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Quantitative effect of leaf damage caused by downy mildew (*Plasmopara viticola*) on growth and yield quality of grapevine 'Merlot' (*Vitis vinifera*)

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Summary

The impact of downy mildew (*Plasmopara viticola*) epidemics on the plant growth and yield quality was analysed during three years under field conditions in order to show a relationship between disease severity on leaves and yield quality losses. Three different treatments 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 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 epidemic progress in the treatment A has shown the same tendency during the three years with an increase starting from the beginning of the ripening phase. The disease severity was more important on the lateral than on the main leaves. During the three years of the study, the disease did not influence the amount of total healthy leaf area per plant until veraison. From this phenological stage until harvest, the healthy leaf area per plant decreased rapidly at the same time as the epidemic increased. The yield quantity was not affected indicating that a single fungicide application at the finding of the first sporulation was enough to preserve the crop production. Among the yield quality parameters, the sugar content has been negatively influenced by the downy mildew leaf damage. The difference was particularly evident between the treatments A and C with differences from 1.4 to 2.04 °Brix. Generally, treatment B didn't differ from C. Sugar uptake in the berries begun to show a different dynamic between 7 and 14 days after the onset of ripening. No correlation between disease severity progress on the canopy and sugar accumulation in the berries from veraison until harvest was found, indicating the capacity of the vine to compensate a stress situation induced by the downy mildew damage on leaf canopy.

K e y w o r d s : Downy mildew, sugar content, disease severity, shoot growth.

Introduction

Downy mildew of grapevine, caused by *Plasmopara viticola* Berk. & Curt. (Berl. and de Toni), is one of the most important fungal diseases of European grapevine (*Vitis vinifera* L.). The causal agent attacks all green parts of the vine. Cluster infections are the most important factor for quantitative yield reduction. Leaf damage is, on the contrary, responsible for an indirect yield loss through a reduction of the carbohydrate production that negatively influences the grape quality, the reserve accumulation and the plant vigour in the next season (Goidanich 1983). These are the reasons for which downy mildew, from its introduction in Europe, has been considered a disease with high destructive potential, which is still mostly controlled by chemical sprays without quantifying its real impact on the plant. Studies have been undertaken to compare the vine response at various levels of defoliation stress during the season (Kliewer 1970, Candolfi-Vasconcelos 1990, Candolfi-Vasconcelos *et al*. 1994, Koblet *et al*. 1994, Ollat and Gaudillere 1998), but the dynamic character of disease epidemics and pest populations make it impossible to apply these results to estimate their influence on the grapevine. Progress in the actual application of the concept of Integrated Production (IP) requires knowledge about the quantitative interactions between pests or diseases and the crop system. In viticulture, this type of study has been undertaken for foliar pests with the aim of relating the population dynamics with vine growth, yield and fruit quality (McNally *et al*. 1985, Boller *et al*. 1989, Boller and Candolfi 1990; Candolfi 1991, Candolfi *et al*. 1993, Linder and Jermini 2001, Martinson *et al*. 1997). In the pathological branch, some authors have compared differences of the yield quality parameters between healthy and infected plants for virus (Kliewer *et al*. 1976, Wolpert and Vilas 1992, Credi and Babini 1997, Guidoni *et al*. 1997, Reynolds *et al*. 1997, Cabaleiro *et al*. 1999), Esca disease (Chinnici *et al*. 1999) and powdery mildew (*Erysiphe necator*) (Piva *et al.* 1997) without considering the epidemic development. For Eutypa dieback (*Eutypa lata*) and Phomopsis cane (*Phomopsis viticola*) the disease progress has been related to yield quantity and vegetative growth (Kast 1989, Munkvold *et al*. 1994). Calonnec *et al*. (2004) have quantified the effect of different bunch infection levels of powdery mildew on grape yield, juice and wine quality, while Gadoury *et al*. (2004) have analysed the influence of powdery mildew on vine growth, yield and crop qual-

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ity. Today it is exceptional to find important yield quantity losses caused by downy mildew epidemics in commercial vineyards. It is more common to observe epidemics causing different levels of leaf damage, which effect on plant growth and yield quality is generally unknown and therefore not quantified (Jermini *et al*. 1997). Such knowledge is important for improving our IP strategies and in providing the basis for implementation of the plan in the new disease management systems which integrate the effect of disease on the plant.

Following the concept of crop system analysis (Delucchi 1990, Jermini *et al.* 2006), we conducted a study during the period 1996-1998 with the aim of quantifying the impact of downy mildew epidemics on the grapevine, considering the disease as a stress factor for the plant. The first step was to quantify the influence of the downy mildew infection on gas exchange capacity of the leaves (Jermini *et al*. 2009). This second work aims to analyze under field conditions the impact of downy mildew epidemics on the plant growth and yield quality in order to show a relationship between disease severity on leaves and yield quality losses.

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 planted with 'Merlot' grafted on 3309 rootstock. The vines were double cane pruned and vertical trained (double Guyot).

Three different treatments 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 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 in different but homogenous blocks of the vineyard to avoid stress influence due to a repetition of the trials on the same place.

Three applications of Slick (250 $g \cdot L^{-1}$ difenoconazol) were made starting from bloom to prevent powdery mildew (*Erysiphe necator*) and black rot (*Guignardia bidwellii*) infections and one with Switch (25 % fludioxonyl + 37.5 % cyprodinil) on clusters at the end of July to control grey mold (*Botrytis cinerea*) infections. The fungicide applications for downy mildew control in the treatments are summarised in Tab. 1. On the canopy, the fungicides were applied with sprayer Fischer Mini-trac (Fischer Sarl, Collombey-le-Grand, Switzerland) with using a water volume 400 $L \cdot ha^{-1}$ and on the clusters with a motorized backpack sprayer Birchmeier M125 (Birchmeier Sprühtechnik AG, Sutten, Switzerland) using a water volume 1,100 $L \cdot ha^{-1}$ always at the ha rate indicated by the manufacturer.

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 (221 Julianday) to result in a homogeneous theoretical production for each sub-plot of 1.2 $kg \cdot m^{-2}$, corresponding at the low potential yield estimated in the experiment. A first topping was done on June 18 (170 Julianday), a second one on July 16 (198 Julianday) and a last one on August third (226 Julianday).

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 (234 Julianday) so as to obtain a theoretical production per subplot of 1.1 $kg \cdot m^{-2}$, corresponding to the low potential yield estimated in the experiment. The first topping was done on June 23 (174 Julianday) and a second one on August 4 (216 Julianday).

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 48 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 (211 Julianday) with the aim of obtaining a theoretical production per subplot of 1.2 $kg \cdot m^{-2}$, corresponding to the low potential yield estimated in the experiment. The first topping was done on June 30 (181 Julianday) and a second one on July 30 (211 Julianday).

Vegetative growth and disease assessment: One 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. Leaf area was measured on plant using the method proposed by Carbonneau (1976). Disease severity was estimated with the extended Horsfall scale (Horsfall and Cowling, 1978), in which a supplementary class for the lower disease level was introduced. In this way, the scale was divided into 12 classes: class 0 (0 % damaged leaf area), class 1 (0*-1 % damaged leaf area), class 2 (1* - 3 % damaged leaf area), class 3 (3* - 6 % damaged leaf area), class 4 (6* - 12 % damaged leaf area), class 5 (12* - 25 % damaged leaf area), class 6 (25* - 50 % damaged leaf area), class 7 (50* - 75 % damaged leaf area), class 8 (75* - 88 % damaged leaf area), class 9 (88* - 94 % damaged leaf area), class 10 (94* - 97 % damaged leaf area) and class 11 (97* - 100 % damaged leaf area). The asterisk indicates a value slightly exceeding the indicated value.

Yield quality analysis: Samples of 25 berries were taken in each sub-plot choosing 2 berries on the upper, 2 in the middle and 1 on the lower part of the

Table 1

Fungicide used, concentration and application date in the treatments "Untreated canopy", "Reduced fungicide schedule" and "Standard schedule" for the experimental years 1996, 1997 and 1998. A fungicide application on clusters at the appearance of the first symptoms to avoid yield quantity losses was made on the plants of the treatment "Untreated canopy" and at the first application of the experimental year 1996

Year	treatments	Application date	Fungicide used	Active ingredients	Concentration use
1996	Reduced fungicide schedule	10.07	Curado D	6 % cymoxanil + 40 % folpet + 1.25 % pyriphenox	4.0 kg·ha^{-1}
		20.08	Ridomil Viti	60 % folpet + 7.5 % methalaxyl	3.6 kg·ha^{-1}
		29.08	Quadris	22.9 % azoxystrobin	1.6 L·ha^{-1}
	Untreated canopy	10.07	Curado D	6 % cymoxanil + 40 % folpet + 1.25 % pyriphenox	4.0 kg·ha^{-1}
	Standard schedule	24.05	Cyrano	25 % folpet + 4 % cymoxanil + 50 % Phosethyl-Al	3.2 kg·ha^{-1}
		05.06	Cyrano	25 % folpet + 4 % cymoxanil + 50 % Phosethyl-Al	3.2 kg·ha^{-1}
		18.06	Cyrano	25 % folpet + 4 % cymoxanil + 50 % Phosethyl-Al	3.2 kg·ha^{-1}
		03.07	Ridomil Viti	60 % folpet + 7.5 % methalaxyl	3.6 kg·ha^{-1}
		17.08	Ridomil Viti	60 % folpet + 7.5 % methalaxyl	3.6 kg·ha^{-1}
		02.08	Ridomil Viti	60 % folpet + 7.5 % methalaxyl	3.6 kg·ha^{-1}
		20.08	Ridomil Viti	60 % folpet + 7.5 % methalaxyl	3.6 kg·ha^{-1}
		29.08	Quadris	22.9 % azoxystrobin	1.6 L·ha^{-1}
1997	Reduced fungicide schedule	16.06	Cyrano	25 % folpet + 4 % cymoxanil + 50 % Phosethyl-Al	3.2 kg·ha^{-1}
		16.07	Remiltine F pepite	37.5 % folpet + 20 % mancozeb + 6 % cymoxanil	3.0 kg·ha^{-1}
	Untreated canopy	16.06	Remiltine F pepite	37.5 % folpet + 20 % mancozeb + 6 % cymoxanil	3.0 kg·ha^{-1}
	Standard schedule	23.05	Cyrano	25 % folpet + 4 % cymoxanil + 50 % Phosethyl-Al	3.2 kg·ha^{-1}
		02.06	Cyrano	25 % folpet + 4 % cymoxanil + 50 % Phosethyl-Al	3.2 kg·ha^{-1}
		20.06	Cyrano	25 % folpet + 4 % cymoxanil + 50 % Phosethyl-Al	3.2 kg·ha^{-1}
		01.07	Ridomil Viti	60 % folpet + 7.5 % methalaxyl	3.6 kg·ha^{-1}
		14.07	Cyrano	25 % folpet + 4 % cymoxanil + 50 % Phosethyl-Al	3.2 kg·ha^{-1}
		30.07	Cyrano	25 % folpet + 4 % cymoxanil + 50 % Phosethyl-Al	3.2 kg·ha^{-1}
		20.08	Cyrano	25 % folpet + 4 % cymoxanil + 50 % Phosethyl-Al	3.2 kg·ha^{-1}
1998	Reduced fungicide schedule	29.06	Phaltan 80	80 % folpet	2.0 kg·ha^{-1}
		10.07	Cyrano	25 % folpet + 4 % cymoxanil + 50 % Phosethyl-Al	3.2 kg·ha^{-1}
		04.08	Ridomil Viti	60 % folpet + 7.5 % methalaxyl	3.6 kg·ha^{-1}
	Untreated canopy	29.06	Phaltan 80	80 % folpet	2.0 kg·ha^{-1}
	Standard schedule	02.06	Cyrano	25 % folpet + 4 % cymoxanil + 50 % Phosethyl-Al	3.2 kg·ha^{-1}
		09.06	Cyrano	25 % folpet + 4 % cymoxanil + 50 % Phosethyl-Al	3.2 kg·ha^{-1}
		24.06	Cyrano	25 % folpet + 4 % cymoxanil + 50 % Phosethyl-Al	3.2 kg·ha^{-1}
		10.07	Cyrano	25 % folpet + 4 % cymoxanil + 50 % Phosethyl-Al	3.2 kg·ha^{-1}
		23.07	Cyrano	25 % folpet + 4 % cymoxanil + 50 % Phosethyl-Al	3.2 kg·ha^{-1}
		04.08	Ridomil Viti	60 % folpet + 7.5 % methalaxyl	3.6 kg·ha^{-1}
		19.08	Cyrano	25 % folpet + 4 % cymoxanil + 50 % Phosethyl-Al	3.2 kg·ha^{-1}

cluster. Each sample was crushed and soluble solids (°Brix at 20 °C), pH and titratable acidity (TA, as g·L^{-1} tartaric acid) immediately measured. This control was carried out weekly from the beginning of veraison until the harvest (only for the 1996 experiment, the first control was made starting at full veraison). At vintage, each sub-plot was harvested individually and weighed. The crop was crushed to determine soluble solids, pH, TA, L-malic and tartaric acid. Soluble solids measurements were made with a refractometer (ERMA) with temperature correction. The pH was measured with a Metrohm 691 pH-meter (Metrohm AG Herisau, Switzerland) equipped with a microelectrode. TA was determined on 15 ml must by titration with 0.2 mol·l^{-1} NaOH until pH 7.0. L-malic acid was analyzed by the enzymatic method (Boehringer Mannheim) and tartaric acid by the colorimetric method according to Rebelein (Lipka and Tanner 1974). 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

Disease progress: In 1996, 1997 and 1998 the first downy mildew sporulation appeared in the plots on June 25, 11 and, respectively, 24 corresponding to the phenological stages of full flowering for 1997 and fruit set for 1996 and 1998. The epidemic progress in the "Untreated canopy" treatment, expressed as disease severity (percentage of diseased leaf area/shoot), has shown the same tendency, independently of the late (1996 and 1998) or early (1997) apparition of the first sporulation in the field and increased starting from the beginning of the ripening phase

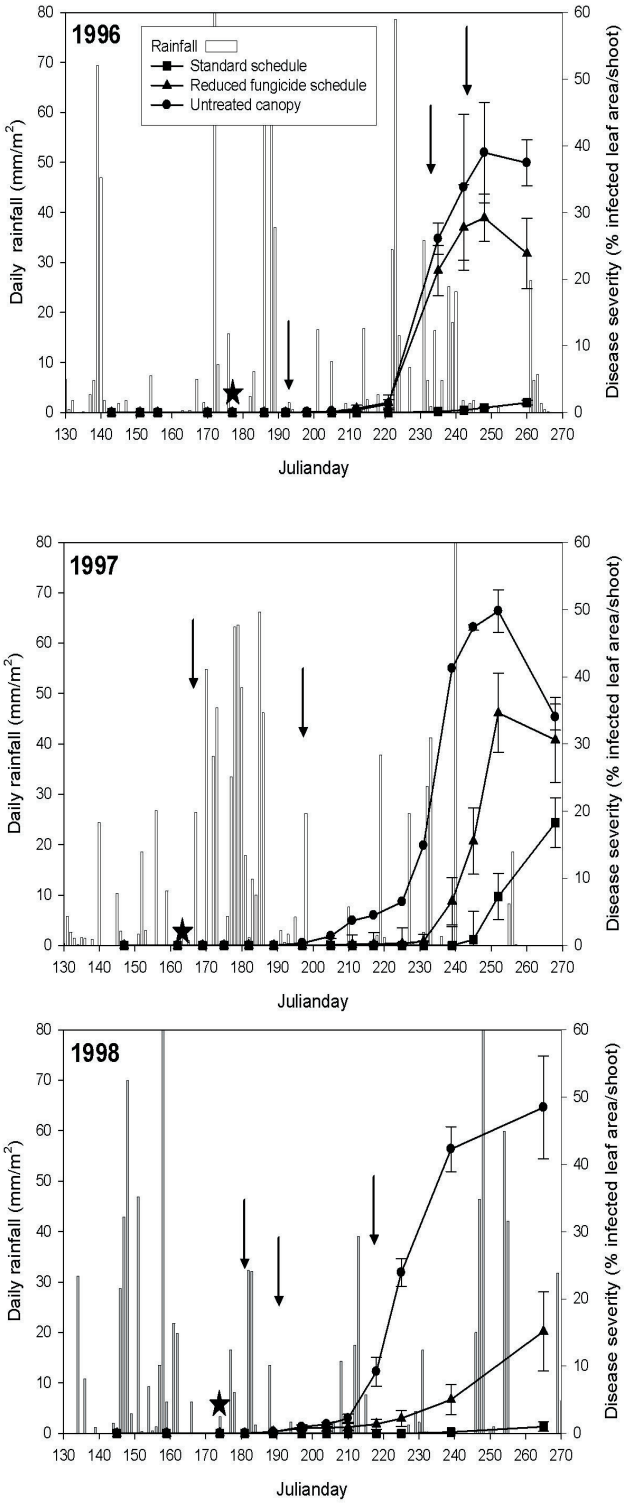

Fig. 1: Daily rainfall (mm·m^{-2}) and disease severity progress, expressed as percentage of diseased leaf area per shoot on cultivar 'Merlot'. Three *P. viticola* control strategies are presented: "Untreated canopy", "Reduced fungicide schedule" and "Standard schedule" for the experimental years 1996, 1997 and 1998. Each point represents the average of 6 for 1996 and 1997 and 8 replications for 1998 with standard deviation. The star indicates the apparition of the first downy mildew sporulation in field and the arrow indicates the fungicide applications in the treatments "Untreated canopy" and "Reduced fungicide schedule". The fungicide applications in the "Untreated canopy" and the first made in 1996 in the treatment "Reduced fungicide schedule" were made only on clusters in correspondence to the first arrow.

(Fig. 1). At this phenological stage, the disease severity corresponded to 9.17 %, 4.46 % and 1.29 % diseased leaf area/shoot for 1996, 1997 and, respectively, 1998 (Fig. 1). From veraison to harvest, the epidemic progressed rapidly and at the last control before harvest a disease severity of 37 %, 34 % and 48 % of diseased leaf area/shoot was measured. The epidemic progress on main and lateral leaves followed a similar pattern and the final disease damage resulted higher on the lateral than on the main leaves, even though the disease increased 1-2 weeks before on the main leaves than on lateral leaves (data not shown). In 1996, the first fungicide application in the "Reduced fungicide schedule" treatment was made only on the clusters to avoid yeld quantity losses and the first one on canopy was delayed with the aim to reduce a minimum the number of applications. The epidemic progress never increased until the beginning of veraison (August 6 = 221 Julian day) and at this phenological stage the disease severity was 1.5 % and 1.3 % in the "Reduced fungicide schedule" and, respectively, in the "Untreated canopy" treatments. Unfortunately, a very rapid increase was observed in the next fourteen days, so that the two later fungicide applications were inefficient in delaying the epidemic (Fig. 1). On the basis of this experience we changed the approach in 1997 and in 1998, applying the fungicides at the beginning of the epidemic and so achieve an important delay of the epidemic progress (Fig. 1). In the "Standard schedule" plots an increase of the disease was observed only after the end of the fungicide application, in Switzerland corresponding to the second half of August (Fig. 1).

Canopy development and vine vigour: The influence of downy mildew epidemics on the canopy development can be described by the amount of healthy leaf area per plant. This is an important parameter because it indicates the amount of photosynthetic leaf area at the disposal to the vine for carbohydrate production. During the three studied years, the disease did not influence the amount of total healthy leaf area per plant until veraison (Fig 2 A). From this phenological stage until harvest, the healthy leaf area per plant decreased rapidly at the same time as the epidemic increased (Fig. 2 A). At the control before harvest, the average healthy leaf area/plant available for a vine in the "Untreated canopy plots" was 27.1 % in 1996 and that of a plant in the "Standard schedule" plot was of 32.7 % and 22.9 % for 1997 and, respectively, 1998. The application of a limited number of fungicides in the "Reduced fungicide schedule" plots has permitted keeping, on average, a healthy leaf area/plant of 56.6 %, 54.8 % and 88.1 % for 1996, 1997 and, respectively, 1998 in relation to leaf area of a normally treated grapevine. During the ripeness phase, the decrease of healthy leaf area on the plant was attributed to the increase of the epidemic, which induced the leaf fall and a standstill of the new leaf formation (Fig. 2 B). The leaf fall became important generally starting 3-4 weeks after veraison (Fig. 2 B) and consequently, the plants in the "Untreated canopy" plots lost the 70.3 % of the total leaves at harvest in 1996, 65.1 % and 61.8 % in 1997 and, respectively, 1998 in comparison with the "Standard schedule". In the "Reduced fungicide schedule", the effect of the fungicide application was more

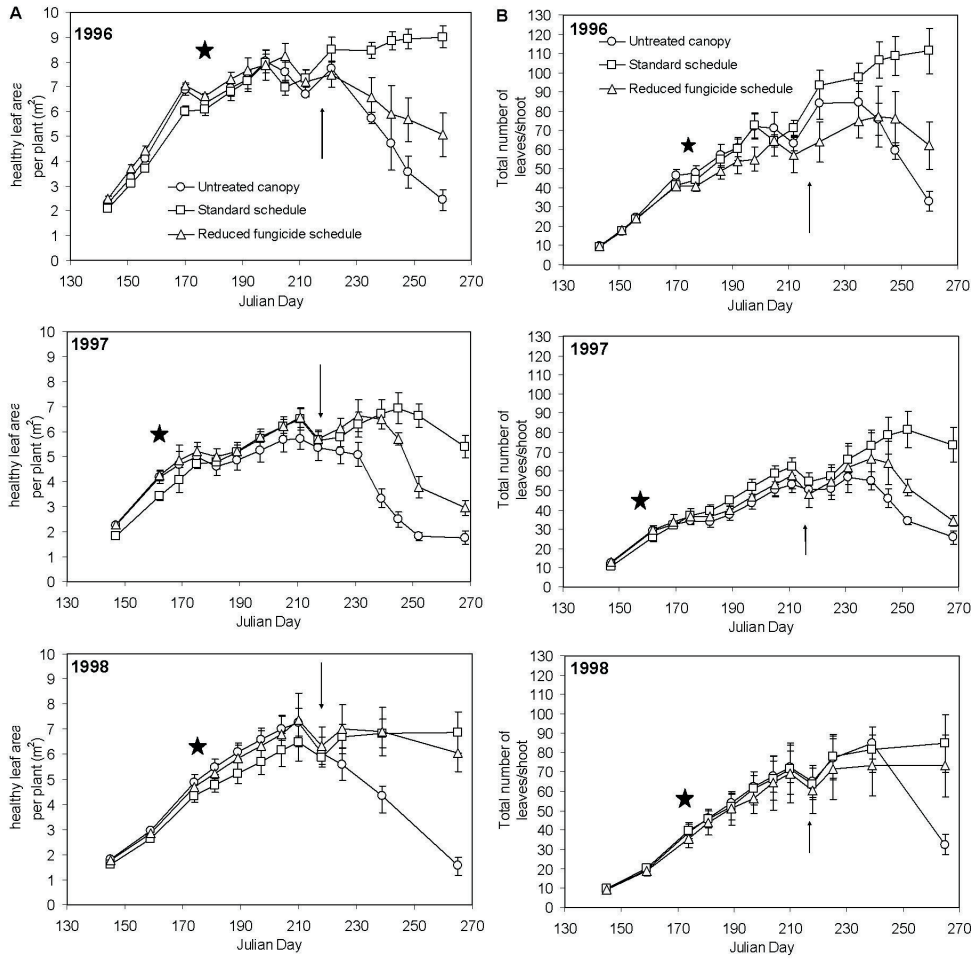

Fig. 2: Evolution of the healthy leaf area/vine, expressed in m^2 per vine of 'Merlot', where healthy leaf area = leaf area without downy mildew symptoms, yellowing or presence of sporulations (**A**) and of the total number of leaves/shoot (**B**) in the treatments "Untreated canopy", "Reduced fungicide schedule" and "Standard schedule" for the experimental years 1996, 1997 and 1998. Each point represents the average of 6 for 1996 and 1997 and 8 replications for 1998 with standard deviation. The star indicates the finding of the first downy mildew sporulation in field and the arrow the beginning of the ripening phase (veraison).

evident with a delay of the leaf fall, which had an intermediary dynamic with the exception of 1998 where the total leaf number remained stable until harvest (Fig. 2 B).The plant vigour, expressed from the total pruning and one year shoot weight, did not show a clear effect following the important leaf area reduction due to downy mildew infection (Tab. 2).

Effect of downy mildew leaf infection on yield quantity and quality: The yield quantity didn't statistically differ between treatments for the experimental years 1996 and 1997 (Tab. 3). A significant difference in the production was found only in 1998 between the "Standard schedule" plot and the two other treatments probably due to an insufficient level of yield regulation in the "Standard schedule" plots and a greater berry weight (Tab. 3).

Among the yield quality parameters, the sugar content, which is one of the most important, has been negatively influenced by the downy mildew leaf damage. The difference was particularly evident between the "Untreated canopy" and the "Standard schedule" plots with differences from 1.4 °Brix for 1996, 0.57 °Brix for 1997 and 2.04 °Brix for 1998. The "Reduced fungicide schedule" didn't differ from the "Standard schedule" plot with the exception of 1996, where the result was intermediary between the two other treatments (Tab. 3). Fig. 4 shows the sugar accumulation dynamic during the three experimental years. The comparison between "Standard schedule" and "Untreated canopy" treatments emphasized, with exception of 1996 where the controls started later, how sugar accumulation in the berries begins to show a different dynamic 14 d (1997) and 7 d (1998) after the onset of ripening (Fig. 3). The increase in the difference of sugar content between these two treatments was generally regular and only in 1998 it remained constant between the end of August and the middle of September before decreasing in the last week before harvest.

The sugar uptake dynamic of the crop in the "Reduced fungicide schedule" did not show, for 1997 and 1998, differences with the "Standard schedule" treatment. In 1997, a dynamic similar to that of the "Untreated canopy" treatment was observed (Fig. 3). Contrary to expectations, no correlation between disease severity progress on the canopy and sugar accumulation in the berries from veraison until harvest was found in 1997 and 1998 (1996 not considered) (Fig. 4).

For the other yield quality parameters measured at harvest (Tab. 3), only the titratable acidity showed a certain influence with values generally higher in the "Untreated

Table 2

Effect of downy mildew epidemic on plant vigour of Merlot grapevine, expressed with the fresh weight of one year old cane (g) and the total pruning per vine (kg/vine), for the experimental years 1996, 1997 and 1998. Each value represents the average of 6 for 1996 and 1997 and 8 replications for 1998 with standard deviation. Means followed by same letter not significantly different at $p < 0.05$ (Tuckey test)

Attribute	Year	Treatment		
		Untreated canopy	Reduced fungicide schedule	Standard schedule
One year old cane fresh weigh (g)	1996	45.36 ± 2.86 a	44.42 ± 3.57 a	42.51 ± 2.67 a
	1997	57.46 ± 4.28 a	60.50 ± 9.74 a	48.74 ± 5.55 a
Total pruning fresh weight (kg·vine^{-1})	1998	56.40 ± 8.51 b	72.40 ± 8.31 a	63.00 ± 8.15 ab
	1996	0.613 ± 0.024 a	0.613 ± 0.046 a	0.576 ± 0.053 a
	1997	0.497 ± 0.042 ab	0.556 ± 0.092 a	0.411 ± 0.038 b
	1998	0.546 ± 0.095 b	0.694 ± 0.089 a	0.662 ± 0.083 ab

Table 3

Effect of downy mildew epidemic on yield quantity and juice quality of 'Merlot' grapevine at harvest during the experimental years 1996-1998. The harvest was made on October 2 for 1996, September 23 for 1997 and September 29 for 1998. Each value represents the average of 6 for 1996 and 1997 and 8 replications for 1998 with standard deviation. Means followed by same letter are not significantly different at $p < 0.05$ (Tuckey test)

Attribute	Year	Treatment		
		Untreated canopy	Reduced fungicide schedule	Standard schedule
Yield (kg·m^2)	1996	1.150 ± 0.151 a	1.155 ± 0.149 a	1.013 ± 0.112 a
	1997	0.893 ± 0.130 a	1.044 ± 0.068 a	1.005 ± 0.050 a
Berry weight (g)	1998	1.022 ± 0.076 b	1.105 ± 0.123 b	1.357 ± 0.198 a
	1996	2.30 ± 0.28 a	2.24 ± 0.15 a	1.96 ± 0.03 a
	1997	1.67 ± 0.07 a	1.74 ± 0.11 a	1.64 ± 0.11 a
Soluble solids (°Brix)	1998	1.72 ± 0.06 b	1.91 ± 0.06 b	1.97 ± 0.05 a
	1996	17.8 ± 0.33 c	18.3 ± 0.15 b	19.20 ± 0.26 a
	1997	18.2 ± 0.11 b	18.8 ± 0.17 a	18.77 ± 0.10 a
Juice pH	1998	17.4 ± 0.46 b	19.1 ± 0.36a	19.46 ± 0.16 a
	1996	3.37 ± 0.017 b	3.35 ± 0.014 b	3.39 ± 0.005 a
	1997	3.32 ± 0.015 a	3.27 ± 0.016 b	3.33 ± 0.004 a
Titratable acidity (g·L^{-1})	1998	3.58 ± 0.040 a	3.40 ± 0.024 b	3.44 ± 0.025 c
	1996	7.83 ± 0.17 a	7.70 ± 0.09 a	7.20 ± 0.14 b
	1997	7.15 ± 0.19 a	7.03 ± 0.16 a	6.67 ± 0.08 b
Malic acid (g·L^{-1})	1998	5.46 ± 0.19 b	5.92 ± 0.20 a	5.56 ± 0.20 b
	1996	4.98 ± 0.13 ab	5.08 ± 0.13 a	4.82 ± 0.09 b
	1997	3.37 ± 0.22 a	3.03 ± 0.19 b	3.12 ± 0.17 ab
Tartaric acid (g·L^{-1})	1998	3.47 ± 0.31 a	3.47 ± 0.17 a	3.22 ± 0.16 b
	1996	5.42 ± 0.20 a	5.13 ± 0.29 ab	4.95 ± 0.16 b
	1997	6.82 ± 0.09 ab	6.88 ± 0.23 b	6.50 ± 0.17 a
	1998	4.32 ± 0.11 a	4.45 ± 0.10 a	4.37 ± 0.08 a

canopy" and "Reduced fungicide schedule" treatments in comparison with the "Standard schedule". The pH and the malic and tartaric acids didn't show a clear effect due to the downy mildew leaf damages (Tab. 3).

Discussion

Contrary to the expectations, the impact of downy mildew leaf damage on plant canopy on plant growth and on yield quality parameters were most pronounced only in the sugar content of berries. The plant growth and vigour wasn't affected by the important leaf area reduction due to downy mildew epidemics. In fact, Vasconcelos and Castagnoli (2000) indicate that vines in balance should have one year canes each weighing 30 to 40 g with 40 g fresh weight being preferred in cool climates. For each experimental year we always measured cane weight greater than 40 g fresh weight demonstrating the lower impact of the epidemics on this factor. The same observations have been made by Wolpert and Vilas (1992) and Cabaleiro *et al.* (1999), which have shown that grapevine leafroll didn't influence the plant vigour expressed by pruning weight. These results should be analysed considering our climatic

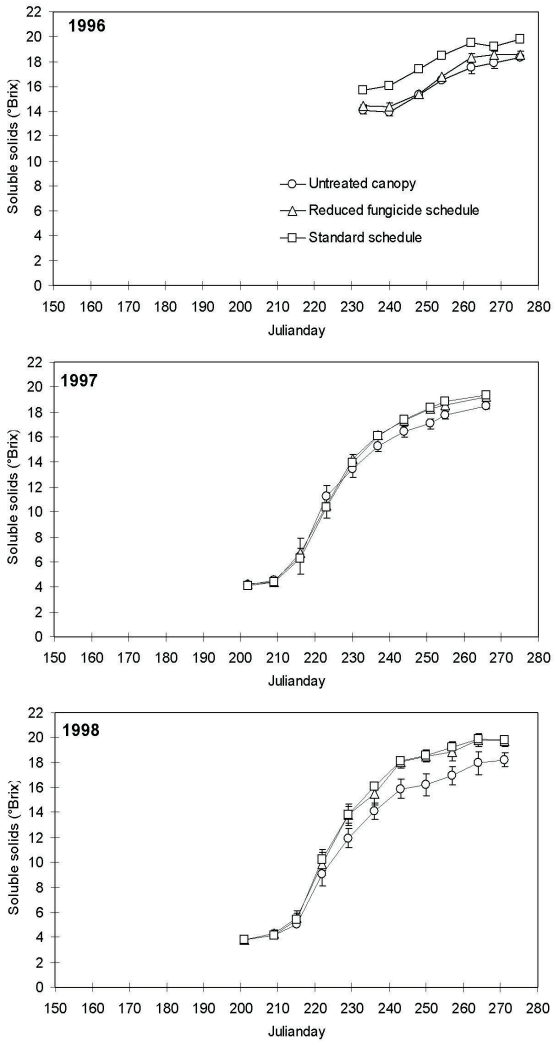

Fig. 3: Accumulation of the must soluble solids (°Brix) in the berries of 'Merlot' during the ripening phase for the treatments "Untreated canopy", "Reduced fungicide schedule" and "Standard schedule" for the experimental years 1996, 1997 and 1998. Each point represents the average of 6 for 1996 and 1997 and 8 replications for 1998 with standard deviation.

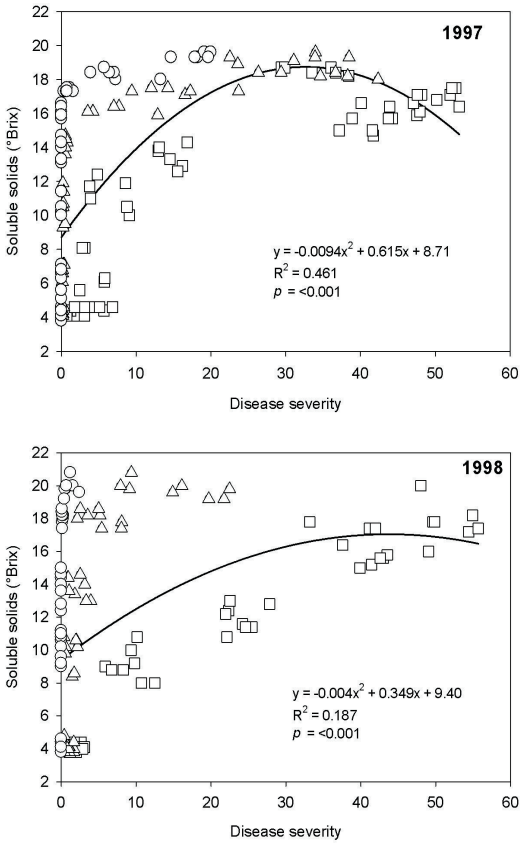

Fig. 4: Relation between the must soluble solids and disease severity of *P. viticola* on 'Merlot' measured weekly from veraison to harvest for 1997 and 1998 experimental years. Squares correspond to "Untreated canopy", triangles to "Reduced fungicide schedule" and circles to "Standard schedule" treatments. Each data point represents a single sample. For each of one replication, 6 in 1997 and 8 in 1998.

conditions, which influenced the dynamic character of the downy mildew epidemics, the cultural methods applied and the variety cultivated and consequently the plant response to a stress. The role of these elements has been reported by different authors. Credi and Babini (1997), for single and mixed virus infections, and Reynolds *et al*. (1997), for the Rupestris stem pitting virus, have observed differences due to the type of virus combinations, their source and, respectively, to the variety. Kliewer and Fuller (1973) emphasise that with defoliation at veraison or later, the pruning weight of canes would not be a good indicator of reduced vine capacity due to loss in leaf area, because dry matter accumulation is more reduced in the trunk than in the canes. Under our climatic and growth conditions the exponential increase of the epidemics during the ripening can only partially influence the plant vigour of 'Merlot' cultivar. We have also applied each year a plot rotation and this choice could also have had an influence on the plant response, because, as demonstrated by Reynolds *et al*. (1989) in trials of different summer hedging levels, the effect of time and severity on the plant vigour is not substantially influenced by timing of hedging, but the severity consistently reduced vigour each season. An analysis of the real impact of the downy mildew epidemics on growth parameters needs a repetition in time.

One single application of a contact fungicide on clusters at the apparition of first sporulation has permitted preserving the crop production, with the exception of 1998, where a lower level of the crop limitation resulted in the differences observed. This result can not be generalised, because most early apparition of the downy mildew in the field requires certainly one more fungicide application. Nevertheless, the choice of a good timing for the cluster protection permits preserving yield quantity with a very limited number of fungicide applications. The leaf area at disposal to the plant also has a major role on the crop formations. Studies on artificial defoliation (Buttrose 1966, Kliewer 1970, Candoli-Vasconcelos 1990, Hunter *et al*. 1995, Koblet *et al*. 1994) have demonstrated that yield quality at harvest depends on the combination effect of time and defoliation severity. Main leaves appear to play a main role for the yield formation and sugar accumulation in the berries seems to depend on the available active leaf area of lateral leaves (Candoli-Vasconcelos, 1990). Our results confirm these observations, but it is important

to consider that a downy mildew epidemic has a dynamic character. The climatic conditions influence the oospores maturation during the season, the epidemic progress and, consequently, the time and severity of the leaf damage. It is therefore logical that the epidemic character of the downy mildew observed during these three experimental years, associated with the efficacy of the fungicide application on the clusters, has permitted preserving until the ripening an adequate main leaf area to supply the carbohydrates required by the cluster for the crop formation. Sugar accumulation is the main quality factor which was negatively influenced from downy mildew, but the content in the berries isn't proportional to the decrease of the leaf area. Hunter *et al*. (1995) showed that a 33 % defoliation level at veraison had no effect on soluble solid accumulation but increased titratable acidity and reduced pH. Our results show a different situation. The factors influencing pH and total acidity are complex and the dynamic character of the epidemics could influence in time the chemical and enzymatic processes responsible for acid composition of the berries. Nevertheless, we could assume that the differences observed are probably due to the effect of a different K^+ content of the musts, because a different K^+ concentration influences the pH value. This behaviour of titratable acidity and pH is an example of the complex interaction between disease and plant. For the grapevine, some studies have been undertaken to compare the impact of disease on yield components (Kliewer *et. al*. 1976, Wolpert *et al*. 1992, Credi and Babini 1997, Guidoni *et al*. 1997, Piva *et al*. 1997, Reynolds *et al*. 1997, Chinnici *et al*. 1999), but the symptom expression and the impact of the epidemic development in relation to yield formation have not been taken into account. Other authors (Duso and Belvini 1992) have tried to artificially simulate pest leaf damage by applying a progressive defoliation from veraison until harvest with different intensity. They have observed a negative influence on berry weight and fruit quality with defoliation levels between 25 and 50 %, but the damage also seems to depend on the relationship between crop load and leaf area. Even though these experimentations partially confirm our results, it is impossible to extract indications explaining the grapevine behaviour, because they consider a fixed defoliation level made at a defined time. On the contrary, the healthy leaf area reduction caused by downy mildew has a dynamic evolution depending on the epidemic increase, which is modulated by weather. Measurements of leaf gas exchange have furthermore indicated that healthy leaf parts of an infected leaf of the lateral shoot react more negatively than main leaves and that photosynthesis decreases with the increase of leaf damage severity (Jermini *et al*. 2009). If we associate this impact factor with the major role of the lateral leaves during the berry ripening phase on the sugar accumulation (Candolfi-Vasconcelos 1990), the low plant capacity of reconstructing the assimilating apparatus (Candolfi-Vasconcelos 1990) at this time of the season and the rapid development of the epidemic with a colonisation of the new formed leaves, it is difficult to understand the low correlation between sugar accumulation and disease severity. This apparent contradiction is in accordance with the results of Koblet *et al*. (1994), which, in experiments made with different defoliation levels, have demonstrated that sugar accumulation is not proportional to the decrease in leaf area. They found that reserves might be exported from woody parts of the plant to the fruit under defoliation stress conditions to compensate for the carbohydrate requirements of the berries. The capacity of the vines to apply compensation mechanisms has also been demonstrated for abiotic (Buttrose 1970, Candolfi-Vasconcelos 1990, Candolfi-Vasconcelos *et al*. 1994, Murisier 1996) and biotic stress factors as the grape leafhopper *Empoasca vitis* (Candolfi *et al*. 1993), the spider mite *Tetranychus urticae* (Candolfi 1991) and eastern grape leafhopper *Erythroneura comes* (Martinson *et al*. 1997). In fact, during the ripening phase the berries represent the main sink for the plant and lateral leaves generally play the main role in supplying the fruit requirements (Candolfi-Vasconcelos 1990). Our results emphasize the potential capacity of the grapevine to compensate for the stress induced by downy mildew and the importance of the timing of a fungicide application in delaying the epidemics. The comparison of the ripening dynamic between "Untreated canopy" and "Standard schedule" treatments indicates a constant increase of the sugar content of the berries until the end of the first ripening phase. Afterwards, the difference remains generally constant. In this case the stress situation is probably too high to permit the plant to compensate for the deficiency. The application of a reduced control schedule depends on the timing of the fungicide application. The 1996 trial stresses this importance, because during the two other experimental years a choice of the good timing delayed the epidemic, leaving the plant the possibility to supply the carbohydrate requirement of the berries. Fungicide applications at the first epidemic phase therefore contribute greatly in delaying the epidemic. Gadoury *et al*. (2001) have shown the same results with powdery mildew. Multiple fungicide applications during the peak period of fruit susceptibility give the most efficient control. It is therefore possible to assume that for downy mildew there exists a damage threshold during the ripening phase which limits the stress situation permitting the plant to enhance a compensatory mechanism. Our data show no significant differences in the soluble solids contents at harvest between the treatments "Reduced fungicide schedule" and "Standard schedule" if the disease severity is limited to between 1% at the beginning of ripening and 5 % at the end of August, corresponding to the end of the first ripening phase. This hypothesis must be validated and its application should be supported by a simulation model that integrates, on a quantitative basis, the epidemic progression and the interactions between disease and crop growth (Dietrich *et al*. 1997). It is also important to analyse this strategy on the same plot for a long period in order to better evaluate the disease impact on the plant growth.

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