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The latent period of Septoria nodorum in wheat. 2. The effect of temperature and moisture under field conditions

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Abstract

The effects of temperature and moisture (duration of leaf wetness) on the latent period of *Septoria nodorum* (Berk.) Berk. in seedlings of 'Felix' wheat were studied in the field. Throughout the autumn 1969 plants were inoculated at regular intervals. For each inoculation day the subsequent latent period was determined. Variation in temperature was caused by the seasonal decrease of temperature. Variation in the duration of leaf wetness was caused by the variability of the weather in general, and by covering and irrigation in special. Within the range of the experiment, an increase of temperature and an increase of the duration of leaf wetness both caused a decrease of the latent period. The magnitude of the effect (up to about 7 days) was approximately the same as in growth chamber experiments. Relations between variables were tested by means of multiple regression equations; the effects of temperature, duration of leaf wetness, and sometimes of their interaction were significant. For the prediction of the latent period, duration of leaf wetness combined with minimum temperature provided the best results.

Introduction

In a previous paper (Shearer and Zadoks, 1972), an experiment was described on the effect of constant temperature and a constant rhythm of changes in moisture (duration of leaf wetness) on the latent period of *Septoria nodorum* (Berk.) Berk., as studied in growth chambers. From the observed values equations were derived to predict the latent period, within the range of temperature and moisture conditions imposed.

In the experiment reported here, the effect of fluctuating temperature and moisture on the latent period of *S. nodorum* was studied in the field. Temperature and moisture were varied by sequential inoculation. Moisture was also varied by manipulation of natural moisture conditions by irrigation and covering. From the observed data prediction equations were derived by regression analysis.

Materials and methods

Host and pathogen. Details of host cultivar, host plants and pathogen were as described by Shearer and Zadoks (1972). In order to prevent contamination, plants for inoculation of cv. Felix were grown in the growth chambers at 18°C, and 85% r.h. The plants were transplanted into the field one to two days prior to inoculation and were at the two to three leaf stage at the time of inoculation.

Experimental design. There were two independent variables: temperature and moisture. The dependent variable was latent period. In this study the term 'moisture' refers to the duration of leaf wetness. Temperature and moisture were varied by using a sequential inoculation procedure. In addition, three moisture treatments were applied simultaneously (see below).

Inoculum and inoculation. Healthy plants were inoculated with *S. nodorum* every two days, between 16.00 and 18.00 h. Details on the preparation of inoculum, and on the inoculation procedure were as in Shearer and Zadoks (1972). However, in this study the spore suspensions were not standardized. Agar and pycnidia from one quarter to one sixteenth of an agar plate were macerated in 100 ml of deionized water and filtered through one layer of muslin. After inoculation, the plants were incubated in clear polythene bags for 72 hours to provide a water saturated atmosphere conducive to infection.

Temperature treatment. Inoculated plants were exposed to outdoor temperature. Variation in temperature was obtained by repeating the experiment every two days between August and November, 1969, during which time the temperature gradually decreased. Air temperature at leaf height (about 12.5 cm) and temperature within a plastic bag were measured with the aid of thermocouples and a recorder.

Moisture treatments. The moisture treatments were called 'natural', 'wet' and 'dry'. In the 'natural' treatment, the plants were exposed to the normal variation of leaf wetness between August and November, 1969. A 'wet' treatment was imposed by periodically irrigating a section of the plot using a stationary sprinkler at 80 cm height. The plants were irrigated at 18.00 h for one to two minutes. A 'dry' treatment was imposed by covering plants with a linen cover to prevent dew formation (Rotem and Reichert, 1964), and to protect the plants from light rain. The linen cover was supported on a 115 × 220 cm Dexion frame, 75 cm above ground level.

The duration of leaf wetness (DLW) was recorded by DeWit's leaf wetness recorders (Post, 1959); one recorder for each moisture treatment. The sensing elements of the recorders were situated 50 cm above ground level. DLW was obtained from the recorder traces by drawing a reference line halfway between the saturation and the dryness level, and measuring the period of leaf wetness along this line to the nearest quarter of an hour. Measurement of DLW along the reference line was considered the best estimate that would take into consideration variation in the measurement of DLW caused by different wetting and drying conditions on the sensing element. Because of frost interfering with the sensing element, the measurement of DLW was discontinued after the middle of October.

Measurement of latent period. The latent period was measured as the period in days from the time of inoculation to the first appearance of mature pycnidia. The criteria used in the measurement of latent period are described by Shearer and Zadoks (1972).

Statistical analysis. The basic unit in this study is the latent period (LPD), determined per inoculation day ($n = 22$ in most cases) and per moisture treatment ($m = 3$). The data for all LPD's ($n \times m = 66$ in most cases) were pooled so that the prediction equations would include the range of moisture conditions observed in the experiment.

Table 1. The meaning of the symbols used for the dependent variable and for the independent variables in the multiple regression equations relating the effect of temperature and moisture on the latent period of *Septoria nodorum* in seedlings of wheat cv. Felix, under field conditions.

	Variable/ *Variabele*	Abbreviation/ *Afkorting*
Dependent/ *Afhankelijk*	Observed latent period in days/ *Waargenomen latente periode in dagen*	OLPD
	Predicted latent period in days/ *Berekende latente periode in dagen*	PLPD
Independent *Onafhankelijk*	Mean daily duration of leaf wetness during the latent period, in h/ *Gemiddelde dagelijkse bladnatperiode gedurende de latente periode, in h*	DLW
	Mean daily maximum temperature during the latent period in °C/ *Gemiddelde dagelijkse maximumtemperatuur gedurende de latente periode in °C*	MAXTEMP
	Mean daily minimum temperature during the latent period, in °C *Gemiddelde dagelijkse minimum temperatuur gedurende de latente periode in °C*	MINTEMP
	(MAXTEMP + MINTEMP)/ 2	AVTEMP
	Mean daily difference between maximum and minimum temperature during the latent period, in °C/ *Gemiddeld dagelijks verschil tussen maximum en minimum temperatuur gedurende de latente periode, in °C*	DIFTEMP
	Mean hourly temperature during the latent period, in °C/ *Gemiddelde uurlijkse temperatuur gedurende de latente periode in °C*	METEMP

Tabel 1. De betekenis van de symbolen gebruikt voor de afhankelijke variabele en de onafhankelijk variabelen in de multipele regressievergelijkingen voor het effect van temperatuur en bladnatperiode op de latente periode van Septoria nodorum in kiemplanten van 'Felix' tarwe te velde.

The independent variables, given in Table 1, were calculated for each LPD, and multiple regression equations relating LPD to the selected independant variables calculated. The form of the multiple regression equations was chosen to include linear and quadratic effects and a linear interaction effect of the two independant variables. The calculated equations are of the form:

$$\hat{Y} = b_0 + b_1X_1 + b_2X_2 + b_3X_1^2 + b_4X_2^2 + b_5X_1X_2$$

where: Y is the independent variable, $\hat{Y}$ the 'predicted' value of Y, X_1 and X_2 the independent variables (Table 1), and b_0 to b_5 the partial regression coefficients.

Details for the calculation of the partial regression coefficients are given in Searle (1966; p. 225 to 243). The level of significance of the multiple correlation coefficient was determined by the F test for n-3 degrees of freedom (Steel and Torrie, 1960).

Results

Prediction equations. The multiple correlation coefficients for the prediction equations are shown in Table 2; the partial regression coefficients are given in Table 3. Although

Table 2. Multiple correlation coefficients, percentage variation explained by the relationship, number of observations, and ranges of the independent variables for the multiple regression equations relating the effect of temperature and moisture on the latent period of *Septoria nodorum* in seedlings of wheat cv. Felix, under field conditions. The meaning of the symbols used for the independent variables is given in Table 1.

Independentvariables X_1	X_2	Multiple correlation coefficient (R)	% variation explained ($R^2 \times 100$)	Number of observations (n)	Range
DLW	MAXTEMP	0.67	45	66	$5 \leqslant$ DLW $\leqslant 18; 15 \leqslant$ MAXTEMP $\leqslant 28$
DLW	MINTEMP	0.72	52	66	$5 \leqslant$ DLW $\leqslant 18; 5 \leqslant$ MINTEMP $\leqslant 13$
DLW	METEMP	0.70	49	66	$5 \leqslant$ DLW $\leqslant 18; 11 \leqslant$ METEMP $\leqslant 18$
DLW	DIFTEMP	0.56	31	66	$5 \leqslant$ DLW $\leqslant 18; 5 \leqslant$ DIFTEMP $\leqslant 18$
MAXTEMP	MINTEMP	0.61	37	66	$15 \leqslant$ MAXTEMP $\leqslant 28; 5 \leqslant$ MINTEMP $\leqslant 13$
MAXTEMP	MINTEMP	0.83	69	87	$8 \leqslant$ MAXTEMP $\leqslant 28; 2 \leqslant$ MINTEMP $\leqslant 13$

Tabel 2. Multipele correlatiecoëfficienten, percentage van variantie verklaard, aantal waarnemingen, en meetbereiken van de onafhankelijke variabelen in de multipele regressievergelijkingen voor het effect van temperatuur en bladnatperiode op de latente periode van Septoria nodorum bij kiemplanten van 'Felix' tarwe te velde.

the correlation coefficients are significant ($P < 0.01$) for all equations, the proportion of the total sums of squares which can be attributed to the regression decreases from 69% for the relationship PLPD-MAXTEMP-MINTEMP ($n = 87$) to 31% for the relationship PLPD-DLW-DIFTEMP. The meaning of the symbols is given in Table 1. For the relationship between leaf wetness period DLW and temperature, the size of the interaction term is related to the correlation coefficient; multiple regression equations with the greatest interaction terms explain the greatest proportion of the variance (Table 2 and 3). Because of the low proportion of the variance explained by the relationships PLPD-DLW-DIFTEMP and PLPD-MAXTEMP-MINTEMP ($n = 66$), these relationships will not be considered further.

Scatter diagrams of predicted latent period (PLPD) plotted against observed latent period (OLPD) for four of the relationships are given in Fig. 1. The equation for the relationship PLPD-MAXTEMP-MINTEMP tends to consistently overestimate PLPD for the 'wet' moisture treatment and under-estimate PLPD for the 'dry' moisture treatment. The equations for the relationships between DLW and temperature do not show such a tendency. Ideally, the plots of PLPD against OLPD should fall on the 45° bisector, whith a slope of 1. The slopes of the linear regression lines fitted to the plots of PLPD against OLPD (Fig. 1) are significantly less than 1 (determined by the t-test), and suggest that all relationships overestimate PLPD for OLPD $\leqslant$ about 13 days. Nevertheless the majority of points are clustered around the 45° bisector. This is illustrated in Table 4 which gives the magnitude of the absolute differences between observed and predicted LPD. For all relationships the difference is < 2 days for approximately 70% of the observations and < 3 days for about 90% of the observations.

Table 3. Partial regression coefficients calculated for the multiple regression equations representing the effect of temperature and moisture on the latent period of *Septoria nodorum* in seedlings of wheat cv. Felix, under field conditions. The meaning of the symbols used for the independent variables is given in Table 1.

Independent variables		Intercept	Partial regression coefficients				Interaction	n
		b_0	Linear		Quadratic		b_5	
X_1	X_2		b_1	b_2	b_3	b_4		
DLW	MAXTEMP	+10.5343	−1.2585	+1.4709	+0.0271	−0.0428	+0.0063	66
DLW	MINTEMP	+39.1012	−1.5252	+2.6244	+0.0185	+0.0636	+0.0650	66
DLW	METEMP	+46.0523	−1.4547	−2.6404	+0.0273	+0.0653	+0.0214	66
DLW	DIFTEMP	+15.2316	−0.3867	+0.5674	−0.0012	−0.0266	−0.0027	66
MAXTEMP	MINTEMP	+37.2217	−1.4254	−0.7420	−0.0034	−0.1523	+0.1353	66
MAXTEMP	MINTEMP	+33.7385	−0.8909	−1.9860	−0.0017	−0.0023	+0.0758	87

Tabel 3. Partiële regressiecoëfficienten berekend voor de multipele regressievergelijkingen voor het effect van temperatuur en bladnatperiode op de latente periode van Septoria nodorum in kiemplanten van 'Felix' tarwe te velde.

Fig. 1. The relationship between observed latent period (OLPD) and predicted latent period (PLPD) from multiple regression equations relating the effect of temperature and moisture (independent variables X_1 and X_2) on the latent period of *Septoria nodorum* (dependent variable) in seedlings of wheat cv. Felix under field conditions. The meaning of the symbols used for the independent variables is given in Table 1. (Moisture treatments: ■ natural, ● wet, ▲ dry). The observations plotted above the curve ab are the 87–66 = 21 observations not included in the other graphs (see under 'moisture treatments'). ** means significant at P ⩽ 0.01.

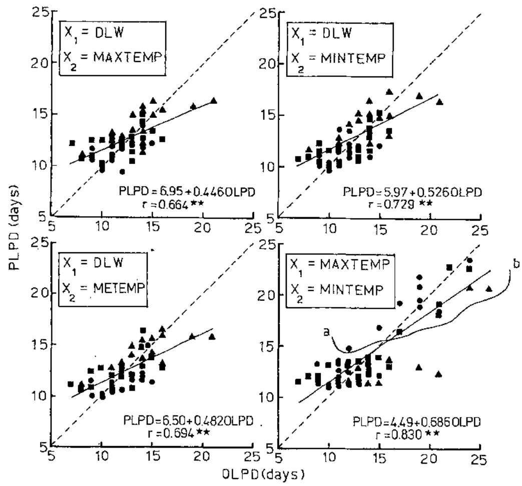


*Fig. 1. Het verband tussen de waargenomen latente periode (OLPD) en de berekende latente periode (PLPD) volgens de multipele regressievergelijkingen voor het effect van temperatuur en bladnatperiode (onafhankelijke variabelen X_1 en X_2) op de latente periode van Septoria nodorum (afhankelijke variabele) in kiemplanten van 'Felix' tarwe te velde. (Bladnat-behandelingen: ■ normaal, ● nat, ▲ droog). ** betekent significant bij P ⩽ 0,01.*

Table 4. The proportion of observations falling within the class limits indicated of the absolute difference between observed latent period and latent period predicted from the multiple regression equations representing the effect of temperature and moisture on the latent period of *Septoria nodorum* in seedlings of wheat, cv. Felix, under field conditions. The meaning of the symbols used for the independent variables is given in Table 1.

Independent variables		Class limits (in days) for the absolute difference between observed and predicted latent period (d)				n
X_1	X_2	$d < 1$	$1 \leqslant d < 2$	$2 \leqslant d < 3$	$d \geqslant 3$	
DLW	MAXTEMP	0.47	0.21	0.24	0.08	66
DLW	MINTEMP	0.45	0.27	0.20	0.08	66
DLW	AVTEMP	0.35	0.41	0.14	0.10	66
MAXTEMP	MINTEMP	0.38	0.33	0.21	0.13	87

Tabel 4. De fractie van de waarnemingen vallende binnen de aangegeven klassegrenzen van het absolute verschil tussen de waargenomen latente periode en de latente periode berekend uit de multipele regressievergelijkingen voor het effect van temperatuur en bladnatperiode op de latente periode van Septoria nodorum in kiemplanten van 'Felix' tarwe te velde.

Responses of the dependent variable to the independent variables. The relationship between the dependent variable, PLPD, and the independent variables X_1 and X_2 can be represented by a response surface. Substituting different values of X_1 and X_2 into the multiple regression equation will give the co-ordinates of the response surface, the elements of which will be PLPD for combinations of X_1 and X_2. PLPD response surfaces for selected independent variables are shown in Fig. 2 to 6.

Relationship between latent period, leaf wetness and temperature. The form of the response surface relating the effect of DLW and temperature on PLPD depends on the choice of the temperature variable, X_2 (Figs. 2 to 4).

If X_2 = MAXTEMP (Fig. 2), the DLW $\times$ MAXTEMP interaction is relatively

Fig. 2 (left). The response surface derived from the multiple regression equation relating the effect of duration of leaf wetness (DLW) and maximum temperature (MAXTEMP) on the predicted latent period of *Septoria nodorum* (PLPD) in seedlings of wheat cv. Felix, under field conditions.
Fig. 3 (right). The response surface derived from the multiple regression equation relating the effect of duration of leaf wetness (DLW) and minimum temperature (MINTEMP) on the predicted latent period of *Septoria nodorum* (PLPD) in seedlings of wheat cv. Felix, under field conditions.

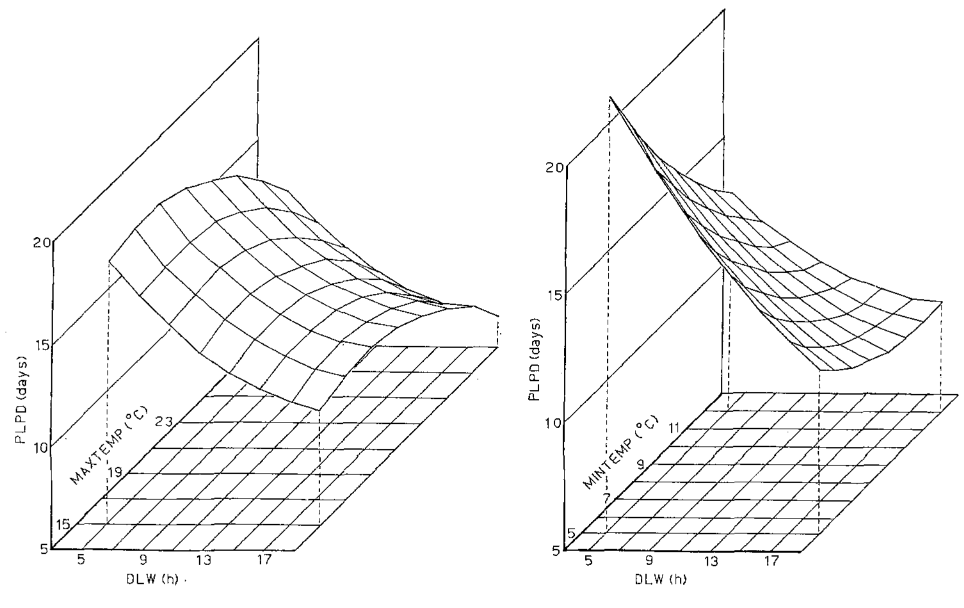


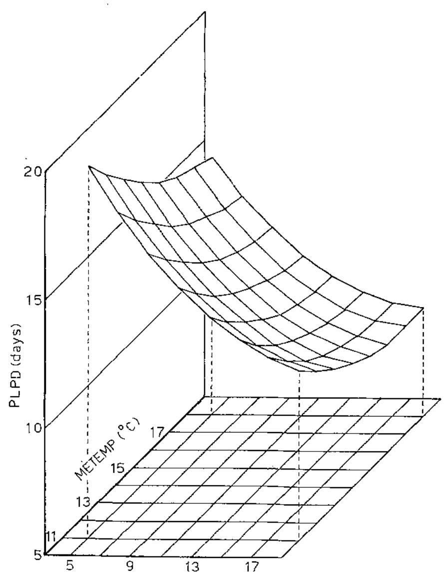
Fig. 2 (links). Het responsie-oppervlak berekend uit de multipele regressievergelijking voor het effect van de bladnatperiode (DLW) en de maximum temperatuur (MAXTEMP) op de berekende latente periode van Septoria nodorum (PLPD) in kiemplanten van 'Felix' tarwe te velde.
Fig. 3 (rechts). Het responsie-oppervlak berekend uit de multipele regressievergelijking voor het effect van de bladnatperiode (DLW) en de minimum temperatuur (MINTEMP) op de berekende bladnatperiode van Septoria nodorum (PLPD) in kiemplanten van 'Felix' tarwe te velde.

small, and the relationship between one independent variable and PLPD is independent of the level of the other independent variable. A difference in DLW of 12 h (17 to 5 h) delays PLPD by 6 to 7 days. The relationship between PLPD and MAXTEMP has the form of an inverted parabola.

If X_2 = MINTEMP (Fig. 3), the DLW × MINTEMP interaction modifies PLPD, the relationship between PLPD and one independent variable depending on the level of the other independent variable. Within the range of the experiment, the optimum for the relationship between PLPD and one independent variable tends to be broad when the other independent variable is optimal, but narrow when the other independent variable is limiting. A decrease in DLW of 12 h (from 17 to 5 h) increases PLPD by 4 days at MINTEMP = 12°C and 9.5 days at MINTEMP = 5°C. A decrease in

Fig. 4 (left). The response surface derived from the regression equation relating the effect of duration of leaf wetness (DLW) and mean temperature (METEMP) on the predicted latent period of *Septoria nodorum* (PLPD) in seedlings of wheat cv. Felix, under field conditions.

Fig. 5 (right). The response surface derived from the regression equation, for n = 87, relating the effect of maximum temperature (MAXTEMP) and minimum temperature (MINTEMP) on the predicted latent period of *Septoria nodorum* (PLPD) in seedlings of wheat cv. Felix, under field conditions. Line pq represents the MAXTEMP-MINTEMP combinations with average temperature (AVTEMP) = 15°C. Curve rs is the projection of line pq on the response surface. Curve xy connects the points with the highest PLPD per AVTEMP.



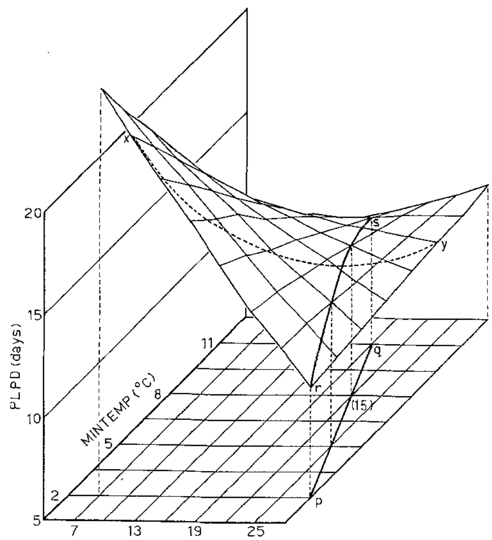


Fig. 4 (links). Het responsie-oppervlak berekend uit de multipele regressievergelijking voor het effect van de bladnatperiode (DLW) en de gemiddelde temperatuur (METEMP) op de berekende latente periode van Septoria nodorum (PLPD) in kiemplanten van 'Felix' tarwe te velde.

Fig. 5 (rechts). Het responsie-oppervlak berekend voor n = 87 uit de multipele regressievergelijking voor het effect van de maximum temperatuur (MAXTEMP) en de minimum temperatuur (MINTEMP) op de berekende latente periode van Septoria nodorum (PLPD) in kiemplanten van 'Felix' tarwe te velde. Lijnstuk pq geeft de MAXTEMP-MINTEMP combinaties aan met een gemiddelde temperatuur (AVTEMP) = 15°C. Curve rs is de projectie van lijnstuk pq op het responsie-oppervlak. Curve xy verbindt de punten met de hoogste PLPD per AVTEMP.

MINTEMP of 7°C (from 12 to 5°C) increases PLPD by 2 days at DLW = 17 h and 8.5 days at DLW = 5 h. The rate of increase of PLPD increases as DLW and MINTEMP approach the lower limits of their range, suggesting that the effect of the DLW × MINTEMP interaction is additive.

The form of the response surface when X_2 = METEMP (Fig. 4), is intermediate between the response surface described when X_2 = MAXTEMP or MINTEMP, but resembles the latter more than the former.

The response surface for the relationship between PLPD, MAXTEMP and MINTEMP (n = 87) has the form of a flat surface, which has been bent up at two opposite corners and deflected down at the remaining two corners (Fig. 5). The form of the response surface reflects the small quadratic component and the relatively large interaction component (Table 3). PLPD increases as MINTEMP and MAXTEMP approach the lower limits of their range, but decreases as they approach the upper limits. If MINTEMP = 2°C, a decrease in MAXTEMP of 21°C (from 28 to 7°C) increases PLPD by 14 days. Conversely, if MINTEMP = 12.5°C a decrease in MAXTEMP of 15°C (from 28 to 13 ;C) decreases PLPD by 1.9 days. If MAXTEMP = 7°C, a decrease in MINTEMP of 4.5°C (from 6.5 to 2°C) increases PLPD by 7 days. However if MAXTEMP = 28°C, a decrease in MINTEMP of 10.5°C (from 12.5 to 2°C) decreases PLPD by one day.

It can be shown that curves on the response surface, given in Fig. 5, represent the variation of PLPD with combinations of MAXTEMP and MINTEMP which give equal average temperature (AVTEMP). An example is given by the curve rs which is the projection of the line pq representing an AVTEMP = 15°C. In Fig. 6 the PLPD-MAXTEMP-MINTEMP response surface has been redrawn, but the points of equal AVTEMP on the response surface have been joined. The variation of PLPD for equal AVTEMP is such that PLPD increases with combinations of decreasing MAXTEMP and increasing MINTEMP.

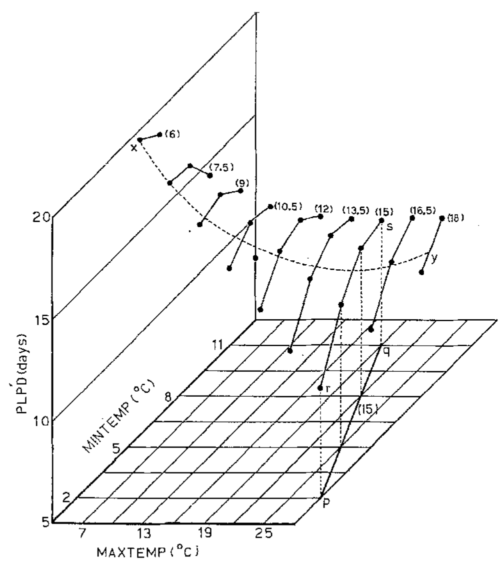


Fig. 6. The variation of predicted latent period of *Septoria nodorum* in seedlings of wheat cv. Felix with average temperature AVTEMP under field conditions. Fig. 5 redrawn to show the variation of predicted latent period of *Septoria nodorum* (PLPD) with combinations of maximum temperature (MAXTEMP) and minimum temperature (MINTEMP) which give equal average temperature (selected values indicated in parenthesis). For the line pq and the curves rs and xy, see Fig. 5.

Fig. 6. De variatie van de berekende latente periode van Septoria nodorum in kiemplanten van 'Felix' tarwe te velde. Fig. 5 werd opnieuw getekend om de variatie te laten zien van de berekende latente periode (PLPD) bij combinaties van maximum temperatuur (MAXTEMP) en minimum temperatuur (MINTEMP), die gelijke gemiddelde temperaturen geven (de gekozen gemiddelde temperaturen AVTEMP zijn tussen haakjes aangegeven). Voor het lijnstuk pq en de curves rs en xy, zie fig. 5.

It can be shown, again, that there is a curve xy on the response surface with an asymmetrical U-shaped form connecting the highest values of PLPD per AVTEMP (Fig. 5 and 6); the meaning of the curve is not known.

Discussion

Multiple regression equations were fitted to the data to determine the relationship(s) between the latent period of *S. nodorum* and temperature and moisture, in seedlings of wheat, 'Felix', under field conditions. The size of the multiple correlation coefficient and the form of the response surfaces derived from the multiple regression equations indicate that the effect of temperature and duration of leaf wetness on the predicted latent period (PLPD) depends on the choice of the temperature variable. The multiple regression equation with MINTEMP as the second independent variable gives a better estimate of PLPD than the equation in which MAXTEMP is the second independent variable (Table 2). Similarly, Hill and Green (1965) observed in growth chamber studies that minimum temperature was the best guide to the development (incubation period) of *Peronospera tabacina* in tobacco seedlings.

The response surfaces derived from the respective multiple regression equations indicate the relative effect of MAXTEMP and MINTEMP on PLPD. The form of the response surface for the relationship between PLPD, DLW and MAXTEMP (Fig. 2) suggests that either the observed MAXTEMP range ($15 \leqslant$ MAXTEMP $\leqslant 28$) is within the optimal range for the development of *S. nodorum* or that MAXTEMP is a poor estimator of fungal development. On the other hand the response surface for the relationship between PLPD and DLW and MINTEMP (Fig. 3) suggests that the observed MINTEMP range ($5 \leqslant$ MINTEMP $\leqslant 13$) varies from optimal to sub-optimal. The optimum range of MINTEMP is relative, being dependent on the level of DLW.

In the case of the relationships between leaf wetness period DLW and temperature, the interaction term is an important determinant of the latent period of *S. nodorum*; multiple regressions with the greatest interaction term explain the greatest proportion of the variance. Relatively little interaction occurs between DLW and MAXTEMP, as could be expected for both dew as well as for rain. In the case of dew, DLW and MAXTEMP act independently because they are not simultaneous. In the case of rain, although DLW and MAXTEMP can occur simultaneously, under such conditions MAXTEMP deviates relatively little from MINTEMP, and there is no specific interaction with DLW. A high interaction between DLW and MINTEMP may be expected especially in the case of dew, when DLW and MINTEMP occur simultaneously.

The average temperature is often used in studies on the effect of temperature on fungal development. However the latent period of *S. nodorum* varies with maximum and minimum temperature combinations which give the same average temperature (Fig. 6). In growth chamber studies on *P. tabacina* Hill and Green (1965) also found that the plant × pathogen interaction varied with temperature combinations which gave the same average temperature.

This study confirms our previous conclusions that the duration of leaf wetness (DLW) is an important determinant of the latent period of *S. nodorum*. In growth chamber studies with a constant rhythm of change in DLW, a decrease in DLW of 12 h (from 24 to 12 h) prolonged latent period by about 6 days (Shearer and Zadoks, 1972). Under fluctuating conditions in the field a decrease in DLW of 12 h (from 17 to 5 h) prolonged latent period by approximately 7 days.

The error associated with this type of study is large. The size of the error term will affect the proportion of the variance explained by the multiple regression equations fitted to the observed data; the greater the error term, the greater the proportion of variance unexplained. Since no values can be assigned to the components of the error term, we can only speculate on possible sources of error. Error can be introduced in the measurement of latent period, the measurement of environmental variables, the effect of environmental variables not measured, and variation in the inoculum density and host. The latent period, as defined in 'materials and methods', is the 'shortest latent period' in plant samples of a given size. As noted by Shearer and Zadoks (1972) this estimate of latent period does not take into consideration the variance between leaves in the appearance of the first sporulating pycnidium nor the variance within a leaf in the time to the appearance of successive pycnidia. Furthermore the 'shortest latent period' is an estimate situated at one end of the normal curve representing the variation of latent period between and within leaves, and hence is subject to large errors of measurement (Zadoks, 1961). The sources of error in the measurement of environmental variables would be: differences between wetting of the sensing element of the leaf wetness recorders and wetting of the infected leaf surface, variation between recorders, and differences between air temperature measured by the thermocouples and actual leaf temperature. Light intensity and relative humidity are unmeasured variables that could affect the length of the latent period. Not only did light intensity differ between the covered 'dry' moisture treatment and the uncovered 'natural' and 'wet' moisture treatments but also between days. As the experiment progressed the number of cloudy days increased, and day length decreased. The failure to control the inoculum density will introduce a variation in the length of the latent period. Shearer and Zadoks (1972) found that a tenfold reduction in inoculum density (5×10^5 to 5×10^4 spores ml^{-1}) increased the latent period by about 2 days.

The multiple regression equations derived in this study can be used to predict the development of an epidemic of *S. nodorum*; environmental conditions which favour short latent periods will favour the development of an epidemic. Constraints on the extrapolation of predicted latent period to wheat cultivars other than 'Felix' and to plant parts other than the 2nd to 3rd leaves have been discussed by Shearer and Zadoks (1972). Unfortunately, in this study the multiple regression equations calculated for all relationships underestimate latent period for observed latent periods of $\leqslant$ about 13 days. This is a serious disadvantage of the equations since if (for example) the latent period is predicted on a daily basis, the error in overestimating short latent periods ($\leqslant$ about 13 days) will be compounded. Because the rate of increase of an epidemic is essentially exponential, a small error in prediction at the beginning of a growing season will result in a large error at the end of that season.

Because of the complexity of the relationship between latent period temperature and moisture, we chose a regression model that included linear and quadratic effects, and a linear interaction effect. Because of the relatively low precision of the observations, the use of other, and more complicated regression models was not considered worthwhile. An estimate of error is given in Table 4. The authors consider the error in prediction to be of the same order of magnitude as the error in observation. Although regression equations are empirical relationships and do not necessarily have biological meaning, they are useful in that they indicate the variables with the greatest effect on fungal development and hence give leads for further experimentation.

In conclusion, the duration of leaf wetness period greatly influences the length of the latent period of *S. nodorum* in the field – under fluctuating conditions – as well as in the growth chamber – under constant conditions –, both in the same order of magnitude.

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Samenvatting

De latente periode van Septoria nodorum bij tarwe. 2 Het effect van temperatuur en vochtigheid onder veldomstandigheden

Klimaatkamerstudies met kiemplanten van 'Felix' tarwe en *Septoria nodorum* onder constante of constant wisselende omstandigheden toonden aan dat de latente periode van *S. nodorum* afhing van de temperatuur en de duur van de bladnatperiode. In een veldproef werd nagegaan of deze relaties ook onder wisselende omstandigheden aantoonbaar waren. Gedurende de herfst 1969 werden in de klimaatkamer opgekweekte kiemplanten geïnoculeerd en buiten uitgepoot. Voor iedere inoculatiedag werd de latente periode bepaald voor elk van drie bladnat-behandelingen. Variatie in de temperatuur werd bereikt door de seizoensmatige daling van de temperatuur gedurende de herfst. Variatie in de duur van de bladnatperiode werd bereikt door de natuurlijke variaties van het weer in het algemeen, en door drie behandelingen in het bijzonder, onbehandeld (normaal), afgeschermd (droog) en beregend (nat).

Voor de statistische berekeningen werd gebruik gemaakt van multipele regressievergelijkingen met twee onafhankelijke variabelen, hun lineaire en kwadratische effecten en hun lineaire interactie. De multipele correlatiecoëfficienten zijn gegeven in Tabel 2, de partiële regressiecoëfficienten in Tabel 3. Voor een aantal vergelijkingen zijn in Fig. 1 de puntenzwermen gegeven, waarbij per punt een berekende latente periode is vergeleken met de corresponderende waargenomen latente periode. In driedimensionale figuren worden de vergelijkingen weergegeven door gekromde responsie-oppervlakken (Fig. 3 t/m 6). De berekende latente periode is afhankelijk van de bladnatperiode, de temperatuur, en soms van hun interactie. De combinatie van bladnatperiode met minimum-temperatuur geeft het beste resultaat voor de berekening (voorspelling) van de latente periode, binnen de grenzen van de in deze proef gemeten variatiebreedte.

Enkele voorbeelden van resultaten zijn als volgt. Een afname van de bladnatperiode van 12 h (van 17 tot 5 h) doet de berekende latente periode toenemen met 4 dagen bij een minimumtemperatuur van 12°C en met 9,5 dagen bij een minimum temperatuur van 5°C. Een afname van de minimum temperatuur van 7°C (van 12 naar 5°C) doet de berekende latente periode toenemen met 2 dagen bij een bladnatperiode van 17 h en met 8,5 dagen bij een bladnatperiode van 5 h. Deze effecten zijn van dezelfde orde van grootte als de effecten waargenomen in klimaatkamerproeven onder constante of constant wisselende omstandigheden.

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