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An analysis of the effects of environmental factors on conidial dispersal of *Uncinula necator* (grape powdery mildew) in vineyards

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Aerial spore concentration of *Uncinula necator* (the causal agent of grape powdery mildew), weather data and cropping practices were monitored during two consecutive seasons in two vineyards of the Bordeaux area. During days with no rain, spore dispersal was mainly diurnal and showed variations that followed the same pattern as that of wind speed, and a reverse pattern to that of relative humidity. Light falls of rain, of approximately 2 mm, coincided with increased spore densities in the air. Pesticide sprays using high pressure equipment generated high wind speeds at the canopy level. This may trigger high spore dispersal. High conidial stocks were produced under spontaneous conditions in the canopy. These stocks were released only under particular events, such as heavy rains, or pesticide applications with high pressure sprayers. Other cropping practices causing leaf shaking, such as pruning, may enhance spore dispersal. Over the observation period, the onset of spore dispersal was observed during a period with no rain following a rainy period, suggesting the detrimental effect of rains on epidemic onset. Epidemiological and disease management implications are discussed.

Introduction

Determining the timing, conditions and intensity of spore release provides useful information for the better understanding of disease epidemics. Liberation of propagules is one important process in the temporal spread of polycyclic diseases (Gregory, 1961). Under field conditions, the aerial spore concentration is a suitable epidemiological variable for studying the effects of environmental factors on spore dispersal.

Grape powdery mildew, caused by *Uncinula necator*, is a major disease in many areas of grape production (Pearson & Goheen, 1988). Although dissemination of conidia in *U. necator* has not been studied in detail, the spores are considered to be mainly released by wind, and dispersed over vineyards for appreciable distances (Bulit & Lafon, 1978). The conditions required for conidial liberation have been studied in other powdery mildews (Schnathorst, 1965; Butt, 1978), but factors responsible for spore dispersal in *U. necator* have not been quantitatively documented. However, the rapid spread of the disease when it was introduced into Europe in the last century suggests that the pathogen is readily dispersed.

The objective of the present study was to describe powdery mildew spore dispersal patterns in vineyards, and to assess the effect of environmental conditions on these patterns. Toward this aim, aerial spore concentration, environmental parameters, disease severity and cultural practices were monitored during two growing seasons in vineyards located in the Bordeaux area of France.

Materials and methods

Initial conditions and vine management

Aerial concentration of powdery mildew conidia was monitored in two vineyards planted with the susceptible *Vitis vinifera* cultivar Cabernet–Sauvignon (Galet, 1977). One vineyard, monitored in 1991 and 1992, was located 10 km South of Bordeaux, France, at the INRA research farm of Couhins. The plot consisted of four rows of 40 vines. The distance between rows and between vines was 1 m. The vineyard had been heavily infected by powdery mildew during previous years. During these years, as well as in 1991 and 1992, diseased flag shoots, grown from naturally infected buds, were observed at the beginning of the growing season (12 in

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1991, at the beginning of June, the first one being detected on April 28; and 20 in 1992, recorded on May 15). Cleistothecia were observed on infected leaves and grapes at the end of the growing season in 1990, 1991 and 1992.

Another, commercial, vineyard planted in Creon, was situated 30 km east of Bordeaux, and was monitored in 1991. Within the vineyard, four plots of two rows of 10 vines each were randomly selected, and used for assessments. The distances between rows and between vines were 2·5 m and 1 m, respectively. The vineyard was heavily infected by powdery mildew in 1990. No flag shoots were detected in 1991. Cleistothecia were observed at the end of the growing season on infected leaves and grapes in 1990 and 1991.

Following current recommendations, the vines were pruned during the growing season, to heights of 1·5 and 1·7 m at Couhins and Creon, respectively. Pruning was carried out on 19 July 1991 and 24 July 1992 at Couhins, and in three bouts at Creon in 1991: between July 3 and 10, between July 24 and 31, and between August 7 and 21. Before pruning, at Couhins, the average number of leaves per main cane were 21 in 1991 and 32 in 1992. At Creon, before the first pruning, the average number was 16. After pruning, averages of 15, 16 and 15 leaves per main cane were left at Couhins 1991, Couhins 1992 and Creon 1992, respectively.

In both fields it was necessary to use fungicides against downy mildew (*Plasmopara viticola*) (but not effective against powdery mildew), a mixture of cymoxanil and mancozeb (120 g and 1400 g a.i./ha, respectively) being applied every 10–15 days. At Couhins, the fungicide was sprayed with a motorized knapsack mistblower, which blew an air/fungicide suspension at a speed of 30 m s^{-1} at the level of the canopy. At Creon, a tractor-drawn sprayer applied the suspension at 9–10, 4–5 and 2–3·6 m s^{-1} at 1 m (grape height), 1·5 m and 1·7 m (top of the canopy) above ground level respectively.

Aerial spore concentration

In 1991, spore catches were made throughout the growing season (April to September), in both vineyards and over the same period in 1992 at Couhins. Burkard 7-day recording volumetric spore traps (Burkard Manufacturing Co., Rickmansworth, Hertfordshire, UK) were placed between two grapevine rows in the middle of the experimental plots, with the sampling orifice at a height of 60 cm. One trap was used in each vineyard in 1991, and two traps were used at Couhins in 1992.

The traps were adjusted to sample 10 l of air per minute. Each week, a tape coated with Vaseline supplemented with paraffin (10% v/v) was placed on the trap drum. The tape was removed after a 7-day exposure period. Segments corresponding to 1 day exposure were cut, mounted on glass slides and stained with cotton blue. Five straight lines, 4 mm apart, were drawn on the glass slides with a fine pen to divide the tape in six periods of 4 h. For each segment, two strips 2 mm wide, parallel to the direction of movement of the trap drum, were examined under the microscope (×100 objective), and the number of conidia caught within each 4-h time-step was recorded. Within each day, the six consecutive 4-h periods started with that from 22·00 hours to 02·00 hours, and are referred to as time-steps 1 to 6. The number of spores per m^3 of sampled air was calculated, representing the 4-hourly aerial conidial concentration. In 1992, the average of number of spores collected from both traps was computed. The mean daily spore concentration was calculated as the mean over the six time-steps within each day.

Weather data

Temperature and relative humidity were measured with a 7-day recording hygrothermograph placed at a height of 1·5 m in a standard weather shelter. Rainfall was recorded with a rain gauge located at a height of 0·5 m. Both instruments were installed beside the experimental plots. Hourly maximum wind speed data (at a height of 10 m), provided by the National Meteorological Office, were recorded by stations located 500 m and 12 km away from the experimental vineyards of Couhins and Creon, respectively. Mean values for temperature, relative humidity, maximum wind speed and accumulated rainfall were computed for each 4-hourly time-step.

Disease assessment

Ninety six, 92 and 48 canes, representing approximately 1/10 of the total cane population, were randomly selected at the beginning of the growing season and assessed every week at Couhins in 1991, Couhins in 1992 and Creon in 1991, respectively. In the three observation periods, disease severity (i.e. percentage diseased area) on grape clusters was assessed. Mean disease severity on the grapes was calculated over all the canes examined at each assessment. In 1992, the number of leaf faces (abaxial plus adaxial) infected per cane was also monitored, representing the intensity of the disease on leaves.

Variations of 4-hourly spore concentration within selected periods

The 4-hourly raw spore concentration data and weather were plotted over time. These graphs were analysed visually to identify periods that could give general indications of the relationship between weather conditions and patterns in the dynamics of aerial spore concentration.

Average daily variation of wind speed, relative humidity and aerial spore concentration

During each of the three monitoring exercises, periods of high spore concentration were selected; these were from

20 May to 25 July 1991 and 15 June to 27 July 1992 at Couhins, and from 10 May to 25 July 1991 at Creon. Within these periods of high spore concentration, rainy days and dates where sprays or pruning occurred were not included in the analyses, as they could induce strong disturbances in the diurnal patterns of spore dispersal. The 4-hourly data of wind, relative humidity, and log-transformed data of aerial spore concentration were averaged on a time-step basis. The means of log-transformed spore concentration were compared by the Student–Newman–Keuls multiple range test ($P = 0{\cdot}05$).

Results

Variation of daily aerial spore concentration and disease intensity throughout the growing season

In the three data sets, the daily variation in spore concentration showed irregular patterns (Figs 1b, 2b, 3b). High peaks of spore concentration were observed, for example at Couhins on 24 June, 12 July, 31 August, 1991 (Fig. 1b), at Creon on 29 June 1991 (Fig. 2b), and at Couhins on 30 June, and 9, 18 and 22 July 1992 (Fig. 3b).

At Couhins in 1991, spores were first detected in the air on 15 May, and could be observed until the end of September (Fig. 1b). Spore densities higher than 30 spores per m^3 of sampled air (SMSA) were regularly observed from 15 May to 31 July. After this period, except for a peak on 31 August, the average spore concentration was lower. The cumulated spore density

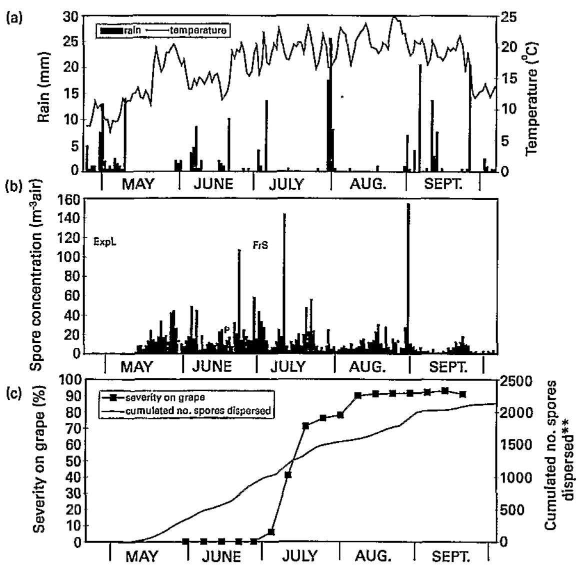

Figure 1 Patterns of weather, spore dispersal, and disease on grape over time for Couhins 1991. (a) Rain and temperature; (b) spore dispersal; (c) cumulated daily spore dispersal and severity on grape. ExpL and Frs: phenological stages of expanded leaves and fruit set, respectively (Baggiolini, 1952). *Missing data; **cumulated 7-day moving average of daily spore dispersal.

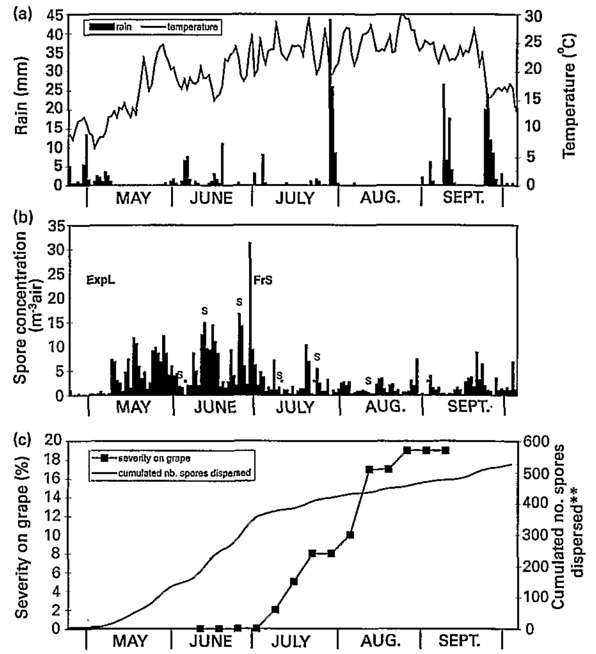

Figure 2 Patterns of weather, spore dispersal, and disease on grape over time for Creon 1991. (a) Rain and temperature; (b) spore dispersal; (c) cumulated daily spore dispersal and severity on grape. ExpL and Frs: phenological stages of expanded leaves and fruit set, respectively (Baggiolini, 1952). S, application of fungicide against downy mildew. **Cumulated 7-day moving average of daily spore dispersal.

increased linearly from 15 May until the end of September, and the total number of spores trapped during the season was 2150 SMSA (Fig. 1c). The onset of epidemic on grape occurred between 29 June and 6 July, when spore release was at an average of 26 SMSA. Within 3 weeks from the onset of the visible epidemic, disease severity was 72%, which was 78% of the final severity.

At Creon in 1991, similar patterns were observed, but with lower spore concentrations. Values higher than 10 SMSA occurred regularly from 15 May to 1 July (Fig. 2b). After this date, the values remained lower than 10 SMSA. The transition period corresponds to the first pruning operations (3–10 July). This is also reflected by a change in the slope of cumulated spore concentration at this time (Fig. 2c). The total number of spores trapped during the season was 520 SMSA. Within the 6 days when the fungicide against downy mildew was sprayed, 3 corresponded with local peaks of spore density (13 June, 26 June and 24 July). The epidemic on grapes started between 4 and 11 July, when spore release was lower than 10 SMSA. Within 6 weeks of detection of the first symptoms, severity was 17% (90% of the final severity).

At Couhins in 1992, spores were observed from 4 May to 2 October (Fig. 3b), release being high between 15 June and 1 August. This was also reflected in the pattern of cumulated spores dispersed (Fig. 3c), which

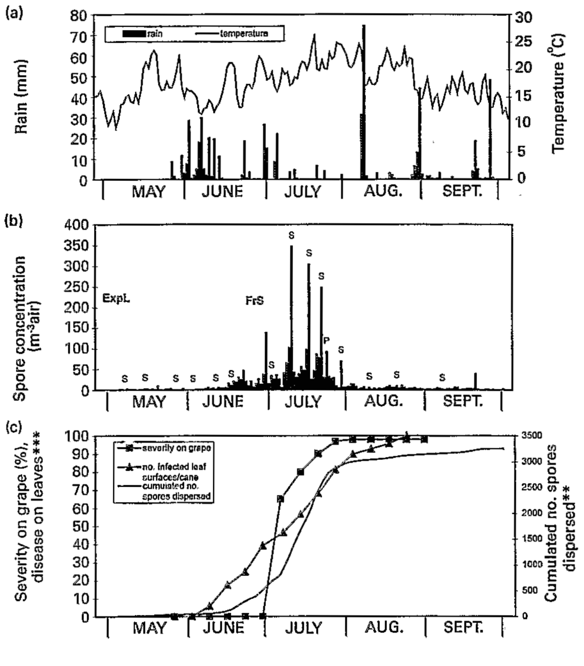

Figure 3 Patterns of weather, spore dispersal, and disease on grape over time for Couhins 1992. (a) Rain and temperature; (b) daily spore dispersal; (c) cumulated daily spore dispersal, disease intensity on leaves, and severity on grape. ExpL and Frs: phenological stages of expanded leaves and fruit set, respectively (Baggiolini, 1952). S, application of fungicide against downy mildew. **Cumulated 7-day moving average of daily spore dispersal; ***cumulated disease intensity on leaf, as a percentage of the final number (34·5).

showed the steepest slope for this period. During this period, the spore concentration was regularly higher than 50 SMSA. Five peaks were detected on 30 June, 10 July, 17 July, 22 July and 31 July. Four of them corresponded to days when sprays against downy mildew were applied. During these days, the peaks were concentrated in one 4-h period, corresponding with the spray timing (data not shown). The day on which pruning was performed also corresponded with a peak of spore release. The period of high spore release coincided with that of disease appearance on leaves and on grapes. The pattern of cumulated number of spores caught was similar to that of the development of leaf disease intensity. At the end of the growing season, a total of 3300 SMSA had been trapped. Within 1 week of the appearance of symptoms, disease severity on grapes increased from 0 to 67%, which was 90% of the final severity. Among the canes sampled for assessment, the first powdery mildew lesions were recorded on 7 June. Until 24 July (pruning date), the intensity of disease on leaves increased linearly. After this date, it increased at a lower rate. Spores were caught before the first powdery mildew lesions were observed on the leaves.

Three common features were observed in the three monitorings: (1) the aerial concentration of conidia started to increase during the first period with no rain (3 weeks in 1991, 1 week in 1992); (2) the onset of the epidemics on grapes started a few days after fruit set, i.e. when the grain size was 3–6 mm; and (3) the dynamics of disease on grape and cumulated spore concentration were similar only at Couhins in 1992.

Variations of 4-hourly spore dispersal within selected periods

Figures 4 and 5 show the variations of aerial spore concentration and weather factors observed at Couhins between 19 June and 2 July 1992, and between 18 and 23 July 1992, respectively. During days with no rain, spore density patterns generally showed a daily, sinusoidal shape, with highest values between 10·00 hours and 18·00 hours, and lowest values between 18·00 hours and 06·00 hours. These patterns were similar to that of wind speed. The spore catch pattern was negatively correlated with that of relative humidity.

Very high numbers of spores were trapped during the 4-hourly periods when fungicides were applied against downy mildew (2 July, fourth time-step and 22 July, third time-step). Rain events were generally associated with higher aerial spore concentrations, even for low rainfalls (e.g. 2 mm on 21 June, last time-step and 1·5 mm on 30 June, first time-step). When rain was recorded during successive periods (on 22 June and 30 June), spore density was the highest during the first rainy interval, and then decreased over the successive ones. However, in spite of rainfalls, low spore concentration was observed on 24 June and 1 July.

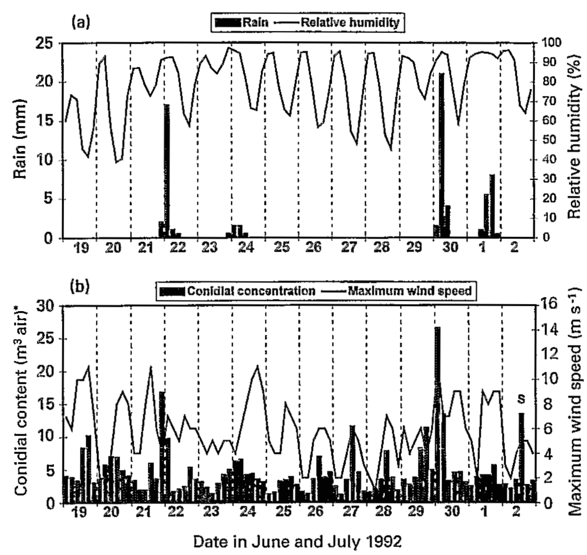

Figure 4 Aerial spore concentration and 4-hourly variations in weather for Couhins from 19 June to 2 July 1992. S, application of fungicide against downy mildew. *Square root transformed values. Each bar represents one time-step.

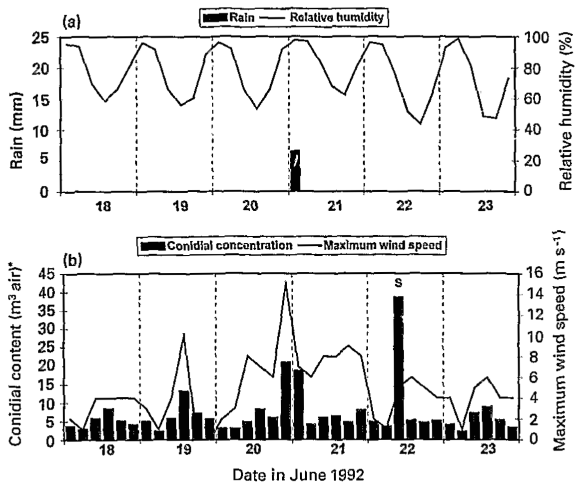

Figure 5 Aerial spore concentration and 4-hourly variations in weather for Couhins from 18 to 23 July 1992. S, application of fungicide against downy mildew; *Square root transformed values. Each bar represents one time-step.

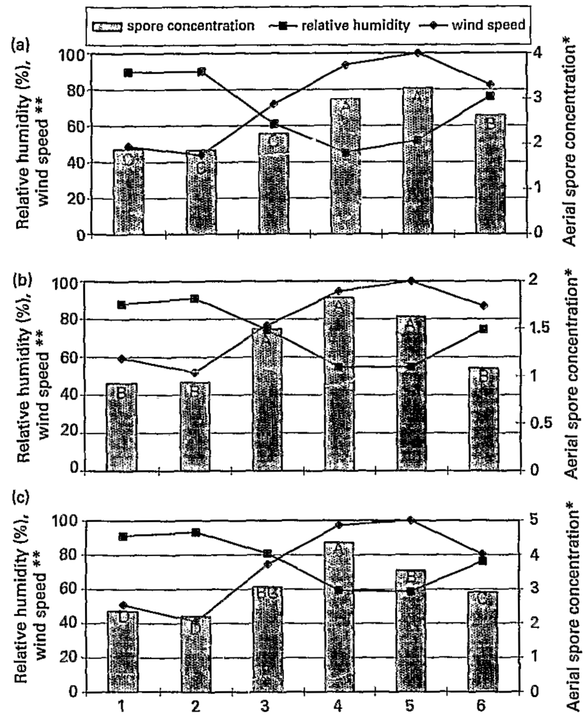

Figure 6 Four-hourly values of aerial spore concentration and weather factors, averaged per time-step (a) for Couhins from 20 May to 25 July 1991, (b) for Creon from 10 May to 25 July 1991, and (c) for Couhins from 15 June to 27 July 1992. Rainy days and days when the canopy was disturbed by spray application or pruning were excluded for the analysis. *Mean over log-transformed air spore content values; **wind speed relative to maximum average, i.e. 8·3 m s-1 for Couhins in 1991 (a), 8·1 m s-1 for Creon (b), and 6·9 m s-1 for Couhins in 1992 (c). In each monitoring, bars from 4-hourly log-transformed air spore content values, labelled with the same letter, are not significantly different according to the Student–Newman–Keuls multiple range test ($P = 0{\cdot}05$).

Average daily variation of wind speed, relative humidity and aerial spore concentration

The range and variation of weather variables over time were similar in the three monitorings (Fig. 6). Wind speed was minimum from 22·00 hours to 06·00 hours, increased during daytime, and was maximum from 14·00 hours to 18·00 hours (8·3, 8·1 and 6·9 m s^{-1} at Couhins in 1991, Creon in 1991, and Couhins in 1992, respectively). Relative humidity showed an opposite pattern, with minimum values of 50 to 60% recorded between 10·00 hours and 18·00 hours.

Aerial conidium concentration was noticeably lower at Creon. Concentrations were highest between 10·00 hours and 18·00 hours, and was lowest from 22·00 hours to 06·00 hours, but was above zero. The pattern of variation in spore dispersal within a day was similar to that of wind speed. Spore dispersal appeared to be primarily a diurnal phenomenon.

Discussion

Daily spore dispersal dynamics, weather patterns and disease epidemics throughout the growing season

In all three observation periods spores were trapped continuously between the onset of spore dispersal and the end of the growing season. This suggests that inoculum was always available, and was not a limiting factor for epidemics.

The patterns of rainfall and spore catches suggested that the onset of spore dispersal occurred during a period of consecutive days with no rain. At Couhins, ascospores and infected buds may be considered as the two sources of primary inoculum. Although flag shoots were observed quite early, no dispersal occurred before the first period with no rain. At Creon, where no flags were observed, ascospores appear to be seen the main source of primary inoculum. At the beginning of the growing season, when the canopy density is still low, even light rain may wash off conidia. In other words, disease increase would be more sensitive to rainfall at the beginning of the growing season. However, the period of rainfall occurring before the onset of spore dispersal may have triggered the liberation of ascospores (Gadoury & Pearson, 1990).

The timing of onset of the epidemics on the grapes seemed to be strongly connected to the phenological stage of the host plant. In the three observation periods, the first infections were observed at fruit set. Epidemics occurred within 3 weeks at Couhins, and no further increase in disease was observed at Creon 5 weeks after epidemic onset. Delp (1954) and Chellemi & Marois (1992) showed that the susceptibility of grapes to powdery mildew declined sharply after fruit set.

The difference in magnitude of the terminal disease severity on grapes between Couhins and Creon could be explained by two main factors. First, the temperature at Creon was on average 5°C higher than at Couhins and temperatures above 30°C occurred more often. Above this level, higher temperatures are unfavourable to grape powdery mildew (Delp, 1954; Chellemi & Marois, 1991). Second, the cropping practices used at Couhins produced a denser, more shady canopy (i.e. higher relative humidity, less radiation and lower temperature), with more young, susceptible leaves. All these factors are favourable to grape powdery mildew (Delp, 1954; Chellemi & Marois, 1991; Willocquet *et al.*, 1996).

At Couhins in 1992, the spores trapped before powdery mildew was detected on the sampled canes were probably dispersed from the flag shoots. A comparison of cumulated spore catches, and grape and leaf disease intensity curves, indicates that the dispersed spores originate from the leaves throughout the growing season, and from the grapes also when the disease epidemic occurs.

Fungicide application and rain effects on spore dispersal

Fungicide application against downy mildew at Couhins in 1992 induced a high wind speed at the level of the canopy (30 m s^{-1}). It may be assumed that nearly all the powdery mildew conidia were removed from the colonies, by the direct effect of air turbulence and also by shaking of infected leaves. The observed high spore density shows that an important stock of conidia was then present in the vineyard, that had not previously been spontaneously dispersed. This suggests that grape powdery mildew conidia are not easily removed under conditions prevailing naturally.

In contrast, at Creon, sprays did not cause such high spore release. There may be two main reasons for this: either disease severity on grapes and leaves was low, and thus the stock of spores was also low, or the sprayer produced lower wind speeds and disturbances than the one used at Couhins.

Sprays operated with equipment blowing a mixture of air and pesticide suspension at high flow rates are likely to induce high turbulence within the canopy. This may result in shaking of infected leaves, in addition to high air speeds at the sites of sporulating powdery mildew lesions. Spraying preventive fungicides against powdery mildew with high pressure sprayers might enhance fungicide efficiency as it induces spore dispersal and spore deposition when fungicide concentration is highest. In contrast, high pressure sprays applied against other harmful agents (insecticides, or fungicides specific to other diseases such as downy mildew) could enhance powdery mildew epidemics.

Light rainfall may induce high spore dispersal. Two main mechanisms are involved, the splash effect (Gregory, 1961) and the rain tap and puff effect (Hirst & Stedman, 1963). The latter can disperse dry spores in two ways, by mechanical shaking (tap) and radial air movements due to droplets dispersal (puff) (Hirst & Stedman, 1963). This tap and puff mechanism was shown to be important in the dispersal of groundnut rust (Savary & Janneau, 1986) and is likely to be important for the dispersal of powdery mildews. In the case of grape powdery mildew, the rain tap effect might be important both quantitatively and qualitatively for two reasons. First, germination of *U. necator* conidia is negatively affected by the presence of free water (Delp, 1954; Weltzien-Stenzel, 1959). Thus, the germination of conidia dispersed by rain splash may be hampered compared with that of dry spores. Second, powdery mildew colonies are mostly located on the lower surface of leaves, especially at the beginning of the growing season. As these colonies are not likely to be hit by rain drops, the rain tap effect may be the most important mechanism of spore dispersal by rain. In the vineyard, light rainfall can thus be considered as favourable to the fungus, as it would allow dispersal without the drawbacks associated with heavy or continuous rain.

Under continuous rain, the conidial stock is likely to decrease and conidia may be washed off leaves, leading to a decrease in spore concentration, as observed on 22 and 30 July 1922 at Couhins. Such decreases during rain have been reported for other powdery mildews (Fernando, 1971; Hammett & Manners, 1971; Sutton & Jones, 1979; Pauvert, 1986). Continuous rainfall is also likely to be unfavourable to grape powdery mildew because of physical damage to leaf surface mycelium and conidiophores.

In spite of rain events, low spore densities were observed on 24 June and 1 July 1992 at Couhins. This could be explained by the fact that large amounts of spores had been released 2 days earlier in both cases. At the time of these rainfalls, the stock of conidia may not have been replenished. In contrast, fungicide applications on 2 July 1992 at Couhins, 2 days after a high spore release, led to high aerial spore density (1485 SMSA). Possible explanations for this difference in effect of rainfall and fungicide application might be that either the spore stock had already been replenished by the time the fungicide was applied, or only a fraction of the spores present 2 days previously had been released during the rainfall.

Patterns during days with no rain

Dispersal in *U. necator* is a process with daily periodicity and occurs mainly during daytime. Such a trend has been reported for other powdery mildews, on barley (Sreeramulu, 1964; Pauvert, 1986), wheat (Hammett & Manners, 1971), rose (Packham, 1969), tobacco (Cole, 1966), apple (Sutton & Jones, 1979) and rubber (Fernando, 1971), and for many other diseases (Aylor, 1990).

High wind speed and low relative humidity seem to be the main factors associated with the diurnal spore dispersal. This pattern is common to many aerial fungi (Zadoks & Schein, 1979). Similar associations were observed in apple powdery mildew (Sutton & Jones,

1979) and wheat powdery mildew (Hammett & Manners, 1971).

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