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Production of conidia by *Peronosclerospora sorghi* on sorghum crops in Zimbabwe

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Factors affecting the production of conidia of *Peronosclerospora sorghi*, causing sorghum downy mildew (SDM), were investigated during 1993 and 1994 in Zimbabwe. In the field conidia were detected on nights when the minimum temperature was in the range 10–19°C. On 73% of nights when conidia were detected rain had fallen within the previous 72 h and on 64% of nights wind speed was $< 2{\cdot}0\ m\ s^{-1}$. The time period over which conidia were detected was 2–9 h. Using incubated leaf material, conidia were produced in the temperature range 10–26°C. Local lesions and systemically infected leaf material produced $2{\cdot}4–5{\cdot}7 \times 10^3$ conidia per cm^2. Under controlled conditions conidia were released from conidiophores for 2·5 h after maturation and were shown to be well adapted to wind dispersal, having a settling velocity of $1{\cdot}5 \times 10^{-4}\ m\ s^{-1}$. Conditions that are suitable for conidia production occur in Zimbabwe and other semi-arid regions of southern Africa during the cropping season.

Introduction

Sorghum downy mildew (SDM), caused by *Peronosclerospora sorghi*, is a serious disease of maize (*Zea mays*) and sorghum crops (*Sorghum bicolor*, Frederiksen *et al*., 1969; Williams, 1984). Plants may be infected either systemically or with local lesions. Systemic infection may arise from soil-borne oospores (Tuleen *et al*., 1980), or aerially dispersed conidia (Cohen & Sherman, 1977; Ramalingham & Rajasab, 1981). Systemically infected plants are usually barren. Yield loss has been shown to have a linear relationship with incidence of systemic SDM (Craig *et al*., 1989). Local lesion infection, caused by conidia, occurs as discreet lesions on the leaf surface, and has not been implicated directly with yield loss, although it may act as a source of conidial inoculum for subsequent systemic infection of younger plants (Cohen & Sherman, 1977). Young plants remain susceptible to systemic infection for only a few weeks after germination (Williams, 1984), and so in areas where crops are ratooned or planted over a period of weeks there is a risk of infection by air-borne conidia from early oospore- or conidia-infected plants (Cohen & Sherman, 1977; Ramalingham & Rajasab, 1981).

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In Zimbabwe and other countries in southern Africa there are reports of localized epidemics of SDM on sorghum (de Milliano, 1992). Because of the arid conditions during the noncropping season there may be no host for much of year. In these areas oospores, which are commonly formed in systemically infected sorghum plants (Williams, 1984), may be important in initiating epidemics. However, if conidia are produced on these plants they may play a major role in infecting later planted crops, as the conditions supporting conidia production are also conducive to conidia germination and infection of the host (Bonde *et al*., 1985). In southern Africa there is a paucity of information on the aerobiology and epidemiology of *P. sorghi*. If conidia are produced and dispersed in large numbers from sorghum plants infected at the beginning of the season, these conidia may play a major role in subsequent epidemic development of SDM in southern Africa.

In India and Israel long-term sampling of the air in the vicinity of crops infected by *P. sorghi* has produced information on the pattern, frequency and quantity of asexual spore production in these regions (Kenneth, 1970; Shenoi & Ramalingham, 1979). Conidia were released for 2–6 h from 24·00 to 06·00 hours when the relative humidity was > 80%, leaves had surface water, and the temperature was in the range 18–23°C. Conidia from early planted, oospore-infected plants were found to be responsible for the bulk of infections as the season progressed (Cohen & Sherman, 1977; Ramalingham & Rajasab, 1981).

Although conidia have been detected in the air adjacent to infected sorghum crops (Rajasab *et al.*, 1979), there is no information on how effectively they may be dispersed by the low wind speeds in crop canopies at night. The aerodynamic diameter of a particle dictates its settling velocity and is a major factor determining suitability of the particle for aerial dispersal (Chamberlain, 1975; McCartney *et al.*, 1993). The settling velocity of *P. sorghi* is unknown.

The following experiments were undertaken to investigate characteristics of the aerobiology of conidia of *P. sorghi* during the sorghum cropping season in semi-arid southern Africa. Some factors affecting production of conidia are investigated. The settling velocity of conidia is also calculated to confirm the suitability of conidia of *P. sorghi* for dispersal at low wind speeds.

Materials and methods

Periodicity of conidia production in the field

Spore sampling

A 7-day volumetric Burkard spore sampler (Burkard Manufacturing Co., Rickmansworth, Hertfordshire, England) was used to detect conidia. The sampler was operated in sorghum fields during 1993 (28 January to 3 April 1993) and 1993/4 (24 November 1993 to 31 March 1994) in Zimbabwe at the Matopos SADC/ICRISAT/SMIP (Southern African Development Co-operation/International Crops Research Institute for the Semi-Arid Tropics/Sorghum and Millet Improvement Program) farm. The air was sampled at a height of 1 m. The Burkard was run from a 12-V car battery, which was replaced weekly. The sampler operates by drawing air through an orifice at a rate of 10 L min^{-1}, causing particles to be impinged on a rotating drum immediately posterior to the orifice. The drum was prepared by attaching a strip of melinex with double-sided sticky tape. A coating of vaseline wax (150 mL) and paraffin wax (18 g) dissolved in hexane was painted on the melinex strip using a paint brush. This acted as the surface to entrap the spores. The drum rotates at 2 mm h^{-1}, each 48-mm section accounting for a 24-h period. The drum was changed every 7 days or less. After sampling, the melinex tape was cut into 1-day strips (48 mm) and mounted on slides with a gelvatol/methylene blue slide mountant (35 g gelvatol, 100 mL distilled water, 50 mL glycerol, 0·16 g methylene blue). The numbers of conidia on the strips were then counted by microscopic observation at ×100 magnification. The spore count was made on an hourly basis by taking a 100-μm traverse every 2 mm, and the number of spores detected per m^3 of air was subsequently calculated.

In 1993 the sampler was located immediately south-west (predominant wind direction from the north-east) of an experiment planted on 28 January 1993. In the 1993/4 season the sampler was approximately 600 m from the previous site, immediately leeward of an experiment planted on 16 January 1994. An infected ratoon crop from the previous season was situated 30 m north-east and was showing symptoms of systemic infection when spore sampling commenced on 24 November 1994.

Disease assessments of systemic and local lesion infection were made in the adjacent crop experiment areas on five occasions during both years. Systemic infection was estimated by counting the number of infected plants in four replicate transects of 10 plants each in all plots of the experiment, and calculating the mean value. The incidence of local lesion infection was estimated by assessing the proportion of leaves infected on 10 plants chosen at random in each of the plots, and taking means. Both experiments were planted with the var. Marupantse.

Weather data

Meteorological data were obtained from the SADC/ICRISAT/SMIP automated weather station situated in an open area at a height of 2·0 m. It was located approximately 100 m distant from the Burkard sampler in 1993 and 800 m in 1993/4. Data were recorded on a 4-h basis. Variables recorded included maximum and minimum temperatures, and wind speed and direction. Daily records of rainfall were obtained for this site from the Department of Meteorology, Harare.

Factors that affect production of conidia

Temperature

The effect of temperature on sporulation of systemically-infected leaf material was investigated. Thirty-day-old systemically infected container-grown plants (var. DMS 652), pre-inoculated at emergence, were held under light overnight to condition them for sporulation (400 W high pressure sodium lights 19·00–07·30 hours). Counting from the first leaf produced, leaves 6, 7 and 8 were used. Uniform systemically infected leaf material was removed from the plants, cut into 7-cm sections and placed immediately in distilled water. Leaf sections were mixed randomly, wiped dry with tissue paper and placed abaxial surface uppermost, in Petri dishes lined with moistened tissue paper. Four leaf sections were placed in each Petri dish, with three replicate dishes for each temperature. The leaf sections were incubated in the dark at 6, 10, 14, 18, 20, 22, 24, 26, 30, 34 and 38°C. A further set of dishes was kept aside to test for maturity of conidia. Every 30 min, from 5 to 8 h, leaf sections were taken from these dishes and the conidia were tested for maturity (conidia were assumed to be mature when freely released from the conidiophores). The experiment was fully randomized. At maturity of conidia, the petri dishes were removed from the incubator and the leaf sections placed in a desiccator jar containing 40% formaldehyde to kill the conidia and prevent germination. The leaf-pieces from each Petri dish were placed in a bijou bottle containing 5 mL distilled water, and agitated vigorously to release conidia from the leaf surface. The concentration of conidia was estimated by

microscopic observation using a haemacytometer. The width of each leaf section in the bottle was measured and the number of conidia produced per cm^2 of leaf was calculated.

Time period of release of conidia

Systemically infected leaf material was used to investigate the time period over which conidia were released from conidiophores under still conditions. The leaf material was selected and prepared as described for the previous experiment. The leaf sections were pinned abaxial surface uppermost to the inside of a rectangular plastic container (15 × 10 cm) lined with moist tissue paper. Enough leaf sections were used to cover the base of the container. A sheet of plastic covered with a layer of moist tissue paper was prepared. A glass microscope slide was placed on this layer, and the container inverted on the plastic sheet over the slides. Five replicate containers were randomly placed on two shelves of the incubator at 22°C. After 3 h a fresh plastic sheet, prepared in a similar manner, was placed under each container. This was repeated every 30 min for 11 h, causing minimal disturbance to the container. Slides were mounted as described previously. The number of spores deposited was counted by microscopic observation by taking the mean of six 100-μm transects across each slide at × 100 magnification.

Conidia production from systemically infected leaves and local lesions

The spore production of field-grown systemically infected and local-lesion infected leaf material, and container-grown systemically infected leaf material was investigated (leaf number 6–10). Two leaf sections (var. DMS 652) were placed in each of eight replicate Petri dishes. The experiment was fully randomized. The incubation period was 6·5 h at 22°C, as previous experiments had shown this to be the time at which conidia achieved maturity (indicated by germination), and 22°C the optimal temperature for sporulation. Methods to prepare and incubate the leaf material were as previously described.

The settling velocity of conidia

The settling velocity was calculated from the aerodynamic diameter (d_a) of conidia, estimated using a May Ultimate Impactor (MUI, May, 1975), a cascade impactor that separates particles of different settling velocity onto microscope slides. The slides are on different stages separated by different sized jets, which sort the particles according to their d_a. The operation of the instrument was previously described by Bock *et al.* (1997). The apparatus was tested using *Lycopodium* spores to confirm that it produced results comparable to previous reports (McCartney *et al.*, 1993). Leaves producing mature conidia were shaken over a funnel attached to the MUI by a flexible hosing. The experiment was replicated three times. The microscope slides were removed from the MUI and mounted, and the number of spores deposited on each stage was counted by taking 8 × 50 μm traverses across each slide at × 100 magnification. The d_a was ascertained from the proportion (P) of spores detected on the different slides. The estimate of d_a was made by taking that value of d_a that minimized the chi-squared value of P, where $(P_{observed} - P_{expected})^2/P_{expected}$ was summed over all the stages collecting spores in each replicate (McCartney *et al.*, 1993). The physical diameters of 100 conidia counted from three 50-μm transects across a slide were also measured at × 400, and the mean compared with the estimate of the d_a from the MUI.

Data analysis

Statistica (Statsoft Inc., Tulsa, Oklahoma 1994) was used to fit regression models to describe the effect of temperature on the production and time of deposition of conidia of *P. sorghi*. Prior to regression analysis the data from the conidia deposition experiment was log transformed, because of heterogeneity of the sample variance. For other data presented standard errors of the means were calculated.

Results

Periodicity of production of conidia

The results of the spore sampling in Zimbabwe in 1993 and 1993/4 are shown in Figs 1(a) and (b). Temperature data and rainfall for the Matopos site during this period are also shown. Mean disease incidence in the adjacent fields is shown in Table 1. Conidia were detected intermittently in both seasons. In 1993 conidia were detected on 25 nights (sampling period 66 days), and in 1994 on 33 nights (sampling period 130 days). In 1993 conidia were detected 7 days before disease was observed in the crop. In 1993/4 many conidia were detected prior to planting the adjacent field, probably because of an infected ratoon crop of sorghum about 30 m distant from the sampling site. Few conidia were detected after mid-February 1994. Rain fell regularly during the 1993 sampling period, but in 1994 a drought started in mid-February, and disease incidence fell after Julian date 55, as a result of plant death. Conidia were detected less frequently after this time. The number of conidia recorded during a particular day varied greatly within both seasons. During the different nights when conidia were detected, the minimum temperature ranged from 10 to 19°C.

The production of conidia shows marked periodicity (Fig. 2). Conidia were detected between 00·00 and 08·00 hours only, the number being highest between 02·00 and 05·00 h, when mean wind speed was less than 2·5 m s^{-1} and mean temperature was in the range 15–17°C.

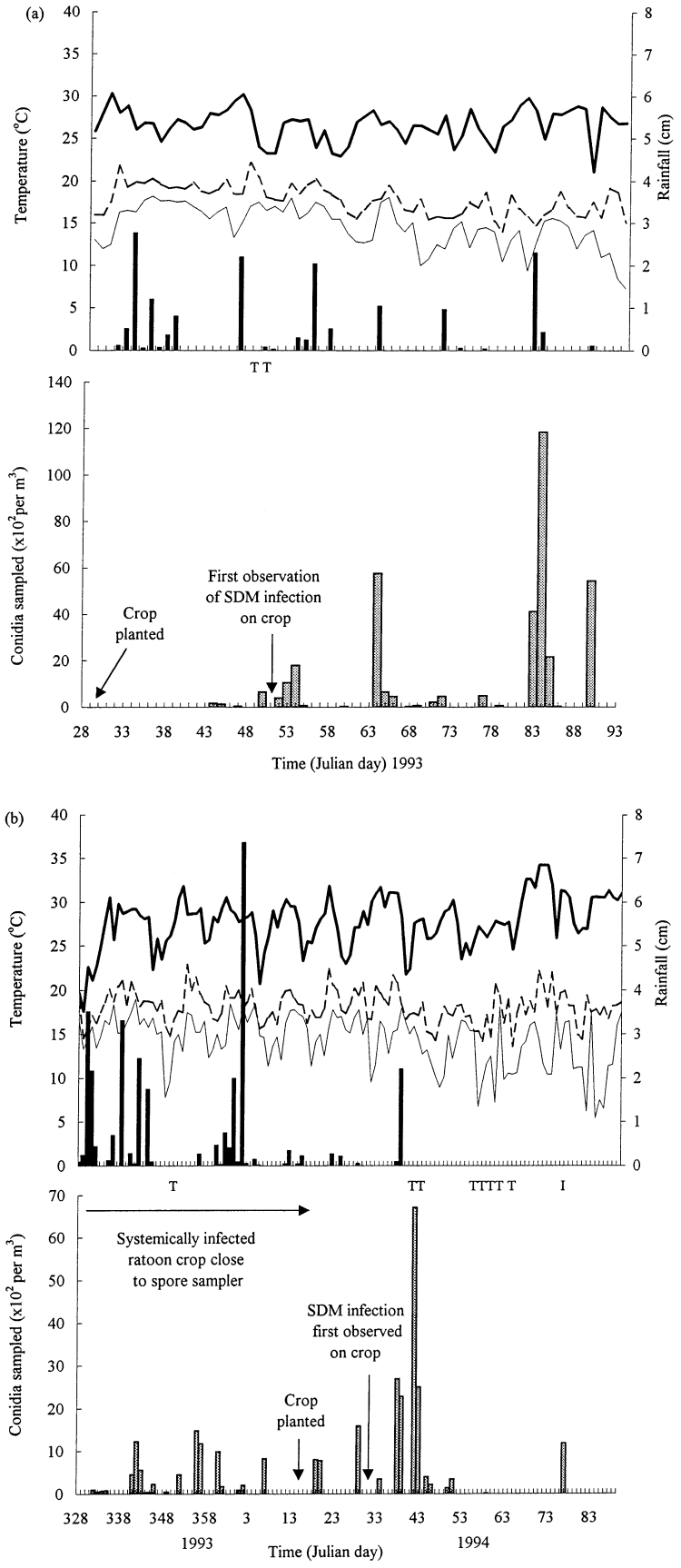

Figure 1 Temperature (maximum, heavy solid line; minimum, light solid line; 4-h mean (20:00–24:00 h) medium dashed line), rainfall (solid histogram) and daily concentration of conidia (shaded histogram) of *Peronosclerospora sorghi* in the air adjacent to infected sorghum crops during the 1993 (a) and 1994 (b) growing seasons at Matopos, Zimbabwe. T, trace of rain; I, irrigation applied.

Experiment year	Day of assessment (Julian date)	Mean disease incidence[a] Systemic infection (% plants infected)	Local lesions (% leaves infected)
1993			
	50	3·4 (2·74)[b]	12·3 (7·85)
	63	4·6 (2·01)	39·9 (4·10)
	81	5·9 (2·72)	57·0 (3·18)
	96	7·3 (2·70)	70·7 (2·79)
	120	7·2 (2·68)	84·7 (2·53)
1994			
	31	0 (0)	3·5 (2·64)
	55	8·7 (1·30)	32·0 (5·70)
	73	6·3 (4·66)	25·5 (7·69)
	98	9·7 (3·15)	17·1 (10·13)
	117	9·8 (4·95)	16·2 (9·40)

Table 1 The incidence of sorghum downy mildew in sorghum crops adjacent to spore sampling locations at Matopos, Zimbabwe in 1993 and 1994
[a]Disease incidence averaged over all plots of adjacent area.
[b]Standard errors of the mean in parentheses.

Conidia tended to be produced immediately after rain. The number of days with rain and the days when conidia were recorded are shown in Table 2. The fraction of the total nights on which conidia were detected and the number of days since the previous rain (both seasons combined) is shown in Fig. 3(a). Conidia were detected on 72% of nights between 1 and 3 days after the last rain, and on 8% of nights more than 6 days after the last rain. The greatest proportion of nights (81%) when conidia were detected had a mean temperature between 14 and 20°C (Fig. 3b). None were detected below 12 or above 22°C. For 64% of nights when conidia were found the wind speed was less than 2 m s^{-1} (Fig. 3c) and for 73% of nights conidia dispersal lasted less than 5 h (Fig. 3d).

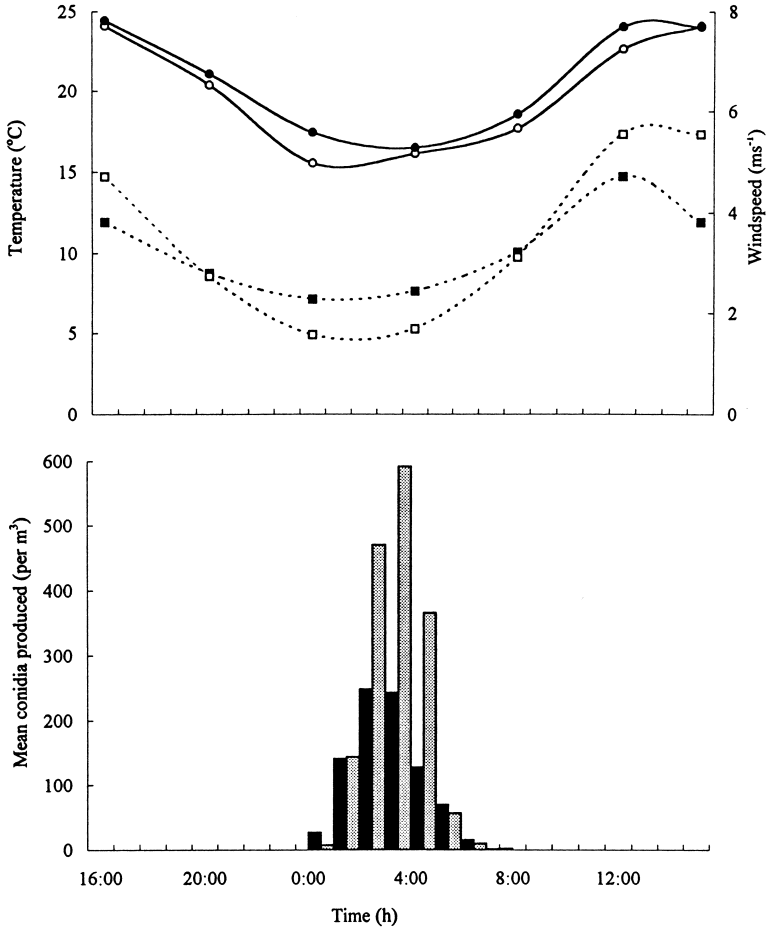

Figure 2 Mean diurnal periodicity of conidia production of *Peronosclerospora sorghi* adjacent to a sorghum crop at Matopos, Zimbabwe during the sampling periods in the 1993 (shaded histogram) and 1994 (solid histogram) growing season. Temperature (1993,○;1994,●) and wind speed (1993,□; 1994,■). Temperature and windspeed are based on 4-h means.

Table 2 The number of days with rain and the number of days on which conidia of *Peronosclerospora sorghi* were detected during the spore sampling periods at Matopos, Zimbabwe in 1993 and 1994

		Days with rain		Days without rain		
year	Total number of days with sampling	Number of days	Days conidia detected	Number of days	Days conidia detected	Total days when conidia detected
1993	66	24	19	42	6	25
1994	130	41	23	89	10	33

Factors that influence production of conidia

Effect of temperature on sporulation

The effect of temperature on sporulation of SDM from Matopos, Zimbabwe is shown in Fig. 4. The relationship between temperature and spore production was described by a third-order polynomial regression model. Maximum sporulation occurred at 22°C (>4000 conidia per cm^2). No sporulation occurred above 26°C or below 10°C over the 8-h period of incubation.

Time period of release of conidia

The time period of release of conidia from systemically infected leaves under controlled environment conditions is shown in Fig. 5. The release of conidia was described by a third-order polynomial regression model. Maximum deposition occurred 8 h after commencing incubation. No conidia were deposited with incubation periods of less than 7 h, and deposition ceased after 10 h.

Production of conidia from systemically infected leaves and local lesions

Examination of sorghum leaf material with local lesions and systemically infected field- and container-grown plants showed that container-grown plants produced 5666 conidia per cm^2 (standard error = 1078). Leaf material of a similar age from the field with local lesions produced 2437 conidia per cm^2 (standard error = 785) and systemically infected leaves from the field produced 2846 conidia per cm^2 (standard error = 1177).

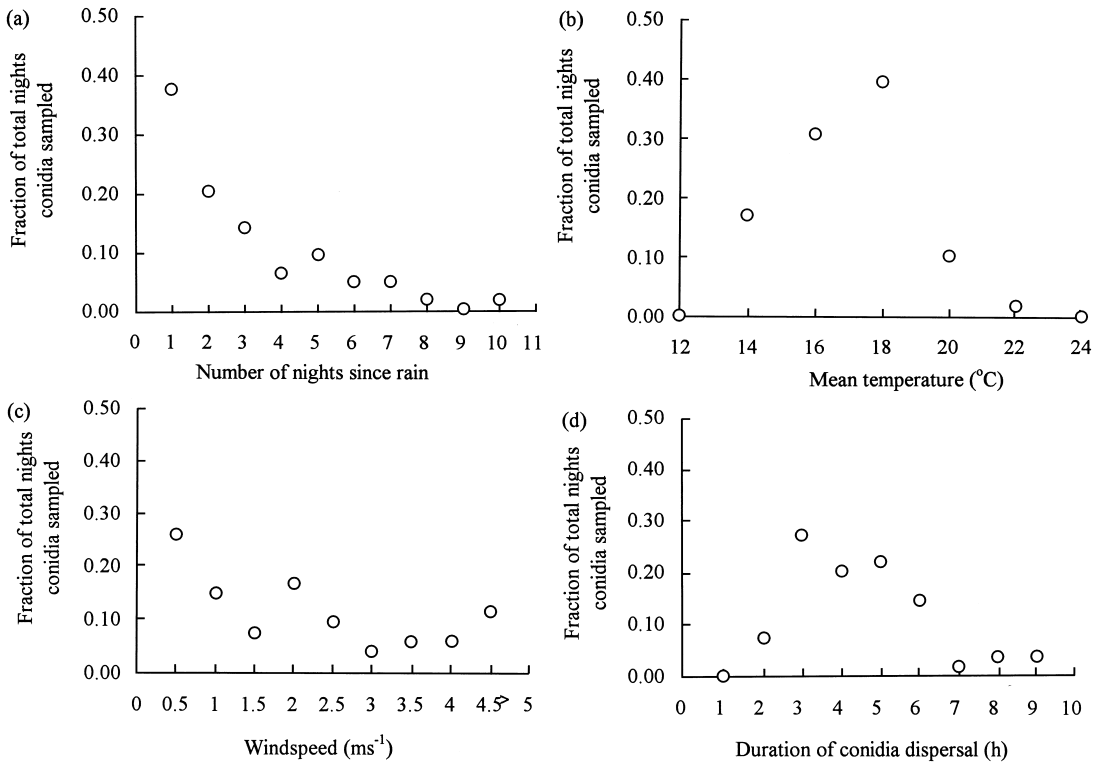

Figure 3 The frequency of detecting conidia of *Peronosclerospora sorghi* (○) in relation to (a) number of nights since the last rainfall, (b) mean nocturnal temperature (20·00–24·00 hours), (c) mean wind speed (20·00–24·00 hours) and (d) duration of conidia release (all data from both 1993 and 1994 growing seasons at Matopos, Zimbabwe).

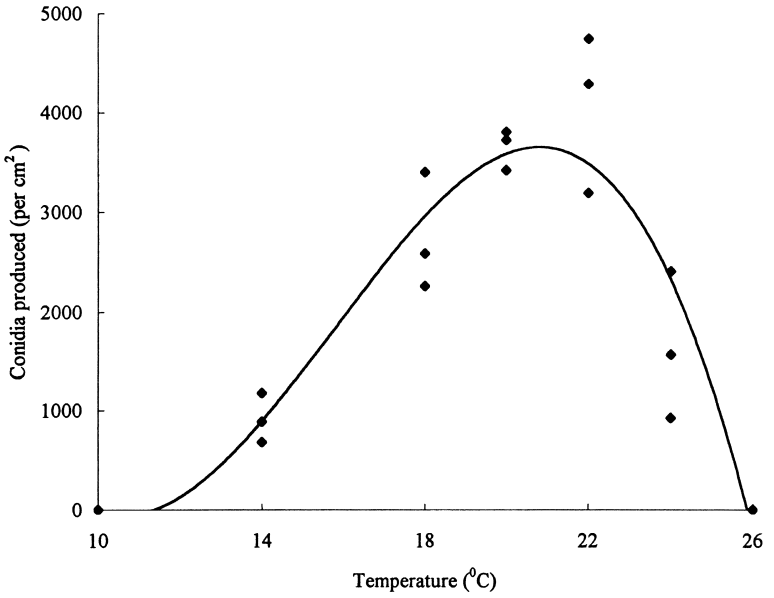

Figure 4 The effect of temperature on sporulation of *Peronosclerospora sorghi*. Sporulation was assessed on detached, systemically infected leaf pieces. Regression solution is a third-order polynomial model ($y = -7{\cdot}032x^3 + 331{\cdot}68x^2 - 4469x + 20548$, $R^2 = 0{\cdot}89$).

The settling velocity of conidia

The d_a of conidia as estimated using the MUI was 23·3 μm. The results from measuring the physical diameter are similar (21·8 × 19 μm, range 14·2–23·0 × 15·0–33·0 μm, standard error = 1·72 × 2·51). The estimate of d_a for *Lycopodium* (41 μm) is similar to the observation (43·8 μm) of McCartney *et al.* (1993). The settling velocity can be calculated from the d_a of the spore (Chamberlain, 1975; McCartney *et al.*, 1993):

$$V_s = (d_a \boldsymbol{g} \rho)/(18\nu\rho_a),$$

where d_a = the aerodynamic diameter of conidia estimated from the MUI, g = rate of fall due to gravity (9·81 m s^{-1}), ρ = density of the spore (assumed to be 1·0 × 10^3 kg m^{-2}), (ν = kinematic viscosity of air (1·5 × 10^{-4} m^2 s^{-1}) and (ρ_a = the density of air at 20°C (1·175 kg m^{-2}). The settling velocity for a conidium of *P. sorghi* is calculated to be 1·5 × 10^{-4} m s^{-1}.

Discussion

These data suggest that conidia of *P. sorghi* may play a major role in the epidemiology of SDM in the semi-arid regions of southern Africa. The daily pattern of conidia release was similar to that described in India and Israel (Kenneth, 1970; Shenoi & Ramalingham, 1979). The time at which conidia were released was typical, although the maximum time period over which they were detected was greater (9 h) than previously reported (6 h, Shenoi & Ramalingham, 1979). In the laboratory, conidia were deposited for up to 3 h, which is similar to

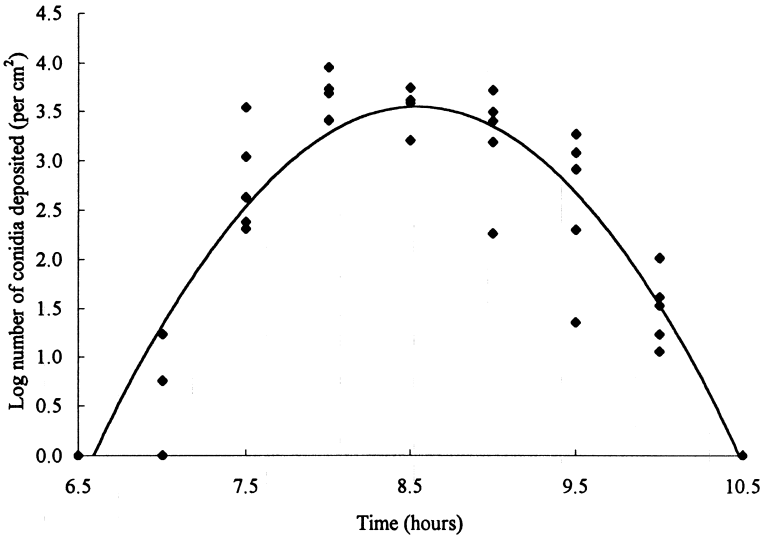

Figure 5 Time period of *Peronosclerospora sorghi* conidia release from systemically infected leaves incubated at 22°C. Regression solution is a third-order polynomial model ($y = -0{\cdot}0011x^3 - 0{\cdot}909x^2 + 15{\cdot}76x - 64{\cdot}072$, $R^2 = 0{\cdot}88$).

the period of deposition observed by Safeeulla (1976). In the field, conditions are less uniform and this would result in staggered and, overall, prolonged sporulation on plants. Conidia cease to be detected after 08·00 h, and although the lesion may produce further crops of conidia when conditions are favourable, only a single event takes place each day. Perhaps the periodic conidia production is dependent on the food reserves built up in the previous light period, or an innate periodicity within the fungus itself.

Previous work illustrated the importance of relative humidity and leaf wetness for conidia production of *P. sorghi* (Kenneth, 1970; Shenoi & Ramalingham, 1979), when temperature was adequate for spore production. In this study conidia were generally produced during the first few nights after rain, when relative humidity would be greatest. Unfortunately data on relative humidity were not available at the site, but the relationship between rainfall, temperature and wind speed indicate that the mean temperature (12–22°C) and wind conditions (mostly $< 2{\cdot}5\ m\ s^{-1}$) that supported spore production would also be likely to support high relative humidity within the crop. Conidia were not produced at night during prolonged periods of dry weather. This was especially noticeable during the dry, latter part of the 1993/4 season when there were few occasions when conidia were detected.

The results of the controlled environment laboratory investigations presented in this study indicate that sporulation of SDM from Zimbabwe could take place between 10 and 26°C (optimally at 22°C). In the field conidia were most frequently detected when the mean temperature was between 15 and 19°C. Much of the process of conidiophore development and conidia production may take place at a temperature greater than 15°C as the mean temperature reflects the range between the maximum and minimum temperatures during the entire day.

Conditions of temperature and moisture that support conidia production have been shown to be conducive to conidia survival, germination and infection (Bonde *et al*., 1985). Although the effects of temperature and moisture on infection were not investigated in this study, the observations on the production of conidia suggest that conditions in these semi-arid regions of southern Africa are also likely to be suitable for conidial infection of susceptible hosts. Further work is needed to confirm that healthy plants are infected under natural conditions in Zimbabwe.

The production of conidia of *P. sorghi* from systemically infected sorghum leaf material is in agreement with previous observations (Futrell & Bain, 1968; Duck *et al*., 1987), although less than that reported in India, where in excess of 10 000 conidia per cm^2 was reported (Shetty & Safeeulla, 1981). Different varieties of sorghum may affect the ability of *P. sorghi* to produce conidia. However, in Uganda, Bigirwa *et al*. (1997) found no effect of host on conidia production when comparing Johnson grass, sorghum and maize. All produced about 4000 conidia per cm^2 of lesion. It remains possible that different isolates of *P. sorghi* vary in their ability to produce conidia.

Duck *et al*. (1987) assessed the risk of the graminaceous downy mildews to other crops by their capacity for asexual sporulation. They observed that *P. sorghi* had a comparatively low sporulation ability compared with both *P. philippinensis* and *P. maydis*. However, it is worth noting that neither *P. philippinensis* nor *P. maydis* produce local lesion infections (Williams, 1984). Local lesions possibly contribute significantly to the epidemic potential of *P. sorghi* within an infected sorghum crop. Local lesion infections can cover a significant proportion of the leaf area within an infected crop which may have only a very low incidence of systemic infection (Cohen & Sherman, 1977). This may become even more important, considering the short latent period of local lesions (about 8 days, Cohen & Sherman, 1977; Rajasab *et al*., 1980). Within the crops from which conidia were detected in this study, there was a rapid increase in incidence of local lesion infection, except in 1994 when severe drought conditions later in the season resulted in a reduction in disease. It is likely that local lesions were a major source of the conidia detected in these studies, at least until the incidence of systemic infection had risen to a significant level.

It is not known whether the release of conidia is active or passive. Kenneth (1970) suggested that conidia were actively released as in other downy mildews, but no studies have been undertaken to confirm this. Once the conidia have left the leaf surface they enter air currents. A combination of the settling velocity of the spore and the nature of the air currents then determines dispersal (Chamberlain, 1975; McCartney *et al*., 1993). The settling velocity of $1{\cdot}5 \times 10^{-4}\ m\ s^{-1}$ for conidia of *P. sorghi* suggests that they can be readily dispersed by lower wind speeds at night, and supports the observations of Rajasab *et al*. (1979), who detected conidia some distance from an infected crop.

Information on the aerobiology of the asexual phase of *P. sorghi* in a particular area can aid in disease management decisions. In Zimbabwe conditions early in the season are favourable for conidia production and infection (Bonde *et al*., 1985), and planting in many areas may span a period of at least a few weeks. Ratoon cropping should be avoided and the risk of systemic SDM infection, and yield loss may be minimized by planting susceptible crops early in the season, when airborne inoculum from early infected plants is likely to be lowest.

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