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Removal of urediniospores of brown (*Puccinia recondita* f.sp. *tritici*) and yellow (*P. striiformis*) rusts of wheat from infected leaves submitted to a mechanical stress

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Abstract

The passive spore removal from colonies due to mechanical stress was compared in the brown (*Puccinia recondita* f.sp. *tritici*) and yellow (*P. striiformis*) rusts of wheat. Mechanical stress was applied using either a miniaturized wind tunnel or a centrifuge. In wind-tunnel experiments, a wind of minimum velocity of 1.3 and 1.8 m s^{-1} for *P. recondita* f.sp. *tritici* and *P. striiformis*, respectively, applied for at least 10 seconds, was necessary to remove spores. The interaction between wind velocity and cumulated duration was significant for both rusts. At low wind velocity, a longer duration was required to remove the spores than at high wind velocity, and vice versa.

In centrifugation experiments, the maximum spore removal occurred for angular velocities of 10^3 and 2 10^3 rotations min^{-1}, for *P. recondita* f.sp. *tritici* and *P. striiformis*, respectively, applied for 5 min. Calculation of the aerodynamic and centrifugal forces showed that the forces necessary to remove spores are greater for *P. striiformis* than for *P. recondita* f.sp. *tritici*. This difference can be related to the size of the dispersal unit, which is larger in *P. striiformis* than in *P. recondita* f.sp. *tritici* due to spore clustering. These observations are consistent with the differences in the mean spore dispersal distance, which is usually smaller in *P. striiformis* than in *P. recondita* f.sp. *tritici*.

Introduction

Efficient propagule dispersal is a prerequisite for the spatial spread of plant disease epidemics. Aerial spore dispersal is one important mechanism beside splash dispersal and contacts between plants. Dispersal of airborne fungal spores can be divided into three successive, but interrelated phases of spore removal, transport, and deposition (Aylor, 1990). The biological characteristics of the disease on the source plant (e.g. spore and fructification type) interact with the physical characteristics of the environment during spore removal (McCartney, 1994). The asexual spores (urediniospores, hereafter called spores), which cause the epidemic spread of many rust fungi, are produced by the intercellular mycelium and accumulate in a sorus erupting through the host plant cuticle. The spores are borne singly on pedicels (Laundon, 1967). They are, however, abscised some time before removal and are presented for dispersal as a floccose powder of detached spores (Hirst, 1961). Removal of spores from the sorus, therefore, is passive and mainly assured by wind gusts of various velocity and duration (Aylor, 1990). An increase in velocity (above a minimum threshold) or duration of air flow led to an increase in spore removal of many passively removed fungi, such as *Erysiphe graminis* DC. f.sp. *hordei* (Hammett and Manners, 1974; Pauvert, 1984), *Cochliobolus heterostrophus* (Drechs.) Drechs. (Waggoner, 1973), and *Botrytis fabae* Sardiña (Harrison and Lowe, 1987). Similar results were obtained for the cereal rust fungi *Puccinia recondita* Roberge f.sp. *tritici* (Srivastava et al., 1987), *P. striiformis* Westend. (Rapilly et al., 1970), and *P. graminis* Pers. f.sp. *tritici* (Hirst, 1961; Smith, 1966). The interaction between wind velocity and duration was only tentatively studied (Waggoner,

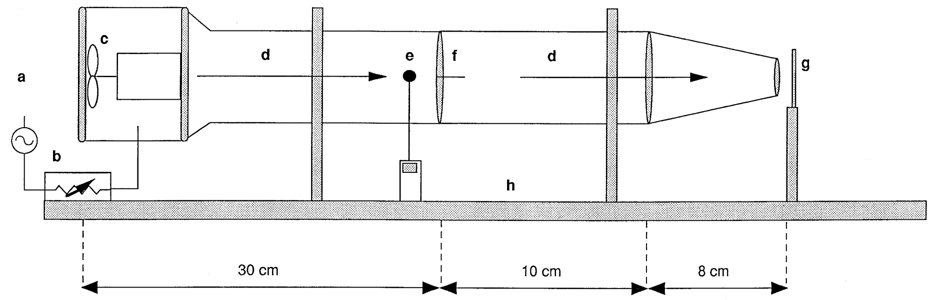

Figure 1. Schematic representation of the miniaturized wind tunnel used to remove cereal rust spores. a) power supply; b) monitoring unit; c) electric fan; d) air flow; e) thermoanemometric probe; f) leaf fragment with sporulating lesions; g) collection unit; h) wooden frame. Inner diameter of the tunnel is 3 cm in the main part and 1.33 cm at the outlet.

1973). From the physical point of view, removal can be seen as the result of a mechanical stress conducing to an irreversible strain (Levitt, 1980). Compared to biotic stresses, most abiotic stresses can be characterized quantitatively with no major difficulty. A mechanical stress can be characterized very easily by its magnitude as a function of time; such a stress can be obtained by applying aerodynamic or centrifugal forces to the fungal lesions on leaf surfaces.

The goal of the experiments was a comparison of the efficiency of passive spore removal from colonies due to mechanical stress in *P. recondita* f.sp. *tritici* (wheat brown rust) and *P. striiformis* (wheat yellow rust) in controlled conditions. From wind-tunnel and centrifugation experiments, aerodynamic and centrifugal forces necessary to remove the spores from sorus were calculated for both wheat rusts.

Materials and methods

Host, fungi and inoculation procedure

Experiments were undertaken on seedlings of wheat cv. Michigan Amber, highly susceptible to brown (*P. recondita* f.sp. *tritici*) and yellow (*P. striiformis*) rusts. Seedlings were grown in square pots (7×7×8 cm, 5 seeds per pot along one side) in a greenhouse maintained at 15 ± 5 °C, until the unfolding of the second leaf. Inoculation was done in a settling tower (Eyal et al., 1968). Primary leaves were attached horizontally with their adaxial side up on a Plexiglas sheet with plasticine (de Vallavieille-Pope et al., 1995). For each rust fungus, seedlings were inoculated by forcibly discharging 3 mg of spores, to ensure an homogeneous density of 345 ± 30 spores cm^{-2} on the inoculated leaves. Inoculated plants were incubated for 24 h in the dark at 100% relative humidity, at 15 °C for *P. recondita* f.sp. *tritici* and 8 °C for *P. striiformis*. These temperatures are optimal for spore germination and penetration (de Vallavieille-Pope et al., 1995). The seedlings were then transferred to a growth chamber maintained at 17 ± 1 °C during a 16-h light period with a light intensity of 250 μE $m^{-2}s^{-1}$ and a temperature of 15 ± 1 °C during a 8-h dark period. *P. recondita* f. sp. *tritici* and *P. striiformis* sporulated profusely on seedlings 8 and 15 days after inoculation, respectively.

Miniaturized wind-tunnel experiments

Experimental design

The tunnel was a 48-cm long Plexiglas tube (Willocquet, 1994) (Figure 1). A 1-cm long leaf fragment of a primary leaf with 60–80 sporulating lesions cm^{-1} was fixed with a piece of double-sided adhesive tape to a plastic sheet held horizontally in the middle of the tunnel. The leaf fragment was not allowed to flutter. Wind was produced by an electric fan. A spherical hot-wire thermoanemometric probe (NTC TESTO 491, Testo SARL, Forbach, France) was introduced through an orifice in the tunnel wall to measure wind velocity and temperature very close to the leaf fragment. Calibration experiments showed a linear relationship between the measured wind velocity u (ms^{-1}) and voltage v (V) [$u = 0.287 \pm 0.002\, v$ ($R^2 = 1.00$, $n = 18$)]. The plastic sheet was present in the tunnel during calibration experiments. The thermoanemometric probe was omitted during further experiments to avoid flow perturbations within the wind tunnel. The Reynolds number ($Re = u\ d\ /\ \nu$, with d the tunnel inner diameter [m], and ν the kinematic viscosity of the air [$m^2\ s^{-1}$]) ranged between 1400 and 6600 in the studied range of wind velocity. For such values of *Re*, the air flow within the tunnel can be considered as laminar (Charnay and Scon, 1978). A microscopic slide coated with Tween® 20 was held vertically 0.5 cm from the tunnel outlet to collect the removed spores. The removed spores impacted on a 1.3-cm diameter, disc-shaped target area. When the target area was conspicuously colored by spores, the collecting slide was washed with a solution of water including a few droplets of Tween® 20 and the washed-off spores were counted with a Coulter Counter® (ZM Model, Coultronics France, Margency) (Sache and de Vallavieille-Pope, 1993). When the spore deposit on the slide was not visible, the spores were directly counted with an optical microscope (magnification × 100). Preliminary studies showed that the spore losses by sedimentation on the tunnel walls or escape in the air around the collecting slide were low and apparently not related to the wind velocity. Therefore, no correction for velocity-dependent impaction efficiency was attempted.

Wind velocity threshold
A leaf fragment with sporulating lesions was exposed to the lowest available wind velocity during 10 s. The collecting slide, but not the leaf fragment, was changed and the next higher wind velocity was applied during 10 s and so on, until the highest available wind velocity had been applied. The six tested wind velocities were 0.7, 1.3, 1.8, 2.3, 2.8, and 3.3 m s^{-1}. Therefore, the total duration of each experiment was one minute, excluding the time necessary to change the slides. For each 10-s period, the percentage of the total number of spores collected during the whole experiment was calculated. For each wind velocity, the experiment was performed three times.

Interaction between intensity and cumulated duration of the drag force
A leaf fragment with sporulating lesions was exposed to wind of constant velocity during increased exposure periods of 10, 20, and 30s. Therefore the total duration of each experiment was one minute, excluding the time necessary for changing the slides. The collecting slide was changed after each exposure period. For each exposure period, the percentage of the total number of spores collected during the whole experiment was calculated. The experiment was done for each of the six available wind velocities, and with lesions of different age, 11, 13 and 15 days after inoculation for *P. recondita* f.sp. *tritici*, and 16, 18 and 20 days after inoculation for *P. striiformis*. Aging was expected to induce changes in lesion morphology for both rust fungi, and thus influence removal efficiency. For each wind velocity, the experiment was performed three times. The whole experiment was replicated once.

Data were analyzed using two-way analysis of variance after angular transformation to stabilize variance. When the interaction velocity x duration of the wind was significant ($P < 0.05$), treatment means were compared with Scheffé's test.

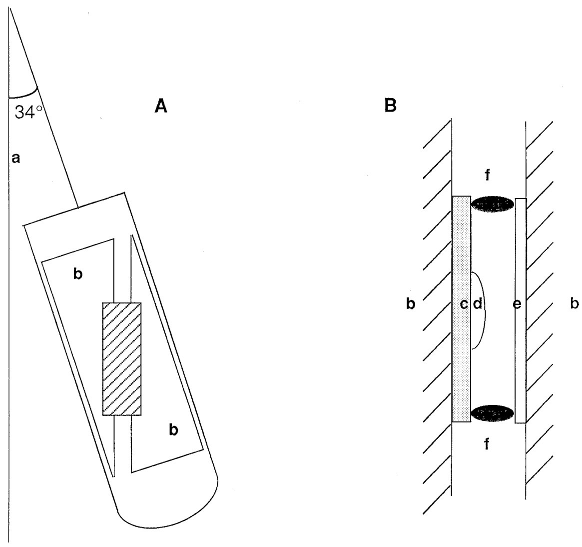

Figure 2. Schematic representation (longitudinal section) of the centrifugation device used to remove rust spores. A. General view of the device. B. Details of the hatched part of A. a) rotation axis; b) wooden frames; c) leaf fragment; d) sporulating lesions; e) collecting coverslip; f) toric rubber seal.

Centrifugation experiments

Experimental design (Figure 2)
A cylinder of wood (length 72 mm, diameter 22 mm) was cut into two beveled pieces. A 2-cm long leaf fragment with sporulating lesions was attached with a double-sided adhesive tape to the first piece. A circular coverslip (diameter 1.8 cm) used as collection unit was attached in the same way to the second piece. A toric rubber seal was inserted to avoid any contact between the leaf fragment and the coverslip. The two pieces were placed in capped tubes with the sporulating lesions facing downward, and centrifuged in a fixed angle head (34 °) centrifuge (J2–21 M, Beckman Instruments, Inc., Fullerton, USA). The centrifuge

included five leaf fragments. Spores were counted as described in the wind tunnel experiment.

Angular velocity threshold

A leaf fragment with sporulating lesions was exposed to the lowest available angular velocity during 5 min, including acceleration and deceleration of the centrifuge. The collecting slide, but not the leaf fragment, was changed, and the next higher angular velocity was applied for 5 min, and so on, until the highest available angular velocity had been reached. The tested angular velocities were 10^2, 1–2–$\cdots$–9 10^3, and 10^4 rotations min^{-1} (rpm). The corresponding centrifugal accelerations were 8.6, 860, 3.4 $10^3 \cdots$ 6.9 10^4, and 8.6 10^4 *g*, respectively (the acceleration is proportional to the square of the angular velocity, therefore doubling the angular velocity quadrupled the acceleration). Angular velocities higher than 10^4rpm caused cracks in the collecting slides. For each angular velocity, the percentage of the total number of spores collected during the whole experiment was calculated. The whole experiment was replicated once.

Interaction between intensity and exposure time of the centrifugal force

A leaf fragment with sporulating lesions was centrifuged at a constant angular velocity for 11 successive periods of 5 min. The collecting coverslip was changed after each period of 5 min. Therefore, the total duration of the experiment was 55 min, excluding the time necessary to change the slides. The angular velocity was set at 10^3 rpm for *P. recondita* f.sp. *tritici* and 2 10^3 rpm for *P. striiformis*, the respective angular velocity giving the maximum spore removal according to the results of the threshold experiment. The experimentations were done with lesions of different age, 11, 15, 19 and 23 days after inoculation for *P. recondita* f.sp. *tritici* and 15, 19, 23 and 27 days after inoculation for *P. striiformis*. The whole experiment was replicated once.

A linearized exponential model was fitted to the data, following:

$$1\text{n}(y) = a - bt \tag{1}$$

where:
y is the proportion of removed spores after a cumulated centrifugation time of *t* min;
a is the intercept of the linear regression; *b* is the slope of the linear regression.

As parameter values obtained for the five leaf fragments centrifuged during the same experiment were not different ($P > 0.5$), results for the five leaf fragments were pooled for each experiment.

Calculation of the drag and centrifugal forces leading to spore removal

A spore in an air flow of velocity *u* (ms^{-1}) is submitted to a drag force F_D(N), estimated as (Aylor, 1975):

$$F_D = \frac{1}{2}\rho_a u^2 \pi r^2 C_D(Re) \tag{2}$$

where:
ρ_a is the air density (kg m^{-3});
r is the radius of a spore (π r^2 is the projected area of the spore);
C_D is the drag coefficient (nondimensional);
Re is the Reynolds number (nondimensional), as *Re* = 2 *u r* / ν;
ν is the kinematic viscosity of the air (m^2 s^{-1}).
The relationship between C_D and *Re* is given by Leclair et al. (1970) for solid spheres as follows:

$$\begin{aligned} C_D = 24/Re\{1 + \exp[(-2.029)+ \\ 0.8222\ 1\text{n}(Re) + (-0.02253\ 1\text{n}^2(Re))]\} \end{aligned} \tag{3}$$

To estimate the average force able to remove spores, *u* was set to the value able to remove 50% of the spores (Aylor, 1975).
The centrifugal force F_R (N) applied to the spores by an angular velocity ω (rd s^{-1}) is estimated as:

$$F_R = \rho 4/3\pi r^3 gRCF \tag{4}$$

where
ρ is the density of a spore (kg m^{-3})
g is the gravitational acceleration (m s^{-2})
RCF is the relative centrifugal force, according to:
RCF = $\omega^2 d$ / *g*, with *d* the distance between the spore and the axis of rotation (m).
To estimate the average force able to remove spores, ω was set to the value able to remove 50% of the spores (Aylor, 1975).

Results

Wind velocity threshold

Spores were not removed at the lowest wind velocity (0.7 m s^{-1}) (Figure 3). About 3% of *P. recondita* f.sp.

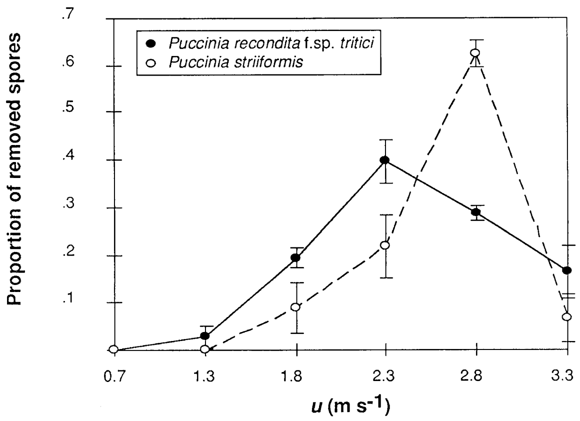

Figure 3. The effect of increasing wind velocity (u) on the removal of spores of two wheat rust fungi. The six wind velocities were applied successively in increasing order during 10 s each. Means and standard errors of 3 repetitions are presented.

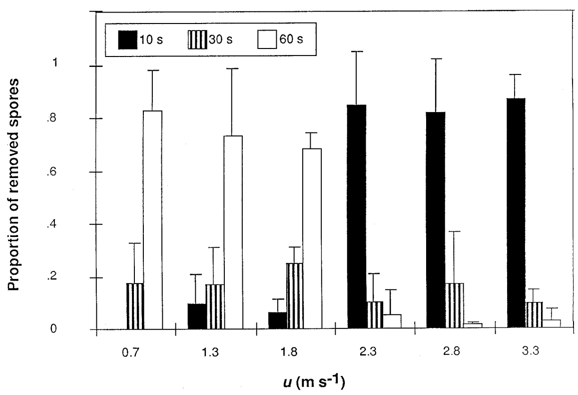

Figure 4. The effect of the interaction of wind velocity (u) and duration on the removal of spores of *Puccinia striiformis* from 16-day old lesions. Means and standard errors of three repetitions are presented.

tritici spores were removed at a wind velocity of 1.3 m s^{-1}. The theoretical threshold of wind velocity necessary to remove *P. recondita* f.sp. *tritici* spores, therefore, occurred between 0.7 and 1.3 m s^{-1}. Similarly, the theoretical threshold of wind velocity necessary to remove *P. striiformis* spores occurred between 1.3 and 1.8 m s^{-1}. With increasing wind velocities most spores were removed at 2.3 and 2.8 m s^{-1} for *P. recondita* f.sp. *tritici* and *P. striiformis*, respectively.

Interaction between intensity and cumulated duration of the drag force

The temporal pattern of spore removal depended on the interaction between wind velocity and duration. Spore removal was similar for the two rust fungi and was not influenced by lesion age. Therefore, results obtained with 16-day old yellow rust lesions are thought to be representative of the whole experiment and will be illustrated here (Figure 4). Spores were not removed at 0.7 m s^{-1} wind velocity during the first 10-s period. At the same wind velocity, spores were removed during the next periods (30 and 60 s), 80% of the total spores being removed during the last period. Increased but low, wind velocities of 1.3 and 1.8 m s^{-1} were able to remove 5-13% of total spores during the first 10-s period. At the three highest wind velocities (2.3, 2.8 and 3.3 m s^{-1}), most spores (about 90%) were removed during the first 10-s period. Spore removal then decreased with increased duration of exposure to become very low (only 0.3% of *P. striiformis* spores were removed at 3.3 m s^{-1} during the last period). Analysis of variance showed no effect of wind velocity (P = 1.00) but a significant ($P < 0.05$) effect of wind duration and a significant interaction wind velocity $\times$ duration ($P < 0.05$).

In general, the effect of wind velocity on spore removal depended on the wind duration. For wind durations of 10 s and 60 s and at the first three wind velocities (0.7, 1.0 and 1.8 m s^{-1}) the proportion of removed spores increased with wind duration. For the intermediate wind duration of 30 s, the proportion of removed spores was low and homogenous, since no difference between the 6 wind velocities was noticed. In one experiment with 16-day old yellow rust lesions, wind duration had no significant effect ($P > 0.05$). This particular case was further characterized by a very low total number of removed spores and may not affect the general conclusions drawn from the whole experiment. In all other experiments, the total number of collected spores was quite variable, but increased with increasing wind velocities. The total number of collected spores at the higest wind velocity (3.3 m s^{-1}) was 5-10 times the total number of collected spores at the lowest wind velocity (0.7 m s^{-1}).

Centrifugation at increasing angular velocity

After 5 min of centrifugation at 100 rpm, the proportion of removed spores varied from 0.7 to 3%. With increasing angular velocities, most spores were removed at 10^3 rpm for *P. recondita* f.sp. *tritici* and 2 10^3 rpm for *P. striiformis*, respectively (Figure 5). After centrifugation at 10^4 rpm, observation of the centrifuged leaf fragments under binocular lens suggested that lesions

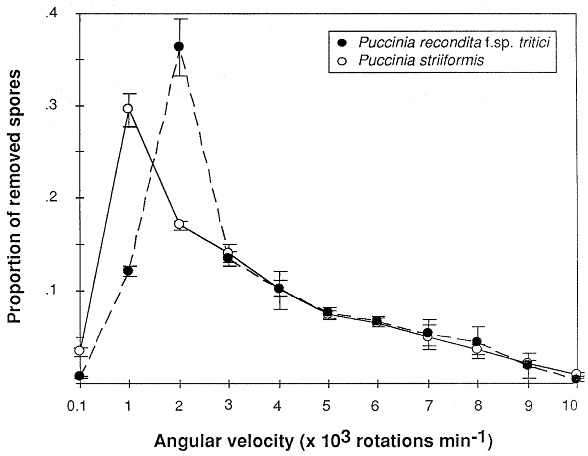

Figure 5. The effect of increasing angular velocity on the removal of spores of two wheat rust fungi in a centrifuge. Means and standard errors of five leaf fragments centrifuged during the same run are presented.

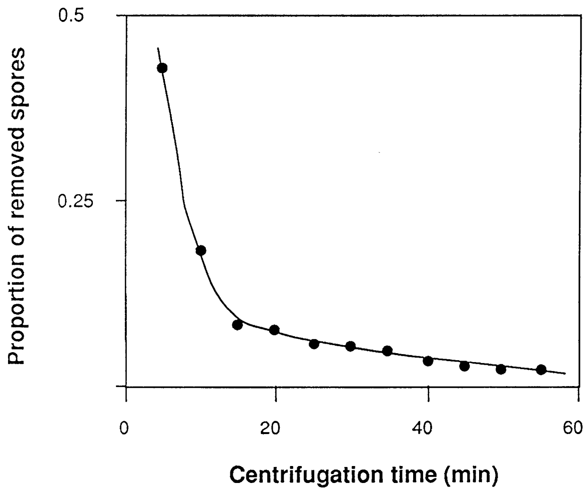

Figure 6. The exhaustion of 11-day old sporulating lesions of *Puccinia recondita* f. sp. *tritici* in a centrifuge rotating at 10^3 rpm. The equation of the curve is: y = 5.724 $x^{-1.249}$, R^2 = 0.97 (for the linearized model). Each dot is the mean of five leaf fragments centrifuged during the same run. Standard errors are too small to be represented.

were totally exhausted from spores, but not damaged. This was confirmed by the total number of collected spores, which was 5-10 times the number of collected spores in the wind tunnel experiment at the highest wind velocity.

Centrifugation at constant angular velocity

After the first 5 min of centrifugation at an angular velocity promoting maximal removal efficiency (10^3 and 2 10^3 rpm for *P. recondita* f.sp. *tritici* and *P. striiformis,* respectively), 35-50% of the spores of the two rusts had been removed. Figure 6 shows the example of 11-day old sporulating lesions of *P. recondita* f.sp. *tritici*. With increasing centrifugation times, the proportion of removed spores decreased according to a power-law model (*P. recondita* f.sp. *tritici*: R^2= 0.74–0.97; *P. striiformis*: R^2 = 0.74–0.93, $P < 0.001$ in all cases). The total average number of removed spores for the 11 durations was greatest for 15-day old lesions in *P. recondita* f. sp. *tritici* and 19-day old lesions in *P. striiformis*. In very old lesions (with these experimental conditions, 23-day old in *P. recondita* f.sp. *tritici* and 27-day old in *P. striiformis*), the removal of spores did not cease (Figure 7) indicating that sporulation continued so far plant hosts were still alive and environmental conditions favourable. Analysis of variance, performed on the slope of the linearized power-law model showed significant effects of lesion age (P = 0.001) and experiment (P = 0.001), as well as a significant interaction between these two factors (P = 0.019) for *P. recondita* f.sp. *tritici*. Conversely, no effect of experiment was observed for *P. striiformis* (P = 0.677), but the effect of lesion age and the interaction between lesion age and experiment remained significant (P =0.001).

Calculation of the forces able to remove the spores from sorus

The comparison of both drag and centrifugal forces was made for values of u and RCF promoting maximum spore removal efficiency.

Aerodynamic (drag) force
The air characteristics were:
ρ_a = 1.2 kg $m^{-3}$and ν =1.5 10^{-5} m^2 s^{-1}
For *P. recondita* f.sp. *tritici*:
u = 2 m s^{-1}, r = 2.5 10^{-5} m, Re = 6.6 and C_D = 5.7, according to equation (3), giving:
F_D = 2.7 10^{-8} N, according to equation (2).
For *P. striiformis*:
u = 2.5 m s^{-1}, r = 2.7 10^{-5} m, Re = 8.9 and C_D= 4.7, according to equation (3), giving:
F_D = 4 10^{-8} N, according to equation (2).

Centrifugal force
For both rusts, g = 9.8 m s^{-2} and d = 7.8 10^{-2} m.
For *P. recondita* f.sp. *tritici*:
RCF = 88, giving

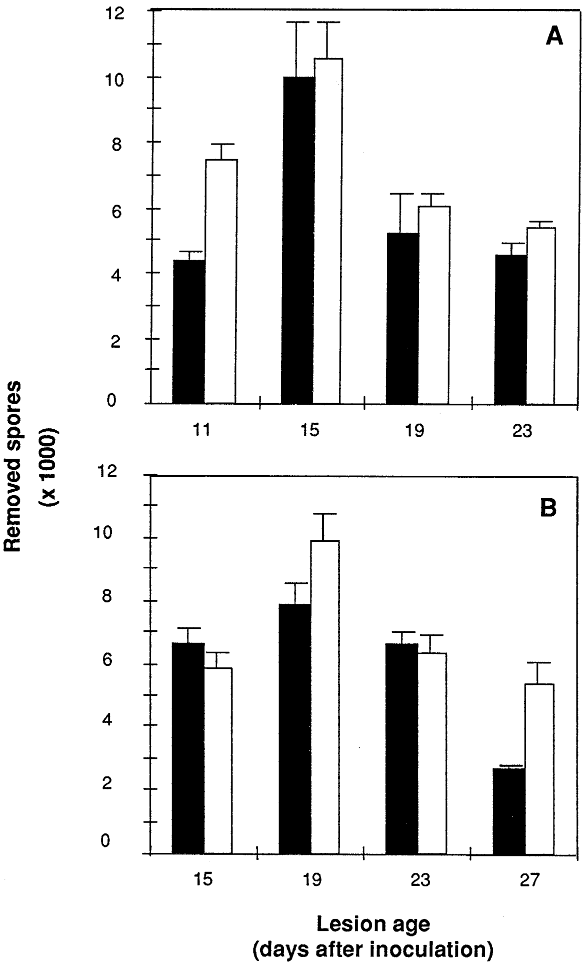

Figure 7. The total spore removal from sporulating lesions of two rust fungi during 55 min of centrifugation at constant angular velocity. A. *Puccinia recondita* f. sp. *tritici*, 10^3 rpm. B. *P. striiformis*, 2×10^3 rpm. For both fungi, black and white bars correspond to two different experiments. Each bar (with standard error) is the mean of five leaf fragments centrifuged during the same run.

$F_R = 0.72\ 10^{-8}$N, according to equation (4).
For *P. striiformis*:
$RCF = 350$, giving
$F_R = 3.4\ 10^{-8}$N, according to equation (4).

Discussion

Wind-tunnel experiments indicated that a minimum wind velocity was required to remove the rust spores (Figure 3). The numerical values of this threshold (between 0.7 and 1.3 m s^{-1}for *P. recondita* f.sp. *tritici* and between 1.3 and 1.8 m s^{-1}for *P. striiformis*) were slightly higher than those found in previous studies (brown rust: 0.5-0.7 m s^{-1} (Stepanov, 1935, in Gregory, 1973; Srivastava et al., 1987), yellow rust: 1 m s^{-1} (Rapilly et al., 1970)). Wind velocity thresholds measured in controlled conditions, however, might have limited field significance, since many other factors as wind gusts (Shaw and McCartney, 1985; Aylor, 1990), sporulation intensity (Pauvert, 1984), relative humidity (Rapilly et al., 1970), leaf shaking (Bainbridge and Legg, 1976), and rain drop impacts (Carter et al., 1970ab; Rapilly et al., 1970) may decrease the minimum wind velocity required to remove spores.

Interaction between wind velocity and duration was clearly demonstrated in the wind-tunnel experiments (Figure 4). Such an interaction was reported for the spore removal in *Trichothecium roseum* Link (Zoberi, 1961). Similarly, Waggoner (1973), comparing two wind velocities, found that conidia of *Cochliobolus heterostrophus* were removed massively during a single wind outbreak of high velocity or during successive wind outbreaks of low velocity. Hammett and Manners (1974) reported the overwhelming importance of the first wind outbreak for the removal of *Erysiphe graminis* conidia when wind velocity was high. All these results can be interpreted in terms of mechanical stress: a minimum stress, such as a short period of fast wind or an extended period of slower wind, must be applied to break the boundary layer and enhance spore removal.

Aerodynamic and centrifugal forces necessary to remove the spores were derived from the wind-tunnel (Figure 3) and centrifugation (Figure 5) experiments, respectively. It should be noted that the calculated aerodynamic force, using the free air velocity, may underestimate the actual force experienced by the spore due to the flow gradient complicating the drag on it. Both kinds of forces were one magnitude order smaller than those required to remove *C. sativus* conidia (Aylor, 1975) and two-three magnitude orders larger than those required to remove *E. graminis* conidia (Bainbridge and Legg, 1976). These differences may be related to the biophysical characteristics of spore attachment to the sporulating structure. Conidia of *C. sativus* are borne on stalks (Aylor, 1975), whereas those of powdery mildews build chains protruding from the leaf surface (Pauvert, 1984). Rust spores may represent an intermediate case, since they are already detached from their pedicels (Laundon, 1967) before the dispersal act but still embedded in the leaf boundary layer (Aylor, 1990). The consistent differences observed between *P. recondita* f. sp.

tritici and *P. striiformis* in wind and angular velocity threshold and therefore in aerodynamic and centrifugal forces necessary to remove spores may be related to the size of the dispersal unit (Rapilly, 1977) in both rusts. The spore surface of *P. striiformis* is covered with a mucilaginous layer which becomes thicker when relative humidity increases (Rapilly, 1979). Therefore, under high relative humidity, spores stick together and are dispersed mostly as clusters of 2-10 spores (Rapilly et al., 1970). The size of the dispersal unit is, thus, larger in *P. striiformis* than in *P. recondita* f.sp. *tritici*, which is dispersed mainly as single spores (Rapilly, 1979). Relative humidity was not controlled in our experiments. However, the diameter of *P. recondita* f. sp. *tritici* spores was about 25 μm, corresponding to fully hydrated spores (Littlefield and Schimming, 1989). This indicated that ambient relative humidity was conducive to spore clustering in *P. striiformis*. The size of dispersal units influenced only the beginning of removal act in exhaustion experiments (Figure 6). Later on, the decrease in the number of removed spores was qualitatively equivalent for both rust fungi.

The controlled experiments reported here are quite far from field conditions, but their results may explain some features of disease spread in the field. Disease gradients (i.e. the linear plot of disease severity according to increasing distance from the focus, after a suitable linearization (Gregory, 1968)), usually have a larger slope in yellow rust than in brown rust (Rapilly, 1979), indicating a lesser mean distance of spore dispersal in *P. striiformis* than in *P. recondita* f.sp. *tritici*. The larger dispersal units of *P. striiformis* require a stronger force to be removed and travel on shorter distance than those of *P. recondita* f.sp. *tritici*. Moreover, removal at high wind velocities may also enhance the impaction efficiency of spores, and therefore reducing the dispersal distance within the canopy. Near the top of the crop, deposition will be less important and removal at high wind velocities will increase the dispersal distance, thus explaining the appearance of daughter foci far from the primary disease focus.

To conclude, there is correct agreement between controlled conditions and field experiments when comparing the dispersal strategy of both wheat rusts. More attention has now to be paid in hitherto neglected dispersal factors, such as leaf fluttering [Bainbridge and Legg, 1976), rain-puff (Hirst and Stedman, 1963) and splash dispersal (McCartney, 1994).

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