

Inoculum density – host response relationships of spring wheat cultivars to infection by *Septoria tritici*

B. L. SHEARER

Western Australian Department of Agriculture, Jarrah Road, South Perth, Australia

Accepted 27 May 1977

Abstract

Eight inoculum densities (ID), increasing in geometric progression from 0.1×10^5 to 12.8×10^5 conidia ml^{-1} of *Septoria tritici* were sprayed onto the leaves of five cultivars of *Triticum aestivum*, differing in resistance to *S. tritici*. Host response to infection by *S. tritici*, measured as either the latency period (LPD) or percentage of leaf area covered by lesions with pycnidia (PLAL), was significantly linearly correlated with \log_{10} ID ($r = 0.84$ to 0.96 , with 6 degrees of freedom). As the ID increased from 0.2×10^5 to 12.8×10^5 conidia ml^{-1} , LPD decreased by 1 to 2 days for the susceptible and resistant cultivars and by 3 to 5 days for the moderately susceptible cultivars. Within the same ID range, PLAL increased from 73% to 90% for the susceptible cultivar and 2 to 12% for the resistant cultivar. The ID_{50} value (the number of conidia required for 50% PLAL) calculated from the regression equations relating \log_{10} ID to PLAL for each cultivar, ranged from 6.42×10^3 conidia ml^{-1} for the susceptible cultivar to 7.13×10^{13} conidia ml^{-1} for the resistant cultivar. Estimates of the number of conidia ml^{-1} required to initiate a lesion (obtained by substituting 1% PLAL into the regression equations relating \log_{10} ID to PLAL) ranged from 16 conidia ml^{-1} for the susceptible cultivar to 1.0×10^4 conidia ml^{-1} for the resistant cultivar. Using the change of PLAL with ID, the restriction of lesion development for each cultivar could be partitioned into that due to host resistance and that due to interaction between lesions. \log_{10} LPD was significantly correlated negatively with PLAL. As a general rule when screening cultivars for resistance to *S. tritici*, it is advisable to inoculate them with several inoculum densities and to determine the latency period.

Introduction

In studies on resistance of *Triticum* spp. to infection by *Septoria tritici* Rob. ex Desm., little attention has been given to the effect of inoculum density on host response to infection. Morales (1957) studied the effect of four inoculum densities on infection of three wheat (*Triticum aestivum* L.) cultivars by *S. tritici*, and found that host response increased in a curvilinear relationship with increase in inoculum density. Non-standardized inoculum of *S. tritici* has been applied by dipping fingers or cotton swabs into the inoculum and rubbing them over the surface of wheat leaves (Beach, 1919; Renfro and Young, 1956; Hilu, 1956) or by spraying the inoculum onto the surfaces of leaves with an atomizer (Weber, 1922; Fellows, 1962; Rillo et al., 1970; Rosielle, 1972). The failure to standardize inoculum density in studies on the *S. tritici* – *Triticum* spp. interaction may have resulted in contradictory conclusions in the literature (Shipton et al., 1971).

The objective of this study was to quantitatively determine the effect of inoculum density of *S. tritici* on the response of five cultivars of spring wheat to infection. The serial dilution method was used, because the response of the cultivars to infection by

S. tritici, at different levels of inoculum, could be determined quantitatively, and analysed statistically by regression analysis. A preliminary report has been published (Shearer, 1974).

Materials and methods

Experimental design. The experiment was a 5×8 split plot design with 3 replicates. The independent variables were host cultivar (5) and inoculum density (8). The dependent variable was host response measured as either the latency period or percentage of leaf area covered by lesions with pycnidia.

Host. The cultivars used were: Kondut (resistant to moderately susceptible), Festiguay (moderately susceptible), Heron (moderately susceptible), Gamenya (moderately susceptible to susceptible) and Federation (susceptible). Resistance to *S. tritici* infection is manifest as the rate of development of the lesions, the size of the lesion, and the size and number of pycnidia formed within the lesion. In the resistant cultivar, Kondut, lesion development in seedling leaves is restricted, and the pycnidia are lighter in colour and smaller than those formed in leaves of the susceptible cultivar Federation (Fig. 1).

The cultivars were grown in a sandy loam in 8 cm diameter pots, 5 plants per pot, in a temperature and humidity controlled glasshouse at 19.6 (range 14 to 27) °C and programmed for 90% relative humidity. Fifty ml of a complete balanced fertilizer was added to each pot at the time of seedling emergence.

Inoculation. The method of single conidium isolation was as described by Shearer

Fig. 1. Difference in the number and size of pycnidia in leaves of seedlings of the resistant spring wheat cultivar Kondut (K) and the susceptible cultivar Federation (F), 22 days after inoculation with *Septoria tritici*. Note that the pycnidia formed in leaves of Kondut (arrow) are fewer in number and smaller than those formed in leaves of Federation.

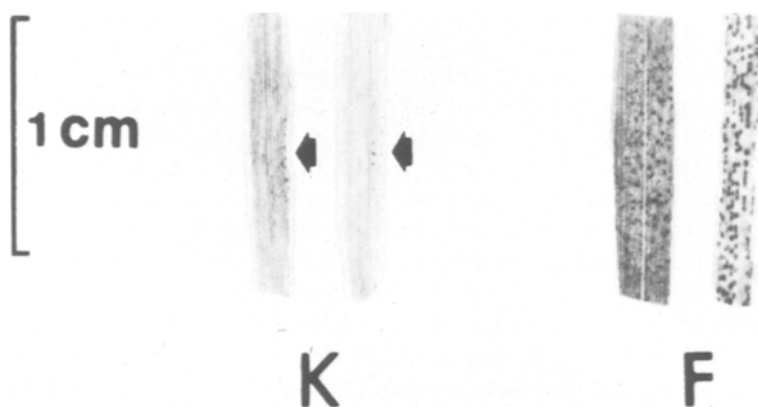


Fig. 1. Verschil in aantal en afmetingen van pycniden in kiemplantbladeren van de resistente zomertarwecultivar Kondut (K) en de vatbare cultivar Federation (F) 22 dagen na inoculatie met *Septoria tritici*. De pycniden die gevormd zijn in de bladeren van Kondut (pijl) zijn geringer in aantal en kleiner dan die in de bladeren van Federation.

et al., (1974). Inoculum of a single conidium isolate was increased on Elliot-V-8 juice agar, incubated at 20°C and 0.13×10^4 ergs $\text{cm}^{-2} \text{sec}^{-1}$ continuous irradiation from 40 W incandescent lights. Preparation of inoculum was as described by Shearer et al., (1974). Inoculum density (ID) of the conidial suspension was adjusted to the desired density, from ca. 10×10^3 conidia ml^{-1} , increasing in geometric progression to 12.8×10^5 conidia ml^{-1} , and uniformly sprayed until run off onto plants at the 3 to 4 leaf growth stage. After inoculation, the plants were kept moist in plastic bags for 96 h and then the bags were removed. Immediately following inoculation, samples from the suspensions of each ID used for inoculation, were incubated at 20° for 12 h and the percentage of conidia germinating determined. All ID's used in the calculation of the results were corrected for the percentage of conidium germination.

Disease assessment. Assessment of disease severity was confined to observations of the latency period (LPD), and the percentage of the leaf area covered by lesions with pycnidia (PLAL). The LPD was determined as the period, in days, from inoculation to the observation of the first black mature pycnidia (Shearer and Zadoks, 1972b), in leaves of each ID-cultivar combination. The PLAL was estimated, using the Tehon scale (Tehon, 1927), on the third and fourth leaf, 22 days after inoculation.

Statistical analysis. Linear regression equations of the form $\hat{Y} = b_0 + b_1 \log_{10} \text{ID}$ were fitted to the data by least squares, where Y is LPD or PLAL and \hat{Y} the 'estimated' value of Y, b_0 is the y intercept and b_1 the slope of the linear regression line. All linear correlation coefficients were significant ($P < 0.01$ on 6 degrees of freedom) and between 0.84 to 0.96. Homogeneity of the b_1 values was tested with Student's *t* test (Steel and Torrie, 1960).

Results

Effect of cultivar on the relationship between ID and LPD. The relationship between \log_{10} ID and LPD, for the 5 cultivars, is shown in Fig. 2. The LPD for the cultivar Kondut was the longest (19 to 21 days) whilst that for Federation was the shortest (12 to 14 days). Cultivars in order of decreasing LPD are: Kondut > Festiguay > Heron > Gamenya > Federation.

As the ID increased from 0.2×10^5 to 12.8×10^5 conidia ml^{-1} , LPD decreased by 1 to 2 days for both susceptible and resistant cultivars and by 3 to 5 days for the moderately susceptible cultivars (Fig. 2). The change in LPD with increasing \log_{10} ID (Table 1) was least for Federation, which was not significantly different from those for Festiguay or Kondut. It was greatest for Gamenya, which was not significantly different from that for Heron (Table 1).

Effect of cultivar on the relationship between ID and PLAL. The susceptible cultivar Federation, had the greatest PLAL (39 to 90%) while the resistant cultivar, Kondut, had the lowest PLAL (2 to 12%). Cultivars ranked in order of decreasing PLAL are: Federation > Gamenya > Heron > Festiguay > Kondut; this ranking being opposite to that observed for LPD.

PLAL increased in a curvilinear relationship with increase in ID; the mean PLAL

Fig. 2. The relationship between inoculum density (ID) and the latency period (LPD) of *Septoria tritici* in leaves of seedlings of five spring wheat cultivars. (Cultivars: \square = Kondut, \blacktriangle = Festiguay, \triangle = Heron, \bullet = Gamenya, \circ = Federation; \times indicates overlap of observations).

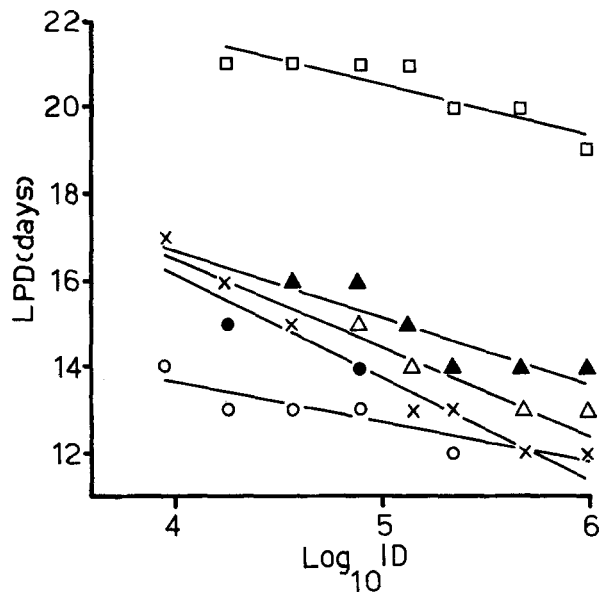


Fig. 2. Het verband tussen inoculumdichtheid (ID) en latentie periode (LPD) van *Septoria tritici* in de bladeren van kiemplanten van vijf zomertarwecultivars. (Cultivars: \square = Kondut, \blacktriangle = Festiguay, \triangle = Heron, \bullet = Gamenya, \circ = Federation; \times duidt op het samenvallen van waarnemingen).

Table 1. Regression analysis between inoculum density (ID) and either the latency period (LPD) or the percentage of leaf area covered by lesions with pycnidia (PLAL) of *Septoria tritici* in leaves of five spring wheat cultivars.

Cultivar	LPD:	PLAL		Estimated number of conidia ml ⁻¹ required for 1% PLAL
	slope (b ₁) \pm cl ₉₅ ¹	slope (b ₁) \pm cl ₉₅	ID ₅₀ (antilog) ³	
Federation	-0.91 \pm 0.44 a ²	+19.58 \pm 11.96 b	6.42 \times 10 ³	16
Gamenya	-2.39 \pm 0.66 c	+29.44 \pm 8.77 b	3.01 \times 10 ⁴	660
Heron	-2.08 \pm 0.61 bc	+23.01 \pm 7.75 ab	1.88 \times 10 ⁵	1440
Festiguay	-1.57 \pm 0.57 ab	+15.85 \pm 6.76 a	4.24 \times 10 ⁵	270
Kondut	-1.14 \pm 0.71 a	+ 4.88 \pm 2.59	7.12 \times 10 ¹³	9640

¹ \pm 95% confidence limits.

² Values with the same letter are not significantly different ($P \leq 0.01$).

³ Antilog of estimated ID at 50% PLAL, in conidia ml⁻¹.

Tabel 1. Regressie-analyse van de inoculumdichtheid (ID) en de latentie periode (LPD), of het percentage van het bladoppervlak ingenomen door vlekken met pycniden (PLAL) van *Septoria tritici* binnen bladeren van vijf zomertarwecultivars.

for the five cultivars increased from 22 to 57% as ID increased from 0.1×10^5 to 3.0×10^5 conidia ml^{-1} , but levelled off between 57 to 61% as ID increased from 3.0×10^5 to 12.8×10^5 conidia ml^{-1} . For 3.0×10^5 conidia $\text{ml}^{-1} \leq \text{ID} \leq 12.8 \times 10^5$ conidia ml^{-1} , PLAL levelled off between 87 to 90% for Federation, 80 to 85% for Gamenya, 57 to 65% for Heron, 52 to 54% for Festiguay and 9 to 12% for Kondut.

PLAL increased linearly with \log_{10} ID (Fig. 3). The rate of increase of PLAL, with increase in \log_{10} ID, was greatest for the cultivar Gamenya (Table 1), but this value was not significantly different from those for Federation and Heron. The rate of increase was least for the resistant cultivar Kondut and this value was significantly different from the rest.

The position of the linear regression lines, relating PLAL to \log_{10} ID, can be expressed as the ID_{50} ; that is the ID giving 50% PLAL. Estimated ID_{50} values, from the linear regression equations are given in Table 1. Cultivars, ranked in order of decreasing ID_{50} are: Kondut > Festiguay > Heron > Gamenya > Federation.

From the Tehon scale (Tehon, 1927) one lesion of *S. tritici* covers approximately 1% of the leaf area. Substituting 1% PLAL into the regression equations will give an estimate, for each cultivar, of the number of conidia ml^{-1} required for one lesion (Table 1). The cultivars, ranked in order of decreasing number of conidia ml^{-1} required for one lesion are: Kondut > Heron > Gamenya > Festiguay > Federation.

Fig. 3. The relationship between inoculum density (ID) and the percentage of leaf area covered by lesions with pycnidia (PLAL) of *Septoria tritici* in leaves of seedlings of five spring wheat cultivars. (Cultivars: ○ = Federation, ● = Gamenay, △ = Heron, ▲ = Festiguay, □ = Kondut).

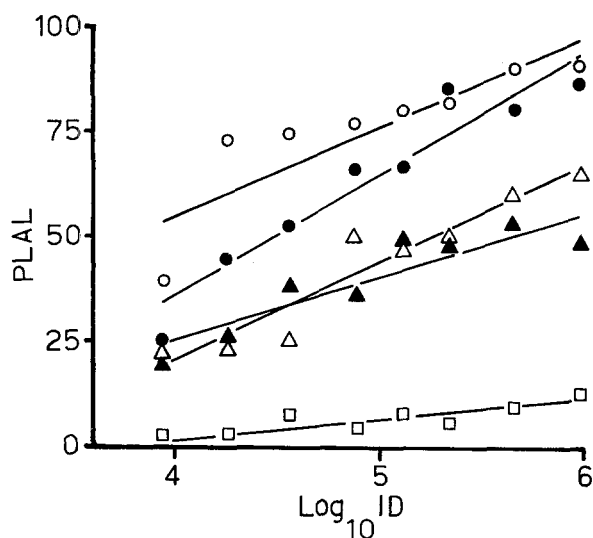


Fig. 3. Het verband tussen inoculumdichtheid (ID) en het percentage bladoppervlak ingenomen door vlekken met pycniden (PLAL) van *Septoria tritici* in bladeren van kiemplanten van vijf zomertarwe-cultivars. (Cultivars: ○ = Federation, ● = Gamenay, △ = Heron, ▲ = Festiguay, □ = Kondut).

Relationship between change in ID and corresponding change in PLAL. The amount of change between two quantities, reduced to a common base, can conveniently be represented by $10 \log_{10} Q_i/Q_j$, where $Q_i > Q_j$. This ratio can be used (Shearer and Zadoks, 1972a) to compare the relationship between change in ID and the corresponding change in PLAL.

If the $10 \log_{10} \text{PLAL}_i/\text{PLAL}_j$ values are plotted against the corresponding $10 \log_{10} \text{ID}_i/\text{ID}_j$ value, for all combinations of ID_i and ID_j ($i = 2$ to 8 , $j = 1$ to 7), the points fall on a straight line. Plots of $10 \log_{10} \text{PLAL}_i/\text{PLAL}_j$ against $10 \log_{10} \text{ID}_i/\text{ID}_j$ for the susceptible cultivar Federation and resistant cultivar Kondut, are given in Fig. 4.

Ideally, if a change in ID gave an equivalent change in PLAL, the plot of $10 \log_{10} \text{PLAL}_i/\text{PLAL}_j$ against $10 \log_{10} \text{ID}_i/\text{ID}_j$ will fall on the 45° bisector AB (Fig. 4). However, if lesion development is restricted by lesion interaction or cultivar resistance, the ratio $10 \log_{10} \text{PLAL}_i/\text{PLAL}_j$ will be $< 10 \log_{10} \text{ID}_i/\text{ID}_j$ and the plot will not fall on the 45° bisector.

The extent to which lesion development is restricted is proportional to the difference between the line AB and the observed line AC (Fig. 4). Thus the area ABC in Fig. 4 is proportional to the restriction in lesion development caused by either lesion interaction or cultivar resistance, or both.

The ratio of the area ABC/area ABD in Fig. 4, is the proportionate restriction in lesion development. In the ideal case the area ABC will be 0 and there would be no proportionate restriction in lesion development. However if lesion development is restricted, area ABC will be smaller than area ABD and the proportionate restriction

Fig. 4. Relationship between change in inoculum density (ID) of *Septoria tritici*, expressed as $10 \log_{10} \text{ID}_i/\text{ID}_j$, and the corresponding change in the percentage of leaf area covered by lesions with pycnidia (PLAL) of *S. tritici*, expressed as $10 \log_{10} \text{PLAL}_i/\text{PLAL}_j$, in leaves of seedlings of the spring wheat cultivars (a) Federation and (b) Kondut. See text for the significance of area ABC and ABD.

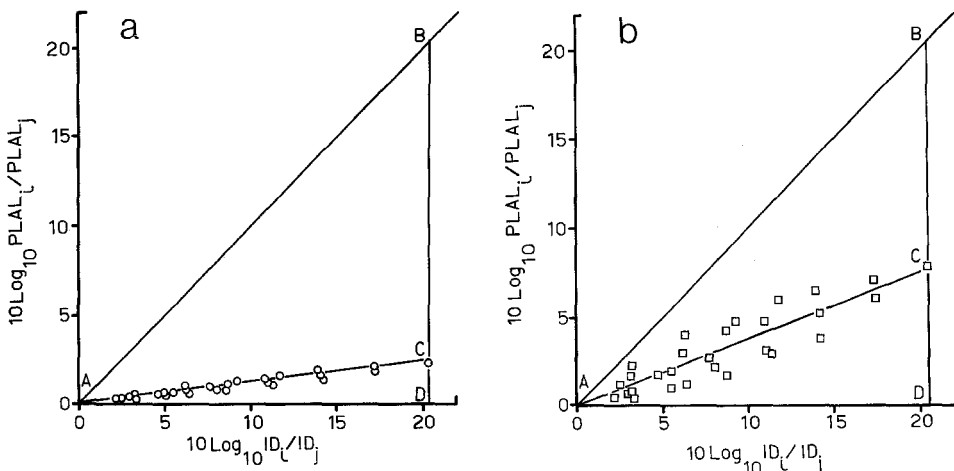


Fig. 4. Het verband tussen de verandering in inoculumdichtheid (ID) van *Septoria tritici*, uitgedrukt als $10 \log_{10} \text{ID}_i/\text{ID}_j$, en de overeenkomstige verandering in het percentage van het bladoppervlak, ingenomen door vlekken met pycnidien (PLAL) van *S. tritici*, uitgedrukt als $10 \log_{10} \text{PLAL}_i/\text{PLAL}_j$, in bladeren van kiemplanten van de zomertarwecultivar (a) Federation en (b) Kondut. Zie de tekst voor de betekenis van het gebied ABC en ABD.

Table 2. Regression analysis of the change in inoculum density (ID) of *Septoria tritici* expressed as $10 \log_{10} ID_i / ID_j$, with the corresponding change in the percentage of leaf area covered by lesions with pycnidia (PLAL) of *S. tritici*, expressed as $10 \log_{10} PLAL_i / PLAL_j$, (see text and Fig. 4) and the partitioning of the proportionate restriction in lesion development (the ratio of area ABC/area ABD – Fig. 4) into that due to host resistance and that due to interaction of lesions. See text for the method of partitioning proportionate restriction in lesion development.

Cultivar	Slope	Coefficient of determination	Proportionate restriction in lesion development (area ABC/area ABD)	Partitioning of restriction in lesion development into proportion due to:	
				host resistance	lesion interaction
Federation	0.12	0.96	0.88	0.00	0.88
Gamenya	0.21	0.92	0.79	0.22	0.57
Heron	0.17	0.94	0.74	0.34	0.40
Festiguay	0.25	0.89	0.83	0.15	0.68
Kondut	0.38	0.81	0.62	0.62	0.00

Tabel 2. Regressie-analyse van de verandering in inoculumdichtheid (ID) van *Septoria tritici* uitgedrukt als $10 \log_{10} ID_i / ID_j$ met de overeenkomstige verandering in het percentage bladoppervlak ingenomen door lesies met pycniden (PLAL) van *S. tritici*, uitgedrukt als $10 \log_{10} PLAL_i / PLAL_j$ (zie tekst en Fig. 4) en de toedeling van bijdragen in de remming van de vlekuitbreiding aan de resistentie en aan de interactie van de lesies (de verhouding tussen de oppervlakken ABC en ABD, Fig. 4). Voor de wijze waarop de berekening van de beide componenten in de remming van de vlekuitbreiding tot stand zijn gekomen wordt verwezen naar de tekst.

in lesion development will be > 0 , but < 1 . The proportionate restriction in lesion development for each cultivar is given in Table 2.

Of the cultivars used in this study, Federation is the most susceptible to *S. tritici* infection. Thus, relative to the other cultivars used, the effect of host resistance in restriction lesion development in Federation will be minimal (Fig. 1) and lesion interaction will be maximal since the lesions will develop in leaves of finite size. Thus the proportionate restriction in lesion development for Federation will be proportional to the amount of lesion interaction. Conversely in the case of the resistant cultivar Kondut, the effect of host resistance will be maximal, relative to the other cultivars used in the study, and the effect of lesion interaction will be minimal (Fig. 1). Thus for the cultivar Kondut, the proportionate restriction in lesion development will be proportional to restriction in lesion development by host resistance.

Using the proportionate restriction in lesion development obtained for the cultivars Federation and Kondut, the proportionate restriction in lesion development obtained for the moderately susceptible cultivars can be partitioned into the amount of restriction in development due to host resistance and that due to interaction of lesions. In Fig. 5 the proportionate restriction in lesion development are plotted for each cultivar. Within the range of the experiment, the limits of which are set by the use of the susceptible cultivar Federation and the resistant cultivar Kondut, the line A'B' (Fig. 5) represents the change in the proportionate restriction in lesion development with increasing susceptibility of the host to *S. tritici* infection, A'B the influence of host resistance, and AB' the effect of interaction of lesions, on restricting lesion development. The relative values for the influence of host resistance and lesion inter-

Fig. 5. Difference in the proportionate restriction in lesion development (the ratio area ABC/area ABD) between the spring wheat cultivars inoculated with *Septoria tritici*. See text for the meaning of the ratio, area ABC/area ABD, and the significance of lines A'B, AB', and A'B'. (Cultivars: K = Kondut, H = Heron, G = Gamanya, Fe = Festiguay, and F = Federation).

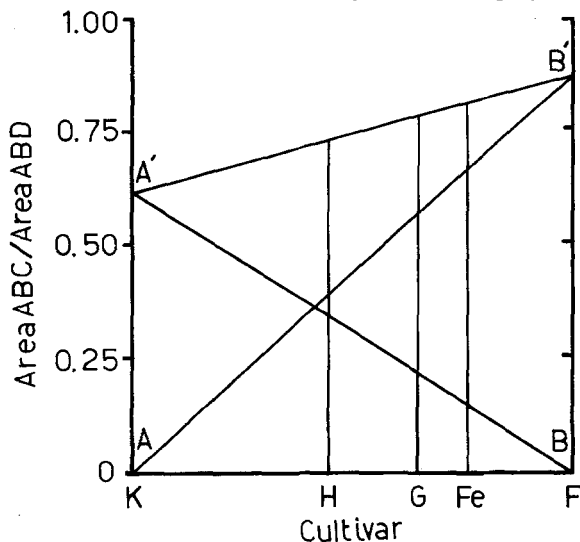


Fig. 5. Verschil tussen de cultivars geïnoculeerd met *Septoria tritici* in de remming van de vlekuitbreiding toegeschreven aan resistentie en vlekinteractie en uitgedrukt als de verhouding tussen het oppervlak ABC en het oppervlak ABD. Voor een nadere verklaring van de verhouding tussen de oppervlakken ABC en ABD en voor de betekenis van de lijnen A'B, AB', en A'B' wordt verwezen naar de tekst. (Cultivars: K = Kondut, H = Heron, G = Gamanya, Fe = Festiguay, en F = Federation).

Fig. 6. Relationship between the latency period (LPD) of *Septoria tritici* and the percentage of leaf area covered by lesions with pycnidia (PLAL) of *S. tritici* in leaves of seedlings of five spring wheat cultivars. (Cultivars: ○ = Federation, ● = Gamanya, △ = Heron, ▲ = Festiguay, □ = Kondut).

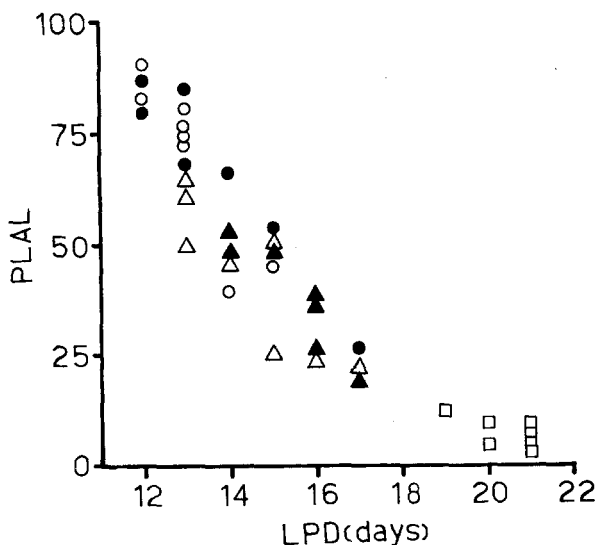


Fig. 6. Het verband tussen de latentie periode (LPD) van *Septoria tritici* en het percentage van het bladoppervlak ingenomen door vlekken met pycniden (PLAL) van *S. tritici* in de bladeren van kiemplanten van vijf zomertarwecultivars. (Cultivars: ○ = Federation, ● = Gamanya, △ = Heron, ▲ = Festiguay, □ = Kondut).

action on lesion development can be read off from Fig. 5, and are given in Table 2. For Heron, the influence of host resistance, in restricting lesion development, is about equal to the influence of lesion interaction. However for the cultivars Gamenya and Festiguay, lesion interaction has a greater influence than host resistance in restricting lesion development.

Relationship between LPD and PLAL. The relationship between LPD and PLAL, for all ID treatments and cultivars, is curvilinear (Fig. 6) and of the form: $\log_{10} \text{PLAL} = 3.67 - 0.14 \text{ LPD}$ ($r = -0.96$, on 37 degrees of freedom).

Discussion

The spray inoculation procedure used in this study is similar to that used in the routine evaluation of wheat cultivars for resistance to *S. tritici*. This inoculation procedure is in contrast to that used in previously reported studies on the effect of ID on infection, where drops of water of known volume and containing a known number of conidia were applied to the surfaces of plant parts and the amount of infection assessed by determining the incubation or latency period, and the percentage of plant parts infected (McKee, 1964; Lapwood and McKee, 1966; Evans and Griffiths, 1971). While the droplet method has the advantage that the number of conidia per unit leaf area is accurately known, this method is too laborious to be suitable for screening in a breeding programme (Lapwood and McKee, 1966). The procedure of spraying inoculum of known ID onto plant surfaces can be used in a breeding programme, but suffers from the disadvantage that the number of conidia deposited per unit surface area is not accurately known, because conidia will be shed from the leaf surface during inoculation. Also, as noted by Evans and Griffiths (1971), plants sprayed on separate occasions may receive different conidium deposits due to difficulties in obtaining accurate and consistent performance from the spraying apparatus, or due to variation in the surface characteristics of the plants. However, the effect of plant surface characteristics on the deposition of conidia can be minimized by the incorporation of gelatin into the inoculum (Rosielle, 1968).

The ID_{50} value (the ID required for 50% PLAL) used in this study is not equivalent to the ED_{50} (the number of conidia required to infect 50% of the replicates) used in the previously reported studies. At the ID_{50} values found in this study, all of the leaves inoculated (with the possible exception of leaves of Kondut) were infected. Thus the ID_{50} is greater than the ED_{50} .

The shortest LPD of 12 days, observed for the susceptible cultivar Federation, is longer than the shortest LPD of 7 days observed in the glasshouse by Hilu (1956). This difference, in shortest LPD, may be due to differences in inoculation method (Hilu, 1956), cultivar, ID, or environmental conditions under which the infected plants were incubated. The LPD of *S. tritici* decreases with an increase in the length of the period of a water saturated atmosphere following inoculation (Shearer, 1969, unpublished) and increases with lowering incubation temperatures (Weber, 1922). The LPD for the cultivar Kondut was 7 to 8 days longer than that for Federation, which is in agreement with the 4 to 10 days observed by Hilu (1956), for the difference between resistant and susceptible cultivars inoculated and incubated under glasshouse conditions.

In this study, the severity of infection by *S. tritici*, measured by PLAL, increased in a curvilinear relationship with increase in ID and a linear relationship with $\log_{10}ID$. The form of the relationship was independent of the resistance of the cultivar. Morales (1957) also found a similar relationship between ID and the severity of *S. tritici* infection on leaves.

Susceptibility of a cultivar to infection by *S. tritici* appears to be dependent on the amount of hyphal development within the leaf tissue following penetration, rather than on the number of penetrations. Hilu (1956) found that in susceptible and resistant cultivars inoculated with the same ID, the conidia of *S. tritici* penetrated the two cultivars equally, but the development within the leaf following penetration was restricted in the resistant cultivar. The factors affecting the development of the fungus following penetration are not known. According to Hilu (1956) some hyphae escape an 'unknown barrier' in resistant and intermediate cultivars and form a lesion. The response of a cultivar to an increase in ID is probably dependent on the increase in the number of penetrations that can escape the 'unknown barrier', resulting in a decrease in LPD and an increase in PLAL. However, the curvilinear relationship between ID and PLAL indicates that the number of successful penetrations resulting in PLAL may level off, suggesting that the 'unknown barrier' may be composed of more than one component.

Little is known of how many conidia of *S. tritici* are required to initiate a lesion. Inasmuch that relatively few conidia would be expected to survive between cropping cycles, knowledge of the number of conidia required to initiate a lesion is of importance in understanding and predicting the beginning and outcome of an epidemic. The $\log_{10}ID$ -PLAL linear regression equations for each cultivar can be used to estimate the number of conidia required to initiate a lesion by extrapolation to 1% PLAL. A better estimate of the number of conidia required to initiate a lesion could be obtained by the drop inoculation method described previously. More work is needed to accurately determine the number of conidia required to initiate a lesion in relation to cultivar resistance and environment.

Inoculation of cultivars with more than one level of ID gives an indication of the various factors affecting lesion development and hence aides in the interpretation of infection data. For example, although Gamenya is rated as susceptible and Festingway as moderately susceptible, fewer conidia ml^{-1} are required for 1% PLAL on Festingway than Gamenya. Furthermore, Festingway has a lower resistance component than Gamenya, when the change in ID is related to change in PLAL (Tables 1 and 2). Festingway is less sensitive to an increase in ID than Gamenya (Fig. 2) and the change in PLAL appears to be due to crowding of lesions (Fig. 5, Table 2).

The significant correlation between LPD and PLAL has implications in screening programmes. In a study of 323 wheat cultivars inoculated with 2×10^4 conidia of *S. tritici* ml^{-1} , I found (Shearer, 1969 unpublished) a significant linear correlation between LPD and mean disease score for each LPD class ($LPD = 8.494 - 0.308$ mean disease score, $r = 0.97$). Unfortunately, in reports on screening wheat cultivars for resistance to *S. tritici* in the glasshouse, LPD's are rarely given. In glasshouse tests, determination of LPD is less tedious than assessment of PLAL and can be used to cull out susceptible cultivars before PLAL assessments can be made. Furthermore LPD may be a better estimator, than PLAL, of the resistance of a wheat cultivar in the field to *S. tritici* infection. In studies on the effect of ID on the infection of potato

tuber discs by *Phytophthora infestans* (Mont.) de Bary, LPD (incubation period) was found to be more closely related to the resistance of the cultivar in the field, than was the incidence of infection in inoculated discs (McKee, 1964). In the field, the length of the LPD would be a factor affecting the number of secondary cycles of infection; cultivars with relatively long LPD's would have fewer secondary cycles of infection than those with relatively short LPD's. When screening for resistance to *S. tritici*, it is advisable to inoculate cultivars with several inoculum densities and determine the latency period.

Samenvatting

Het verband tussen inoculumdichtheid en responsie van zomertarwecultivars bij inoculatie met Septoria tritici

Sporensuspensies van *Septoria tritici* die in dichtheid (ID) varieerden volgens een geometrische reeks van $0,1$ tot $12,8 \times 10^5$ sporen.ml⁻¹, werden gebruikt bij de inoculatie van kiemplanten van vijf cultivars van *Triticum aestivum* die verschilden in resistentie tegen *S. tritici*.

De reactie van de waardplanten werd gemeten aan de latentie periode (LPD) en aan het percentage bladoppervlak dat ingenomen werd door vlekken met pycniden (PLAL). Beide grootheden toonden een significante lineaire correlatie met log₁₀ ID ($r = 0,84$ tot $0,96$ bij 6 vrijheidsgraden). Bij een toename van ID van $0,2 \times 10^5$ tot $12,8 \times 10^5$ sporen.ml⁻¹ nam de lengte van de latentie periode af met 1 tot 2 dagen bij de vatbare en de resistente cultivars, en met 3 tot 5 dagen bij de matig vatbare cultivars (Fig. 2).

In hetzelfde traject van inoculumdichtheid nam de PLAL toe van 73 tot 90% bij vatbare cultivars, en van 2 tot 12% bij de resistente cultivars (Fig. 3). De ID₅₀-waarde, het aantal sporen dat nodig is om 50% aantasting te verkrijgen, werd berekend uit de regressievergelijkingen die voor iedere cultivar het verband aangeven tussen log₁₀ ID en het aantastingspercentage (PLAL). Deze waarde varieerde van $6,42 \times 10^3$ sporen per ml voor vatbare tot $7,13 \times 10^3$ sporen per ml voor de resistente cultivars (Tabel 1). Schattingen voor het aantal sporen dat nodig is om een vlek te doen ontstaan werden verkregen door de 1% aantastingswaarde te substitueren in de eerder genoemde regressievergelijkingen. Deze waarden varieerden van 16 sporen.ml⁻¹ voor de vatbare cultivar tot 10000 sporen.ml⁻¹ voor de resistente cultivar (Tabel 1). Via de toename van de aantastingsgraad (PLAL) per eenheid stijging in de inoculumdichtheid kon de remming op de vlekontwikkeling opgesplitst worden in een gedeelte dat toegeschreven werd aan de resistentie van de plant en een gedeelte dat te wijten was aan de interactie tussen de vlekken (Fig. 4 en 5; Tabel 2).

Log₁₀ LPD was negatief gecorreleerd met PLAL (Fig. 6). Bij het toetsen van cultivars op resistentie tegen *S. tritici* zouden sporensuspensies van verschillende dichtheden gebruikt moeten worden en zou de latentie periode, evenals de aantastingsgraad bepaald moeten worden.

Acknowledgments

The research was supported by a grant from the Commonwealth Wheat Industry Research Council and the Commonwealth Extension Services of Australia.

References

- Beach, W. S., 1919. Biologic specialization in the genus *Septoria*. *Am. J. Bot.* 6: 1–33.
- Evans, R. L. & Griffiths, E., 1971. Infection of barley with *Rhynchosporium secalis* using single droplet infection technique. *Trans. Br. mycol. Soc.* 56: 235–242.
- Fellows, H., 1962. Effects of light, temperature and fertilizer on infection of wheat leaves by *Septoria tritici*. *Pl. Dis. Repr* 46: 846–848.
- Hilu, H. M., 1956. Inoculation, life cycle and host-parasite relationship of *Septoria tritici* Rob. on *Triticum* species. (Ph. D. Diss.) Univ. Illinois, ix + 98 pp.
- Lapwood, D. H. & McKee, R. K., 1966. Dose-response relationship for infection of potato leaves by zoospores of *Phytophthora infestans*. *Trans. Br. mycol. Soc.* 49: 679–686.
- McKee, R. K., 1964. Observations on infection by *Phytophthora infestans*. *Trans. Br. mycol. Soc.* 47: 365–374.
- Morales, I. N., 1957. Studies on *Septoria* leaf blotch of wheat. (Ph. D. Diss.), Purdue University, xi + 101 pp.
- Renfro, B. L. & Young, H. C., 1956. Techniques for studying varietal response to *Septoria* leaf blotch of wheat. *Phytopathology* (Abstr.) 46: 23.
- Rillo, A. O., Caldwell, R. M. & Glover, D. V., 1970. Cytogenetics of resistance to wheat leaf blotch (*Septoria tritici*) in backcross derivatives of an *Agroticum* line. *Crop Sci.* 10: 223–227.
- Rosielle, A. A., 1968. Studies in the breeding of wheat for resistance to *Septoria nodorum* Berk. (Hons. thesis), Univ. Western Australia, 171 pp.
- Rosielle, A. A., 1972. Sources of resistance in wheat to speckled leaf blotch caused by *Septoria tritici*. *Euphytica* 21: 152–161.
- Shearer, B. L., 1974. The effect of inoculum density on the response of spring wheat cultivars to infection by *Septoria tritici*. *Proc. Am. phytopath. Soc.* 1: 106 (Abstr.).
- Shearer, B. L. & Zadoks, J. C., 1972a. Observations on the host range of an isolate of *Septoria nodorum* from wheat. *Neth. J. Pl. Path.* 78: 153–159.
- Shearer, B. L. & Zadoks, J. C., 1972b. The latent period of *Septoria nodorum* in wheat. 1. The effect of temperature and moisture treatments under controlled conditions. *Neth. J. Pl. Path.* 78: 231–241.
- Shearer, B. L., Zeyen, R. J. & Ooka, J. J., 1974. Storage and behaviour in soil of *Septoria* species isolated from cereals. *Phytopathology* 64: 163–167.
- Shipton, W. A., Boyd, W. J. R., Rosielle, A. A. & Shearer, B. L., 1971. The common *Septoria* diseases of wheat. *Bot. Rev.* 37: 231–262.
- Steel, R. G. D. & Torrie, J. H., 1960. Principles and procedures of statistics, with special reference to the biological sciences. McGraw-Hill, New York, 481 pp.
- Tehon, R. L., 1927. Epidemic diseases of grain crops in Illinois, 1922–26. *Bull. Ill. nat. Hist. Surv.* 17: 63–66.
- Weber, G. F., 1922. *Septoria* diseases of cereals. II. *Septoria* diseases of wheat. Speckled leaf blotch of wheat. *Phytopathology* 12: 558–585.

Address

Department of Agronomy, Institute of Agriculture, the University of Western Australia, Nedlands 6009, Australia.