Plant Pathology (1994) **43**, 112–120

Effects of leaf wetness and temperature on late leaf-spot infection of groundnut

D. R. BUTLER, K. D. R. WADIA *and* D. R. JADHAV
Resource Management Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru PO, Andhra Pradesh 502 324, India

Experiments are described to quantify the effects of temperature and leaf wetness duration on infection of groundnut by *Phaeoisariopsis personata*. Temperature response curves for conidial germination and infection were similar, with optima close to 20°C and minimum and maximum temperatures of about 8°C and 34°C, respectively. The effect of temperature on infection between 15°C and 26°C was slight. Lesions developed only if the leaf wetness period exceeded about 20 h, and the total wetness period necessary for maximum infection exceeded 160 h. The number of lesions resulting from a fixed amount of inoculum was several times greater if leaves were exposed to alternate wet and dry periods (intermittent wetness), compared with continuous wetness. With intermittent wetness the length of the dry period had little effect on the number of lesions, providing it exceeded 2 h. The response curve relating total wetness periods to lesion density was an exponential asymptote.

INTRODUCTION

Groundnut (*Arachis hypogaea*) is a major oil-seed and food crop of the semi-arid tropics, where the production constraints include unreliable rainfall, diseases and pests. Late leaf-spot disease, caused by *Phaeoisariopsis personata*, is globally widespread, and the most important foliar disease. Recent conservative estimates of yield losses caused by the disease are in the order of 0·5 million tonnes per year for India alone, which is about 7% of the total production (T. G. Kelley, ICRISAT, unpublished data, 1992). Chemical control of foliar diseases is common in the USA, but use of fungicides is not widespread in many tropical regions where the crop is grown by resource-poor farmers. Recent advances in screening (Subrahmanyam *et al.*, 1989) and breeding for resistance to late leaf spot have resulted in a number of promising lines being released (Wynne *et al.*, 1991). However, the degree of resistance shown by a given genotype may vary between locations, possibly owing to differences in climate and/or pathogen race (L. J. Reddy, ICRISAT personal communication, 1992).

A thorough understanding of the way in which weather affects disease should lead to improved screening methods for resistance breeding programmes, reliable systems to forecast disease epidemics (Jones, 1986) and the means to classify climate according to disease risk (Coakley, 1988). Disease forecasting systems would enable timely and efficient use of fungicides. This is of particular importance where the possible number of applications is severely restricted by cost, pesticide availability or restricted water supply in remote areas. In areas where regular use of pesticides is common, reductions in the number of applications will reduce both environmental degradation from fungicides and the likelihood of resistance to pesticides (Bent, 1978).

Two weather variables that strongly affect the infection process in late leaf spot are temperature and leaf wetness. The percentage of conidia that germinate is known to decrease with increasing temperature above 20°C, and at 20°C it takes about 12 h for 50% of the conidia to germinate (Sommartya & Beute, 1986). Shew *et al.* (1988) found slightly more infection at 20°C than at 24°C, and much less at 28°C. They also found that infection increased with the number of hours that plants were exposed to high relative humidity (r.h. > 93%) each day for a 6-day period. They wetted the leaves at the start of each daily period of exposure to high r.h. Lannou & Blizoua Bi (1989) examined techniques to infect groundnut plants with *P. personata* and found that the

Table 1. Details of inoculation experiments to examine the effects of leaf wetness and temperature on late leaf-spot infection of groundnut

Experiments	Total wetness periods[a] (h)	Wet/dry sequence[b] (h)	Temperature (°C)
Continuous versus intermittent wetness	16C	**16**	23
	24I	**16** 8 **8**	23
	24C	**24**	23
	32I	**16** 8 **16**	23
	32C	**32**	23
	40I	**16** 8 **16** 8 **8**	23
	40C	**40**	23
	48I	**16** 8 **16** 8 **16**	23
	48C	**48**	23
	64I	**16** 8 **16** 8 **16** 8 **16**	23
	64C	**64**	23
Length of dry periods	80	**80**	23
	80	**22** 2 **22** 2 **22** 2 **14**	23
	80	**20** 4 **20** 4 **20** 4 **20**	23
	80	**18** 6 **18** 6 **18** 6 **18** 6 **8**	23
	80	**16** 8 **16** 8 **16** 8 **16** 8 **16**	23
	80	**14** 10 **14** 10 **14** 10 **14** 10 **14** 10 **10**	23
Intermittent wetness periods	16	**16**	13 15 20 23 26 30
	24	**16** 8 **8**	13 15 20 23 26 30
	32	**16** 8 **16**	13 15 20 23 26 30
	48	**16** 8 **16** 8 **16**	13 15 20 23 26 30
	80	**16** 8 **16** 8 **16** 8 **16** 8 **16**	13 15 20 23 26 30
	112	**16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16**	13 15 20 23 26 30
	160	**16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16**	13 15 20 23 26 30

Table 1. (*Cont.*)

Experiments	Total wetness periods[a] (h)	Wet/dry sequence[b] (h)	Temperature (°C)
Minimum wetness periods	16	**16**	13 15 20 23 26 30
	20	**16** 8 **4**	13 15 20 23 26 30
	24	**16** 8 **8**	13 15 20 23 26 30
	28	**16** 8 **12**	13 15 20 23 26 30
	32	**16** 8 **16**	13 15 20 23 26 30
	36	**16** 8 **16** 8 **4**	13 15 20 23 26 30
	40	**16** 8 **16** 8 **8**	13 15 20 23 26 30
	44	**16** 8 **16** 8 **12**	13 15 20 23 26 30
	48	**16** 8 **16** 8 **16**	13
Temperature	160	**16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16**	10
	160	**16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16**	15
	160	**16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16**	20
	160	**16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16**	25
	160	**16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16** 8 **16**	30

[a] I denotes intermittent wetness; C denotes continuous wetness.
[b] Bold type denotes wet periods; roman type denotes dry periods

infection process took longer than 6 days They also found greater infection efficiency with alternate high and low r h They observed free water on the leaves in the high r h treatment, which suggests that leaf wetness may be an important variable Cook (1981) observed germ tube growth of *P personata* towards stomata from the first day after inoculation of detached groundnut leaves However, this only occurred when condensation inside the Petri dish dried during part of the day With continuous condensation, when Petri dishes were enclosed in plastic bags, germ tube growth was not directional

Current knowledge of the effects of temperature and leaf wetness on infection is incomplete, and this paper describes studies to elucidate and quantify relationships between these two weather variables and infection

MATERIALS AND METHODS

Five sets of experiments were carried out to examine how temperature and leaf wetness periods affect infection The plant material and inoculation technique described below were the same in all experiments

Plant material

Groundnut plants (cv TMV 2) were grown in 13-cm diameter pots in a glasshouse The potting medium, 50% loam, 25% sand and 25% compost, was steam pasteurized and Broughton's nutrient solution (Broughton & Dilworth, 1971) was applied weekly Healthy plants were maintained without the use of pesticides and insect damage was eliminated by removing affected plants Four-week-old plants (two per pot) were used for inoculation experiments

The maximum air temperature in the glasshouse did not exceed 35°C and the minimum air temperature varied between 12°C and 20°C The minimum r h ranged from 30 to 50% during the day and from 60 to 90% at night The average irradiance in the glasshouse was about 60% of daylight

Inoculation

Late leaf-spot inoculum was multiplied on groundnut leaves (cv TMV 2) using isolates derived from conidia collected locally The inoculum was harvested with a cyclone spore collector and stored at 4°C

On each plant the third and fourth leaves from the top (four leaves per pot) were tagged prior to inoculation Immediately before inoculation, a suspension of conidia in about 200 ml of distilled water with a few drops of Tween 80 wetting agent was prepared The spore concentration was determined with a haemocytometer and adjusted to give approximately 10 000 spores per ml The suspension was sprayed with an atomizer, ensuring that both surfaces of the tagged leaves were completely wetted The retention of suspension per unit leaf area, estimated by weighing, was approximately 6 μl/cm^2, so the number of conidia deposited on both surfaces was about 60 per cm^2

Controlled environment

Immediately after inoculation (while still wet) plants were placed in dew chambers to ensure the presence of liquid water on the surface of the leaves The dew chambers were based on the design of Clifford (1973) with a cooled outer cabinet and heated water bath in the inner chamber The temperature of the inner chamber was controlled by switching on the water bath heater only when the air temperature at the height of the plants was below the set value This resulted in the temperature always remaining within 0 5°C of that required The temperature sensor was a thermocouple attached to a data logger (CR10, Campbell Scientific Inc , Logan, UT, USA) It is normally dark inside the dew chambers, but lights were fitted to one chamber used for the continuous wetness treatment (see below)

After removing plants from the dew chamber, leaves were dried in front of a fan before transfer of the plants to a controlled environment cabinet or a glasshouse, where they were kept during dry periods within the experimental treatment or to wait for symptoms to develop after the end of the treatment The conditions in the glasshouse were as described above Plants were inspected and the number of lesions on inoculated leaves were counted daily Discrete, incipient lesions (necrotic specks) were counted as soon as they could be detected Where more than one lesion coalesced during growth, a single count was recorded After the number of lesions had stopped increasing, inoculated leaves were removed and the leaf area determined with a leaf area meter (Delta-T Devices, Cambridge, UK) The maximum number of lesions on any day was used to calculate lesion density

Experiments

The five sets of experiments are summarized in

Table 1. Each experiment was repeated to provide two replicates and, as similar patterns of results among replicates were obtained in the first four sets of experiments, no further repetition was undertaken. However the fifth set was repeated three times, giving four replicates. In each experiment of the first four sets, three pots per treatment were used to provide 12 inoculated leaves. In the fifth set either six or eight pots were allocated to each treatment to provide 24 or 32 inoculated leaves.

Separate experiments were carried out to determine the effect of temperature on germination of conidia.

Continuous versus intermittent wetness

Continuous wetness was compared with alternate wet and dry periods (referred to as intermittent wetness). The sequence of wet and dry periods in the intermittent wetness treatment is given in Table 1 Dry periods were achieved by moving the pots to a plant growth cabinet (E15 Conviron Cabinet, Winnipeg, Canada) set to 23°C, 80% r.h. and an irradiance of 59 μmol/m^2.s. In the continuous treatment, dew chamber lights which gave 54 μmol/m^2.s were operated during the same periods.

Duration of dry periods

The effect of varying the daily duration of dry periods while maintaining a constant total wetness period of 80 h was assessed (Table 1). Treatments were achieved by moving plants between a dew chamber (23°C) and a plant growth cabinet (23°C, 80% r.h.), and lights were operated in both the dew chamber and the plant growth cabinet, so that plants in all treatments were illuminated for 8 h each day.

Intermittent wetness periods

To examine the effect of different intermittent wetness periods on infection at different temperatures, three dew chambers were operated simultaneously, with one at 23°C (standard temperature, thought to be close to the optimum), and the others at two treatment temperatures between 13°C and 30°C (Table 1). For the 23°C treatment, a second dew chamber was operated at the same temperature as the standard. Pots were kept in the dew chambers at night (16 h) and moved to a plant growth cabinet during the day (8 h).

Minimum wetness periods

To determine the minimum period of leaf wetness for infection to begin, plants were subjected to intermittent wetness, as shown in Table 1. Two dew chambers were used at one time with different temperature settings.

Temperature

To examine the effect of temperature on infection with non-limiting leaf wetness, five dew chambers were used, each at a different temperature. Preliminary experiments had indicated that maximum infection occurred with a total of about 160 h intermittent wetness, so all plants were subjected to 10 consecutive nights (16 h) in a dew chamber and moved to a growth cabinet each day (8 h).

Germination of conidia

A suspension of conidia (50000 spores per ml) was prepared, one drop of which was placed on each of 14 glass slides. Each slide was placed in a covered Petri dish lined with moist tissue to prevent the drop drying. The dishes were put on a thermogradient plate (Garcia-Huidobro *et al.*, 1982), set to give temperatures in the range 8–34°C. The temperature in each Petri dish was monitored with a copper constantan thermocouple connected to a data logger (CX21, Campbell Scientific Inc.). The slides were removed after 48 h and the numbers of germinated and non-germinated conidia were counted using a microscope. The average number of conidia assessed per treatment was about 300, and the experiment was repeated twice.

Data analysis

In the first four sets of experiments, replicates were combined to give the mean and standard error for all leaves in each treatment. In the fifth set of experiments, the mean lesion density was calculated for each treatment in each replicate separately.

Response curves (equations 1 and 2 below) were fitted using the Simplex method to obtain non-linear least squares estimates (Wilkinson, 1990).

RESULTS

Continuous versus intermittent wetness

The number of lesions increased with the total period of leaf wetness with both continuous and

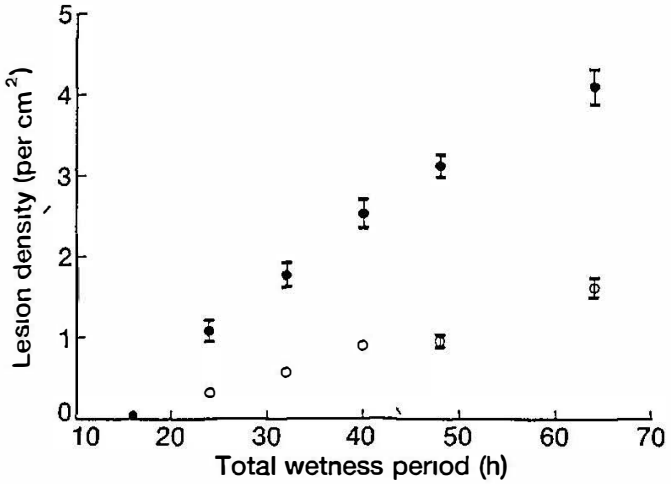

Fig. 1. The effect of leaf wetness periods on infection by *Phaeoisariopsis personata* at 23°C Groundnut leaves were inoculated with a conidial suspension and the maximum number of resulting lesions per unit leaf area was used to assess infection ●, Intermittent wetness, ○, continuous wetness Bars indicate standard errors

intermittent treatments, but about three times as many lesions formed with intermittent wetness (Fig 1)

Duration of dry periods

Lesion density increased as the daily dry period increased from 0 h to 4 h, and thereafter it remained constant (Fig 2)

Intermittent wetness periods

Lesion densities in Fig 3 were normalized with respect to the lesion density at the standard temperature (23°C) with 160 h total wetness This allowed comparisons between sequential experiments when the absolute number of lesions varied considerably Lesion density increased with the total period of intermittent wetness up to 160 h, but the rate of increase was usually greatest between 30 h and 80 h (Fig 3) The final lesion density was similar to that at 23°C for all temperatures except 30°C, where consistently fewer lesions developed At 13°C, results from sequential experiments were inconsistent and two results are shown for comparison in Fig 3a

When individual experiments were repeated with the same conditions of temperature and wetness, there was some variation in the pattern of increase in lesion density However, at 23°C (the standard temperature), we repeated the same procedure eight times and the average result produced a smooth curve (Fig 4) The equation

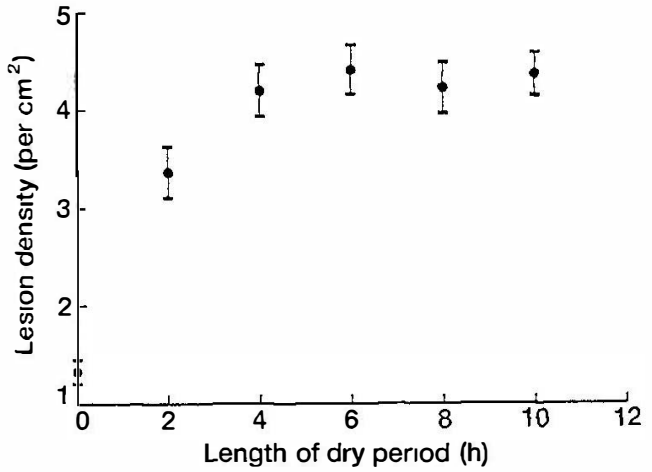

Fig. 2. The effect of different lengths of daily dry periods on lesion density at 23°C Groundnut leaves were inoculated with a conidial suspension and the total wetness period was 80 h in all treatments

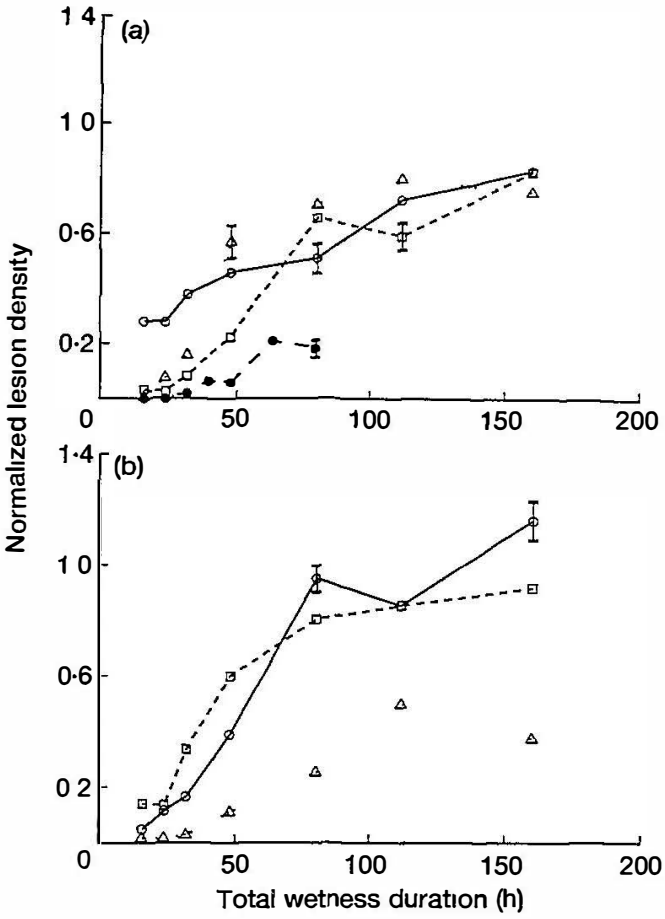

Fig. 3. The effect of varying the total wetness period on lesion density, with intermittent wetness at different temperatures At each temperature the lesion density was normalized with respect to the lesion density at 23°C with 160 h of wetness To illustrate the variability at 13°C, the results of two separate experiments are shown Bars indicate standard errors (a) – ● –, 13°C, —○—, 13°C, - - - -□- - - -, 15°C, △ , 20°C (b) —○—, 23°C, - - - -□- - - -, 26°C, △ 30°C

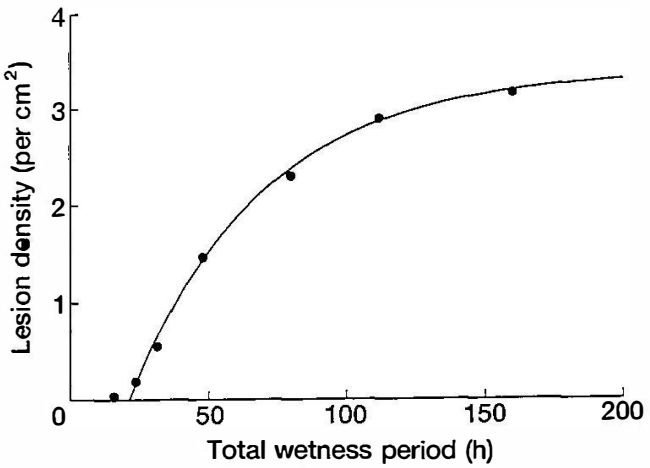

Fig. 4. The relationship between infection by *Phaeoisariopsis personata* and leaf wetness duration at 23°C for inoculated groundnut leaves. The fitted line is given by equation 1.

of an exponential asymptote fits the mean values very closely ($r^2 = 0{\cdot}99$):

$$L = L_{max}\{1 - a[\exp(-bW)]\} \qquad (1)$$

where L is the lesion density, $L_{max} = 3{\cdot}37$ lesions per cm² is the asymptote, $b = 0{\cdot}021$ is the rate of increase of lesion density and $a = 1{\cdot}57$, is related to the minimum period of wetness before infection occurs; $(1/b)\log(a) = 21{\cdot}5$ h. The 16 h value in Fig. 4 was excluded from the fitting procedure since this was less than the minimum wetness period required for infection.

Minimum wetness periods

No lesions were produced at any temperature with 16 h of leaf wetness. The initial increase in lesion density with wetness period was approximately linear, and regressions were used to indicate minimum wetness periods for infection to occur. These periods were not significantly different from each other between 15°C and 30°C (Table 2), for which the mean minimum wetness period was 19 h. At 13°C the minimum wetness period of 33 h was significantly greater ($P = 0{\cdot}02$) than at any other temperature. There was an abrupt change between 15°C and 13°C.

Temperature

Temperature had little effect on lesion density between 15°C and 25°C when non-limiting wetness (160 h) was provided (Fig. 5). Mean values of lesion density were significantly ($P < 0{\cdot}001$) less at 10°C and 30°C; however, there was considerable variation between individual experiments. A response curve fitted to the data gave three

Table 2. The effect of temperature on the minimum wetness period (W_{min}) for infection, given by linear regression relationships between total wetness period and lesion density: m is the slope of the line, c is the intercept, and r^2 is the coefficient of determination.

Temperature (°C)	W_{min} (h)	m	c	r^2
13	32·9	0·064	−2·10	0·65
15	19·4	0·025	−0·49	0·84
20	15·8	0·102	−1·61	0·87
23	21·0	0·092	−1·93	0·86
26	18·1	0·116	−2·09	0·78
30	21·4	0·038	−0·81	0·79

cardinal temperatures: the minimum (T_{mm}), the optimum (T_{opt}) and the maximum (T_{max}).

$$Y = Y_{max}\frac{(T - T_{mm})(T_{max} - T)}{[(T_{max} + T_{mm})/2]^2} \qquad (2)$$

where $T_{opt} = (T_{max} + T_{mm})/2$, Y is the dependent variable (in this case Y is the normalized lesion density) and Y_{max} is the value of Y at T_{opt}. The values of T_{mm} and T_{max} (with standard errors) are $6{\cdot}9 \pm 1{\cdot}0$ and $32{\cdot}8 \pm 0{\cdot}9$°C respectively and T_{opt} is 19·8°C.

Equation 2 is a quadratic equation, applicable to cases where T_{opt} is midway between T_{mm} and T_{max}. Written in this form, it is a simple equation with biologically meaningful parameters, which adequately describes the effect of temperature on lesion density and germination of conidia.

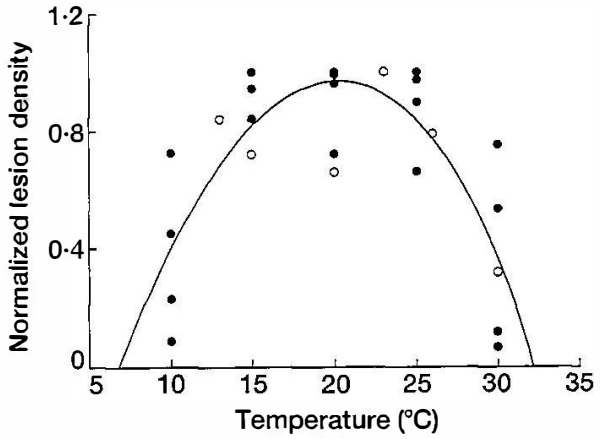

Fig. 5. The relationship between infection by *Phaeoisariopsis personata* and temperature for inoculated groundnut leaves with non-limiting leaf wetness. ●, Data obtained from the experiments described in Set 4; ○, data from other experiments when the total period of leaf wetness was 160 h. The fitted line is given by equation 2.

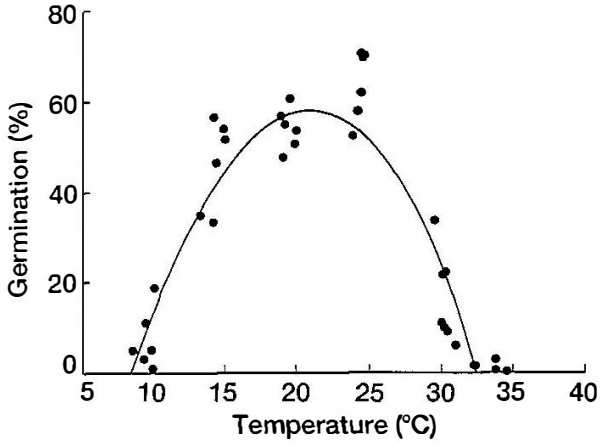

Fig. 6. The effect of temperature on germination of *Phaeoisariopsis personata* conidia on glass slides. The fitted line is given by equation 2.

Germination of conidia

The temperature response curve for percentage germination of conidia (*in vitro*) had a similar form to the response for infection (Fig. 6). The fitted line is equation 2 (where Y is percentage germination) and the values of T_{min} and T_{max} are $8{\cdot}8 \pm 0{\cdot}4$°C and $32{\cdot}1 \pm 0{\cdot}4$°C respectively and T_{opt} is 20·4°C. There is less scatter than was the case for infection, so the cardinal temperatures are more closely defined; differences between values for lesion density and conidial germination are not statistically significant.

DISCUSSION

These results indicate that the effect of temperature on *P. personata* infection is slight between 15°C and 26°C (Figs 3 and 5). At 13°C, after prolonged wetness periods, the final number of lesions varied greatly between experiments. The minimum wetness period for infection to occur at 13°C was usually longer than at other temperatures (Table 2), although in some experiments lesions developed after only 16 h of wetness. The two contrasting situations are shown in Fig. 3a. Lesions from 13°C were generally small and poorly developed, and included many hypersensitive specks, so although the lesion number was sometimes large, disease severity was slight.

Variability in individual experiments masked the smooth relationship between lesion density and total wetness period (Fig. 4). The data fit an exponential asymptote with a minimum period for infection of about 20 h, similar to independently determined values from 15 to 30°C. The number of lesions reached about 90% of the maximum with a total wetness period of 130 h.

It is important to the epidemiology of the late leaf spot pathogen that the infection process continues for as long as 10 days. Our results support the conclusion of Lannou & Blizoua Bi (1989) that this process continues for longer than 6 days. With early leaf spot of groundnut caused by *Cercospora arachidicola*, Alderman & Beute (1986) observed a continuing increase in the number of lesions for 20 days after inoculation. Conidial germination of *C. arachidicola* was virtually complete in the first 30 h, but substantial stomatal penetration was observed only after 4 days and the number of penetrations continued to increase up to 12 days. Our results suggest that *P. personata* behaves similarly, but microscopic studies of the pathogen on leaf surfaces are needed to confirm this.

Since the amount of inoculum was constant, the large difference in lesion density following continuous and intermittent wetness can be ascribed to a difference in infection efficiency. The difference in lesion density agrees with the observation of Lannou & Blizoua Bi (1989) who compared alternating high (100%) and low (60–80%) r.h. with continuously high r.h. They always found the largest lesion densities with alternating high and low r.h. and, since they observed free water on the leaves in the 100% r.h. treatment, it would be reasonable to equate high r.h. in their experiments to leaf wetness.

Shew *et al.* (1988) examined the effect of different daily periods of high and low r.h. on infection by *P. personata.* They continued the treatment for 6 days and found maximum lesion numbers with 24 h of high r.h. per day (i.e., continuously high r.h.). This is in contrast to the results of Lannou & Blizoua Bi (1989) and to the present study. A possible explanation is that r.h. in their high humidity chamber varied between 93% and 99% and, although the leaves were wetted each evening, they may have subsequently dried. Illumination within the growth cabinet would have increased evaporation from the leaves.

Alderman & Beute (1986) observed the effect of intermittent wetness on germ tube growth of *C. arachidicola*. Germ tube length was greatest with continuous wetness and growth was affected by the r.h. during the dry period. With a r.h. $>65\%$, growth stopped (or was minimal) during the dry period and resumed in subsequent wet periods. With a r.h. of 30–40%, growth did not resume during subsequent wet periods. Germ tubes of other fungi such as *Cercospora musae* are able to survive exposure to extremely low humidity and

then resume growth (Good & Zathureczky, 1967). In our experiments the r h. was 70–80% during the dry periods and the increase in *P. personata* lesion number over repeated wet–dry cycles strongly suggests that germ tube growth was continuing.

Providing the dry period between subsequent wetness periods is longer than 2 h, it appears not to matter how long the plants remain dry (Fig. 2). In an experiment not reported here, similar lesion densities were found when plants were exposed to wetness for 16 h on each of five days, and with 16 h on alternate days over a 10-day period. In both cases the total wetness period was 80 h. The available evidence indicates that the total wetness period is a major factor in determining the number of successful infections

Temperature responses were similar for conidial germination and infection. Both response curves indicate an optimum temperature of about 20°C; however, between 15°C and 25°C there were no statistical differences in lesion densities. Sommartya & Beute (1986) reported a similar temperature response curve for conidial germination of *P. personata* between 16°C and 36°C. However their values of maximum germination were larger than this study (63%) for isolates from both the USA (76%) and Thailand (87%).

Night-time temperatures during the rainy season in the groundnut-growing regions of south India are normally between 20°C and 25°C and are optimal for infection by *P. personata*. In the dry season when the crop is irrigated, night-time temperatures of less than 15°C occur, which may limit infection when adequate leaf wetness is provided by dew. Continuous wetness periods greater than 20 h are uncommon, since the majority of rainfall events are of short duration and evaporation rates are high. Our results suggest that the pathogen is not only adapted to survive dry periods during the infection process, but that the process is enhanced by wet–dry cycles. The mechanisms by which this is achieved have yet to be investigated.

REFERENCES

Alderman SC, Beute MK, 1986 Influence of temperature and moisture on germination and germ tube elongation of *Cercospora arachidicola Phytopathology* **76,** 715–19

Bent KJ, 1978. Chemical control of plant diseases some relationships to pathogen ecology. In· Scott PR, Bainbridge A, eds. *Plant Disease Epidemiology* Oxford, UK Blackwell Scientific Publications, 177–86

Broughton WJ, Dilworth MJ, 1971 Control of leghaemoglobin synthesis in snake beans. *Biochemistry Journal* **25,** 1075–80

Clifford BC, 1973. The construction and operation of a dew-simulation chamber *New Phytologist* **77,** 619–23

Coakley SM, 1988. Variation in climate and prediction of disease in plants *Annual Review of Phytopathology* **26,** 163–81

Cook M, 1981 Susceptibility of peanut leaves to *Cercosporidium personatum Phytopathology* **71,** 787–91.

Garcia-Huidobro J, Monteith JL, Squire GR, 1982. Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. & H.) I Constant temperature. *Journal of Experimental Botany* **33,** 288–96

Good HM, Zathureczky PGM, 1967 Effects on the viability of germinated spores of *Botrytis cinerea, Cercospora musae*, and *Monilinia fructicola. Phytopathology* **57,** 719–22.

Jones AL, 1986. Role of wet periods in predicting foliar diseases In: Leonard KJ, Fry WE, eds. *Plant Disease Epidemiology Population Dynamics and Management.* Vol. 1 New York, USA: Macmillan Publishing Company, 87–100

Lannou C, Blizoua Bi P, 1989 Conditions for the development of *C personatum* leaf lesions on groundnut after artificial infection. *Oléagineux* **44,** 531–5

Shew BB, Beute MK, Wynne JC, 1988 Effects of temperature and relative humidity on expression of resistance to *Cercosporidium personatum* in peanut *Phytopatholgoy* **78,** 493–8.

Sommartya T, Beute MK, 1986 Temperature effects on germination and comparative morphology of conidia for Thai and USA isolates of *Cercosporidium personatum Peanut Science* **13,** 67–70.

Subrahmanyam P, Ramnatha Rao V, McDonald D, Moss JP, Gibbons RW, 1989 Origins of resistances to rust and late leaf spot in peanut (*Arachis hypogaea*, Fabaceae) *Economic Botany* **43,** 444–55

Wilkinson L, 1990. *SYSTAT The System for Statistics.* Evanston, IL, USA. SYSTAT Inc.

Wynne JC, Beute MK, Nigam SN, 1991. Breeding for disease resistance in peanut (*Arachis hypogaea* L.). *Annual Review of Phytopathology* **29,** 279–303.