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Effects of wind, relative humidity, leaf movement and colony age on dispersal of conidia of *Uncinula necator*, causal agent of grape powdery mildew

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A wind tunnel was designed to study the effect of wind, relative humidity, leaf movement and colony age on dispersal of conidia of *Uncinula necator.* Wind speed as low as $2{\cdot}3\,\mathrm{m\,s^{-1}}$ instantaneously triggered dispersal of conidia from fixed leaf discs of 18-day-old infections. Conidia were observed on sporulating leaf discs even after exposure to $17\,\mathrm{m\,s^{-1}}$ wind. The fraction of conidia dispersed at a given wind speed increased with colony age from 12 to 24 days. Conidia of 27-day-old colonies were less easily dispersed. No gradient of maturation of conidia along the conidial chain was observed, suggesting that even newly formed conidia were able to germinate after dispersal. Germination of dispersed conidia decreased slightly with greater colony age. Both wind and simulated rain drops caused dispersal of conidia from infected leaves. Leaf movement at wind speed of $3{\cdot}5$–$4\,\mathrm{m\,s^{-1}}$ increased dispersal, and the first impact of three simulated raindrops caused release of 53% of the total conidia dispersed. Relative humidity had no effect on dispersal of conidia at different wind speeds.

Introduction

Powdery mildew of grape caused by *Uncinula necator* is found in most grape growing areas in the world (Pearson & Goheen, 1988). The disease may reduce plant growth and vine yield (Pool *et al.*, 1984). Fruit and wine quality is also reduced by powdery mildew infections (Ough & Berg, 1979; Pool *et al.*, 1984). Dispersal of conidia is an important factor in polycyclic, aerially dispersed diseases such as grape powdery mildew, as it determines both the temporal and the spatial extension of epidemics (Aylor, 1990).

Dispersal of conidia in powdery mildews is a passive process (Butt, 1978) triggered by various weather factors including wind, humidity and rain. Wind has a major effect in dispersing conidia from leaves as has been shown both in the field (Hammett & Manners, 1971) and under controlled conditions (Hammett & Manners, 1974; Pauvert, 1984). Minimum wind speed for dispersal of conidia depends on density of conidia, as shown for barley powdery mildew (Pauvert, 1984). Wind may indirectly induce dispersal by causing leaf movement in the crop canopy (Bainbridge & Legg, 1976). A decrease in relative humidity (r.h.) has been related to an increase in dispersal of conidia in some cases (Leach, 1975; Adams *et al.*, 1986), but not in others (Hammett & Manners, 1974; Pauvert, 1986). The 'tap and puff mechanism' (Hirst & Stedman, 1963) by which raindrops cause dispersal of dry conidia, also disperses conidia of powdery mildews, as indicated by peaks of conidia concentration observed in the field at the onset of rainfalls (Fernando, 1971; Hammett & Manners, 1971; Sutton & Jones, 1979; Pauvert, 1986). Rainfall was also shown to be an important factor for dispersal of conidia of *U. necator* (Willocquet & Clerjeau, 1998).

The age of conidia that have been dispersed and deposited is also important, as it affects the efficiency of inoculum. For instance, Pauvert (1986) found a maturity gradient along the conidial chain in barley powdery mildew. The oldest conidia, located at the tip of the chain, had the highest germinability. In this case, the spores at the tip of the chain, which are the most readily available for dispersal, also represent the most efficient form of inoculum.

Information on the effect of environmental factors such as wind speed, r.h. and rainfall is important for developing more efficient methods for management of powdery mildew of grape. This paper addresses the relationships between such factors and the dispersal of the pathogen. In particular, the effects of wind, r.h., leaf movement, and colony age on dispersal of conidia are

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investigated under controlled conditions. The effect of the age of conidia on their viability after dispersal is also studied.

Materials and methods

Production of sporulating leaf discs

All experiments used a monoconidial culture (R7) isolated in 1990 in Carregado, Portugal. Discs (14 mm diameter), from leaves of 2-month-old grapevine cuttings (cv. Cinsault) grown in the glasshouse (Steva & Clerjeau, 1990), were surface disinfected and placed in Petri dishes on an agar medium ($20\,\mathrm{g\,L^{-1}}$) supplemented with benzimidazole ($30\,\mathrm{mg\,L^{-1}}$). The inoculations were made in a plexiglass settling tower with a square section (20 or 30 cm) and 60 cm high (Willocquet *et al.*, 1996). Petri dishes containing the leaf discs were placed at the bottom of the tower. Spores were dispersed from a sporulating leaf on the top of the tower. This leaf had been infected 12–14 days earlier and incubated at 21°C ($30\,\mu\mathrm{E\,m^{-2}\,s^{-1}}$, 8 h/16 h photoperiod). Air was blown from the tip of a Pasteur pipette connected to an oxygen pump over the sporulating leaf. The density of deposited conidia was checked with a haemocytometer placed at the bottom of the tower, and ranged from 300 to 600 spores per $\mathrm{cm^2}$. The inoculated discs were incubated at 20°C (light intensity $25\,\mu\mathrm{E\,m^{-2}\,s^{-1}}$, 12 h/12 h photoperiod) for 12–28 days, depending on the experiment.

Equipment

The wind tunnel used in these experiments had three plexiglass components (Fig. 1). Component A consisted of three linked sections, the first, a 72 mm diameter, 30 mm long cylinder, containing an axial fan connected to a tension regulator, allowing regulation of wind speed. The second section was a 100 mm long funnel-shaped tube, tapering from 72 to 30 mm. The third section, a 30-mm diameter, 150 mm long cylinder, was pierced by a hole through which a hot-wire anemometer (TESTO 491, TESTOTERM, Forbach, France; precision of 2·5, 4, and 5% for wind speed ranges of 0–3, 3–10, and $10\text{–}60\,\mathrm{m\,s^{-1}}$, respectively) could be inserted to measure the wind speed near the sporulating leaf disc. Component B, a 30 mm diameter, 100 mm long cylinder, was the sample chamber. On the inner edge of this, next to component A, a removable ring (16 or 30 mm interior diameter, 20 mm long) could be inserted (Fig. 1, shaded). The ring was used to insert two types of sample stands, one being a horizontal, vaseline-coated plastic plate, on which the sporulating leaf disc was placed and remained fixed, and the other a vertical flexible needle onto which the sporulating leaf disc was pinned and was thus free to vibrate when exposed to wind. This second stand was used to study the effects of leaf movement and rain tap. The final component (C) was an 80 mm long funnel-shaped tube, tapering to a 13·3 mm diameter orifice. To simulate wind speeds lower than $4{\cdot}4\,\mathrm{m\,s^{-1}}$, the wind tunnel was used with all three components, and the 30 mm diameter removable ring was installed. To simulate higher wind speeds, (up to $17\,\mathrm{m\,s^{-1}}$), the internal diameter of the wind tunnel had to be reduced. Two adjacent rings (100 mm long and 16 mm diameter each) were then inserted in the components A and B, and the 16 mm diameter removable ring was used. Component C was removed. Given the internal diameter of the wind tunnel, and according to Poiseuille's law, the flow was laminar in all the experiments.

A hole, 2 mm in diameter, drilled above the sample stage in component B, allowed access for investigating the rain tap effect. To simulate the impacts of raindrops, lead beads were dropped on the sporulating leaf disc from the top of a vertical hollow cylinder fixed above the hole.

Humidity control was obtained by mixing dry and saturated air, passed through a drier and humidifier, respectively (Fig. 2). The drier consisted of a 15 cm diameter, 25 cm long plastic cylinder filled with silica gel. The humidifier was a similar cylinder filled with soaked corrugated paper. A 75 W lamp 5 cm away provided heat to increase water evaporation from the paper. The drier and humidifier were extended by 30 cm long parallel plastic tubes, which merged into a main tube (20 cm long) fixed to the wind tunnel, next to the fan. A hole was drilled in the main tube to insert a hygrometer sensor (model H 6·2 sensor connected to a portable hygrometer indicator HUMICOR 1100, CORECI, Lyon, France; precision of 2% within a 20–100%

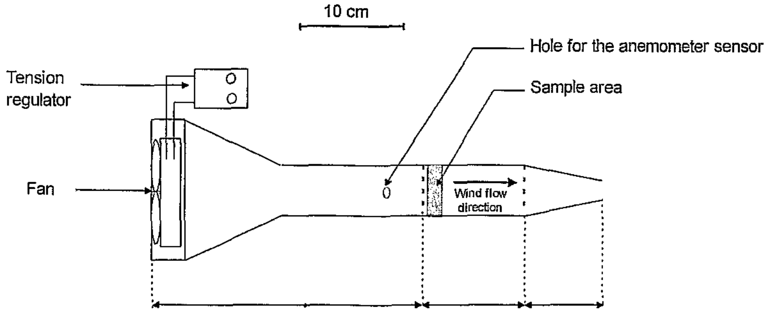

Figure 1 Configuration and structure of the wind tunnel. See text for details.

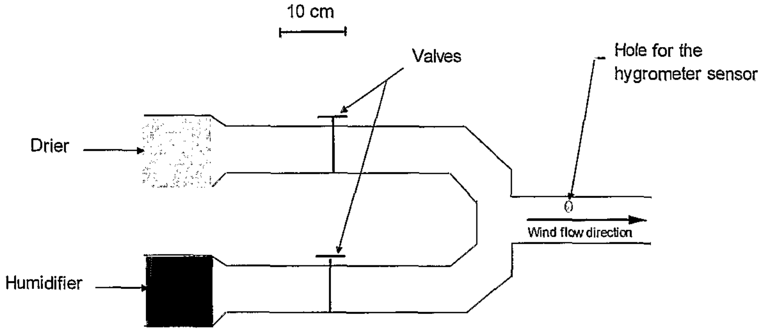

Figure 2 Configuration and structure of the relative humidity regulator. See text for details.

range). Each parallel tube was equipped with a valve. Dry and nearly saturated air could be combined in different proportions by operating the two valves. The r.h. could be lowered or raised within the range of 20%-100% within 3 min. When the humidity device was connected to the wind tunnel, the maximum wind speed achievable, measured with the anemometer, was 3·6 m s^{-1} for low r.h. (20%) and 17 m s^{-1} for high r.h. (>90%).

Conidia traps, sample assessment and conidia viability

Conidia were sampled by two methods, using Petri dishes with water agar on which germination of conidia was assessed and using vaseline-coated glass slides. The sampling surfaces were placed vertically, 7 mm beyond the end opening of the wind tunnel. This allowed sampling of a large fraction of dispersed conidia, without altering the speed of air flowing out of the wind tunnel.

Conidia were concentrated on the slides or Petri dishes in an ellipsoidal zone, the length of which corresponded to the diameter of the sporulating leaf disc. One drop of Cotton Blue was placed on the zone, and covered with a cover slip. The numbers of conidia and their viability were observed under a microscope (100×).

The optimal counting method was chosen depending on the number of conidia sampled. Four counting methods were used, depending on the density of sampled conidia: (a) on the total area of the slide (0 to about 50 conidia), (b) on two strips (2 mm wide), along the whole length of the ellipse (about 50–200 conidia), (c) on one strip only (2 mm), sweeping the length of the ellipse along its central axis (about 200–500 conidia), or (d) on one-quarter of each adjacent microscope field, along the length of the ellipse, on the central axis (more than 500 conidia). The conversion factor to convert counts from method b to method a was set to 6·8, based on counts made on 15 slides using the two methods. As conidia were uniformly distributed on the area swept in method b, the factors to convert counts from method c to b, and from method d to c were set to 2 and 10·18, respectively. Counts were made by methods a and b, b and c, and c and d on a set of 15 slides, 10 Petri dishes, and 10 Petri dishes, respectively, that had sampled the corresponding ranges of conidia numbers (see above). For each of the three comparisons, the two counting methods did not yield statistically different results ($P>5\%$), using the comparison of means test with paired observations.

To assess viability, conidia were sampled on water agar in Petri dishes and incubated at 20°C for 48 h (light intensity 25 μE m^{-2} s^{-1}, 12 h/12 h photoperiod). Conidia were stained with Cotton Blue and germination was measured using a microscope (100×). A conidium was considered germinated when the germ tube was at least as long as the width of the conidium (Manners, 1966). The proportion of germinated conidia was estimated from at least 50 conidia per replication.

Experimental design

In all experiments, a complete randomized block design with five replications was used. One experimental unit consisted of a sporulating leaf disc, and each leaf from which discs had been cut was considered a block. For each experiment, leaf discs were inoculated with the same source of inoculum. For example, in an experiment where dispersal of conidia was compared for colonies of seven ages, seven discs were cut from each of five vine leaves, and the 35 discs were inoculated at the same time. Unless stated otherwise, the number of conidia sampled was expressed as a percentage of the total conidia dispersed during the whole experiment.

Experimental procedure

Each sporulating leaf disc was placed on the chosen stand and then placed in the wind tunnel, and the first trap was positioned at the end of the tunnel. Before each change of experimental conditions the exposed trap was replaced by a new one.

Effect of wind duration on dispersal of conidia

The sporulating leaf discs were exposed to a continuous wind for 5 min. During this period, successive new traps were positioned at time 0, and after 10, 30 and 60 s. The experiment was conducted twice, each time at wind speeds of 5·2, 10·4 and 17 m s^{-1}.

Effect of colony age on the dynamics of dispersal of conidia

Different sets of five leaf discs were tested every third day from day 12 to day 27 after inoculation. A sporulating leaf disc was successively exposed to increasing wind speeds, from 0·4 to 17 m s^{-1} (0·4, 1·4, 2·3, 3, 3·5, 4, 4·4, 5·2, 7·9, 10·4, 12·9, 15·1, 17). A new trap was positioned before any change in wind speed.

Effect of colony age and wind speed on the number and viability of dispersed conidia

Different sets of five sporulating leaf discs were tested every third day from day 15 to day 24 after inoculation. Each infected leaf disc was successively exposed to wind speeds of 5·2, 10·4 and 17 m s^{-1}. A new trap was positioned for each wind speed tested. For each leaf disc and wind speed, the number of conidia dispersed per cm^2 of sporulating leaf disc was determined, and the viability of the dispersed conidia assessed. The total number of conidia dispersed per cm^2 of sporulating leaf disc and the number of viable conidia dispersed per cm^2 were expressed as percentages of the highest value obtained among all the colony age × wind speed combinations. The experiment was repeated.

Effect of leaf movement on dispersal of conidia

A 0·8 × 0·8 cm square and a 0·8 × 4 cm segment were collected from a sporulating leaf. The leaf segment was pinned onto the needle 3 mm from its edge, placed in the wind tunnel, and successively exposed to wind speeds of 0·4–4·4 m s^{-1} (0·4, 1·3, 2·3, 2·9, 3·5, 4, 4·4). The leaf square was placed on a vaseline-coated plate and exposed to wind at 17 m s^{-1}. The number of conidia dispersed from the leaf segment at each wind speed was expressed as the percentage of the number of conidia dispersed at 17 m s^{-1} from the leaf square, after standardizing over the area of the leaf samples. The fraction of spores dispersed was compared with that from leaf discs having a similar spore density that were installed on a vaseline-coated plate and exposed to increasing wind speeds. The data were taken from the experiment on the effect of colony age on the dynamics of dispersal of conidia.

Simulation of the rain tap effect

Each sporulating leaf disc was exposed to a constant wind speed of 2·3 m s^{-1}. This speed was sufficient for conidia to be dispersed through the rain tap effect and transported to the sampling point and only a very small fraction of conidia would be dispersed directly by the airflow at this speed (cf. Fig. 3). Three lead beads were dropped on the leaf disc at 30, 60, and 90 s after applying the wind. New traps were positioned before each bead drop. The experiment was repeated.

Effect of r.h. on minimum wind speed for dispersal of conidia

Relative humidity was fixed at 20% or 100% in still air within 2 min after positioning the sporulating leaf disc. The disc was exposed to six successive wind speeds of 1–3·9 m s^{-1} at 100% r.h. and from 0·6 to 3·6 m s^{-1}, at 20% r.h.

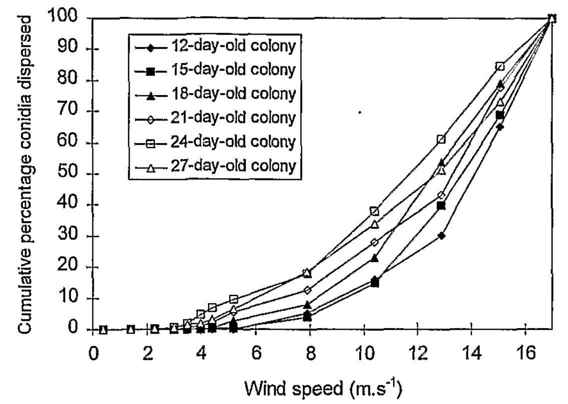

Figure 3 Effect of wind speed and colony age on *U. necator* spore dispersal. Each data point represents the mean of five replicate leaf discs.

For varied r.h., each sporulating leaf disc was exposed to 100% r.h. for 5 min and then to 20% r.h. for 30 min. The experiment was repeated, at wind speeds of 1 and 3 m s^{-1}.

The temperature during the experiments ranged between 26 and 30°C.

Calculation of the required mass of the lead bead for the simulation of the rain tap effect

The height from which the bead was dropped was such that the kinetic energy of the bead was equal to that of a raindrop. The kinetic energy of a raindrop (with mass m_r, in kg; and with speed v, in m s^{-1}) is:

$$Ec_r = 1/2^* m_r^* v^2 \qquad (1)$$

The terminal fallspeed of a raindrop (with diameter d, in cm) is (Atlas & Ulbrich, 1977):

$$v = 17{\cdot}67\ ^*d^{0{\cdot}67} \qquad (2)$$

Considering a raindrop as a sphere, Eqn 1 becomes:

$$Ec_I = 39{\cdot}128\ ^*10^6\ ^*D^{4.34} \qquad (3)$$

where D is the diameter of the sphere (m).

The kinetic energy of a lead bead of mass m_l (kg), dropped from a height H (m) is:

$$Ec_l = m_l\ ^*g^*H \qquad (4)$$

where g is the acceleration due to gravity (9·81 m s^{-2}).

To simulate the kinetic energy of a 2-mm diameter raindrop fall, a 0·18-g lead bead was dropped 4·3 cm onto a sporulating leaf disc. Keklar (1961) showed that raindrops 2–5 mm predominate at high intensity rainfall (> 15 mm h^{-1}), and represent 10% of raindrops at low intensity rainfall (< 5·4 mm h^{-1}).

Estimation of the fraction of dispersed conidia at different wind speeds

If $y(u)$ is the accumulated fraction of conidia dispersed from a sporulating leaf disc at a given wind speed, u, and if the leaf is subject to increasing wind speeds then $y(u)$ reflects dispersal of conidia that occurred at the different wind speeds, until the current wind speed, u, is reached.

Thus dy/du is the fraction of conidia that are dispersed per unit of wind speed increase and is assumed to be proportional to the accumulated fraction of conidia that have been dispersed (y), and to the fraction of conidia still present on the leaf disc $(1-y)$:

$$dy/du = r^{*}y^{*}(1-y) \qquad (5)$$

In this equation, r is the relative increase of dispersed conidia per unit of wind speed increase, relative to the fraction of conidia available for dispersal. Integrating Eqn 5:

$$y = \exp(r^{*}u + b)/(1 + \exp(r^{*}u + b)) \qquad (6)$$

When $u=0$, $b=\ln\ (y/(1-y))$. Therefore the absolute value of b reflects the capacity of a lesion to withhold conidia when there is no wind.

Furthermore, if: (i) N_T is the total number of conidia on an infected leaf disc; (ii) N_{17} is the total number of conidia dispersed after successive exposures to wind speeds from 0 to 17 m s^{-1} (within the duration of one test); (iii) n is the number of conidia dispersed after successive exposures to wind speeds from 0 to u, then $n/\mathrm{N}_{17}=x$, is the running fraction of accumulated, dispersed conidia, relative to the total number of conidia dispersed during one test. y can be written as $y=n/Nt$, hence $y=x^{*}\mathrm{N}_{17}/\mathrm{N}_\mathrm{T}$. $a=\mathrm{N}_{17}/\mathrm{N}_\mathrm{T}$ gives:

$$x = \exp(r^{*}u + b)/(a^{*}(1 + \exp(r^{*}u + b))) \qquad (7)$$

Parameters a, r, and b were estimated from the data collected in the experiment 'Effect of colony age on the dynamics of dispersal of conidia' for each colony age by using the nonlinear regression procedure (NLIN) of SAS (SAS, 1988).

Results

Effect of wind duration on dispersal of conidia

Most conidia were dispersed within the first 10 s of wind exposure (81, 69 and 88% at wind speeds 5·2, 10·4 and 17 m s^{-1}, respectively). Within the first 30 s 90% or more were dispersed (Table 1). In all further experiments, the standard period of exposure to wind for each condition tested was thus set to 30 s, sufficient for dispersal of conidia, and allowing enough time to position a new trap and record wind speed.

Table 1 The effect of wind duration and wind speed on the percentage dispersal of conidia of *U. necator* from leaf discs in the wind tunnel

Sampling period (after initiating wind) (s)	Wind speed (m s^{-1}) 5·2[a]	10·4	17
0–10	81 a[b]	69 a	88 a
10–30	11 b	21 b	7 b
30–60	4 b	6 b	3 b
60–300	4 b	4 b	2 b

[a]Numbers followed by the same letter in each column are not significantly different according to Student–Newman–Keuls multiple range test ($P=5\%$). Each number represents the mean of two experiments. [b]Expressed as a percentage of the total number of spores sampled at each wind speed.

Effect of colony age on the dynamics of dispersal of conidia

Leaf discs were sporulating 12 days after inoculation and most conidiophores carried at least one conidium. Sporulation increased until day 24 after inoculation, when most conidiophores carried four or five conidia. By day 27, conidia began to aggregate between chains.

For all colony ages the accumulated percentage of dispersed conidia increased with wind speed (Fig. 3). Increasing numbers of conidia were dispersed by the successive exposures to greater wind speeds. However, even after successive wind speed exposures up to 17 m s^{-1} sporulating discs still had numerous conidiophores with three or four conidia.

In general, the fraction of conidia dispersed at low wind speed increased with colony age although this was not the case with the 27-day-old colonies. The minimum wind speeds for dispersal of at least one conidium from at least three sporulating leaf discs out of five were 7·9, 7·9, 5·2, 3·5, 2·3, and 3·5 m s^{-1} for colonies aged 12, 15, 18, 21, 24 and 27 days, respectively.

The accumulated fraction of dispersed conidia at different wind speeds was described by Eqn 7. In all regressions, R^2 was greater than 99% (Table 2). For 12-, 15- and 18-day-old colonies, the estimated fraction of conidia dispersed after exposures to wind speeds up to 17 m s^{-1} increased with colony age, r-values being greatest for the youngest colonies. On average, 0·3–0·5 conidia were dispersed per conidium available for dispersal and per wind speed unit. In general, the absolute value of b decreased with colony age. There was no consistent trend in the predicted fraction of spores released as a result of colony age, although the lowest fraction was produced from the shortest incubation period.

The effect of wind on dispersal of conidia is instantaneous, so it may be assumed that $y(u)$, in eqn 6, represents the fraction of conidia instantaneously dispersed by exposure to wind with speed u. This relationship is shown for different colony ages in Fig. 4. The results show that a wind speed of at least 25 m s^{-1} would be necessary to disperse more than 90% of the conidia on infected leaves. Only a very small proportion of the conidia are dispersed for wind speeds lower than 5 m s^{-1}.

Table 2 Nonlinear regression analyses[a] of the cumulative fraction of dispersed conidia of *U. necator* by all wind speeds tested on different colony ages

Colony age (day after inoculation)	a^b	r^b	b^b	Sum of squares (regression)	Sum of squares (residual)	Coefficient of determination (R^2)
12	0·53 (0·08)	0·41 (0·03)	−6·90 (0·26)	1·5431	0·0021	99·8
15	0·72 (0·04)	0·47 (0·02)	−6·99 (0·25)	1·6533	0·0012	99·9
18	0·85 (0·03)	0·47 (0·02)	−6·33 (0·23)	1·9691	0·0015	99·8
21	0·66 (0·09)	0·35 (0·03)	−5·35 (0·27)	1·8842	0·0063	99·5
24	0·84 (0·04)	0·37 (0·02)	−4·65 (0·18)	2·2794	0·0034	99·7
27	0·69 (0·10)	0·32 (0·03)	−4·69 (0·25)	1·9437	0·0093	99·3

[a] The equation tested was $x = \exp(r{*}u + b)/(a{*}(1 + \exp(r{*}u + b)))$. See text for details.
[b] Estimates are followed by their asymptotic standard error.

Effect of colony age and wind speed on the number and viability of dispersed conidia

Sporulation was greater in the second replication than in the first one. The greatest number of dispersed conidia was obtained at 17 m s^{-1} wind speed using 24-day-old colonies, i.e. 5000 and 18 900 conidia per cm^2 of leaf disc for replicates 1 and 2, respectively. The number of conidia dispersed increased with colony age, as well as with wind speed (Fig. 5a). Conidia germination decreased slightly with colony age, from 89–97% for 15-day-old colonies to 69–83% for 24-day-old colonies (Fig. 5). Germination was not affected by wind speed. In spite of the decrease in germination rate with time, the number of dispersed viable conidia increased with colony age (Fig. 5c). The variation of number of dispersed viable conidia with colony age and wind speed was similar to that observed for the number of dispersed conidia.

Effect of leaf movement on dispersal of conidia

The onset of dispersal of conidia occurred at a wind speed of 2·3–2·9 m s^{-1}, when the first leaf segment movement was observed (Fig. 6). At 4·4 m s^{-1}, 23% of conidia were dispersed from the movable leaf segment,

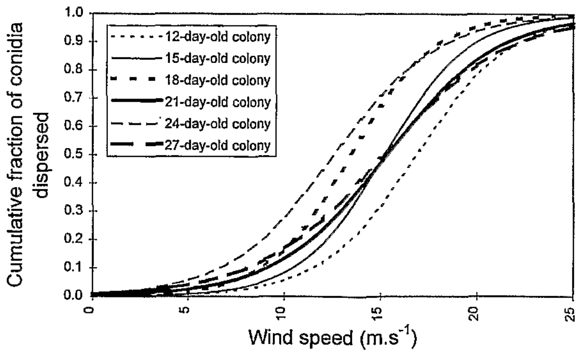

Figure 4 The predicted fraction of dispersal of conidia of *U. necator* relative to wind speed for different colony ages. Values were estimated from Eqn 6 using parameters shown in Table 2.

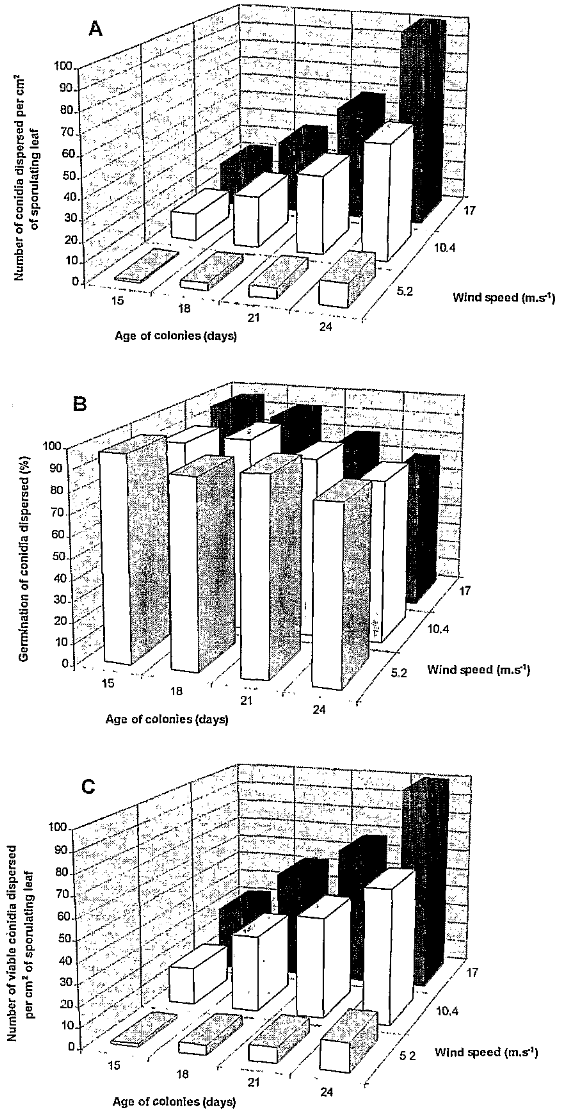

Figure 5 Effect of wind speed and colony age on dispersal and viability of conidia of *U. necator* (A) fraction of conidia dispersed, (B) germination of conidia dispersed, and (C) fraction of conidia dispersed that are viable. Percentage, relative to the maximum conidia dispersed for each experiment.

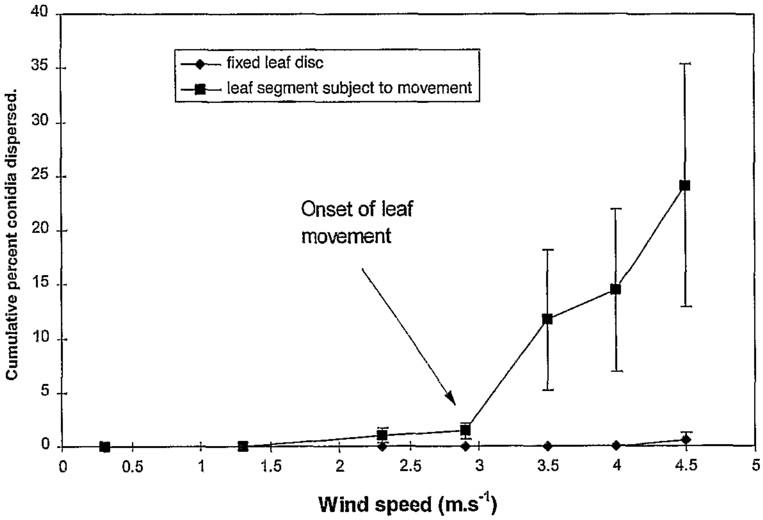

Figure 6 Effect of leaf movement on dispersal of *U. necator* conidia. Each data point represents the mean of five replicate leaf discs. Each bar represents the standard error of the mean. 'Fixed leaf disc' data taken from Fig. 3, 18-day-old colonies.

whereas < 1% were dispersed from leaf discs installed on the vaseline-coated plate.

Simulation of the rain tap effect

The percentage of dispersed conidia (arcsine transformed) did not differ significantly over the two replications ($P = 0{\cdot}79$). The effect of impact of lead beads was significant ($P = 0{\cdot}02$). Before the first impact (control), 2% of conidia were dispersed. Dispersal, according to the Student–Newman–Keuls grouping, was 53% (a), 27% (b) and 18% (c) after the first, second, and third impact, respectively. All three lead beads drops induced significantly greater ($P = 0{\cdot}05$) dispersal of conidia than that of the control (d).

Effect of r.h. on the minimum speed for dispersal of conidia

At fixed r.h., totals of seven and 17 conidia were sampled from the five leaf discs tested at 100% and 30% r.h., respectively. At varying r.h., the total was three conidia from the five leaf discs when the r.h. was varied from 30 to 100% at wind speeds of 1 and 3 m s^{-1}.

Discussion

Effect of wind on dispersal of conidia

These results show that wind causes an instantaneous dispersal of conidia of *U. necator*. Wind dispersal has previously been observed for other powdery mildews (Hammett & Manners, 1974), as well as many other fungi (Zoberi, 1961; Aylor, 1990). Greater wind speed resulted in more conidia of *U. necator* being dispersed. The dispersal may be increased yet further by gusts of wind, as suggested by Aylor (1990), but this was not investigated in this study.

The minimum wind speed required to cause conidial dispersal was 2·3 m s^{-1}, which is noticeably higher than that observed for barley powdery mildew (0·2 m s^{-1}) (Pauvert, 1986). In *U. necator*, conidia seem thus to have a comparatively low ability for wind dispersal. Although high wind speed (17 m s^{-1}) caused dispersal of a high proportion of the conidia, it is unlikely the crop canopy would be subject to such high wind speeds. In the Bordeaux area, maximum wind speeds greater than 10 m s^{-1} (36 km h^{-1}) are infrequent (Willocquet & Clerjeau, 1998) and wind speed at the level of the canopy is generally lower than 2 m s^{-1}. The low ability of *U. necator* for wind dispersal may explain why events of large dispersal were observed at particular times such as during intense rainfall or when pesticides were applied by high pressure sprayers (Willocquet & Clerjeau, 1998). Large numbers of conidia occur in the vineyard canopies but are not dispersed by the prevailing wind until they are dislodged from the leaves by rain or mechanical intervention.

Leaf movement caused by low wind speeds was shown to result in dispersal of conidia. A similar trend was observed in previous experiments with barley powdery mildew (Bainbridge & Legg, 1976). Conidia deposited on the wall of the wind tunnel were not taken into account in the present study when calculating the number of dispersed conidia, therefore the effect of leaf movement on dispersal may have been larger than that measured. Leaf movement by wind may thus represent an important mechanism for dispersal of conidia in grape powdery mildew.

The minimum wind speed for dispersal of conidia decreased with increasing colony age, probably in relation to greater sporulation, and longer chains of conidia. Apical conidia are likely to be placed under conditions more favourable for their liberation, i.e. higher wind speed and lower r.h.. A positive relationship between dispersal of conidia by wind and conidia density was also observed in barley powdery mildew (Pauvert, 1986).

Effect of colony age and conidia age on germination of dispersed conidia

Germination of dispersed conidia was not affected by wind speed. Assuming that apical conidia were dispersed by a low wind speed, and that conidia located close to the conidiophore were liberated only by strong wind, no germination gradient occurred along the conidial chain of *U. necator.* As a result, conidia are able to germinate as soon as they are formed. This contrasts with barley powdery mildew, where germination gradients exist, and the germination rate of less mature conidia is lower than 30% (Pauvert, 1986).

Germination of dispersed conidia declined with colony age, but still remained high, even 12 days after the start of sporulation. This may be explained by favourable conditions to which sporulating leaf discs were exposed before the tests (high r.h., low light intensity, moderate temperature, high leaf susceptibility).

Effect of r.h. on dispersal of conidia

Relative humidity appeared to have no effect on the minimum wind speed for dispersal of conidia. Similar results were obtained with barley powdery mildew (Pauvert, 1986) and wheat powdery mildew (Hammett & Manners, 1974).

Rain tap effect

As in the leaf movement experiment, numerous conidia were found on the wind tunnel wall after the lead bead impacts. The effect of simulation of raindrop fall on dispersal of conidia was thus underestimated in our experiments. However, rain tap clearly triggers dispersal of *U. necator* conidia. This confirms observations made in the vineyard, where conidial dispersal occurred at the onset of rainfall (Willocquet & Clerjeau, 1998). The decline in the number of dispersed conidia over successive lead bead drops suggests that the impacts resulted in exhaustion of conidia populations on the leaf discs. Similar patterns of conidial concentration in the air were observed under field conditions for *U. necator* (Willocquet & Clerjeau, 1998), and for other powdery mildews (Hammett & Manners, 1971; Sutton & Jones, 1979; Pauvert, 1986). In these cases, spore density was the highest at the onset of rainfall, and then decreased over the remaining rainfall period.

Our method allowed simulation of the energy of raindrops according to their size. It thus enabled an accurate and precise quantification of the rain tap effect. Other devices that generate rainfall (Hirst & Stedman, 1963; Fitt *et al.*, 1986; Savary & Janneau, 1986) have produced raindrop sizes ranging from 2 to 5 mm. In these cases, the overall effect of a rainfall (both the splash effect and the rain tap and puff effect) could be quantified. The lead beads simulated the energy of raindrops, but not their mechanical properties: therefore, only the rain tap effect could be quantified. However, the same device could be used with water drops to provide additional information on the effects of rain on dispersal of conidia in *U. necator*, and quantify with precision the relative importance of rain tap, rain puff and rain splash effects. For grape powdery mildew, the rain tap effect might be more important than the rain splash effect, both quantitatively and qualitatively, for two reasons (Willocquet & Clerjeau, 1998). First, germination of conidia of *U. necator* 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 leaf surface, especially at the beginning of the growing season. These colonies are not likely to be hit by rain drops, thus the rain tap effect may be the most important mechanism of spore dispersal by rain. Continuous rainfall is unfavourable to grape powdery mildew, because of disorganization of the mycelial network, weakening conidiophores, wetting of the leaf surface (which hampers spore germination), and washing off of conidia. In the vineyard, light rainfall can thus be considered as favourable to the fungus, allowing its dispersal without the drawbacks associated with heavy rain.

Implications for the disease management

Vine pruning (or other vine management causing leaf movement in the canopy), high-pressure sprays of pesticides, and light rainfalls may represent key events for dispersal of *U. necator* conidia. The last two events also provide a microclimate with high humidity that is conductive to infection. These events favour both the dispersal and the germination of the spores – insofar as sprays are not fungicides effective against powdery mildew – and therefore may enhance powdery mildew epidemics. This information may be useful for grape powdery mildew management, especially to improve the timing of field operations, including antipowdery mildew sprays.

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