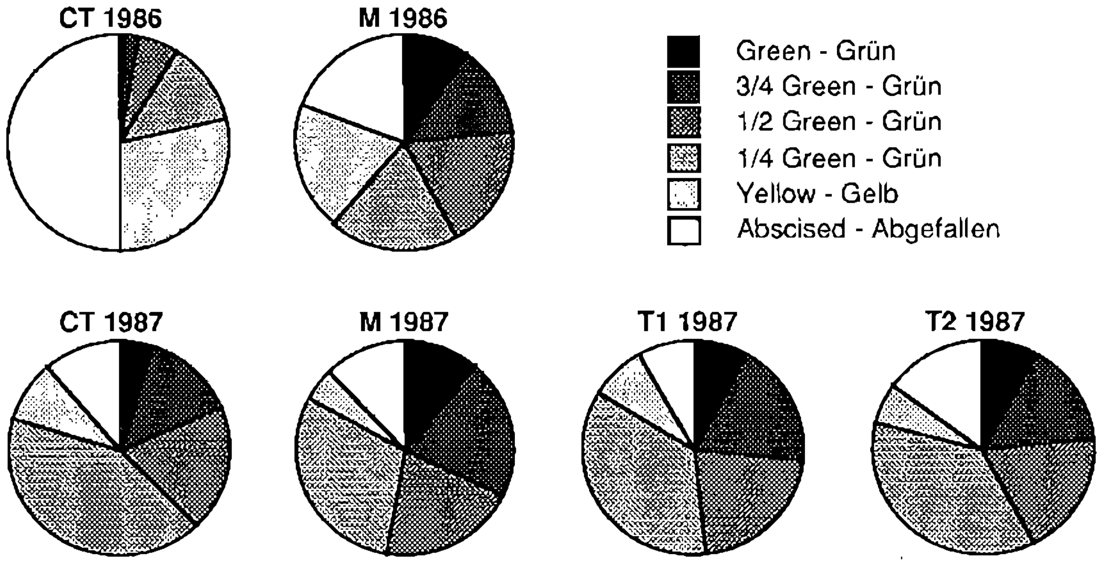

Fig. 1: Influence of removing lateral shoots and of treatment time on leaf coloration and abscission at vintage time. CT: control topped; M: only main leaves left; T1: plants treated 1 week after bloom; T2 plants treated 6 weeks after bloom.

Einfluß des Entfernens von Geiztrieben und des Behandlungszeitpunktes auf Blattverfärbung und Blattfall zur Zeit der Weinlese. CT: Kontrolle gekappt; M: nur Hauptblätter stehen gelassen; T1: Entblätterung 1 Woche nach der Blüte; T2: Entblätterung 6 Wochen nach der Blüte.

Yield and yield components

In 1985, there were practically no significant differences in the yield components of the control and defoliated plants (Table 3). This was probably due to the time of treatment (6 weeks after full bloom), which was later in the season than in 1986, and also to the very high variations of the plants inside the treatments. Berry weight was the only yield component strongly affected by defoliation in 1985. An interesting result in this experiment was that the control plants which were not topped (C) did behave like the plants with all the main leaves removed (L). Both L and C plants showed throughout the season an intense production of new leaves (Table 1) which surely affected the fruit growth. Control topped plants had an advantage over C plants because they did not have the actively growing shoot tip. Probably for this reason they achieved the best yield performance. Topping improves the fruit set because it eliminates a sink which would compete with the fruit for organic nutrients (COOMBE 1962; KOBLET 1966; VERGNES 1981). QUINLAN and WEAVER (1970) showed that the direction of translocation of photosynthates from a newly exporting leaf during berry set stage was reversed after tipping: instead of upwards moving to the shoot tip, the assimilates were diverted basipetally. In 1986 (as in 1985), plants bearing only lateral shoots had approximately one third lower fruit yield as compared with the CT plants, owing to lower berry number and weight (Table 3). Nevertheless, it has to be stated that treatment L represents a tremendous stress for the plant: when the main leaves were removed the lateral shoots were practically non-existent, so that the plants looked completely stripped during the first weeks following the treatment. The first weeks after full bloom proved to be of capital importance for the final berry number and size (Experiment II). COOMBE *et al.* (1987) found that increments in dry matter of pericarp increased with initial berry size. They observed also that defoliation reduced the increments both on a per fruit and a per fresh weight basis. In other words, if stage 1 of berry growth (described by HARRIS *et al.* 1968) is disturbed, the rate of dry matter accumulation will be reduced and the final berry weight will be lighter.

An interesting feature is the fact that treatment M with only 50—60 % (1985 and 1986) and 30 % (1987) of the CT plants' leaf area obtained equivalent results in crop yield and yield components. These results show that defoliation can be compensated by an increase in the physiological efficiency of the remaining leaves.

The final crop yield seems to depend on the existing assimilating surface during the first period of berry growth. During this critical period, plants bearing only main leaves had the entire available leaf surface consisting of fully grown actively assimilating and exporting leaves (KOBLET 1969) and competition from a growing shoot tip or

Table 3

Influence of removing main leaves or lateral shoots on fruit yield and quality during the 1st stressing year (1985 and 1986) · C: control; CT: control topped; L: only lateral leaves left; M: only main leaves left

Einfluß des Entfernens von Hauptblättern oder Geiztrieben auf Traubenertrag, Beeren je Traube, Beerengewicht, Zuckergehalt, Gesamtsäure, Reifeindex, Beerenfarbe, Leistungsindex während des 1. Streßjahres (1985 und 1986) · C: Kontrolle; CT: Kontrolle gekappt; L: nur Geiztriebe stehen gelassen; M: nur Hauptblätter stehen gelassen

	C	CT	L	M	SE[1]
1985					
Yield					
Fruit yield (kg.m^{-2})	0.60 a[2]	0.91 a	0.57 a	0.76 a	0.11
Berries per cluster	55 a	58 a	54 a	52 a	5.6
Berry weight (g)	1.71 a	1.85 b	1.70 a	1.87 b	0.04
Fruit quality					
Must soluble soldis (°Oe) (A)	84.8 a	84.5 a	86.0 a	83.1 a	1.4
Must total acidity (g l^{-1}) (B)	13.3 a	13.2 a	12.0 b	14.0 a	0.4
Maturity index M = (A × 10): B	64 a	64 a	72 b	60 a	2.3
Fruit coloration (% of highest value)	86.4 a	73.0 b	86.7 a	71.2 b	4.2
Yield performance index = (M × yield)	103 a	152 a	107 a	117 a	16.2
1986					
Yield					
Fruit yield (kg.m^{-2})	—	1.32 a	0.87 b	1.37 a	0.09
Berries per cluster	—	78 a	69 a	82 a	5.3
Berry weight (g)	—	1.68 a	1.28 b	1.65 a	0.03
Fruit quality					
Must soluble solids (°Oe) (A)	—	80.1 a	82.0 b	76.7 c	0.6
Must total acidity (g l^{-1}) (B)	—	14.6 a	12.8 b	14.7 a	0.2
Maturity index M = (A × 10): B	—	55 a	64 b	51 c	1.1
Fruit coloration (% of highest value)	—	55.3 a	93.2 b	66.2 a	2.0
Yield performance index = (M × yield)	—	174 a	134 a	169 a	12.9

[1]) Standard error of the mean.

[2]) Mean separation by Duncan's multiple range test. Means followed by the same letter within rows do not differ significantly at 5 % level.

lateral shoots was excluded. That was not the case in the young growing lateral shoots from L plants whose leaves had to provide assimilates for their own growth, diverting them from the fruit.

In 1987, L plants showed a reduction of 50 % in the fruit yield compared with the control (Table 4). They were weakened by 2 consecutive deprivation seasons[2]). Contrary to the predictions (MAY *et al.* 1969), there was no decline of the bud fertility (= number of clusters per shoot and number of shoots per plant). The yield reduction was mainly due to berry fall which was significantly stronger only in L plants, treated 1 week after bloom (L.T1). In treatment L, contrary to M and CT, the berry drop was more severe in case of the first treatment term. This fully agrees with the previous explanation: plants L.T1 were deprived of the main leaves 5 weeks before plants L.T2 and so the latter had the main leaves for a longer time, exactly during the hypothetical critical period. On the other hand, elimination of the immature growing leaves from the shoot tip (treatments CT, M) and lateral shoots (treatment M), which are sharing the same reserve pool with the fruit, represented a favouring circumstance for plants CT and M treated 1 week after bloom, as compared with the same treatments performed later.

Fruit quality

The variation in fruit quality is explained by the differences observed in the leaf surface (Table 1). In the first defoliation season it is evident that lateral leaves were more efficient than main leaves in feeding the clusters during the ripening period and could fully compensate for the absence of main leaves. Fruit maturation was better in plants bearing only lateral shoots in 1985 and 1986 (Table 3). No differences were seen in the maturity index (sugar/acid ratio) in all treatments in 1987 (Table 4) because the lower sugar reading also coincided with a lower level of total acidity. L plants had a significantly lower °Oe in the 2nd stressing season (1987). This fact may be explained by the incapability of this plant group to reconstruct an adequate assimilating apparatus after the defoliation treatment to allow a satisfactory fruit ripening as had been accomplished in the previous season. Treatment M had the poorest sugar reading, but the acid content of the juice was not different from the control plants. Fruit coloration followed more or less the same pattern of the sugar content. Treatment L had the highest color intensity on a per g basis, even in the 2nd defoliation season because of the smaller berries with more specific surface. If expressed on a per fruit basis, fruit coloration in 1987 would be 65, 63 and 52 % for treatments CT, L, M, respectively. Berry skin pigmentation and sugar content of the fruit juice were correlated both in 1985 ($r = 0.62$, $P < 1$ %) and 1986 ($r = 0.64$, $P < 0.1$ %), but no significant interdependence was seen in 1987. WEAVER (1963) reported a parallelism between the curves of sugar accumulation and change in amount of color during the ripening period. PIRIE and MULLINS (1980) state that sugar flux to grape tissues is one of the factors that govern the rate of phenolics accumulation. This relationship is easy to explain since the pigments of grapes are anthocyanidins glycosylated by glucose, forming the anthocyanins. They are synthesized from sugar, via shikimic acid and acetate provided by acetyl-coenzyme A from the glycolytic pathway (SALISBURY and ROSS 1985). Fruit coloration was also negatively correlated with crop level ($r = -0.76$, $P < 0.1$ %; $r = -0.79$, $P < 0.1$ %; $r = -0.61$, $P < 0.1$ % in 1985, 1986, 1987, respectively). Similar findings are reported by PIRIE and MULLINS (1977) and SOMERS (1968).

The accumulation of sugar and color in the berries seems to depend on the available active leaf surface during the period between veraison and harvest. During this

[2]) Plants used in 1987 were the same as in 1986, and the same treatments were made on the same plants.

Table 4

Influence of removing main leaves or lateral shoots at 2 different times on fruit yield and quality in 1987 (2nd stressing season) · CT: control topped; L: only lateral leaves left; M: only main leaves left; T1: treated one week after bloom; T2: treated 6 weeks after bloom

Einfluß des Entfernens von Hauptblättern oder Geiztrieben zu zwei verschiedenen Zeitpunkten auf Traubenertrag, Zahl der Triebe je Rebe, Zahl der Trauben je Trieb, Beeren je Traube, Beerengewicht, Zuckergehalt, Gesamtsäure, Reifeindex, Beerenfarbe, Leistungsindex, in 1987 (nach 2 Streßjahren) · CT: Kontrolle gekappt; L: nur Geiztriebe stehen gelassen; M: nur Hauptblätter stehen gelassen; T1: Blattentnahmen 1 Woche nach der Blüte; T2: Blattentnahmen 6 Wochen nach der Blüte

	CT	L	M	SE[1])	T1	T2	SE	Interaction
1987								
Yield								
Crop yield (kg m^{-2})	0.91 a[2])	0.45 b	0.70 a	0.08	0.67 a	0.70 a	0.06	NS[3])
No. of shoots per vine	11.0 a	11.3 a	11.3 a	0.5	11.0 a	11.3 a	0.4	NS
No. of clusters per shoot	1.9 a	1.8 a	1.9 a	0.1	1.9 a	1.9 a	0.1	NS
Berries per cluster	69 a	46 b	64 a	2.8	58 a	61 a	2.3	**
Berry weight (g)	1.47 a	1.10 b	1.20 b	0.04	1.27 a	1.24 a	0.04	NS
Fruit quality								
Must soluble solids (°Oe) (A)	77.6 a	73.1 b	77.0 a	0.8	77.1 a	74.7 b	0.7	NS
Must total acidity (g l^{-1}) (B)	13.5 a	11.8 b	13.1 a	0.3	12.6 a	13.0 a	0.2	NS
Maturity index M = (A × 10): B	58 a	62 a	59 a	1.5	62 a	58 a	1.2	NS
Fruit coloration (% of highest value)	52.6 a	68.1 b	55.1 a	2.5	63.4 a	53.8 a	2.0	***
Yield performance index (= M x yield)	125 a	65 b	98 a	10.1	96 a	96 a	8.2	*

[1]) Standard error of the mean.
[2]) Mean separation within row sections by Duncan's multiple range test. Means followed by the same letter do not differ significantly at 5 % level.
[3]) NS, *, **, ***, non-significant or significant at 5 %, 1 % or 0.1 % level, respectively.

period, plants L have a canopy composed of relatively young leaves in opposition to plants M which can only count on old leaves for the sugar accumulation in the berries. KOBLET and PERRET (1971) showed clearly a positive influence of lateral shoots on grape quality. STOEV *et al.* (1966), KRIEDEMANN (1968), KRIEDEMANN *et al.* (1970) and ALLEWELDT *et al.* (1982) agreed that photosynthetical activity is higher in recently formed leaves and that the peak of photosynthesis occurs when leaves attain full size. Then it decreases gradually with increasing age. Plants treated earlier in 1987 had a better maturation index and this was probably due to the earlier stimulation of the laterals' growth.

Defoliated plants had no statistically proved reduction of the yield performance index (maturity index × yield per plant) in 1985 and 1986. However, in 1987, after 2

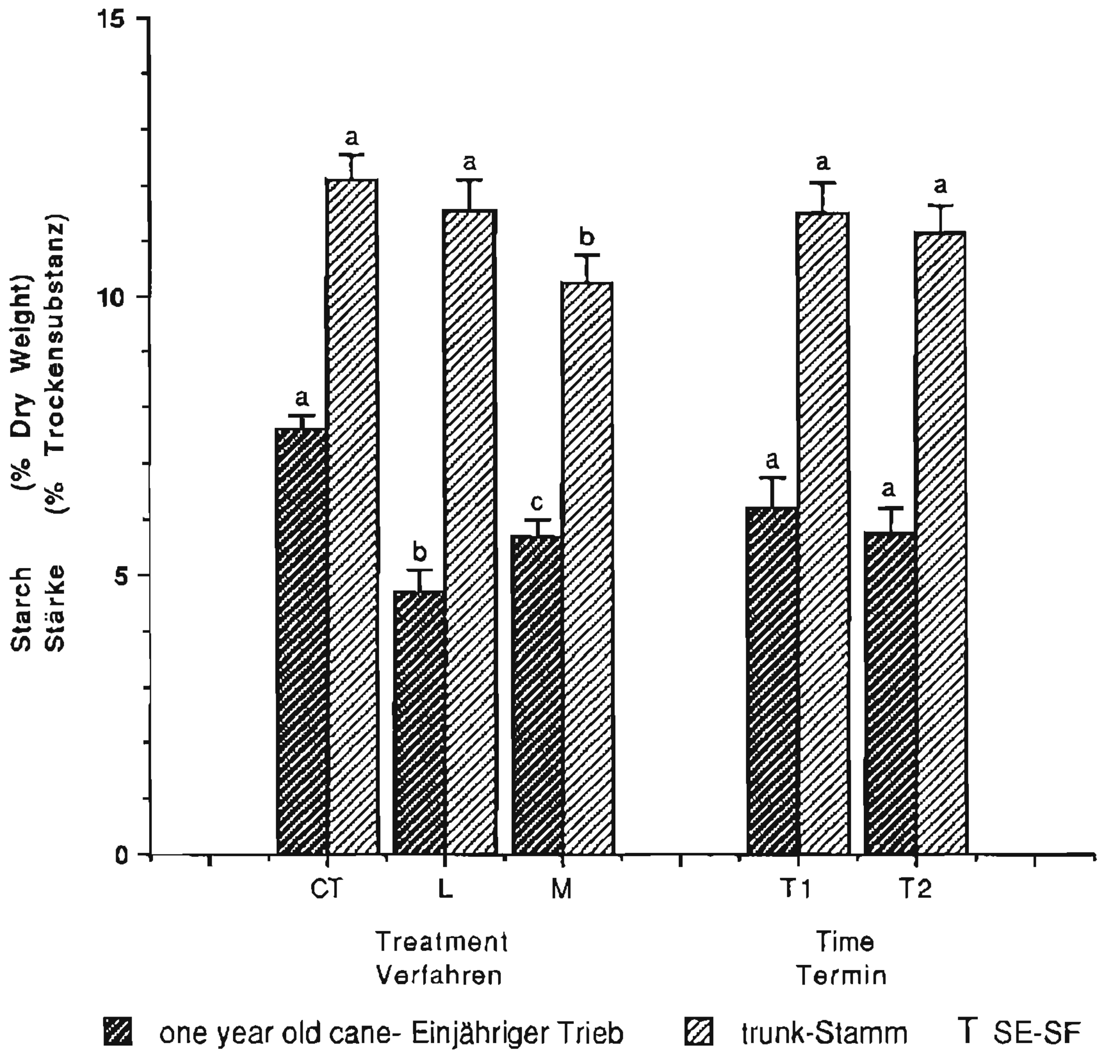

Fig. 2: Influence of removing main or lateral leaves over 2 consecutive seasons on starch reserves in the wood. CT: control topped; L: only lateral leaves left; M: only main leaves left; T1: plants treated 1 week after bloom; T2: plants treated 6 weeks after bloom. Samples were taken on February, 1988. Mean separation by Duncan's multiple range test at 5 % level. Means of the same plant part, headed by the same letter, do not differ significantly.

Einfluß des Entfernens von Haupt- oder Geizblättern während 2 aufeinander folgenden Vegetationsperioden auf die Reservestärke im Holz. CT: Kontrolle gekappt; L: nur Geiztriebblätter stehen gelassen; M: nur Haupttriebblätter stehen gelassen; T1: Entblätterung 1 Woche nach der Blüte; T2: Entblätterung 6 Wochen nach der Blüte. Durchschnittswerte der gleichen Rebteile unterscheiden sich bei gleichen Buchstaben nicht signifikant.

accumulated stressing seasons, plants bearing only lateral shoots revealed a 50 % decrease in comparison to the control, probably due to the 50 % smaller leaf surface observed in this plant group.

Starch reserves in the wood

After 2 stressing seasons, defoliated plants had considerably less reserves than the control plants (Fig. 2). Time of treatment did not influence the reserve content of the wood. The replacement of the carbohydrate reserves in the wood was most probably restrained to allow fruit maturation.

It has to be noted that the plants did not have the possibility to produce carbohydrates and to refill the reserves after harvest because all the leaves had been removed at vintage time for measurement. The fruit clusters are the first sink organs to benefit of the phloem load because they have the advantage of being situated closer to the source organs and, hence, their needs are satisfied before the other reserve organs in the plant. Shoot reserves (1 year old cane) seem to be the most affected by the sink attraction of the fruit in stressed plants since the reduction observed reached 40 % for treatment L compared to the trunk reserves which were utmost 15 % lower than the control. MATSUI *et al.* (1979) found that not only the translocation of photosynthates synthesized in the leaves but also the translocation of sugars converted from polysaccharides in shoots to the berries were responsible for the sugar accumulation in the fruit.

II. Influence of time of defoliation on berry drop, yield, fruit quality and bud fertility

Berry drop

Berry drop was particularly drastic in plants defoliated at full bloom (T1) and 2 weeks after (T2) (Fig. 3). Treatment T1 and T2 had a 50 and 25 % lower berry set respectively as compared to the control. Plants defoliated later did not show increased berry drop in comparison with the control plants. In all the treatments the period of most intense berry abscission occurred between the 2nd and 3rd week after bloom and it stopped completely 6 weeks after bloom.

These results show clearly that the critical period of berry drop due to an insufficient supply of organic nutrients to the inflorescence is limited to 3 weeks after bloom. These findings confirm the results obtained by KOBLET in 1966. This period seems to coincide with the period of rapid cell division which lasts according to HARRIS *et al.* (1968) 3—4 weeks after anthesis in cv. Sultanina and, according to JONA and BOTTA (1988), 12 d in cvs Barbera and Freisa. KASSEMEYER and STAUDT (1982), working with cvs Weisser Burgunder and Gewürztraminer, found that the mitotic cycle of the zygotes requires 20 d. COOMBE (1960) states that most of the cell division in the pericarp occurs on the first 5—10 d after bloom and that meristematic activity is limited to the 1st period of berry growth which lasts 45 d in cv. Muscat. Beginning of cell differentiation, after cessation of cell division, could as well be one of the reasons that stops berry drop.

Yield and fruit quality

At vintage time, mean berry weight was on all defoliated plants lower than in the control (Table 5). Furthermore, the earlier the defoliation was accomplished, the greater was the decrease in weight. KLIEWER reported similar conclusions in 1970. Several investigators (BUTTROSE 1966; MAY *et al.* 1969; COOMBE *et al.* 1987; KINGSTON and VAN EPENHUIJSEN 1989) showed that defoliation affects negatively berry growth and development. The earlier the reduction in assimilating surface is completed, the earlier the scarcity of carbohydrates and the more drastic are the consequences. Even after a possible reconstruction of the assimilating apparatus, the increments in dry matter per fruit would increase with initial berry size (COOMBE *et al.* 1987) and so the final berry weight would be irremediably lower in the defoliated plants. A reduced number of berries together with a lower berry weight contributed to the decrease of the crop yield registered on plants defoliated during bloom and 2 weeks after. Treatments T3 and T4 had also a small reduction of the yield, although not statistically proved.

Soluble solids of the must were not affected by defoliation (Table 5), except for the last treatment time, probably because at this time overall growth is slowed down and lateral shoot production is not efficient enough to enable a complete reconstruction of the assimilating apparatus. Acidity of the juice was lower than that of the control for all defoliated plants, except the group defoliated at the last date. Fruit coloration, expressed on a per berry basis, was lower only for plants treated 6 weeks after anthesis but, if expressed on a weight basis, it was not influenced by defoliation.

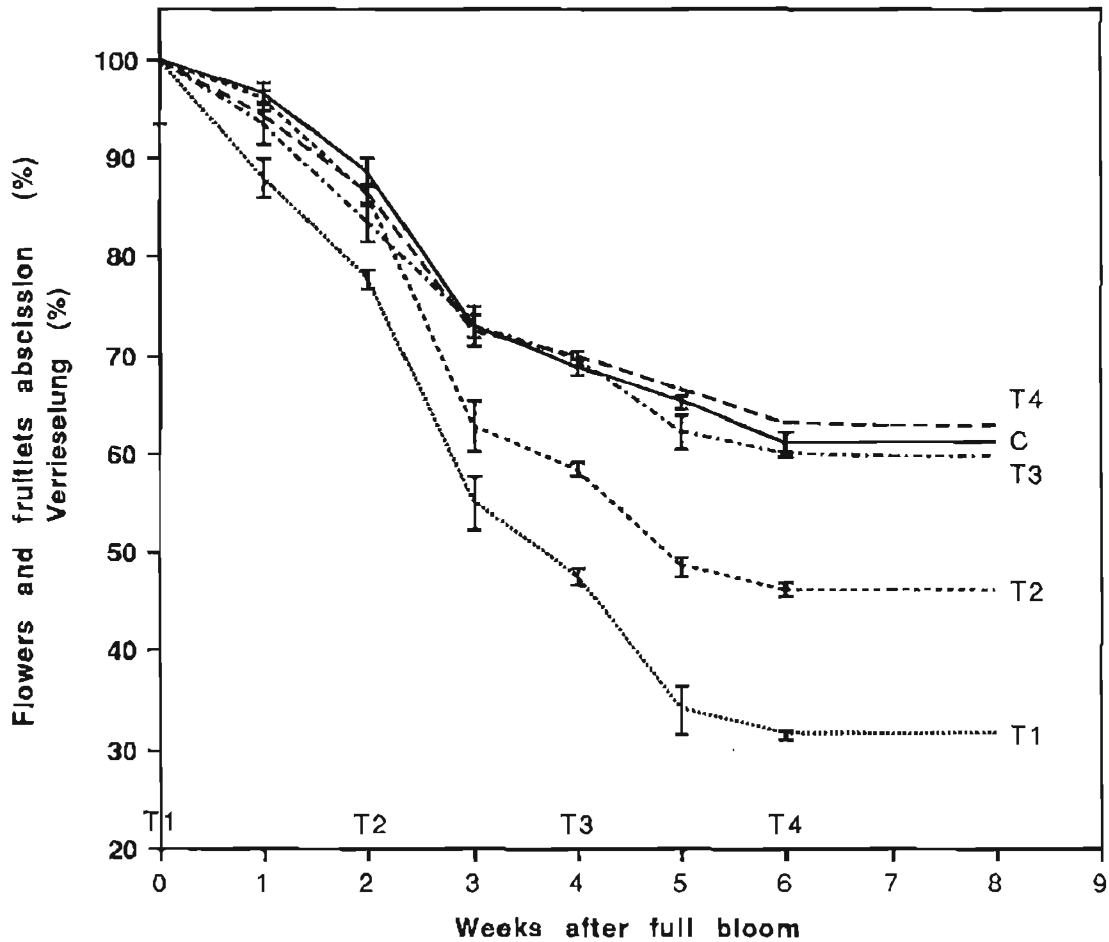

Fig. 3: Influence of time of defoliation on flowers and fruitlets abscission. Vertical bars represent the standard error of the mean. C: control; T1: plants defoliated at full bloom; T2: plants defoliated 2 weeks after bloom; T3: plants defoliated 4 weeks after bloom; T4: plants defoliated 6 weeks after bloom. Defoliation consisted on removing all the main leaves.

Der Einfluß des Entblätterungszeitpunktes auf das Verrieseln. Die senkrechten Striche geben den Standardfehler der Mittelwerte an. C: Kontrolle; T1: Entblätterung zur Zeit der Vollblüte; T2: Entblätterung 2 Wochen nach der Blüte; T3: Entblätterung 4 Wochen nach der Blüte; T4: Entblätterung 6 Wochen nach der Blüte. Die Entblätterung betraf nur die Hauptblätter.

It is clear that elimination of leaves in early stages of berry development causes a decrease of fruit yield, the critical period being limited to 2—3 weeks after full bloom. On the other hand, a strong defoliation stress applied later in the season can cause a decrease of fruit quality.

Bud fruitfulness

Bud burst and number of clusters per node in the following season were severely affected by defoliation (Table 5), in contrast to Experiment I. Flower clusters start to develop during the beginning of bloom of the previous season (SHAULIS and PRATT 1965). Therefore, an adequate supply of assimilates is essential for maximum flower development. The most affected plants were those treated during bloom and 2 weeks after. This period is particularly delicate not only for the current year's fruit production but also for the following season's yield as well. KOBLET (1985) obtained similar results by covering the buds instead of removing the leaves.

Table 5

Influence of time of defoliation on fruit quantity and quality and on bud fruitfulness in the following season · C: control; T1: plants defoliated at full bloom; T2: plants defoliated 2 weeks after bloom; T3: plants defoliated 4 weeks after bloom; T4: plants defoliated 6 weeks after bloom · Defoliation consisted of removing all main leaves

Einfluß des Zeitpunktes der Blattentnahmen auf Beerengewicht, Traubenertrag, Zuckergehalt, Gesamtsäure, Beerenfarbe, Knospenaustrieb, und Traubenzahl je Knospe im folgenden Jahr · C: Kontrolle; T1: Entblätterung der Rebe zur Blütezeit; T2: Entblätterung 2 Wochen nach der Blüte; T3: Entblätterung 4 Wochen nach der Blüte; T4: Entblätterung 6 Wochen nach der Blüte · Die Entblätterung bestand im Entfernen aller Hauptblätter

	C	T1	T2	T3	T4	SE[1])
Fruit yield						
Mean berry weight (g)	1.5 a[2])	0.9 b	1.0 b	1.1 b	1.1 b	0.07
Crop yield (kg m^{-2})	1.2 b	0.3 a	0.5 ac	0.9 bc	0.8 bc	0.16
Fruit quality						
Must soluble solids (°Oe)	77.7 ac	81.7 a	77.8 ab	75.2 bc	64.5 d	1.72
Must total acidity (g l^{-1})	13.4 a	11.7 b	11.6 b	12.0 b	13.5 a	0.35
Fruit coloration (%)	47.5[3]) ac	82.2 b	72.0 b	58.9 a	35.4 c	4.22
	68.4[4]) a	76.5 a	71.9 a	64.0 a	40.1 b	6.56
Bud fruitfulness						
Bud burst (%)	95.0 a	35.0 b	32.5 b	55.0 b	52.5 b	12.58
No. of clusters per node	1.5 a	0.5 b	0.3 b	0.8 b	0.5 b	0.20

[1]) Standard error of the mean.
[2]) Mean separation by Duncan's multiple range test at 5 % level. Means followed by the same letter within rows do not differ significantly.
[3]) Percentage of highest value of optical density on a weight basis.
[4]) Percentage of highest value of optical density on a berry basis.

III. Evidence of recovering capacity after defoliation stress

Yield and yield components

The effects of defoliation during the 2 previous seasons were still visible in 1988, even if the plants were allowed to keep all the leaves (Table 6). Again a 50 % decrease

Table 6

Influence of main leaves or lateral shoots removal on the yield components and quality of the fruit in the 1st season following the defoliation treatment · In 1988, the plants were all treated as the control vines. They had been defoliated in 1986 and 1987 · Treatments were: CT: control topped; L: only lateral leaves left; M: only main leaves left; T1: plants treated 1 week after bloom; T2: plants treated 6 weeks after bloom

Einfluß des Entfernens von Hauptblättern oder Geiztrieben auf Triebzahl je Rebe, Traubenzahl je Trieb, Beeren je Traube, Beerengewicht, Traubengewicht, Traubenertrag, Zuckergehalt, Reifeindex, Beerenfarbe im 1. Jahr nach den Entblätterungen · 1988 wurden die Reben nicht entblättert (= Kontrollen) · Blattentnahmen wurden 1986 und 1987 durchgeführt · Behandlungen: CT: Kontrolle gekappt; L: nur Geiztriebe stehen gelassen; M: nur Hauptblätter stehen gelassen; T1: Entblätterung 1 Woche nach der Blüte; T2: Entblätterung 6 Wochen nach der Blüte

	CT	L	M	SE[1])	T1	T2	SE	Interaction
1988								
Yield components								
No. of shoots per vine	14.1 a[2])	12.2 b	14.0 a	0.5	13.4 a	13.5 a	0.4	NS
No. of clusters per shoot	1.9 a	1.3 b	1.4 b	0.08	1.5 a	1.5 a	0.07	NS
No. of berries per cluster	67.9 a	46.7 b	51.1 b	4.1	55.2 a	55.3 a	3.3	NS
Mean berry weight (g)	1.6 a	1.4 b	1.4 b	0.03	1.5 a	1.4 b	0.03	NS
Mean cluster weight (g)	109 a	69 b	73 b	6.4	86 a	81 a	5.2	NS
Yield (kg m^{-2})	1.2 a	0.5 b	0.6 b	0.08	0.8 a	0.7 a	0.07	NS
Fruit quality								
Must soluble solids (°Oe)	75.3 a	76.7 a	76.8 a	0.6	76.6 a	75.9 a	0.5	NS
Maturity index	54.5 a	58.1 a	57.8 a	1.4	57.0 a	56.6 a	1.1	NS
Fruit coloration (%)	51.3 a	57.7 a	55.1 a	3.7	51.7 a	57.7 a	3.0	NS

[1]) Standard error of the mean.
[2]) Mean separation by Duncan's multiple range test at 5 % level. Means followed by the same letter within row sections do not differ significantly.

Table 7

Influence of main leaves or lateral shoots removal on the yield components and quality of the fruit on the 2nd season following the defoliation treatment · In 1988 and 1989, the plants were all treated as the control vines · They had been defoliated in 1986 and 1987 · Treatments were: CT: control topped; L: only lateral leaves left; M: only main leaves left; T1: plants treated 1 week after bloom; T2: plants treated 6 weeks after bloom

Einfluß des Entfernens von Hauptblättern oder Geiztrieben auf Triebzahl je Rebe, Traubenzahl je Trieb, Beeren je Traube, Beerengewicht, Traubengewicht, Traubenertrag, Zuckergehalt, Reifeindex und Beerenfarbe im 2. Jahr nach den Entblätterungen · 1988 und 1989 wurden die Reben nicht entblättert (= Kontrollen) · Blattentnahmen wurden 1986 und 1987 durchgeführt · Behandlungen: CT: Kontrolle gekappt; L: nur Geiztriebe stehen gelassen; M: nur Hauptblätter stehen gelassen; T1: Entblätterung 1 Woche nach der Blüte; T2: Entblätterung 6 Wochen nach der Blüte

	CT	L	M	SE[1])	T1	T2	SE	Inter-action
1989								
Yield components								
No. of shoots per vine	16.6 a[2])	16.0 a	15.9 a	0.7	16.4 a	16.0 a	0.6	NS
No. of clusters per shoot	2.0 a	1.8 a	1.8 a	0.08	1.9 a	1.9 a	0.07	NS
No. of berries per cluster	73.0 a	71.1 a	65.9 a	3.0	72.2 a	68.4 a	2.4	NS
Mean berry weight (g)	1.5 a	1.6 b	1.6 b	0.04	1.6 a	1.6 a	0.03	NS
Mean cluster weight (g)	110 a	114 a	106 a	4.6	112 a	109 a	3.8	NS
Yield (kg m^{-2})	1.5 a	1.4 a	1.2 a	0.1	1.4 a	1.4 a	0.1	NS
Fruit quality								
Must soluble solids (°Oe)	78.3 a	78.5 a	79.8 a	0.9	78.6 a	78.5 a	0.8	NS
Maturity index	51.4 a	53.0 a	53.2 a	1.5	51.9 a	52.0 a	1.2	NS

[1]) Standard error of the mean.
[2]) Mean separation by Duncan's multiple range test at 5 % level. Means followed by the same letter within row sections do not differ significantly.

of the crop yield was observed on the plants defoliated earlier. This decrease was mainly due to a reduced bud fertility (number of shoots and clusters per plant) and a poor fruit set which caused a lower cluster weight. In 1989, the plants that had been defoliated in 1986 and 1987 showed no yield reduction and even surpassed the control plants with respect to mean berry weight (Table 7). Mean berry weight seems to be the most sensitive measured item to describe the stress status of the plant. It follows that defoliation stress cannot be readily recovered during the following season. The inflorescence primordia are initiated 1 year before they bloom (SHAULIS and PRATT 1965; HUGLIN 1986) and defoliation will affect their development at the very beginning. In consequence, the crop yield is affected not only in the season of defoliation but in the following one as well, even if leaf surface is not limited any more.

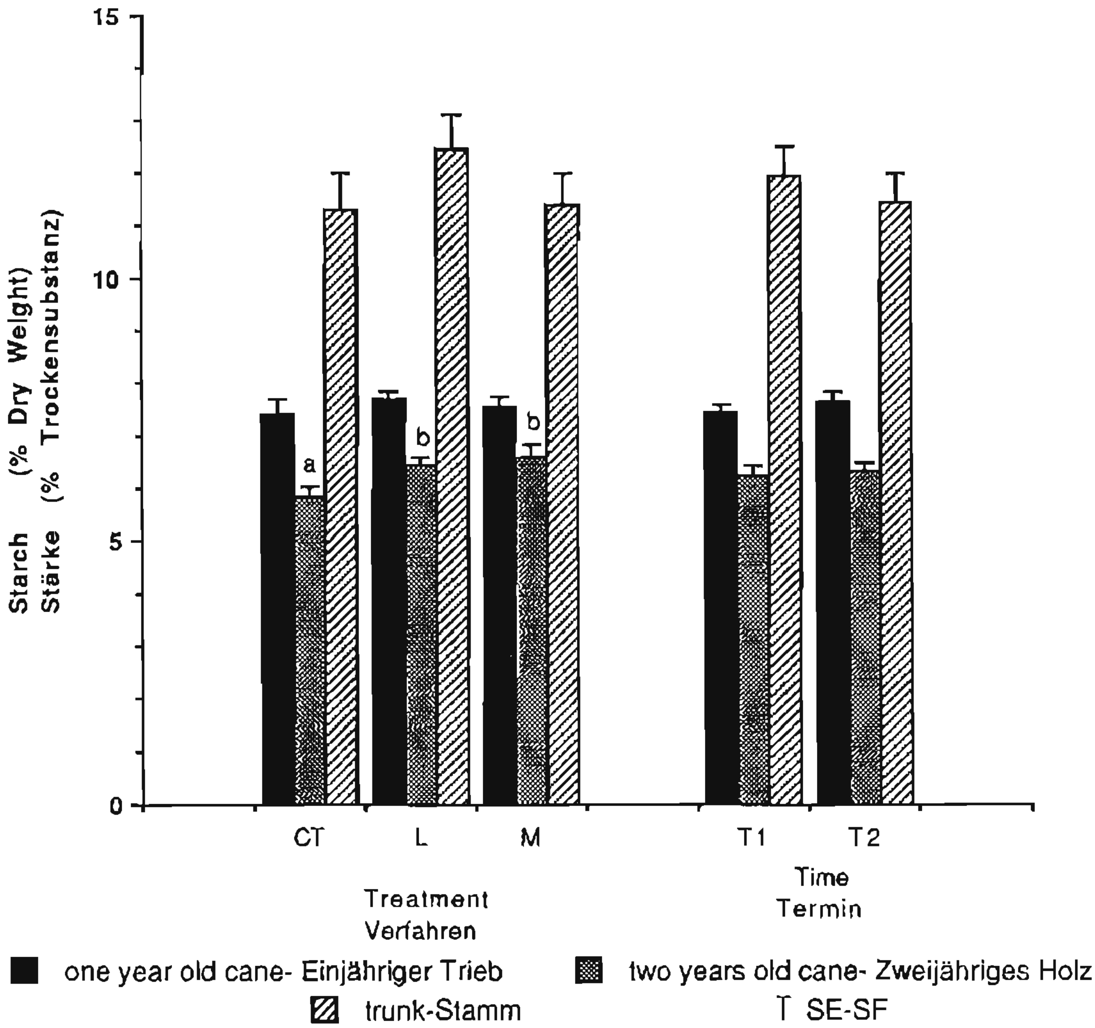

Fig. 4: Starch content of the wood in February 1989. In 1988, the plants were all treated like the control vines. They had been defoliated in 1986 and 1987. Treatments were: CT: control topped; L: only lateral leaves left; M: only main leaves left; T1: plants treated 1 week after bloom; T2: plants treated 6 weeks after bloom. Mean separation by Duncan's multiple range test at 5 % level. Means of the same plant part, headed by the same letter (or none), do not differ significantly.

Stärkegehalt im Holz (% Trockengewicht) im Februar 1989. Im Jahre 1988 wurden die Reben nicht entblättert (= Kontrollen). Sie wurden in 1986 und 1987 entblättert. Behandlungen: CT: Kontrolle gekappt; L: nur Geiztriebe stehen gelassen; M: nur Hauptblätter stehen gelassen; T1: Entblätterung 1 Woche nach der Blüte; T2: Entblätterung 6 Wochen nach der Blüte. Bei gleichen (oder keinen) Buchstaben unterscheiden sich die Durchschnittswerte der gleichen Rebteile bei einer Irrtumswahrscheinlichkeit von 5 % nicht signifikant.

Fruit quality

From 1988, no differences were observed in all plants with respect to must soluble solids, sugar/acid ratio (maturity index) and fruit coloration (Tables 6 and 7). As soon as the leaf area is sufficient during the ripening period, sugar accumulation in the grapes proceeds normally.

Starch reserves in the wood

On February 1989, the starch reserves in the 2 years old canes of the defoliated plants (1986 and 1987) were significantly higher than those of the control plants (Fig. 4). No differences in the starch content of the wood could be observed on the other analyzed plant parts. Comparing these results with those obtained for the same plants in 1988 (Fig. 2), it is evident that an extra effort was undertaken to fill up the wood reserves in order to compensate for the shortage they had suffered during the 2 preceding seasons.

These results show clearly that defoliated plants are able to fill up the reserve pool after 1 season without assimilating surface restrictions. Carbohydrate accumulation in the form of sugar in the fruit and storage as starch in the wood are related. In fact, significant correlations were found between must soluble solids and starch content specially in the 1 year old cane analyzed in the following winter. These correlations were however, rather low: $r = 0.32$, $P < 5\ \%$ in 1987 and $r = 0.46$, $P < 1\ \%$ in 1988. With increasing distance from the fruit to the reserve pool (2 years old cane and trunk) this relationship becomes weaker ($r = 0.32$, $P < 5\ \%$ for the 2 years old cane in 1988 and non-significant in the trunk both in 1987 and 1988). Further experiments on this subject confirmed these assumptions and revealed a very good correlation ($r = 0.81$, $P < 1\ \%$) between must sugar content of the grapes and starch reserves of the wood (publication in prep.). Soluble solids in the fruit juice seem to be a good indicator of the carbohydrate status of the plant. The problem of carbohydrate partitioning in stressed plants needs further investigation. According to our results, the fruit is not necessarily the only first priority sink for assimilates during fruit maturation.

Conclusions

I. Influence of removing main leaves or lateral shoots on yield components, fruit quality and starch reserves in the wood

Final crop yield seems to depend on the existing assimilating surface during bloom and some weeks after. According to YANG *et al.* (1980) retranslocation from the parent vine ceases by the flowering stage. During this critical time, main leaves are the only source organs. The lateral shoots are just starting their growth and act as sink organs. Removal of main leaves during this period means removal of the only available source organs, and a reduction of the crop yield due to flowers and fruitlets abscission is an inevitable consequence. Main leaves are during this critical period actively assimilating and exporting leaves and play the main role for the final fruit quantity. The correlation found between main leaf area and yield per plant in 1987 ($r = 0.87$, $P < 0.1\ \%$) supports this hypothesis.

The accumulation of sugar in the berries probably depends on the available active leaf surface during the period between veraison and fruit harvest. During this period, the lateral shoots are already source organs and provide the bunches with assimilates more efficiently than the main leaves. They represent the young and photosynthetically active part of the canopy, in contrast to the main leaves which have already started the senescence process. These conclusions are based on the fact that the highest content of soluble solids was found in plants bearing only lateral leaves. Hence, the lateral leaves play the main role in fruit ripening. As result of insufficient assimilating surface during fruit maturation, the carbohydrate reserves are not fully replaced in the parent vine. The fruit clusters, being closer to the source organs, benefit of the phloem load before the other reserve organs in the plant.

II. Influence of time of defoliation on berry drop, yield, fruit quality and bud fertility

Flower and fruitlet abscission occurs when the leaves are eliminated in early stages of berry development, causing a decrease of the fruit yield. However, the critical period is limited to 2—3 weeks after full bloom. On the other hand, a strong defoliation stress applied later in the season can cause a decrease of fruit quality.

Defoliation during bloom and 2 weeks after reduces bud fertility in the following season, suggesting that this period is particularly delicate both for the current year's and following season's fruit production.

III. Evidence of recovering capacity after defoliation stress

Prolonged defoliation followed by 1 season with a normal cultural practice is not enough for the complete recovery of the plants because flower bud initiation occurs when the assimilating potential is still being limited. It is therefore affected in its beginning, thus influencing the following season's crop yield. Carbohydrate accumulation in the fruit and in the wood, on the other hand, seems to depend only on the available leaf surface during the ripening period. If the canopy is not restricted, sugar accumulation both in the fruit and in the wood proceeds normally and allows already in the season following the defoliation stress the production of grapes with satisfactory sugar content and adequate starch reserves. Complete recovery occurs therefore in the 2nd season after the stress is released.

For the survival of a perennial plant like the grapevine, to fill the wood reserves seems to be as important a goal as the maturation of the fruit (seeds).

Practical considerations

To obtain a good crop in quantitative and qualitative terms, the plants have to be properly supplied with leaves during two critical periods: fruit set and ripening period. If the main leaves are removed in the period between bloom and 3 weeks after, a reduction in the quantity of the yield of the current and following year is to be expected. In fact, berry drop is responsible for the yield reduction in the season of the stress, and a reduced bud fertility will affect the crop yield of the next year. On the other hand, during the ripening period the main leaves will already have started their senescence process and the main role in the sugar supply to the fruit and reserve organs is played by the lateral leaves. If the lateral shoots are not allowed to grow, a reduction in the sugar content of the fruit and lower starch reserves in the wood is the expected result.

In case that *Botrytis cinerea* presents a threat to the crop, the leaves in the clusters' area should be removed to promote a better aeration. This should, however, not be done until the first critical period is finished. The lateral shoots should be left intact because they can very well compensate for the absence of the main leaves during the ripening period. Lateral shoots should never be removed above the cluster area because they supply sugars for fruit maturation and are thus directly involved in the final fruit quality.

In summary, main leaves should be present during fruit set to assure fruit quantity and bud fertility in the following season and lateral leaves should be present during fruit maturation to assure fruit quality and starch reserves in the wood.

Summary

The effect of removing either main leaves or lateral shoots on final leaf area, yield components, fruit quality and starch reserves in the wood was studied on mature field grown grapevines. The roles of main and lateral leaves were compared, and the sensitive period for induction of berry drop was also examined. The aim of this study was to determine the mechanisms and limitations of compensation for stress induced by defoliation and to find out if the plants can recover after a prolonged defoliation stress.

Plants deprived of main leaves (L) produced more lateral shoots with a greater number of leaves. At vintage time, L plants had approximately the same leaf surface as the control plants. This was not the case during the 2nd defoliation season: L plants still produced more leaves but of smaller size which caused a reduced total final leaf area. Plants bearing only main leaves (M) compensated for the absence of laterals by delaying leaf senescence and abscission. During the 2nd defoliation season this plant group also produced leaves of smaller size.

Fruit yield was little affected by defoliation in the 1st year but was 50 % lower than the control in the 2nd consecutive defoliation season for L plants. M plants showed no reduction on fruit production in both seasons. Must soluble solids and fruit coloration were slightly higher for L plants after the 1st, but were not affected after the 2nd defoliation season.

Final crop yield proved to be dependent on the existing leaf surface during bloom and 2—3 weeks after. The accumulation of sugar in the fruit seems to depend on the available active leaf surface during the period between veraison and fruit harvest.

The level of starch reserves in the wood was greatly reduced after 2 seasons of defoliation. Significant but low correlations were found between sugar content of the must and starch content of the wood.

Defoliation during early stages of berry development causes not only berry drop but also reduces bud fertility in the following season. This critical period is yet limited to 2—3 weeks after bloom.

Prolonged defoliation stress cannot be readily recovered after 1 season with normal cultural practices. This is due to the fact that flower initiation occurs when the defoliation stress is still being applied to the plant. Sugar accumulation in the fruit and replacement of starch reserves proceed normally already in the season following the stress. Complete recovery occurs, therefore, in the 2nd season after the stress is removed.

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