Eur J Plant Pathol (2009) 123:377–386
DOI 10.1007/s10658-008-9374-2

Estimation of soybean rust uredospore terminal velocity, dry deposition, and the wet deposition associated with rainfall

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Received: 25 April 2008 / Accepted: 22 September 2008 / Published online: 16 October 2008

Abstract Using models from atmospheric chemistry and physics, this study examined the wet deposition of single uredospores of soybean rust caused by *Phakopsora pachyrhizi* associated with rainfall and its importance compared with dry deposition. First, a measurement of the terminal velocity of freshly collected *P. pachyrhizi* uredospores was conducted in Nanning, China. The observed terminal velocities associated with different sizes of the uredospore clumps were fitted by negative exponential models. The average terminal velocity of single uredospores (0.0187 m s^{-1}) determined by the fitted models was used to estimate the dry deposition. The wet deposition of single uredospores associated with different rainfall rates was determined numerically using coupled models, in which raindrop capture efficiency of uredospores was based on Slinn's semi-empirical model. The results showed that at a rainfall rate of 0.5 mm h^{-1}, wet deposition can remove 50% of the single uredospores in the air within 1 h. If the rainfall rate is 5 mm h^{-1}, 10 min is sufficient to remove 50% of the uredospores. The dry deposition of the single uredospores was estimated with simplified scenarios: i.e., assuming the uredospore cloud was continuously from 1,000 to 2,000 m in height above a field with a uniform concentration. In the first 16 h, almost no uredospores reached the ground, while the wet deposition caused by 2 mm h^{-1} rainfall within 30 min was even much greater than dry deposition of 24 h duration. The comparisons indicated that the wet deposition of soybean rust uredospores was much more efficient than the dry deposition.

Keywords Epidemiology · Kudzu · *Phakopsora pachyrhizi* · Rainfall rate · Scavenging coefficient

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Introduction

Soybean rust caused by *Phakopsora pachyrhizi* is a fungal disease which is characterised by its airborne uredospores capable of long-distance dissemination (Marchetti et al. 1975, 1976; Tan et al. 1996). *Phakopsora pachyrhizi* uredospores are ovoid, 17 to 45 μm long, and 15 to 27 μm wide for various isolates (Ono et al. 1992; Tan et al. 1994). The spore density is currently unknown. They can be easily carried by winds and become aerosols, i.e., suspensions of solid or liquid matter in air (Wallace and Hobbs 1977). The suspended particles may land either by dry deposition or by wet deposition. In wet deposition, scavenging by rainfall causes most of the removal of aerosols (up to 80% to 90%), and raindrops efficiently collect aerosols that are larger than approximately 2 μm in diam by impaction (Wallace and Hobbs 1977). This aerosol removal process indicated that rainfall could be an important factor for uredospore deposition of *P. pachyrhizi*.

Observations of some fungal pathogens have shown that the wet deposition of their spores due to rainfall was greater than dry deposition in unit time (Gregory 1973; Hirst 1959; Troutt and Levetin 2001; Yang et al. 1993). Gregory (1973) reported that uredospores of *Puccinia* spp. could be collected by raindrops of any size, and the collection efficiency could be as high as 80% to 90% for spores of 20 to 30 μm diam. It is known that wet deposition depends on a scavenging coefficient, which is associated with aerosol diameter, aerosol density, rainfall rate, and raindrop size (Aylor and Sutton 1992; Loosmore and Cederwall 2004; Pruppacher and Klett 1997). The equation of scavenging coefficient (s^{-1}) is described by

$$\lambda(d_p) = \int_0^{\infty} \frac{\pi}{4} d_D^2 V_D E(d_D, d_p) N_{d_D} d(d_D), \tag{1}$$

in which $\lambda(d_p)$ is the integral over all raindrop diameters d_D; $E(d_D, d_p)$ is the capture efficiency for the particles within diameter d_p collected by raindrops within diameter d_D; and N_{d_D} is the number of raindrops within diameter d_D (see Table 1 for the detailed information on equations and notations used in this study) (Aylor and Sutton 1992; Loosmore and Cederwall 2004; Pruppacher and Klett 1997). The capture efficiency, E, is a key variable that is dependent on rainfall rate and the attributes of the aerosols. The capture efficiency indicates how efficiently raindrops are able to capture aerosols. Using a nonlinear regression model to estimate the capture efficiency of ascospores of apple scab (*Venturia inaequalis*), Aylor and Sutton (1992) provided an example of the quantification of fungal spores captured by rainfall. Furthermore, Slinn (1984) developed a more specific semi-empirical model for a more precise estimation of the capture efficiency (Eq. 2), which has been widely used in atmospheric chemistry and physics for air pollution research (Loosmore and Cederwall 2004; Seinfeld and Pandis 2006):

$$E = \frac{4}{R_e S_c}\left[1 + 0.4 R_e^{1/2} S_c^{1/3} + 0.16 R_e^{1/2} S_c^{1/2}\right] + 4\phi\left[\omega^{-1} + \left(1 + 2R_e^{1/2}\right)\phi\right] + \left[\frac{S_t - S*}{S_t - S* + 2/3}\right]^{3/2}\left(\frac{\rho_p}{\rho_w}\right)^{1/2}. \tag{2}$$

In Eq. (2) (see Table 1 for the detailed descriptions of the symbols), the first term stands for Brownian diffusion, which is associated with particle's Brownian diffusivity (D_B in Table 1). Brownian diffusion is due to the movement (Brownian motion) of aerosols caused by impaction of gas molecules. It is significant when the particle size is <1 μm (Seinfeld and Pandis 2006). The second term is for interception, which is due to the contact of aerosols with the surface of raindrops when they pass by the aerosols without direct impaction (Seinfeld and Pandis 2006). The third term stands for the direct impaction of raindrops with aerosols when they stay in the raindrop paths (Seinfeld and Pandis 2006). Specifically, previous studies (Gregory 1973; Loosmore and Cederwall 2004; Seinfeld and Pandis 2006) have pointed out that for particles like fungal uredospores, the capture efficiency is more dependent on impaction than on any other mechanisms due to their size.

Rainfall has been reported to be important in facilitating development of soybean rust in the field (Tan et al. 1994; Tschanz et al. 1983). Since the airborne uredospores of soybean rust can be easily removed by precipitation due to their size, rainfall not only provides free moisture necessary for the uredospore germination and infection, but also facilitates spore deposition, particularly in long-distance dissemination. However, the quantification of wet deposition of soybean rust uredospores associated with rainfall, which may be very important for the determination of initial disease levels in soybean rust forecasting, is currently not available.

Dry deposition is another way by which uredospores of *P. pachyrhizi* land on plants. A general model of particle dry deposition velocity (V_d) is $V_d = V_s + 1/(r_a + r_b + r_a r_b V_s)$, in which V_s is the particle terminal velocity; and r_a and r_b are the aerodynamic resistance and quasi-laminar layer resistance, respectively (Seinfeld and Pandis 2006).

Table 1 Variables and symbols with definitions and equations used in all models

Symbol	Variable (unit)
$Ns(0)$, $Ns(t)$	Uredospore concentration at time 0 and t (m^{-3})
d_p	Aerodynamic diameter of uredospores (m)
d_D	Diameter of raindrop (mm)
ρ_a, ρ_w, ρ_p	Density of air=1.27; water=1,000; and uredospores ($kg\ m^{-3}$)
μ_a, μ_w	Viscosity of air=1.8×10^{-5} and water=1.002×10^{-3} ($kg\ m^{-1}s^{-1}$)
N_T	Parameter of log-normal distribution of raindrops ($m^{-3}mm^{-1}$)
N	Number of raindrops in a certain raindrop diameter range ($d_D+d\ [d_D]$) ($m^{-3}\ mm^{-1}$)
R	Rainfall rate ($mm\ h^{-1}$)
D_r	Representative raindrop diameter (mm)
τ	Particle relaxation time (s) $\tau = (\rho_a - \rho_p)d_p^2 C_c / 18\mu_a$
S_t	Stokes' number (dimensionless) $S_t = 2\tau(V_D - V_s)/d_D$
$\lambda(d_p)$	Scavenging coefficient (s^{-1})
S_*	Critical Stokes' number for impaction (dimensionless) $S_* = [1.2 + (1/12)\ln(1+R_e)]/[1+\ln(1+R_e)]$
V_s	Terminal velocity of uredospore in still air ($m\ s^{-1}$)
V_D	Terminal velocity of raindrop in still air ($m\ s^{-1}$)
E	Capture efficiency
g	Acceleration of gravity: 9.8 ($m\ s^{-2}$)
k	Boltzmann constant: 1.38×10^{-23} ($J\ K^{-1}$)
C_c	Cunningham correction factor (≈1 for particle size of uredospores (Seinfeld and Pandis 2006))
D_B	Particle Brownian diffusivity ($J\ s\ kg^{-1}$) $D_B = kTC_c / 3\pi\mu_a d_p$ T: Temperature in degrees of Kelvin
σ	Variance of raindrop size
R_e	Raindrop Reynold's number for radius (dimensionless) $R_e = d_D V_D \rho_a / 2\mu_a$
S_c	Aerosol particle Schmidt number (dimensionless) $S_c = \mu_a/\rho_a D_B$
ω	Viscosity ratio $\omega = \mu_w/\mu_a$
φ	Diameter ratio $\varphi = d_p / d_D$

All variables associated with environmental temperature are of the values at 20°C. All units in the equations are SI base units except those for rainfall rate and raindrops

Because *P. pachyrhizi* uredospores are large aerosols, the terminal velocity is the dominant factor of their dry deposition velocity (Seinfeld and Pandis 2006). For this reason, a simplified model, $V_d = (1 + \mathrm{LAI})V_s$, described by Aylor and Sutton (1992) was adopted in this study, in which the dry deposition velocity V_d is only associated with the uredospore terminal velocity V_s and soybean leaf area index (LAI). Since dry deposition velocity and wet deposition velocity are both associated with the uredospore terminal velocity V_s, it is necessary to acquire this value first. However, for *P. pachyrhizi* uredospores, this variable is so far unknown. Therefore, the objectives of this study were the following: (1) to measure *P. pachyrhizi* uredospore terminal velocity V_s; (2) to quantify the wet deposition of *P. pachyrhizi* uredospores associated with different rainfall rates; and (3) to compare the wet deposition of *P. pachyrhizi* uredospores with the dry deposition.

Materials and methods

The terminal velocity (V_s) and density (ρ_p) of *P. pachyrhizi* uredospores, and the dry deposition terminal velocity of a spherical particle (V_s) in still air is primarily dependent upon particle size (d_p) and density (ρ_p). Given the properties of uredospores of *P. pachyrhizi* mentioned previously, for simplification in this study, they were treated as spherical particles of a 24 μm diam. Stokes' law (Gregory 1973; Seinfeld and Pandis 2006) can be used to theoretically determine the terminal velocity of *P. pachyrhizi* uredospores if their density is known. The terminal velocity of a smooth spherical particle in still air is determined as

$$V_s = gd_p^2\left(\rho_p - \rho_a\right) / 18\mu_a. \quad (3)$$

However, an exact density of uredospores of *P. pachyrhizi* is unknown currently in the literature. The terminal velocity of these uredospores cannot be determined using Stokes' law (Eq. 3) in this case. Thus, the terminal velocities were obtained using an experimental measurement described below. Based on the experimental measurement of the terminal velocity, *P. pachyrhizi* uredospores density was then derived by Stokes' law, as it was used in other steps of the calculations.

To conduct the experimental measurement, diseased kudzu leaves were collected from a wild kudzu field with natural soybean rust infections in Nanning, China (a soybean rust overwintering region), in March 2006. Disease severity (defined by the area of pustules on the leaves) of the sampled leaves ranged from 10% to 50%. The leaves were placed in a moisture chamber in darkness for 1 day, and then moved to room conditions for a few hours before the experiment. The conceptual design of the experimental device and process of the measurement are illustrated in Fig. 1. A polyvinyl chloride (PVC) cylinder 19 cm in height with a 5 cm inside diameter was used to create a perpendicular tower of still air. The top of the cylinder was left open to facilitate the release of uredospores. Most of the lower end of the cylinder was sealed by wax paper (shaded area in Fig. 1 at the bottom of the cylinder) with only a square opening of 1 cm^2 in the centre. A gliding plastic plate covered by blue wax paper was placed under the cylinder to collect uredospores falling from the top through the square opening. Sequential grids of 1 cm^2 were drawn on the blue wax paper. The distance between the gliding plate and the wax paper sealing the lower end of the cylinder was about 1 mm.

As *P. pachyrhizi* uredospores often form clumps (Melching et al. 1979), the uredospores released from the kudzu leaves included single uredospores and spore clumps. Each uredospore or spore clump would have a different terminal velocity because of size or density difference. To measure the terminal velocity, when the uredospores were released from the top, the gliding plate started moving horizontally (as shown in Fig. 1 by the arrow pointing to the right). Previous studies on the uredospore terminal velocities of other rust fungi showed a terminal velocity range in 0.01 to

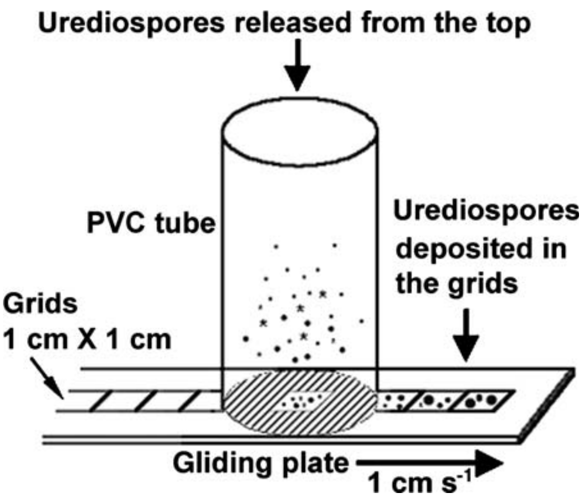

Fig. 1 The experimental scheme for the measurement of terminal velocity of the uredospores of *P. pachyrhizi* and illustration of the uredospore deposition process

0.02 m s^{-1} (Gregory 1973). Thus the speed of the gliding plate was setup at 0.01 m s^{-1}. For each second, the square opening at the bottom of the cylinder scanned over one grid drawn on the plate. Finally, the time needed for any uredospores falling from the top to the plate was correlated with the location of the grids on which they were deposited. Therefore, the terminal velocity of a uredospore or spore clump was derived based on its location on the grids. It should be noted that disturbance to the air in the cylinder caused by the movement of the gliding plate was inevitable to this open system. However, as the gliding plate was moving at 0.01 m s^{-1}, the air on the plate surface would form laminar flows moving parallel to the plate surface causing no turbulence (Yuan 1967). Part of the laminar flows would enter the cylinder through the opening at the base. The friction from the surface of the wax paper would cause decay of these laminar flows and reduce the overall disturbance (Yuan 1967).

The experiments to measure *P. pachyrhizi* uredospore terminal velocity were conducted at midnight under room conditions with minimum indoor illumination to minimise the disturbance of convective air currents in the room to the air in the PVC cylinder. These conditions would be very rare in the field due to the instability of the natural environment; however these were necessary for this study. The uredospores were released by tapping the leaves gently on the top of the PVC cylinder. The measurement was conducted under two different environmental conditions (uncontrolled): at an air temperature of 19°C and 50% relative humidity (RH) using the uredospores from 11 leaflets, and at an air temperature of 20°C and 90% RH with the uredospores from 13 leaflets. To determine the relationship between the terminal velocity and the clump size, the uredospores in each grid were examined under a dissecting microscope with magnifications of 50 to 200 times to determine the spore clump size (number of spores per clump). The velocity values for all the uredospore clumps were averaged by clump size and then fitted by nonlinear models (negative exponential model) for the clump size versus the average terminal velocity of the corresponding clump size. Finally, single uredospore terminal velocity was determined by the fitted models.

An exact density value of *P. pachyrhizi* uredospores was not measured in this study. Alternately, a representative density of the uredospores was estimated using Stokes' law based on the uredospore terminal velocity measured in previous experimentation. Dry deposition was also determined using the measured terminal velocity. Furthermore, because the assessment of the uredospore wet deposition by rainfall for uredospore clumps is quite complicated, this study was only for the case of single uredospores.

The scavenging coefficient estimation and the model fitting the calculation of the scavenging coefficient required several coupled models. These models and their parameters are described below. Rainfall rate R was in a range of 0.5 to 50 mm h^{-1}. Raindrop diameter ranged from 0.1 to 6 mm. For the distribution of raindrop size, an exponential distribution model built by Marshall and Palmer was used in several cases (Marshall and Palmer 1948; Rogers and Yau 1989; Seinfeld and Pandis 2006). However, this model may overestimate the number of raindrops smaller than 1.2 mm (Seinfeld and Pandis 2006). For this reason, a log-normal model of raindrop distribution developed by Cerro et al.(1997) was used in this study:

$$N = \frac{N_T}{\sqrt{2\pi}\sigma d_D} \exp\left[-\frac{1}{2}\left(\frac{\ln(d_D) - \ln(D_r)}{\sigma}\right)^2\right], \quad (4)$$

in which N_T=194$R^{0.30}$, D_r=0.630$R^{0.23}$, $\sigma = (0.191 - 0.01 \ln R)^{0.5}$, and R is the rainfall rate (see Table 1 for more information). A regression model from Willis (1984) was used to calculate the terminal velocity of raindrops of various sizes:

$$V_D = 4.854 d_D \exp(0.195 d_D). \quad (5)$$

Capture efficiency, E, was calculated according to Slinn's model (Eq. 2) for any given raindrop size. All the results from the models above were inputed in the model for scavenging coefficients (Eq. 1). For each rainfall rate R, the scavenging coefficient $\lambda(d_p)$ was determined by integrating over all raindrop diameters (d_D) in the raindrop distribution model (Eq. 4) associated with the given rainfall rate R. This integral was determined numerically using a trapezoid sums approximation (Schatzman 2002), with no error larger than 10^{-5}. Finally, for different rainfall rates from 0.5 to 50 mm h^{-1}, the corresponding scavenging coefficients were fitted with a nonlinear model:

$$\lambda(d_p) = aR^b, \quad (6)$$

as described by Aylor and Sutton (1992), in which a and b are the coefficients determined by model fitting.

The scavenging efficiency associated with rainfall rate and duration assuming that the distribution of raindrop size does not vary with time, and using the fitted model for the scavenging coefficient, the change of *P. pachyrhizi* uredospores left in the air during a rainfall event is estimated by

$$Ns(t) = Ns(0) \exp\left[-\lambda(d_p)t\right], \quad (7)$$

in which $Ns(0)$ is the initial uredospore concentration and $Ns(t)$ is the concentration at time t. If Ns is considered as a fraction instead of a concentration, then $Ns(0)$ is 1, and $Ns(t)$ is the fraction of uredospores at time t during a rainfall event (Beverland et al. 1997; Chate et al. 2003; Pruppacher and Klett 1997; Slinn 1977). Substitution of $\lambda(d_p)$ in Eq. (7) with the fitted scavenging coefficient model leads to the uredospore concentration at time t when the rainfall rate is known. All the computation was conducted with MatLab (The MathWorks, Inc. Natick, MA, USA).

In order to simplify the scenario, an assumption was made that a cloud of *P. pachyrhizi* uredospores from a long-distance dissemination source area was the only initial inoculum source and all uredospores were single. The presence of fungal spores in various altitudes from near the surface to as high as up to 5,000 m has been reported in many earlier studies (Gregory 1973). Lately, model simulations by Pan et al. (2006) suggested that the air movement close to 1,000 m height has a dominant effect in the long-distance dispersal of the uredospores of *P. pachyrhizi*. For this particular simplified case, although it might not be realistic, it was assumed that the uredospores were present from 1,000 m to 2,000 m height above a soybean field with a uniform concentration of 2 uredospores m^{-3}. If uredospores were not deposited within 24 h, they were considered to be diluted in the air and their availability for deposition in this field was lost. For the wet deposition, raindrops fell from a height level above 2,000 m. Based on Eqs. (1) to (7), the number of uredospores landing in a unit area on the ground under different rainfall conditions (0.5, 1, 5, 10, 20 mm h^{-1} rainfall rate, 30-min duration) was estimated. For dry deposition, dry deposition velocity V_d is associated with V_s and leaf area index (LAI). With the assumptions that the uredospores were from the outer sources and present in the air at 1,000 to 2,000 m height levels, the soybean leaf area index did not affect the uredospore deposition in a unit area; thus, the dry deposition velocity V_d in this study was further simplified as $V_d = V_s$. Then for different dry deposition duration times (8, 16, and 24 h) in one day, the numbers of uredospores in a unit area due to dry deposition were estimated based on the uredospore terminal velocity V_s and compared with the wet deposition.

Results

The terminal velocity of uredospores and estimated uredospore density

In the experiment with a temperature of 19°C and 50% RH, 222 single uredospores of *P. pachyrhizi* were collected with terminal velocities ranging from 0.0109 to 0.0345 m s^{-1} and an average of 0.0186 m s^{-1}. With the temperature of 20°C and 90 RH %, 137 single uredospores were collected, with terminal velocities in a range of 0.0115 to 0.0543 m s^{-1} and an average of 0.0225 m s^{-1}. The average terminal velocity for all 359 single uredospores was 0.0201 m s^{-1}.

The size of all the uredospore clumps collected in both experiments ranged from 1 to 100 uredospores/clump by estimation, and their terminal velocity ranged from 0.0109 to 0.076 m s^{-1}. The average size of uredospore clumps at 19°C and 50% RH was 8.31 uredospores/clump, which was significantly smaller (P=0.0096) than the average clump size, 9.94 uredospores/clump, under the conditions of 20°C and 90% RH. Analysis of variance also showed that the average terminal velocity of all single uredospores and uredospore clumps under the conditions of 20°C and 90% RH was significantly larger (P<0.0001) than that of all the uredospores collected at 19°C and 50% RH. These results suggest that uredospores may tend to form clumps more easily and have a higher terminal velocity under humid conditions.

Generally, *P. pachyrhizi* uredospore terminal velocity increases as the uredospore clump size increases, and this increase follows the curves in Fig. 2. The highest terminal velocity measured in the experiments was 0.076 m s^{-1}. Considering that errors of the estimation of clump size increased with the clump size under a dissecting microscope, and that clumps larger than 50 uredospores/clump had a similar velocity of 0.076 m s^{-1}, model fitting was conducted only for clump sizes ranging from 1 to 60 uredospores/clump. Table 2 gives parameter estimates of the two fitted negative exponential models, i.e. $V_s = a - c \cdot \mathrm{EXP}(-bx)$ for the two different experimental conditions. Figure 2a and b shows the measured velocities of different clumps and their model-predicted values. An averaged value of 0.0187 m s^{-1}, as a representative terminal velocity of a single uredospore based on the two models, was used for computation in the next steps. This model-derived terminal velocity of a single uredospore (0.0187 m s^{-1}) was lower than the averaged single uredospore terminal velocity by the experimental measurement (0.0201 m s^{-1}). Given terminal velocity at 0.0187 m s^{-1} for single uredospores, the density of the uredospores was estimated as 1,070 kg m^{-3} according to Stokes' law. With the terminal velocity

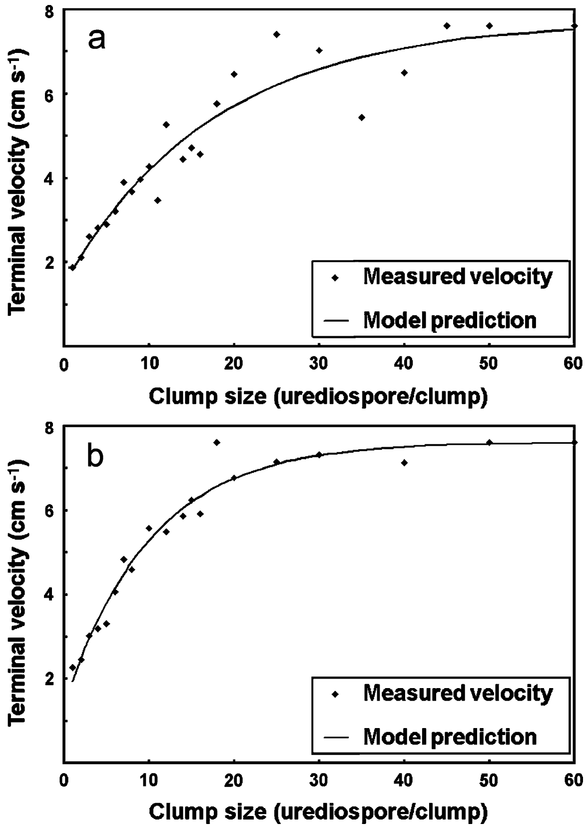

Fig. 2 The measured terminal velocity of different uredospores or clumps of *P. pachyrhizi* and the predicted velocity by negative exponential models for experiments under the different environmental conditions. **a** 19°C and 50% RH. **b** 20°C and 90% RH

Table 2 The parameter estimates of the two fitted negative exponential models $V_s = a - c \cdot EXP(-b \cdot x)$, in which x is uredospore clump size, for the terminal velocity measured under the two different environmental conditions

Environmental condition	Model variable	Parameter estimate	SSE[a]	*R*-square	RMSE[b]	DF[c]
Temp=19°C	*A*	7.734	7.1153	0.9092	0.5821	21
RH=50%*A*	*B*	0.05646				
	C	6.253				
Temp=20°C	*A*	7.619	2.1108	0.9668	0.3524	17
RH=90%	*B*	0.09864				
	C	6.270				

[a] *SSE*=sum of squares

[b] *RMSE*=root mean squared error

[c] DF=degrees of freedom

at 0.0187 m s^{-1}, without other resistance in the atmosphere, a uredospore falling from a 1,000 m height level would take at least 14.8 h to reach the ground, while spores at a 2,000 m height would take more than 1 day.

The uredospore scavenging coefficient by rainfall and the fitted model

The scavenging coefficient $\lambda(d_p)$ was calculated using Eqs. (1), (2), (4), and (6). In Fig. 3, the scavenging coefficient $\lambda(d_p)$ over the rainfall rate from 0.5 to 50 mm h^{-1} increases when the rainfall rate increases. When the rainfall rate is 0.5 mm h^{-1}, $\lambda(d_p)$ is only about 0.0002 s^{-1}. At 50 mm h^{-1}, it reaches 0.094 s^{-1}. The fitted model based on Eq. (6) for the scavenging coefficient is $\lambda(d_p)$=0.0003563$R^{0.8391}$ with r^2=0.999, as the curve in Fig. 3 shows.

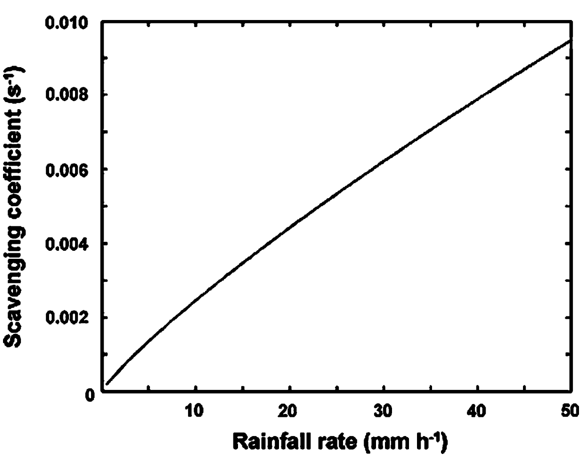

Fig. 3 The scavenging coefficients of single uredospores of *P. pachyrhizi* calculated based on Slinn's model and the log-normal raindrop distribution model for rainfall rates from 0.5 to 50 mm h^{-1}

Change of the uredospore concentration during a rainfall event

According to the fitted model of scavenging coefficient (as shown in Fig. 3), $\lambda(d_p)$=0.0003563$R^{0.8391}$, assuming that the initial concentration of the single uredospore in the air was 100%, the rainfall rate was constant during a rainfall event, and the percentage of total uredospores left in the air at time *t* was estimated by Eq. (7). The changes of the percentage of the spores left in the air versus time (0 to 60 min) for six different rainfall rates (0.5 to 15 mm h^{-1}) are illustrated in Fig. 4. When the rainfall rate is 0.5 mm h^{-1}, it would take 60 min to remove 50% of the uredospores from the air. With an increase of the rainfall rate to 5 mm h^{-1}, 10 min is sufficient to remove 50% of the uredospores.

The comparisons of the uredospore deposition under different dry and rainfall conditions

In a simplified situation, with a dry deposition velocity at 0.0187 m s^{-1}, the numbers of total uredospores landing on the ground by dry deposition and wet deposition from 1,000 to 2,000 m height levels at different times and under different rainfall conditions are given in Table 3. Clearly, dry deposition is much less than wet deposition for the same time length. For example, in the first 16 h, almost no uredospores reach the ground from the 1,000 m height; while with 2 mm h^{-1} rainfall for 30 min, the wet deposition is already greater than the dry

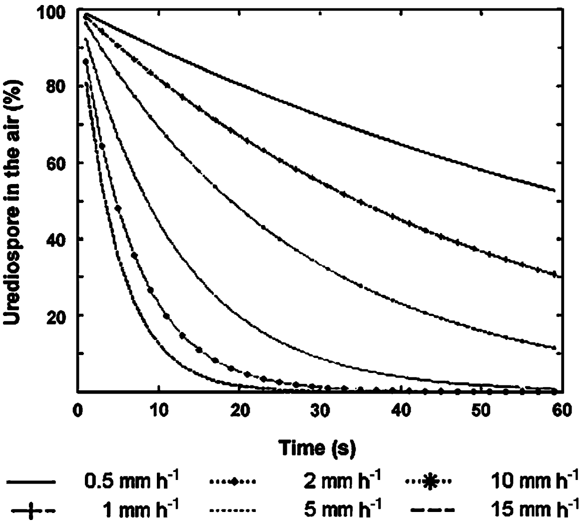

Fig. 4 Percentage of single uredospores of *P. pachyrhizi* in the air at different times *t* in 60 min during six different rainfall events

deposition in 24 h. The uredospores at 2,000 m height cannot even reach the ground in one day with the terminal velocity of 0.0187 m s^{-1}. At 5 mm h^{-1} rainfall rate, 90% of the uredospores in the whole block of the uredospore cloud between 1,000 to 2,000 m height can be deposited within 30 min. After 30 min of rainfall, higher rainfall rates (>10 mm h^{-1}) contribute no significant difference in wet deposition.

Discussion

This study focused on a theoretical estimation with simplified experiments and situations. The results indicated that the velocity of the wet deposition of *P. pachyrhizi* uredospores is much greater than their dry deposition. In reality, the characteristics of the uredospores of *P. pachyrhizi* and rainfall rate always change under different environmental conditions. However, a reasonable conclusion made according to the calculations is that rainfall removes the uredospores quickly. With free moisture brought to the field, rainfall has a double effect on the initial establishment of soybean rust.

Direct field observational or experimental data of the wet deposition of soybean rust uredospores were not available to validate the estimations in this study. However, observations of other fungal spores or plant pollens may validate the results. An hourly observation of *Cladosporium* spp. conidia spore concentration in Tulsa, Oklahoma, showed a decrease of the spore concentration from 3,000 spores m^{-3} to almost zero after a 30 mm rainfall and another case of decrease from 10,000 spores m^{-3} to below 1,000 spores m^{-3} after a 23 mm rainfall (Troutt and Levetin 2001). Observations on several kinds of particles washed down during different time periods in a thunderstorm event ending a 7-day spell of warm, dry weather at the Rothamsted Experimental Station, UK on July 22, 1951, showed similar results (Gregory 1973). These observations generally fit the theoretical calculations in this study. Ascospores of the apple scab pathogen are much smaller than soybean rust uredospores (Aylor and Sutton 1992). Aylor and Sutton's previous work on the ascospores of the apple scab pathogen gave a fitted scavenging coefficient model as $\lambda(d_p)$= $0.000272R^{0.7873}$ (Aylor and Sutton 1992), indicating a smaller scavenging coefficient for the ascospores compared with the uredospores of soybean rust, $\lambda(d_p)$= $0.0003563R^{0.8391}$, consistent with the implication of Slinn's model (Eq. 2) that larger spores are more easily removed by rainfall.

The observed terminal velocity of the single uredospores was in a relatively large range, i.e., 0.0109 to 0.0543 m s^{-1}. This may be due to variability of the fresh spores, i.e., variations in size, environmental changes, or experimental errors. Similarly, in a more precisely conducted study, a wide

Table 3 Comparisons of *P. pachyrhizi* uredospore deposition under the different conditions

Uredospore deposition under different conditions (uredospores m^{-2})								
Dry deposition (h)			Wet deposition in 30 min (mm h^{-1})					
8	16	24	0.5	1	2	5	10	15
0	144	1,231	557	903	1,334	1,825	1,976	1,996

Uredospore cloud is assumed at height levels of 1,000 to 2,000 m with uniform concentration of 2 uredospores m^{-3}. Uredospore terminal velocity is 0.0187 m s^{-1}

range of terminal velocities of *Puccinia graminis* f. sp. *tritici* uredospores which increased from 0.0103 to 0.0154 m s^{-1} when RH increased from 24% to 80% was also reported (Gregory 1973). This increase in the terminal velocity associated with the increase in RH was consistent with the observations in this study. Meanwhile, compared with the terminal velocity of the uredospores of *P. graminis* f. sp. *tritici*, the average terminal velocity (0.0187 m s^{-1}) used in all calculations in this study would be a reasonable representative value. According to Slinn's model, the terminal velocity of uredospores has little effect on raindrop capture efficiency of uredospores even when their difference is very large. However, this velocity is important for the dry deposition and the uredospore release from a field. More precisely controlled conditions would be helpful for better measurement of these uredospore characteristics. The uredospore density of *P. pachyrhizi* (1,070 kg m^{-3}) derived in this study was also similar to that of the uredospores of *P. graminis* f. sp. *tritici*, which was reported in a range of 611.6 to 1,433 kg m^{-3} by various researchers (Gregory 1973; Orr and Tippets 1972). Consistent to the derived density of *P. pachyrhizi*, it was observed in this study that *P. pachyrhizi* uredospores in spore suspensions would descend towards the bottom after staying still for a few minutes without disturbance, which suggested a greater density of the uredospores than that of water (about 1,000 kg m^{-3}).

The model for wet deposition will be useful for disease forecasting in long-distance disease movement, where rainfall is the major mechanism of spore deposition (Nagarajan and Singh 1990; Sun and Tan 1994; Tan et al. 1996; Zeng 1988). If the uredospore concentration of *P. pachyrhizi* in the air could be predicted in a region, by monitoring rainfall events it may be possible to predict an initial disease level before seeing the disease symptoms. Of course, in reality, the rainfall rate always varies during a rainfall event and results in uncertainty of the actual time of spore removal.

Compared with the fast uredospore scavenging during a rainfall event, slow dry deposition indicates that even with a high uredospore concentration in the air, soybean rust may still not be able to establish in the field, as long-time exposure to solar radiation would greatly reduce uredospore viability (Isard et al. 2006). For an area where soybean rust is already established, as a polycyclic disease with a short latent period, a high uredospore scavenging coefficient implies that rainfall would have negative effects on long-distance dispersal of local uredospores by the removal of uredospores from the air, but positive effects on bringing more uredospores back for secondary infections and more local disease development.

Because the scavenging coefficient of uredospores of soybean rust is very high (Fig. 3), not only rainfall but also overhead irrigation may act as a wash-down factor. Tschanz et al. (1983) reported a much higher disease level in a field with overhead irrigation than that in a field with furrow irrigation. Fog could also induce wet deposition. Some observations from the mountainous areas in southern China where fog was frequent indicated severe soybean rust occurrence though rainfall was not abundant (Tan et al. 1996). More research is needed into these phenomena. Rainfall can also flush spores from plant surface, especially during a heavy rainfall event. Meanwhile, heavy rainfall may splash spores that have already deposited on the soil surface to the plants. Although the uredospore scavenging coefficient increases as the rainfall rate increases, the determination of the optimal rainfall rate for overall disease development would be an interesting investigation to address in future studies.

Acknowledgements We thank the United Soybean Board in the U.S. and the National Natural Science Foundation of China (NSFC) for funding. We are grateful to Dr. Paul Esker for assistance.

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