# Response of 'Merlot' (*Vitis vinifera)* grapevine to defoliation caused by downy mildew (*Plasmopara viticola*) during the following growing season

M. Jermini[1)], P. Blaise[2)] and C. Gessler[2)]

[1)] Research station Agroscope Changins – Wädenswil ACW, Centre of Cadenazzo, Contone, Switzerland
[2)] Plant Pathology, Institute of Integrative Biology, Dep. of Agronomy, Swiss Federal Institute of Technology, Zürich, Switzerland

## Summary

The downy mildew (*Plasmopara viticola*) epidemics on leaf canopy during the ripening phase causes a stress situation for the grapevine. The plant compensates the carbohydrate request of the berries mobilising the carbohydrate reserves stored in the woody parts. In this fourth study the impact of the reserves reduction on the growth and fertility and the recovering capacity of the plant were analysed during two consecutive periods of two years (first year = stress; second year = recovering). Two treatments were compared: "Untreated canopy" (to prevent quantity losses, the clusters were treated once with a contact fungicide at the discovery of the first downy mildew sporulation) and "Standard schedule" (schedule normally applied in the vineyard). The impact of decreased reserve contents in the following growth season has negatively influenced only the shoot elongation and the potential crop yield quantity of the "Untreated canopy" treatment. Nevertheless, a single recovery year was enough to rebuild the reserve pool particularly in the roots, confirming the acclimation potential of the grapevine.

K e y   w o r d s :  reserves, growth, yield, epidemic.

## Introduction

Grapevine has a great potential for stress acclimation (Koblet *et al*. 1996), but it needs, as for all the perennial woody plants, to maintain available annual resources in order to mature both reproductive and vegetative tissues. Therefore, each growing season has to be considered in relation to the one prior and the stress level to which the plant is submitted and its impact on the compensatory capacities will influence the vine during the following growing season. A few studies (Candolfi-Vasconcelos 1990, Koblet *et al*. 1993, Howell *et al*. 1994, Murisier and Aerny 1994, Murisier 1996) have been carried out in this field considering only the stress impacts caused by cultural practices. Amongst the compensation mechanisms, the mobilization of the carbohydrate reserves, particularly those stored in the roots is generally employed by the plant to compensate for the strong sink requirements of the berries during the ripening period (Candolfi-Vasconcelos *et al*. 1994, Koblet *et al*. 1997). The roots are the most important sites of carbon accumulation, which is retranslocated

for the early shoot growth in the spring of the following season (Yang and Hori 1979, Yang *et al*. 1980, Koblet *et al*. 1996). Consequently, the reduced availability of the carbohydrate from the reserves could negatively influence the plant in the following growing season as observed by Murisier and Aerny (1994).

Our studies have shown that downy mildew (*Plasmopara viticola*) leaf epidemics reduce the assimilating leaf area during the ripening phase (Jermini *et al*. 2010 a, 2010 b) and, consequently, the plant compensates for the carbohydrate requirement of berries principally by mobilising the reserves stored in the roots (Jermini *et al*. 2010 c). This fourth work aims to investigate and quantify the possible negative influences of the reserve mobilisation on the recovery capacity of grapevine submitted to a downy mildew canopy epidemic during the previous growing season.

## Material and Methods

P l a n t   m a t e r i a l   a n d   e x p e r i m e n t a l
d e s i g n s :  Field-grown grapevine, 'Merlot' grafted on 3309 rootstock, double cane pruned and vertical trained (double Guyot) were used for the investigations. Two trials were made during the years 1995-1996 and 1997-1998 in two different plots of the experimental vineyard of Cugnasco of the Research station Agroscope Changins-Wädenswil ACW Centre of Cadenazzo. For each trial, in the first year plants were subjected to *P. viticola* stress at various intensity, in the second year (recovery phase) all plots were treated in accordance with the normally spray schedule applied in the vineyard so to avoid *P. viticola* stress. The 1995-1996 experiment was placed in a plot of 298 vines planted in 1972, with a vine spacing of 1.80 x 1.40 m between and within the rows, which was divided in the two subplots corresponding to two treatments: 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) and B = "Standard schedule" (normally schedule applied in the vineyard), where 12 grapevines were chosen for treatment A and 10 for B. Controls were carried out for the stress and recovery years on all shoots of the grapevines chosen in 1995 at the phenological stadium 51-53 of the BBCH scale (Baillod and Baggiolini, 1993). The 1997-1998 experiment was placed in a plot planted in 1991 with a vine spacing of 2.00 x 1.20 m between and within the rows and each treatment included 48 plants di-

Correspondence to: Prof. Dr. C. Gessler, Plant Pathology, Institute of Integrative Biology, Department of Agronomy, Swiss Federal Institute of Technology, Universitätstrasse 2, 8092 ETH-Zürich, Switzerland. E-mail: cesare.gessler@agrl.ethz.ch

vided in 6 replications of 8 contiguous plants (Jermini *et al.* 2010 b where, only treatments A and B were considered in the recovery year. For the stress years (1995 and 1997), the number of shoots per plant and the yield quantity were regulated at the same level on each subplot. For 1995, the number of shoots/plant was limited to 11 (minimum 8 and maximum of 15 shoots/plant) and 12 (minimum 8 and maximum 15 shoots/plant) for 1997. In the recovery years (1996 and 1998) the number of shoots/plant was regulated in accordance with the normally practices applied in the vineyard and no yield quantity regulation was carried out.

D i s e a s e   s e v e r i t y : On each main and lateral leaf of the selected shoot, the disease severity was estimated during the stress year using a modified 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 show).

P l a n t   g r o w t h   a n d   l e a f   a r e a : From the phenological stadium 51 BBCH (Baillod and Baggiolini 1993) shoot length was measured weekly until the first topping from the base to the beginning of the apex. The number of main leaves, lateral shoots and leaves on lateral shoots was assessed the first time at the phenological stadium 51 BBCH for main leaves and at the phenological stadium 55 for lateral shoots (Baillod and Baggiolini, 1993), at the shoot topping and at the veraison. Leaf area of main and lateral leaves was estimated on all unfolded leaves of 10 randomly selected shoots using the method described by Carbonneau (1976).

S h o o t   f e r t i l i t y   a n d   n u m b e r   o f f l o w e r s / c l u s t e r : The number of shoots/plant and clusters/shoot was assessed at the phenological stadium 55 BBCH (Baillod and Baggiolini 1993) counting, for 1996, the total number of shoots and clusters present on the plants chosen and for 1998 on a series of 10 consecutive plants. The number of flowers/cluster was calculated with the method described by Casteran *et al.* (1981) on all clusters of the selected plants of 1997 and on 20 consecutive clusters for the 1998 replication.

Y i e l d   q u a n t i t y   a n d   q u a l i t y a n a l y s i s : At vintage, each plot/plant was harvested individually. After weighing, the crop was crushed to determine must soluble solids, pH, titratable acidity and content of malic and tartaric acids. Must soluble solids, expressed by °Brix, was evaluated with a refractometer ERMA with temperature correction, and pH was measured with a Metrohm 691 pH-meter (Metohm AG Herisau, Switzerland) equipped with a microelectrode. Total acidity was determined on a 15 ml must sample by titration with 0.2 mol/l NaOH until pH 7.0.

R e s e r v e   a n a l y s i s : The reserve analysis was carried out only for the 1997-1998 experiment. For each plot, the one-year-old wood sample was taken, during pruning in the February of the year following the experiment, between the 3rd and 6th internode taking one shoot per plant. Samples of the two-year-old wood (cane) included 2 parts of each cane 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. After having dug a profile along the plots from 80-100 cm depth, root samples of fine and middle diameter (0.5-5 mm) were collected from the plants and washed. All samples were cut, oven-dried at 65 °C and then crushed in a hammer mill, obtaining a powder, which was dried at least during 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 were given in mg per g of dry matter.

S t a t i s t i c a l   a n a l y s i s : Statistical analysis of the data was performed utilising the Sigmastat (SSPS) statistical package. The t-test was used to compare the differences between the two treatments.

## Results

T h e   i m p a c t   o f   t h e   s t r e s s   y e a r s   1 9 9 5 a n d   1 9 9 7   o n   t h e   p l a n t : During the stress years, the first downy mildew symptoms were found on June 16 in 1995 and June 11 in 1997. The disease development of the stress year 1997 was more rapid and greater than that of 1995, but their progress was similar with the logit phase during the first ripening period and the terminal phase from the beginning of September until vintage, where a decrease of severity was due to the defoliation (Fig. 1). The consequence of the stress year was a negative influence on yield quality with a significant decrease of the must soluble solids of 1.39 °Brix for 1995 and respectively 0.57 °Brix for 1997 in the "Untreated canopy" plots (Tab. 1). The difference observed in yield production in 1995 (Tab. 1) was due to the difficulty in regulating the crop production on the single plants.
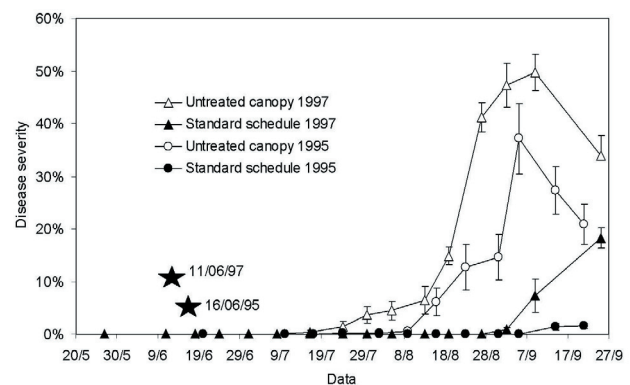


Fig. 1: Disease severity expressed as percentage of diseased leaf area per shoot during the stress years 1995 and 1997 in the "Untreated canopy" plot and "Standard schedule" plot on cultivar 'Merlot'. The star and the date indicate the finding of the first downy mildew sporulation in field.

V i n e   g r o w t h : The most important impact during the recovery season was a significant reduction of the shoot elongation from phenological stadium 55 of the BBCH scale (BAILLOD and BAGGIOLINI 1993) until topping (Tab. 2). The shoot growth difference between the two treatments increased regularly and it was significant starting on May 28 for 1996 and June 2 for 1998 with, at the last control before the topping corresponding to the end of flowering stage, a difference of 22.03 cm in 1996 and 22.4 cm in 1998 (Tab. 2). The slow shoot growth did not always correspond to a delay of main leaves, lateral shoots and leaf apparition. A significant influence on these growth parameters was observed only in the recovery year 1996, where the difference in the shoot elongation corresponded to a decrease in the number of main leaves for the two first controls and, consequently, a delay in the lateral shoot development (Tab. 3). Nevertheless, at the veraison there were no significant differences in the total number of leaves per shoot (Tab. 3). No effects were observed in the recovery year 1998 (Tab. 3). On the contrary, we found a significant reduction of the main and lateral leaf area in 1998 and no differences in 1996 (Tab. 4).

Y i e l d   c o m p o n e n t s   a n d   f r u i t   c o m p o s i t i o n : The effect of downy mildew defoliation did not influence the number of clusters/shoot and the number of flowers/cluster during the recovery year (Tab. 5). Nev-

T a b l e   1

Effect of the downy mildew epidemics on quantity and quality yield parameters of 'Merlot' during the stress years 1995 and 1997 and the recovering seasons 1996 and 1998. Data represent the average ± standard deviation

| | | Treatment | | $t$ | $P$ |
| | | Untreated canopy | Standard schedule | | |
|---|---|---|---|---|---|
| Stress year 1995 | Crop yield (kg·m$^{-2}$) | 1.009 ± 0.151 | 1.198 ± 0.206 | -2.488 | 0.022 |
| | Must soluble solids (°Brix) | 16.97 ± 0.603 | 18.36 ± 0.460 | -5.952 | < 0.001 |
| | pH | 3.24 ± 0.077 | 3.23 ± 0.034 | 0.453 | 0.655 |
| | Total acidity (g·L$^{-1}$) | 7.53 ± 0.381 | 7.47 ± 0.466 | 0.326 | 0.748 |
| Recovering year 1996 | Number shoots/plant | 11.5 ± 1.624 | 11.5 ± 1.509 | 0.000 | 1.000 |
| | Crop yield (kg·m$^{-2}$) | 1.202 ± 0.103 | 1.791 ± 0.029 | -9.468 | < 0.001 |
| | Must soluble solids (°Brix) | 19.45 ± 0.173 | 18.67 ± 0.208 | 5.456 | 0.003 |
| | pH | 3.30 ± 0.022 | 3.38 ± 0.001 | -3.912 | 0.011 |
| | Total acidity (g·L$^{-1}$) | 7.95 ± 0.173 | 7.83 ± 0.115 | 1.000 | 0.363 |
| Stress year 1997 | Crop yield (kg·m$^{-2}$) | 0.893 ± 0.130 | 1.005 ± 0.500 | -1.586 | 0.174 |
| | Must soluble solids (°Brix) | 18.20 ± 0.110 | 18.77 ± 0.103 | -11.461 | < 0.001 |
| | pH | 3.32 ± 0.015 | 3.33 ± 0.004 | -1.387 | 0.224 |
| | Total acidity (g·L$^{-1}$) | 7.15 ± 0.187 | 6.67 ± 0.082 | 6.100 | 0.002 |
| Recovering year 1998 | Number shoots/plant | 11.90 ± 0.626 | 11.85 ± 0.545 | 0.130 | 0.900 |
| | Crop yield (kg·m$^{-2}$) | 1.438 ± 0.081 | 1.815 ± 0.260 | -3.400 | 0.005 |
| | Must soluble solids (°Brix) | 19.02 ± 0.232 | 18.67 ± 0.282 | 2.415 | 0.033 |
| | pH | 3.47 ± 0.027 | 3.47 ± 0.041 | 0.367 | 0.720 |
| | Total acidity (g·L$^{-1}$) | 5.13 ± 0.111 | 5.54 ± 0.273 | -3.395 | 0.005 |

T a b l e   2

Effect of the downy mildew epidemics 1995 and 1997 on shoot length (cm) of 'Merlot' during the recovery season 1996 and 1998. Data represent the average ± standard deviation

| Year | Control data | Treatment | | $t$ | $P$ |
| | | Untreated canopy | Standard schedule | | |
|---|---|---|---|---|---|
| 1996 | May 13 | 12.30 ± 3.650 | 14.89 ± 1.840 | -2.032 | 0.056 |
| | May 21 | 24.20 ± 6.146 | 28.68 ± 3.205 | -2.076 | 0.051 |
| | May 28 | 38.78 ± 7.603 | 46.41 ± 5.771 | -2.604 | 0.017 |
| | June 04 | 55.60 ± 9.202 | 68.58 ± 9.250 | -3.287 | 0.004 |
| | June 13 | 81.99 ± 12.910 | 104.02 ± 17.391 | -3.409 | 0.003 |
| 1998 | May 19 | 25.91 ± 1.864 | 27.91 ± 1.710 | -1.713 | 0.125 |
| | June 02 | 46.14 ± 5.405 | 58.99 ± 7.183 | -3.246 | 0.012 |
| | June 08 | 63.01 ± 8.019 | 77.46 ± 11.136 | -2.396 | 0.043 |
| | June 17 | 78.59 ± 10.920 | 100.97 ± 15.823 | -2.671 | 0.028 |

Table 3

Effect of the downy mildew epidemics 1995 and 1997 on number of main leaves, lateral shoots, leaves/ lateral shoot and total leaves of 'Merlot' during the recovery seasons 1996 and 1998. Data represent the average ± standard deviation

| Year | Attribute | Control data | Treatment | | $t$ | $P$ |
|------|-----------|--------------|-----------|-----------|------|------|
| | | | Untreated canopy | Standard schedule | | |
| 1996 | Main leaves/shoot | May 13 | 4.11 ± 0.506 | 4.74 ± 0.276 | -3.550 | 0.002 |
| | | June 13 | 15.32 ± 1.526 | 16.54 ± 1.041 | -2.134 | 0.045 |
| | | August 05 | 20.91 ± 2.033 | 19.11 ± 2.128 | 1.966 | 0.064 |
| | Lateral shoot/shoot | May 28 | 1.93 ± 0.775 | 2.43 ± 0.661 | -1.584 | 0.130 |
| | | June 13 | 7.27 ± 1.290 | 8.47 ± 1.117 | -2.306 | 0.032 |
| | | August 05 | 13.18 ± 0.956 | 11.75 ± 1.728 | 2.427 | 0.025 |
| | Leaves/lateral shoot | May 28 | 1.03 ± 0.068 | 1.10 ± 0.145 | -1.415 | 0.173 |
| | | June 13 | 1.61 ± 0.156 | 1.76 ± 0.331 | -1.384 | 0.182 |
| | | August 05 | 3.04 ± 0.675 | 4.35 ± 1.927 | -2.188 | 0.041 |
| | Total leaves/shoot | May 13 | 4.11 ± 0.506 | 4.74 ± 0.276 | -3.550 | 0.002 |
| | | June 13 | 10.71 ± 1.598 | 12.66 ± 1.489 | -2.947 | 0.008 |
| | | August 05 | 25.14 ± 3.865 | 26.65 ± 2.980 | -0.978 | 0.340 |
| 1998 | Main leaves/shoot | May 19 | 6.92 ± 0.259 | 6.87 ± 0.433 | 0.208 | 0.840 |
| | | June 17 | 16.29 ± 0.932 | 16.81 ± 0.554 | -0.991 | 0.351 |
| | | August 05 | 19.82 ± 1.483 | 17.50 ± 3.323 | 1.528 | 0.165 |
| | Lateral shoot/shoot | June 02 | 2.42 ± 0.744 | 2.37 ± 0.854 | 0.082 | 0.937 |
| | | June 17 | 6.90 ± 0.903 | 7.56 ± 1.908 | -0.754 | 0.472 |
| | | August 05 | 10.71 ± 1.575 | 11.62 ± 2.487 | -0.722 | 0.491 |
| | Leaves/lateral shoot | June 02 | 1.02 ± 0.031 | 1.04 ± 0.048 | -0.880 | 0.404 |
| | | June 17 | 1.53 ± 0.181 | 1.65 ± 0.295 | -0.859 | 0.416 |
| | | August 05 | 1.82 ± 0.351 | 2.44 ± 1.020 | -1.420 | 0.193 |
| | Total leaves/shoot | May 19 | 6.92 ± 0.258 | 6.87 ± 0.433 | 0.193 | 0.852 |
| | | June 17 | 27.44 ± 3.709 | 30.69 ± 5.060 | -1.180 | 0.272 |
| | | August 05 | 70.73 ± 7.095 | 50.31 ± 14.751 | -1.396 | 0.200 |

Table 4

Effect of the downy mildew epidemics 1995 and 1997 on main and lateral leaf area expressed of cv. Merlot as $cm^2$ during the recovery seasons 1996 and 1998. Data represent the average ± standard deviation

| Year | | Treatment | | $t$ | $P$ |
|------|---|-----------|-----------|------|------|
| | | Untreated canopy | Standard schedule | | |
| 1996 | Main leaf | 143.76 ± 40.353 | 170.19 ± 49.935 | -1.164 | 0.264 |
| | Lateral leaf | 35.05 ± 14.153 | 39.55 ± 4.474 | -0.670 | 0.513 |
| 1998 | Main leaf | 102.49 ± 12.182 | 128.02 ± 6.736 | -3.775 | 0.005 |
| | Lateral leaf | 30.44 ± 3.339 | 3 7.71 ± 6.666 | -2.316 | 0.049 |

Table 5

Effect of the downy mildew epidemics 1995 and 1997 on the number of flowers/cluster and the number of clusters/shoot of 'Merlot' during the recovery seasons 1996 and 1998. Data represent the average ± standard deviation

| Year | | Treatment | | $t$ | $P$ |
|------|---|-----------|-----------|------|------|
| | | Untreated canopy | Standard schedule | | |
| 1996 | n° flowers/cluster | 351.70 ± 25.541 | 371.00 ± 56.074 | -1.071 | 0.297 |
| | n° clusters/shoot | 1.69 ± 0.217 | 1.81 ± 0.191 | -1.367 | 0.187 |
| 1998 | n° flowers/cluster | 365.31 ± 61.737 | 408.35 ± 37.278 | -1.238 | 0.251 |
| | n° clusters/shoot | 1.53 ± 0.106 | 1.66 ± 0.075 | -1.961 | 0.086 |

ertheless, at vintage, the untreated canopy plots presented a significant yield reduction of 0.589 kg·m$^{-2}$ and 0.377 kg·m$^{-2}$ for the recovery years 1996 and, respectively, 1998 (Tab. 1). The final number of berries/cluster always differs from the number of flowers/cluster before bloom, because badly fertilised berries and non fertilised flowers fall off and this drop period is normal in all grapevine cultivars. At vintage, the yield quality showed a significant lower must soluble solid contents of 0.78 and 0.35 °Brix in the unstressed plots (Tab. 1). This result is essentially due to the difference in the crop level between the two plots, which negatively influenced the carbohydrate accumulation in the berries (MURISIER 1996).

Reaccumulation of the assimilate in woody tissue: The impact of the epidemic on the plant reserves during the stress year 1997 showed a significant decrease of 57 % of the starch and of 37 % of the total reserve content of the roots (Fig. 2) as response of the grapevine to a stress situation during the ripening period (JERMINI et al. 2010 c). In the other woody parts, the starch decrease was lower than in the roots, but always 33 % for the shoots (one year wood) and 21 % for the cane (two year wood) and trunk, but the total reserve content did not change significantly between the treatments (Fig. 2). A single recovery year was enough for the grapevine to reconstitute the reserve pool (Fig. 2) and particularly those of the roots, where no differences have been found in the starch and sugar content and, consequently, in the total reserves. The same results have been observed for the cane (two year old wood), but not for the shoot (one year old wood) and the trunk, where a significant lower content of 5.32 % and, respectively, 5.95 % of the total reserves

(Fig. 2) due to significant lower sugar content of 6.1 % and 7.1 % was observed. No differences have been found in the starch content of these woody parts.

**Discussion**

The stress induced by downy mildew in the "Untreated canopy" plot has negatively influenced the shoot elongation in the recovery years. These results are confirmed by MURISIER (1996) in his experimentations on the effect of different crop loads during the recovering year. YANG and HORI (1979) and YANG et al. (1980) also showed that the new shoot growth in the spring depends on carbohydrate reserves stored in the perennial parts of the vine during the previous growing season. This retranslocation reaches a maximum at about the 8-leaf stage and ceases at about the flowering stage, because the carbohydrate requirement is gradually supported by assimilates produced in the leaves. Our previous results indicated clearly that the plant mobilises the carbohydrate reserves in the stress year to compensate for the requirements of the berries with a consequently strong reduction of their content in the perennial parts of the plant and particularly in the roots (JERMINI et al. 2010 c) The moderate shoot growth during the recovery years is probably the result of a limited amount of assimilates from budbreak available in the plant after the stress years. Nevertheless, the dynamic of leaf formation does not seem to follow that observed for the shoot growth, because in the recovery year 1998, contrary to 1996, it doesn't show significant differences in the leaf number between treatments. This result is in contrast to the epidemic dynamic observed
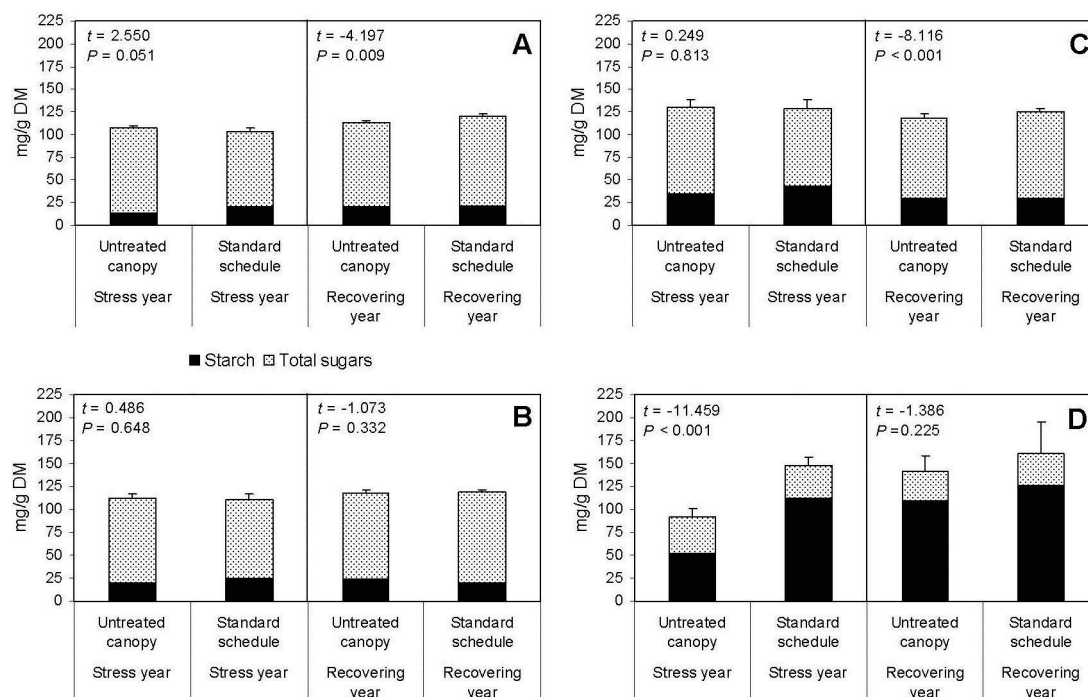


Fig. 2: Comparison of the reserve content (total sugars and starch) in the woody parts of the grapevine 'Merlot' grafted on 3309 for the stress year 1997 and the recovery year 1998. **A** = Shoots (one year old wood), **B** = cane (two year old wood), **C** = trunk and **D** = roots. The t test and significant values refer to total content of the reserves.

in the stress year, because 1997, in comparison with 1995, was characterised by a more important disease severity and consequently by a probably more important stress situation. On the other hand 1998 was characterised, contrary to 1996, by a significant reduction of the leaf area of the main and lateral leaves. Murisier (1996) observed the same tendencies in his experimentation on the chlorosis apparition as an effect of a stress situation due to a high crop load. Howell *et al.* (1994), however did not observe at vintage the influences of six levels of defoliation, occurring six weeks after blooming (berry pea-size), on the vine growth during the recovery year. Nevertheless, it is not possible to exclude for the experiment 1995-1996 that the important difference in the crop load between the treatments could have amplified the stress effect of the downy mildew and consequently the grapevine response in the recovery year. The number of clusters/shoot and flowers/cluster in the recovery years is not influenced by the downy mildew stress. The cluster initiation in the bud takes place generally in June and July (Huglin 1986) and the low disease severity during this period in the stressed years did not influence this physiological process. Nevertheless, differences on yield production at vintage have been found and probably caused by an important berry drop at fruit set induced by a reduced leaf area of the plant or an insufficient carbohydrate uptake of the berries (Huglin 1986). As for the growth parameters, we obtained different outcomes which support or reject these results. Murisier (1996) observed a significant decrease of the yield components of the plants submitted to a high crop load level contrary to Howel *et al.* (1994), which found no differences between these components as in the final crop yield. Our results support the hypothesis proposed by these last authors, which lead us to speculate on the importance of the stress type and duration on the plant response in the recovery year. Independently of the differences observed in the growth and yield parameters, the recovery year permits the plant to reconstitute the reserve pool in the woody parts and particularly in the roots. Candolfi-Vasconcelos (1990) and Koblet *et al.* (1993) have also shown that one year of post-defoliation recovery seems to be sufficient to reconstitute the reserve pool in the woody parts of the plant above the ground without considering the roots, which are the important source for carbohydrate mobilisation in compensating for a stress situation during the ripening phase of the grapevine (Koblet *et al.* 1993, Candolfi-Vasconcelos *et al.* 1994, Murisier 1996). Our results are limited to the first recovery year after the stress which plays a central role because it gives the plant the possibility to reconstitute the reserve pool. Consequently it is only in the second following year that we have a complete recovery as shown by Candolfi-Vasconcelos (1990) in their defoliation experiments.

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