Vitis **49** (4), 153–160 (2010)

Quantification of the influence of the downy mildew (*Plasmopara viticola*) epidemics on the compensatory capacities of *Vitis vinifera* 'Merlot' to limit the qualitative yield damage

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Summary

A preview study on the analysis of the impact of downy mildew (*Plasmopara viticola*) epidemics on the plant growth and yield quality has shown no correlation between disease severity progress on the canopy and sugar accumulation in the berries from veraison until harvest, indicating the capacity of the vine to compensate a stress situation induced by the downy mildew damage on leaf canopy. In this study the compensation capacity of the plant was analysed during three years under field conditions comparing three different downy mildew control strategies: A = "Untreated canopy" (to prevent quantity losses, the clusters were treated once with a contact fungicide at the discovery of the first downy mildew sporulation); B = "Reduced fungicide schedule" (based on a first treatment at the appearance of the first symptoms, to avoid yield quantity losses followed by one or two additional fungicide applications during the early epidemic phase with the aim of delaying the epidemic). C = "Standard schedule" (schedule normally applied in the vineyard). The experimental plot was moved each year to avoid stress influence due to a repetition of the trials on the same place. The grapevine compensated for the carbohydrate requirements of the cluster by mobilizing the starch reserves stored in the woody parts. Roots were the most important site of carbohydrate accumulation used from the grapevine and the mobilisation was higher in treatment A followed by treatment B. This compensation did not completely exhaust the reserves of each woody part and lets suppose a hierarchical pattern of the mobilisation; first a mobilisation of the reserves stored in the roots, and secondly those from the trunk, cane and shoot. The downy mildew could be considered as a stress factor for the grapevine.

Key words: Compensation mechanism, growth, reserves content, starch, downy mildew.

Introduction

Grapevine is subjected to a multitude of stress factors in the field ranging from abiotic factors to pests or diseases. However grape has a great potential for stress acclimation (Koblet *et al*. 1996). In the current grapevine production system, where a maximal quality-quantity yield production over a long period is required, the assimilate allocation system of the plant is manipulated during the season to achieve this objective (Reynolds and Wardle 1989). Canopy management practices are important tools in promoting suitable conditions for optimal quantitative and qualitative yield production. The effect of time and severity of defoliation and the crop load can negatively influence the plant, which applies strategies to compensate for these stress situations (Kliewer 1970, Kliewer and Fuller 1973, Hunter and Visser 1988, Candolfi-Vasconcelos 1990, Koblet *et al*. 1993, Candolfi-Vasconcelos *et al*. 1994, Koblet *et al*. 1996, Murisier 1996, Koblet *et al*. 1997). Stress situations induced during the ripening period modify the sink priority of the vine and, consequently, the priority of the assimilate allocation (Koblet *et al*. 1993, Candolfi-Vasconcelos *et al*. 1994, Koblet *et al*. 1996; Koblet *et al*. 1997). Pests and diseases can be considered biotic stress factors, which are capable of inducing yield losses (Kliewer and Lider 1976, McNelly *et al*. 1985, Boller *et al*. 1989, Kast 1989, Reynolds and Wardle 1989, Boller and Candolfi 1990, Candolfi 1991, Wolpert and Vilas 1992, Candolfi *et al*. 1993, Munkvold *et al*. 1994, Credi and Babini 1997, Guidoni *et al*. 1997, Martinson *et al*. 1997, Piva *et al*. 1997, Cabaleiro *et al.* 1999, Chinnici *et al.* 1999, Linder and Jermini 2001, Calonnec *et al*. 2004, Gadoury *et al*. 2004), but only for the spider mite *Tetranychus urticae* and the green leafhopper *Empoasca vitis* it was demonstrated that the plant was able to compensate for the leaf damages by increasing the leaf area of the lateral shoots (Candolfi 1991, Candolfi *et al*. 1993). In two previews studies we have analysed the impact of down mildew (*Plasmopara viticola*) epidemics on leaf gas exchange (Jermini *et al*. 2010 a) and on the yield quality of grapevine, showing how the plant tried to compensate the stress induced by the leaf damage (Jermini *et al*. 2010 b). This third work aims to investigate the compensation system that the plants use to compensate for the stress situation induced by downy mildew and to quantify the plant response.

Material and Methods

Plant material and experimental designs: The experiments were carried out during the period 1996-1998 in a vineyard of the Research station Agroscope Changins-Wädenswil ACW Centre of Cadenazzo (South part of Switzerland) planted with 'Merlot'

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grafted on 3309 rootstock. The vines were double cane pruned and vertical trained (double Guyot). Three different *P. viticola* control strategies were compared: A = "Untreated canopy" (to prevent quantity losses, the clusters were treated once with a contact fungicide at the discovery of the first downy mildew sporulations); B = "Reduced fungicide schedule" (based on a first treatment at the appearance of the first symptoms, to avoid yield quantity losses followed by one or two additional fungicide applications during the early epidemic phase with the aim to delay epidemic). C = "Standard schedule" (normal schedule applied in the vineyard). The experimental plot was moved each year in different but homogenous blocks of the vineyard to avoid stress influence due to a repetition of the trials on the same place.

Experiment 1996: This trial was placed in a plot planted in 1972 with a vine spacing of 1.80 x 1.40 m between and within the rows. Each treatment consisted of a plot of 48 plants divided in 6 sub-plots of 8 contiguous plants. The number of shoots per plant, including the spurs, was regulated to 11 at the phenological stadium 53 BBCH (Baillod and Baggiolini 1993) and the number of clusters was limited on August 8 to result in a homogeneous theoretical production for each subplot of 1.2 kg·m$^{2-1}$, corresponding to the low potential yield estimated in the experiment. A first topping was done on June 18, a second one on July 16 and a last one on August 13.

Experiment 1997: This trial was placed in a plot planted in 1991 with a vine spacing of 2.00 x 1.20 m between and within the rows. The experimental design and the number of shoots per plant were the same as for the 1996 experiment. The yield regularisation was made on August 22 so as to obtain a theoretical production per subplot of 1.1 kg·m^{-2}, corresponding to the low potential yield estimated in the experiment. The first topping was done on June 23 and a second one on August 4.

Experiment 1998: This trial was placed in a plot planted in 1974 with a vine spacing of 1.80 x 1.40 m between and within the rows. Each treatment consisted of a plot of 32 plants divided in 8 sub-plots of 6 contiguous plants. For this experiment the number of shoots per plant, including the spurs, was regulated to 10 at the same periods as for the other years. The yield regularisation was made on July 30 with the aim of obtaining a theoretical production per subplot of 1.2 kg·m$^{2-1}$, corresponding to the low potential yield estimated in the experiment. The first topping was done on June 30 and a second one on July 30.

Vegetative growth and disease assessment: One main shoot per vine representing the middle vegetative growth of the plant was selected from each treatment replicate at the phenological stadium 53-55 BBCH (Baillod and Baggiolini 1993). The number of main leaves, lateral shoots and leaves on lateral shoots was assessed weekly. Disease severity was estimated with the extended Horsfall scale (Horsfall and Cowling 1978), in which the first class, 0-3 % damaged area, was divided into two new classes from 0-1 % and 1-3 % of damaged area to avoid an overestimation of the low diseased levels (data not shown).

Wood samples harvesting and reserve analysis: Samples were taken for each subplot and treatment during pruning in the month of February of the year following the experiment. One-year-old wood samples were chosen between the 3rd and 6th internode taking one shoot per plant and, where possible, generally the shoot considered for the disease assessment was selected. At the same time, the two-year-wood (cane) samples included 2 parts of each plant taken between the 3rd and 4th node and the 6th and 7th node. The trunk sample consisted of 3-5 g of sawdust produced by perforation at different heights of the trunk with an electric drill fitted with a 3 mm bit. The roots were collected after having dug a profile along the plot of 80-100 cm depth. Roots of fine and middle diameter (0.5-5 mm) were collected from the plants of the plot and washed. All samples were cut and oven-dried at 65 °C and then crushed in a hammer mill. The obtained powder was dried during at least 2 weeks over di-phosphor pentoxide (P_2O_5) before extraction. Glucose, fructose and sucrose were extracted by a hydroalcoholic solution (70 vol.% ethanol) at 80 °C and then analysed by the enzymatic method (Boehringer Mannheim). The solid residue of the extraction was dried over di-phosphor pentoxide (P_2O_5) and starch was extracted with dimethyl sulfoxide in a boiling water bath. Starch was analysed in this second extract by the enzymatic method (Boehringer Mannheim). All results are given in mg sugar per g of dry matter.

Statistical analysis: Statistical analysis of the data was performed utilising the Sigmastat (SSPS) statistical package. Results were subjected to Anova and the Tuckey test was used to compare means.

Results

Compensation through increase of leaf area: The first downy mildew sporulation in the field was found on June 25, June 11 and 24 in 1996, 1997 and 1998 respectively, and the epidemics remained at low level until the beginning of the veraison (first week of august), where we had a severity from 1.3 %, 4.5 % 9.1 % and for 1996, 1997 and 1998 respectively, in the "Untreated canopy" treatment (Jermini *et al*., 2010 b). The "Reduced fungicide schedule" delayed, with the exception of 1996, the epidemic progress and the severity was, at the same periods, from 1.5 %, 0.2 % and 1.4 % for 1996, 1997 and 1998 respectively, in the "Reduced fungicide schedule" treatment (Jermini *et al*. 2010 b). The total number of leaves/shoot and the total number of leaves/lateral shoot did not differ significantly between "Untreated canopy" and "Standard schedule" plots from the first sporulation apparition until ripening (Figure). Low disease level did not induce lateral shoot growth. In August 1996 and 1997 the epidemic progress (Jermini *et al*. 2010 b) reduced the total number of leaves/shoot as a consequence of the high disease severity on the leaves (Figure). The good efficacy obtained in the "Reduced fungicide schedule" plot in 1998 resulted in a total number of leaves/shoot similar to that in the "Standard schedule" plot. In this year leaf abscission

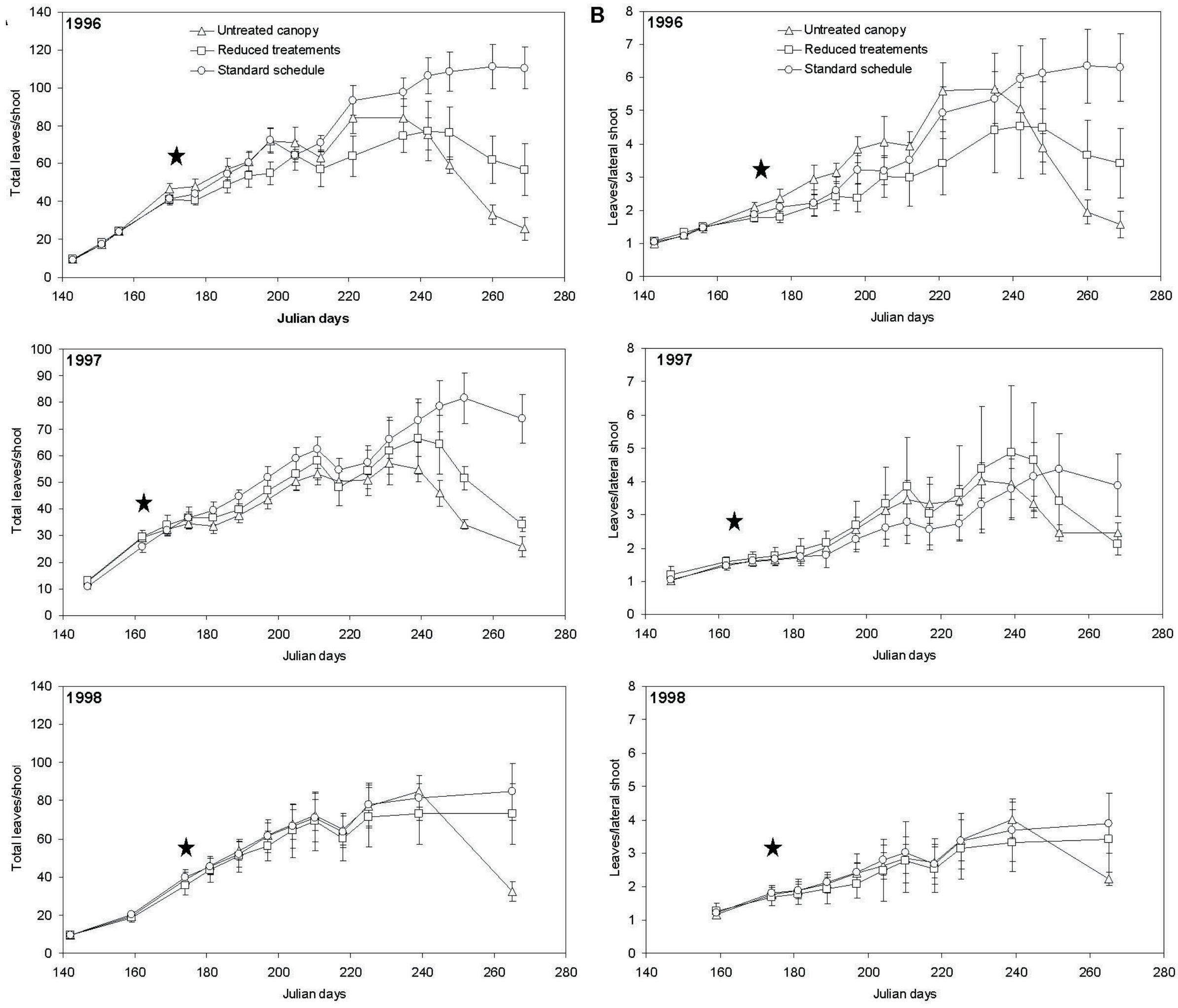

Figure: Effect of the downy mildew epidemics 1996, 1997 and 1998 on **A**) the total number of leaves per shoot and **B**) the total number of leaves per lateral shoot of plants of 'Merlot'. Each point represents the average of 6 for 1996 and 1997 and 8 replications for 1998 ± standard deviation. The star indicates the finding of the first downy mildew sporulation in the field.

was not observed until the last period of ripening and consequently no differences between treatments were found (Figure). Nevertheless, the disease incidence on August 13 was 76.3 % in the "Untreated canopy" plot and 50.1 % in the "Reduced fungicide schedule".

Compensation through mobilisation of the starch reserves: To compensate for the impact of the downy mildew epidemics the grapevine of the "Untreated canopy" plots reduced the total reserve content of the roots between 37 % and 58 % (Tab. 1). For the three experimental years a reduced spray schedule has permitted limiting the amount of the mobilised reserves, while leaving the total reserves stable, although significantly lower than the "Standard schedule" plots. The mobilisation effect was particularly evident for starch, which is the main assimilate storage form of the plant (Hunter *et al.* 1995). In comparison with the "Standard schedule" plot, we observed a significant reduction of the starch contents in the "Untreated canopy" plots varying between 53.2 % for 1997 and 78.5 % for 1998. The application of a reduced number of fungicides has resulted in an intermediary situation but is insufficient in avoiding an important reserve mobilisation. The same situation has been found for the total sugar content of the roots. Between the different sugars, which constitute the most important constituents of the reserves, glucose and fructose content was significantly higher in the plants submitted to the downy mildew epidemics and saccharose was significantly lower. Similarly as for the starch content, the effect of a partial fungicide protection induced an intermediary situation, with no significant differences in the glucose content in some cases. Despite saccharose constituting the most important sugar of the root's reserves, the impact of the epidemics of the "Reduced treatments schedule" plot was less important than on glucose and fructose and significant differences have been found only in 1997. The total sugar content in the roots was generally significantly higher in the "Untreated canopy" and "Reduced treatments schedule" plots with the exception of 1997 where no differences were observed. In the trunk (Tab. 2) a significant reduction of the total amount of reserve components was observed only for 1998 with a difference of 5.3 % between the "Standard schedule" and the "Untreated canopy" plots. No significant differences have been observed between the "Stand-

Table 1

Effect of the downy mildew epidemics on the starch and sugar (glucose, fructose and saccharose) content expressed as mg for g dry matter (DM) of the roots of rootstock plant 3309 grafted with 'Merlot'. Data represent the average of 6 replications for 1996 and 1997 and 8 for 1998. Means followed by same letter are not significantly different at $p < 0.05$ (Tuckey test)

Attribute	Year	Untreated canopy	Reduced fungicide schedule	Standard schedule
Glucose mg·g^{-1} DM	1996	6.00 a	5.25 a	2.60 b
	1997	7.36 a	5.37 b	4.00 c
	1998	11.60 a	3.95 b	2.95 b
Fructose mg·g^{-1} DM	1996	7.85 a	6.85 a	3.35 b
	1997	10.89 a	8.22b	6.09 c
	1998	14.45 a	6.10 b	4.07 c
Saccharose mg·g^{-1} DM	1996	15.40 a	17.07 a	20.50 b
	1997	21.50 a	25.62 ab	25.25 b
	1998	18.16 a	20.45 b	21.85 b
Total sugars mg·g^{-1} DM	1996	29.25 a	29.17 a	26.45 a
	1997	39.75 a	39.21 a	35.34 b
	1998	44.21 a	30.50 b	28.87 b
Starch mg·g^{-1} DM	1996	28.53 a	46.25 b	112.20 c
	1997	52.44 a	91.49 b	112.06 c
	1998	27.67 a	94.54 b	129.79 c
Total reserves mg·g^{-1} DM	1996	57.78 a	75.42 b	138.65 c
	1997	92.19 a	130.70 b	147.40 c
	1998	71.88 a	125.04 b	158.66 c

Table 2

Effect of the downy mildew epidemics on the starch and sugar (glucose, fructose and saccharose) contents expressed as mg for g dry matter (DM) of the trunk of the vine of 'Merlot'. Data represent the average of 6 replications for 1996 and 1997 and 8 for 1998. Means followed by same letter are not significantly different at $p < 0.05$ (Tuckey test)

Attribute	Year	Untreated canopy	Reduced fungicide schedule	Standard schedule
Glucose mg·g^{-1} DM	1996	27.63 a	25.39 b	21.05 c
	1997	37.19 a	32.00 b	26.43 c
	1998	32.32 a	25.32 b	23.49 b
Fructose mg·g^{-1} DM	1996	23.70 a	22.64 a	18.56 b
	1997	34.21 a	29.09 b	24.69 c
	1998	30.06 a	24.31 b	23.54 b
Saccharose mg·g^{-1} DM	1996	27.83 a	30.32 a	26.51 a
	1997	23.94 a	28.32 a	33.52 b
	1998	38.34 a	45.01 b	44.21 b
Total sugars mg·g^{-1} DM	1996	79.16 a	78.35 a	66.12 b
	1997	95.34 a	89.41 ab	84.64 b
	1998	100.72 a	94,64 b	91.24 b
Starch mg·g^{-1} DM	1996	12.69 a	15.38 a	19.98 b
	1997	34.43 a	41.51 ab	43.71 b
	1998	13.50 a	29.64 b	29.39 b
Total reserves mg·g^{-1} DM	1996	91.85 a	93.73 a	86.10 a
	1997	129.77 a	130.92 a	128.35 a
	1998	114.22 a	124.28 b	120.63 b

ard schedule" and the "Reduced fungicide schedule" plots. The trunk did not constitute an important storage point for starch, but, as in the roots, a significant decrease of reserve elements in the plants of the "Untreated canopy" plots was observed. The reduction was 36.6 % for 1996, 21.2 % and 54 % for 1997 and 1998 respectively. The starch content in the plants of "Reduced treatments schedule" plots was significantly lower than the "Standard schedule" plot only in 1996. The total sugar content was more important than starch and in the "Standard schedule" plots constituted

77 % of the total reserves for 1996, 66 % and 76 % for 1997 and 1998 respectively, but showed the same tendencies observed for starch with a significantly higher content in the plants of the "Untreated canopy" plots as response to a stress situation. The saccharose content was variable between the treatments and years. Fructose and glucose content was generally higher in the "Untreated canopy" in comparison with the "Standard schedule" plot. The application of a reduced fungicide schedule induced, as in the roots, an intermediary situation.

The total reserves content of the cane (Tab. 3) did not diverge significantly between the three treatments for each experimental year. This was due, as observed for roots and trunk, to a transformation of the starch, which decreased by 47 % in 1996, 21 % and 63 % for 1997 and 1998 respectively, indicating a marked stressed situation for this last experimental year. The starch degradation corresponded generally with an increase of the sugar content and particularly of glucose and fructose, which was significantly higher in the "Untreated canopy" plot in comparison with the "Standard schedule". The reduced fungicide schedule had an intermediary behaviour, but more closely related to the "Untreated canopy" plot. Only saccharose content, with the exception of 1998, did not show differences between the treatments.

In the shoot (Tab. 4), the total reserves contents showed, with the exception of 1998, the same tendencies as observed for the cane. The starch mobilisation is generally higher, as observed for the other woody parts, in 1998 within the "Untreated canopy" plot a decrease of 63% of the content was noted. With the exception of 1996, the sugar (glucose, fructose and saccharose) content didn't show significant differences between the three treatments. In 1997 and 1998 glucose and fructose content increased in the "Untreated canopy" plot in comparison with the "Standard schedule" plot, and the "Reduced fungicide schedule" showed an intermediary behaviour.

Discussion

Koblet *et al*. (1996) report that leaf physiology modifications, enhancement of the number of new leaves and lateral shoots and reserve mobilization are the most important compensation mechanisms involved in a defoliation stress situation. Considering the possible leaf physiology modifications as a compensation mechanism, different authors (Hunter and Visser 1988, Candolfi-Vasconcelos 1990, Hunter *et al*. 1995, Koblet *et al.* 1996) have shown that grapevine is able to face a stress situation with a photosynthesis or chlorophyll increment or delaying the leaf senescence and abscission. Our preview results (Jermini *et al*. 2010 a) reject this possibility. Moreover, the epidemics increase rapidly starting from beginning of the veraison (Jermini *et al*. 2010 b) and consequently the grapevine does not induce physiological changes during ripening to compensate for leaf damage as also shown by Koblet *et al.* (1993). The enhancement of the number of new leaves and lateral shoots is a compensation mechanism offsetting the leaf area loss as shown in some artificial defoliation stress experiments where the main leaves have been removed (Candolfi-Vasconcelos 1990, Kliewer 1970, Kliewer and Fuller 1973, Reynolds and Wardle 1989). The same compensation mechanism has been observed on 'Merlot' grapevine submitted to a defoliation stress caused by the green leafhopper (*Empoasca vitis*) (Candolfi *et al.* 1993).

Table 3

Effect of the downy mildew epidemics on the starch and sugar (glucose, fructose and saccharose) contents expressed as mg for g dry matter (DM) of the cane (two year old wood) of the vine of 'Merlot'. Data represent the average of 6 replications for 1996 and 1997 and 8 for 1998. Means followed by same letter are not significantly different at $p < 0.05$ (Tuckey test)

Attribute	Year	Untreated canopy	Reduced fungicide schedule	Standard schedule
Glucose mg·g^{-1} DM	1996	24.51 a	22.76 a	19.33 b
	1997	28.26 a	26.05 b	22.08 c
	1998	30.14 a	25.08 ab	23.38 b
Fructose mg·g^{-1} DM	1996	24.70 a	23.89 a	20.15 b
	1997	28.16 a	26.81 a	24.73 b
	1998	29.30 a	25.05 ab	23.75 b
Saccharose mg·g^{-1} DM	1996	22.54 a	23.43 a	20.62 a
	1997	35.63 a	35.35 a	38.32 a
	1998	46.28 a	48.79 ab	50.00 b
Total sugars mg·g^{-1} DM	1996	71.75 a	70.06 a	60.10 b
	1997	92.05 a	88.21 ab	85.13 b
	1998	105.72 a	98.92 b	97.13 b
Starch mg·g^{-1} DM	1996	9.31 a	13.00 b	17.68 c
	1997	20.03 a	25.19 b	25.35 b
	1998	6.56 a	15.25 b	17.98 c
Total reserves mg·g^{-1} DM	1996	81.06 a	83.06 a	77.78 a
	1997	112.08 a	113.40 a	110.48 a
	1998	112.28 a	114.17 a	115.11 a

Table 4

Effect of the downy mildew epidemics on the starch and sugar (glucose, fructose and saccharose) contents expressed as mg for g dry matter (DM) of the shoot (one year old wood) of the vine 'Merlot'. Data represent the average of 6 replications for 1996 and 1997 and 8 for 1998. Means followed by same letter are not significantly different at $p < 0.05$ (Tuckey test)

Attribute	Year	Untreated canopy	Reduced fungicide schedule	Standard schedule
Glucose $mg \cdot g^{-1}$ DM	1996	24.02 a	23.52 a	21.70 a
	1997	30.23 a	26.80 b	23.71 c
	1998	22.76 a	20.25 b	18.69 b
Fructose $mg \cdot g^{-1}$ DM	1996	26.06 a	26.40 a	23.45 a
	1997	31.12 a	26.88 b	25.05 c
	1998	28.26 a	24.38 b	23.09 b
Saccharose $mg \cdot g^{-1}$ DM	1996	15.13 a	13.30 a	13.41 a
	1997	32.88 a	33.79 a	35.03 a
	1998	47.25 a	48.72 a	49.77 a
Total sugars $mg \cdot g^{-1}$ DM	1996	65.21 a	63.22 a	58.56 a
	1997	94.23 a	87.47 a	83.79 b
	1998	98.27 a	93.35 b	91.55 b
Starch $mg \cdot g^{-1}$ DM	1996	10.57 a	12.68 b	17.21 c
	1997	13.41 a	17.98 a	19.94 b
	1998	7.82 a	17.20 b	21.21 c
Total reserves $mg \cdot g^{-1}$ DM	1996	75.78 a	75.90 a	75.77 a
	1997	107.64 a	105.45 a	103.73 a
	1998	106.09 a	110.55 ab	112.76 b

Kliewer and Fuller (1973) showed that defoliation at veraison or later had little or no effect on lateral elongation. The high epidemic level of downy mildew in 1996 and 1997 (Jermini *et al.* 2010 b) has induced leaf abscission that could be more important than the lateral shoot growth. Moreover, the new formed leaves are more susceptible to the pathogen and they are rapidly colonised with an inhibition of their development, which could negatively influence the shoot elongation. Nevertheless, in 1998 the disease epidemic did not cause leaf abscission in the reduced fungicide plot and the plant did not react by increasing the leaf area of lateral shoots. Our results clearly indicate that a stress induced by a regular increase of defoliation during the ripening period causes an important mobilisation of the reserve contents in the woody parts and particularly in the roots. This mobilisation is probably correlated with the carbohydrate requirement of the berries during this period. This is in accordance with Coombe (1992), which indicates that veraison varies between vines within a vineyard and more particularly between berries within each cluster, because each berry appears to develop independently, an independence that may derive from as early as anthesis, maybe earlier. On this basis, Candolfi-Vasconcelos *et al.* (1994) also hypothesize that defoliation when 50 % of the berries are entering the sugar-accumulation phase could block or delay the onset of ripening of the other 50 %. In this way, the sink strength of the whole cluster would be reduced. Our results support this hypothesis. Therefore, a vineyard is composed of an age structured berry population with its own ripening dynamic depending on the berry distribution in age classes and stress is the element capable of transforming a cluster into a more powerful sink. The defoliation level therefore has a central role. Consequently the "Reduced fungicide schedule" provides an intermediary response for the carbohydrate requirement of the berries and this is in agreement with experiments considering different artificial defoliations or crop load levels (Candolfi-Vasconcelos 1990, Koblet *et al.* 1993, Candolfi-Vasconcelos *et al.* 1994, Hunter *et al.* 1995, Murisier 1996, Koblet *et al.* 1997). Candolfi-Vasconcelos *et al.* (1994) have shown that grapevine responds to a defoliation stress by altering the natural translocation pattern and directing carbon stored in the lower parts of the plant to the fruit in order to supply the assimilate requirements of the berries, which represent a very powerful sink during ripening. The reserve mobilisation is also the compensatory mechanism applied by the vine in limiting the stress caused by downy mildew epidemic on leaf canopy and it explains very well why sugar accumulation in the fruit is not proportionally reduced with the increase of the assimilating leaf area loss during the ripening phase (Jermini *et al.* 2010 b). Roots are the most important site of carbohydrate accumulation irrespective of root size (Hunter *et al.* 1995, Yang *et al.* 1980) and the comparison between the total reserve contents of the different woody parts clearly indicates a retranslocation of the stored assimilates. Our results stressed these observations, but they also let us suppose that the grapevine could make some mobilisation priorities: first roots followed by the trunk, cane and one year old wood without completely exhausting the reserves of each woody part. This hypothesis is evident in 1998. Mullins *et al.* (1992) demonstrated that the reserve content of root and trunk is 2 times lower in the 10 than in 25 year old plants. The same observations have been made by Williams (1986) comparing 5 and 20 year old vines. Even reserve contents in the woody parts have a seasonal fluctuation (Mullins *et al*. 1992, Winkler and Williams 1945) and also depend on cultivars, yield, climatic conditions and plant growth (Murisier 1996). Despite the fact that the comparison is not made during the same growing years, our results do not confirm these observations. The 6 year old vines of 1997 present in the "Standard schedule" plot reveal reserve contents of the roots similar to that measured in 1996 and 1998 on 24 old year plants without differences in plant growth and production (Jermini *et al*. 2010 b). Consequently, the mobilisation strategy applied by the vine and the amount of stored compounds retranslocated from the woody parts to fruits depends mainly on defoliation thresholds that induce changes in the source/sink relationship. These defoliation thresholds vary in time as a result of the interactions between disease epidemic and the ripening dynamic of the berry population. Although this work provides a range of data sets on the plant compensation response to downy mildew epidemics, its implementation in a simulation model (Dietrich *et al*. 1997) clashes with the lack of quantitative data on the berry population structure that prevents a quantification of the ripening process and consequently the determination of defoliation thresholds in function of the fruit ripening progress. Nevertheless, these results support the control strategy based on delaying the disease epidemic and limiting a stress situation during the first weeks after veraison, where the fruit represents an important sink in function of damage thresholds.

This type of study needs repeating with other varieties and growing conditions to test the generality of the conclusions, because the influence of the production system is never sufficiently considered and could be greater than expected (Koblet *et a*l. 1993, Murisier 1996).

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Received March 10, 2010