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The latent period of Septoria nodorum in wheat.
1. The effect of temperature and moisture treatments under controlled conditions

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Abstract

The latent period of *S. nodorum* (Berk.) Berk. on seedlings of the wheat 'Felix' was determined in growth chambers under various temperature and moisture treatments, with two inoculum densities. In the wet treatment, where the inoculated plants were placed in continuously water-saturated air, the shortest latent period was 6 days at 23 °C; in the alternate treatment, where 12 h saturated air alternated with 12 h at 85 to 90% r.h., maturity of pycnidia as indicated by extrusion of pycnidiospores was delayed by 5.6 days. In the dry treatment, continuously at 85 to 90% r.h., no sporulation occurred, though infection had taken place. On the average, sporulation at low inoculum density (5.10^4 pycnidiospores.ml^{-1}) was delayed by 2.4 days when compared to sporulation at high inoculum density (5.10^5 spores.ml^{-1}). From the data obtained, equations were derived to predict the latent period within the limits of the experiment. Eventually, these equations can be used in a computer simulator.

Introduction

Latent period, the period from inoculation to sporulation, is a determinant of the speed of an epidemic (Van der Plank, 1963). Latent periods of *S. nodorum* have been reported without specification of temperature and moisture conditions prevailing before and after inoculation, and reports on the factors affecting the latent period are vague. Therefore, experiments were conducted to determine the effect of temperature and moisture on the latent period of *S. nodorum* in leaf tissue.

Materials and methods

Host. In all experiments, the winter wheat 'Felix' was used (Sneep et al., 1969). This cultivar, which was also used in other epidemiological studies, was chosen because of the susceptible response of its leaves to *S. nodorum*. Plants were grown in sterilized sandy peat soil, in 7 cm diam. plastic pots, ten plants per pot. The plants were grown at 18 ± 1 °C, and exposed to a light intensity of 11,500 lux from fluorescent tubes (Philips TLM 40W/33RS) during 16 hours per day. The plants were inoculated with *S. nodorum* at the three leaf stage.

Pathogen. The pathogen studied was *Septoria nodorum* (Berk.) Berk., the imperfect state of *Leptosphaeria nodorum* E. Müller. A well sporulating and virulent isolate was obtained from the Institute of Phytopathological Research (IPO) at Wageningen, by courtesy of E. Ubels.

Experimental design. There were three independent variables: temperature, moisture, and inoculum density. The dependent variable was latent period. Eight temperature treatments were applied in the range of 4 to 25 °C (see below). There were three moisture treatments: wet, dry, and alternating (see below). Two inoculum densities were used: 5×10^4 and 5×10^5 spores.ml^{-1}. Per treatment two pots with ten plants were available, each plant with three inoculated leaves: sixty leaves per treatment. Per treatment there were up to twelve sampling days, with five leaves per daily sample (see under latent period). Each sample of five leaves was chosen at random. At the lower temperature, sampling was begun only after the appearance of the first symptoms. The total number of leaves available for examination was 8 (temperatures) $\times$ 3 (moisture treatments) $\times$ 2 (inoculum densities) $\times$ 12 (sampling days) $\times$ 5 (replicates) $=$ 2880.

Inoculum. The surface of wheat meal agar plates (2% wheat meal + 2% agar; Shearer, 1967) was flooded with a pycnidiospore suspension in sterile deionized water. The plates were incubated at 15 °C, and exposed to light from fluorescent tubes at an intensity of 22,000 lux during 16 hours per day. Within seven to ten days pycnidia, extruding spores in orange-pink cirri abounded. A pycnidiospore suspension was prepared by macerating agar and pycnidia from a number of plates in 100 ml deionized water, followed by filtration through one layer of muslin cloth. The spore suspension was diluted to the desired concentration, 5×10^4 or 5×10^5 spores.ml^{-1}, with the aid of a haemocytometer.

Inoculation. The standardized spore suspension was sprayed onto the plants until run-off by means of a De Vilbiss No 15 adjustable tip atomizer, using compressed air. After inoculation, the plants were enclosed in clear polythene bags for 72 hours to provide a water-saturated atmosphere conducive to infection.

Temperature treatments. The inoculated plants were placed in growth chambers at various constant temperatures (Table 1). Because spores of *S. nodorum* germinate poorly at 5 °C (Thomas, 1962), plants of the 5 °C batch were incubated at 18 °C for twelve hours prior to transfer to the 5 °C environment.

Moisture treatments. In the dry treatments, the pots with plants were placed in the growth chambers at 85 to 90 % r.h. in a metal tray containing water to a depth of 1 cm. The wet treatment was imposed with the aid of $15 \times 15 \times 39$ cm metal frames covered with clear polythene. A water saturated atmosphere was maintained by placing the potted plants in a tray containing water to a depth of 1 cm, and by covering the plants with the polythene cage. The covered plants were placed in the growth chambers. The alternating treatment was obtained by covering and uncovering the plants every twelve hours.

The commencement of the moisture period coincided with the beginning of night in the light cycle. Prior to each covering, the plants were sprayed with deionized water to ensure leaf wetness. After the twelve hours wet period, the free water on the leaves was still visible, but it evaporated within two minutes after removal of the polythene cage.

As the air temperatures tended to rise in the enclosed space of the polythene cages, air temperatures within and outside the cages were measured with the aid of thermocouples and a recorder (Table 1).

Table 1. Temperatures and relative humidities in the growth chambers used for the assessment of the effect of temperature and moisture treatments on the latent period of *Septoria nodorum* in seedlings of wheat 'Felix'.

Programmed temperature (°C)	Measured temperature (°C)						Programmed relative humidity (%)
	air			in polythene covered frame			
	day temp.	night temp.	mean hourly temp.	day temp.	night temp.	mean hourly temp.	
5.0	4.0	3.8	3.9	4.0	4.2	4.1	85
10.0	9.0	8.5	8.8	9.5	8.8	9.2	90
12.5	12.5	12.5	12.5	12.8	12.8	12.8	90
15.0	16.2	16.0	16.2	18.0	16.0	17.3	85
18.0	17.8	17.2	17.6	18.8	17.2	18.2	85
20.0	20.0	19.0	19.9	23.0	18.5	21.5	95
23.0	22.0	21.8	21.9	22.5	22.0	22.3	80
25.0	25.8	24.0	25.0	26.0	24.0	25.3	80

Tabel 1. Temperaturen en relatieve luchtvochtigheden in de klimaatkamers gebruikt voor de bepaling van het effect van temperatuur- en vochtbehandelingen op de latente periode van Septoria nodorum *in kiemplanten van tarwe 'Felix'.*

Light treatment. Ideally, all treatments should be performed under an identical light regime. For various reasons, this could not be accomplished. At all temperature treatments, daylength was 16 hours, except at 20 °C where it was 12 hours. Plants under cover received about 10% less light than uncovered plants.

Latent period. In all experiments, the latent period was measured as the period in days from the inoculation to the observation of the first mature pycnidium. The criterium for pycnidial maturity was the extrusion of spores in a cirrus, after mounting a leaf in water between slide and cover slip. Leaves were examined daily for the presence of mature pycnidia, except those leaves incubated at temperatures below 12.5 °C, which were examined on alternate days. For each examination 5 leaves from intact plants were randomly selected, and discarded after examination.

Results

Dry treatment. During the observation period no pycnidia were observed in leaves of plants receiving the dry treatment. Plants at 18 °C were retained for three weeks without appearance of pycnidia. After three weeks at 18 °C, infected leaves were nearly dead. Formation of pycnidia could be induced by enclosing the plants in a clear polythene bag during 24 hours, thus providing a water- saturated atmosphere. Sporefilled pycnidia were observed within 48 to 72 hours after removal of the bag. No pycnidia had formed in the controls without saturation treatment. This observation confirms a remark by Becker (1963), that a short period in a water saturated atmosphere, applied at the flecking stage, accelerates pycnidium formation.

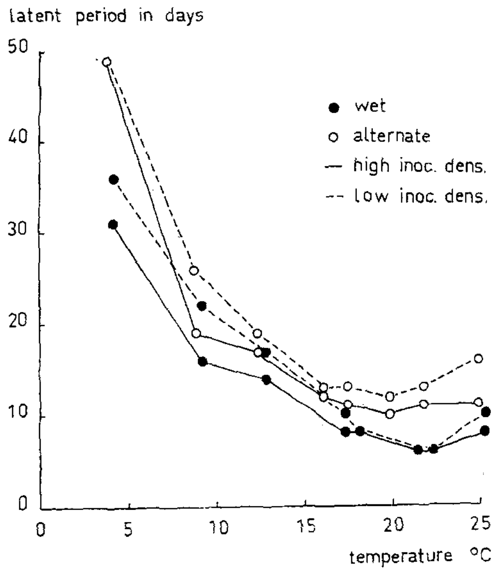


Fig. 1. The effect of temperature and moisture treatments, and of inoculum densities on the latent period of *Septoria nodorum* in seedlings of wheat 'Felix', under controlled conditions. For moisture treatments and inoculum densities, see text under 'Materials and methods'. Moisture treatments are wet and alternate, inoculum densities are high and low.

Fig. 1. Het effect van temperatuur- en vochtbehandelingen en van inoculumdichtheden op de latente periode van Septoria nodorum in kiemplanten van tarwe 'Felix', in klimaatkamers.

Wet treatment. The curve relating latent period to temperature (Fig. 1) has the typical asymmetrical U-shape associated with this type of relationship (Tollenaar and Houston, 1967; Zadoks, 1961). The shortest latent period was 6 days, at 22 °C, whereas at 4 °C the latent period reached values from 31 to 36 days. The latent periods of the low inoculum density treatment were on average 2.25 days longer than those of the high inoculum density treatment. The optimum temperature range of the high inoculum density treatment seemed to be slightly broader than that of the low inoculum density treatment, and in this experiment the optima coincided at a point representing a latent period of 6 days at 22 °C.

Alternating treatment. The curves for the alternating treatment (Fig. 1) show the same characteristics as those of the wet treatments, but the latent periods were, on average 5.58 days longer. The shortest observed latent period was 10 days at 20 °C. At 4 °C, the latent period was 49 days.

Again, the low inoculation density treatment yielded longer latent periods than the high inoculum density treatments. The average difference of 2.62 days was 0.37 days larger than in the wet treatment. It is not known whether this slight difference between the wet and alternating treatments is significant. The temperature optimum ranges in the alternating treatment were broader than in the wet treatment. There seemed to be a shift in the optimum temperature, which was 22 °C in the wet and 20 °C in the alternate treatment. It is not known whether this shift is reproducible and significant.

Relation between various temperatures. As a first approximation, the curve of the wet treatment with high inoculation density, between the lowest temperature applied and the optimum temperature, can be regarded as a hyperbola (Zadoks, 1961). The general equation is $y = a + b. x^{-1}$. Here the equation will be written: $L = A + B. T^{-1}$, where L is the latent period, T is the temperature, and A and B are constants to be determined.

Table 2. The effect of moisture treatments and inoculum densities on the latent period of *Septoria nodorum* in seedlings of wheat 'Felix', under controlled conditions. Table of the parameter B in the hyperbolic regression of latent period on temperature, for the various treatments.

Moisture treatment	Inoculum density	
	high	low
Wet	135	160
Alternate	197	212

Tabel 2. Het effect van vochtbehandelingen en inoculumdichtheden op de latente periode van Septoria nodorum in kiemplanten van tarwe 'Felix 'in klimaatkamers. Tabel van parameter B in de hyperbolische regressie van latente periode op temperatuur.

For the various treatments the values B are given in Table 2; for all treatments A = O. The relationship between L and $B. T^{-1}$ can be plotted on double log paper; it is nearly linear (Fig. 2). The regression coefficient r varies from 0.96 to 0.99, as expected by the original hypothesis of a hyperbolic relationship. The relation between latent period L and temperature T is adequately described, when supra-optimal temperatures are excluded, by the following statement:

$L = 135. T^{-1}$ when $4 \leq T \lesssim 23$

In all cases, the hyperbolic relation between latent period and suboptimal temperatures held good. At the low inoculum densities the scatter is slightly larger than at the high inoculum densities.

Relation between inoculum densities. There was a nearly rectilinear relation between the effects of the two inoculum densities on latent period at all temperatures (Fig. 3).

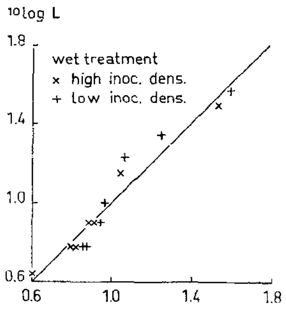


Fig. 2. Observations on the latent period of *Septoria nodorum* in seedlings of wheat 'Felix', under controlled conditions. Relations between the observed latent period L and the calculated latent period B/T, plotted on double logarithmic paper. Ideally, all points coincide with the 45° bisector.

Fig. 2. Waarnemingen over de latente periode van Septoria nodorum in kiemplanten van tarwe 'Felix', in klimaatkamers. Verband tussen waargenomen latente periode L en berekende latente periode B/T.

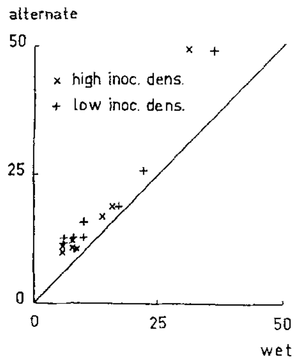


Fig. 3. Observations on the latent period of *Septoria nodorum* in seedlings of wheat 'Felix', under controlled conditions. Relation between the effects of the two inoculum densities for each of two moisture treatments. Figures along ordinate and abscissa represent latent periods in days for the respective treatments. Regression coefficients are: $r_{wet} = 0.99$; $r_{alternate} = 0.99$.

Fig. 3. Waarnemingen over de latente periode van Septoria nodorum in tarwe 'Felix', in klimaatkamers. Verband tussen de gevolgen van de twee inoculumdichtheden voor ieder van de twee vochtbehandelingen. De getallen langs ordinaat en abscis geven de latente perioden in dagen weer voor de diverse behandelingen.

Relation between moisture treatments. Again, there was a nearly rectilinear relation between the effects of two moisture treatments, though there was a deviation at 4.1 °C (Fig. 4). The wet treatment can be regarded as the reference with a *w*etness *int*erruption WINT = 0 days per day, and without *del*ay of sporulation due to interruption of wetness, i.e. DEL = 0 days. The alternate treatment can be considered as a wet treatment with an interruption of the wetness of WINT = 0.5 days per day, and the average delay in the latent period DEL = 5.71 days. The dry treatment can be regarded as a reference but with WINT = 1 day per day, and DEL = ∞: no sporulation. An arbitrary but convenient relation between DEL and WINT permitting interpolation for non-measured values of WINT is:

$\mathrm{WINT} = 1 - e^{-P \cdot \mathrm{DEL}}$, where P is a constant.

After calculation of P and rearrangement, the equation can be written:

$\mathrm{DEL} = -P^{-1} \cdot \ln(1-\mathrm{WINT})$ with $P = 0.121$

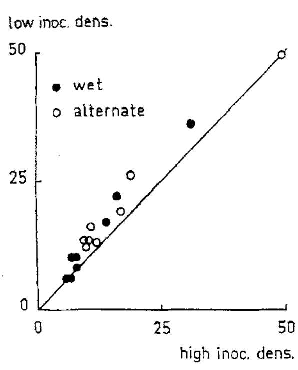
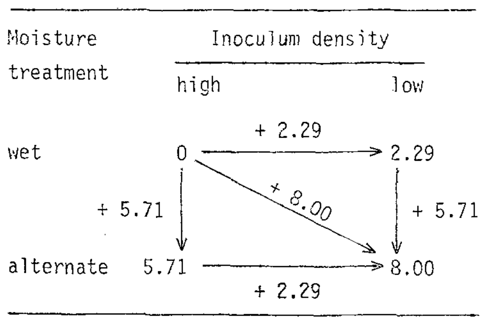


Fig. 4. Observations on the latent period of *Septoria nodorum* in seedlings of wheat 'Felix', under controlled conditions. Relations between the effects of two moisture treatments for each of the two inoculum densities. Figures along ordinate and abscissa represent latent periods in days for the respective treatments. Regression coefficients are: $r_{high} = 0.98$; $r_{low} = 0.98$.

Fig. 4. Waarnemingen over de latente periode van Septoria nodorum in kiemplanten van tarwe 'Felix', in klimaatkamers. Verband tussen de gevolgen van twee vochtbehandelingen voor ieder van de twee inoculumdichtheden. De getallen langs ordinaat en abscis geven de latente perioden in dagen weer voor de diverse behandelingen.

Relation between moisture treatments and inoculum densities. The effects of the various moisture/inoculum combinations in the temperature range $4 \leq T \leq 23$ can be compared with the moisture/inoculum combination that gives the shortest latent period (wet/high). Since all other moisture/inoculum combinations caused longer latent periods, the mean delays of sporulation could be calculated (Table 3).

Table 3. The effect of moisture treatments and inoculum densities on the latent period of *Septoria nodorum* in seedlings of wheat 'Felix', under controlled conditions. Table showing the values in days of the average delays of sporulation due to treatments other than the wet treatment with high inoculum density in the temperature range $4 \leqslant T \leqslant 23\,°C$.



Tabel 3. Het effect van vochtbehandelingen en inoculumdichtheden op de latente periode van Septoria nodorum *in kiemplanten van tarwe 'Felix' in klimaatkamers. Tabel van het gemiddelde uitstel van de sporulatie, uitgedrukt in dagen, ten gevolge van behandelingen anders dan de natte behandeling met hoge inoculumdichtheid in het temperatuurtraject $4 \leqslant T \leqslant 23\,°C$.*

Relation between moisture treatments and temperatures. According to Fig. 1, the *del*ay of sporulation due to *i*nterruption of *w*etness DELIW is temperature dependent. This can be expressed by the following equation, in which the delay is averaged over the two inoculum densities:

$$\begin{aligned} \text{DELIW} &= L_{alt} - L_{wet} \\ &= \frac{197 + 212}{2} \times T^{-1} - \frac{135 + 160}{2} \times T^{-1} \\ &= 57 \times T^{-1} \text{ days,} \end{aligned}$$

in which DELIW is the delay of sporulation due to the interruption of wetness, L is the latent period calculated according to the hyperbolic equation, and T is the temperature. The constants are taken from Table 2. If DELIW is divided bij the *av*erage *del*ay (AVDEL) of sporulation due to the alternate treatment, a dimensionless *co*rrection *f*actor COFIT can be derived relating the delay caused by *i*nterruption to *t*emperature:

$$\text{COFIT} = \text{DELIW}/\text{AVDEL} = 57 \times T^{-1}/5.71 = 10.0 \times T^{-1}$$

Relation between inoculum density and temperatures. According to Fig. 1, the delay of sporulation due to the decrease inoculum density is somewhat temperature dependent. This can be expressed by the following equation, in which the delay is averaged over the moisture treatments:

$$\begin{aligned} \text{DELID} &= L_{low} - L_{high} \\ &= \frac{160 + 212}{2} \times T^{-1} - \frac{135 + 197}{2} \times T^{-1} \\ &= 20 \times T^{-1} \end{aligned}$$

in which DELID is the *del*ay of sporulation due to a difference in *i*noculum *d*ensity, L = the latent period calculated according to the hyperbolic equation, and T is the temperature. The constants are taken from Table 2.

Relation between latent period and all other variables. In Table 3, it was shown that DELIW and DELID can be considered as additive factors. Taking the wet treatment as a starting point, the following equation can be developed and written in FORTRAN

LPD = 135/T + DEL * COFIT + DELID
= 135/T + ALOG (1. – WINT) /–0.121 * 10.0/T + 20./T
when $4 \leq T \leq 23$.

LPD is the latent period in days; for the other symbols see Table 4. The last term, 20./T, is to be used only when there is a tenfold reduction of inoculum density, from 5×10^5 to 5×10^4 spores.ml^{-1}.

Tabel 4. Table of symbols

A	Constant in the hyperbolic equation.
ALOG	Natural logarithm (to base e).
AVDEL	*Av*erage *del*ay of sporulation due to 12 hours of wetness interruption.
B	Constant in the hyperbolic equation.
COFIT	*Co*rrection *f*actor relating delay of sporulation due to wetness *i*nterruption to *t*emperature.
DEL	*Del*ay of sporulation due to wetness interruption in days.
DELID	*Del*ay of sporulation due to a decrease in the *i*noculum *d*ensity in days.
DELIW	*Del*ay of sporulation due to *i*nterruption of *w*etness with temperature dependency, in days.
e	Base of natural logarithms.
L	Observed *l*atent period in days.
LPD	Calculated *l*atent *p*erio*d* in days.
P	Constant in equation.
T	Temperature in °C.
WINT	*W*etness *int*erruption in days per day.
*	Multiplication symbol.
/	Division symbol.

Tabel 4. Verklaring der symbolen.

Discussion

References on the latent period of *S. nodorum* are few. Weber (1922) reported that the latent period varied from 12 to 16 days, and was longer than 14 days at temperatures 'below the optimum for the development of the fungus'. However, this optimum was mentioned only for mycelial growth of the fungus on PDA. Scharen (1964) reported that at 21 °C the latent period was 10 to 14 days. The results reported here place these remarks in another perspective: any report on the latent period of *S. nodorum* without mention of the moisture treatment is rather meaningless.

The cultivar used, 'Felix', is susceptible to *S. nodorum*. The results can not be extrapolated to other cultivars, except, maybe, those of the susceptible class. Nevertheless, it is felt that the general shape of the response curves will be applicable to other cultivars that are moderately to highly susceptible. If this feeling is correct, extrapolation of the results to other cultivars of equal or higher susceptibility is feasible after the determination of a few cardinal points in the response curves of these cultivars. What is said on extrapolation to other cultivars also holds true for extrapolation to other plant parts and growth stages. Results obtained with seedlings cannot be applied to mature plants of the same cv. without further tests.

The asymmetrical U-shaped curves of Fig. 1 are, in a way, the inverses of optimum curves. In the U-shaped curve, the dependent variable reaches a minimum, and in the optimum curve a maximum at a certain value of the independent variable. The relationship between the two types of curves becomes evident if we define the rate of development of the fungus in vivo as the inverse of the latent period: Fig. 5. The rate of development is expressed in units.day^{-1}, assuming that the total development from inoculation to the first sporulating pycnidium has a value of 1 unit. The curve of Fig. 5 is a typical optimum curve.

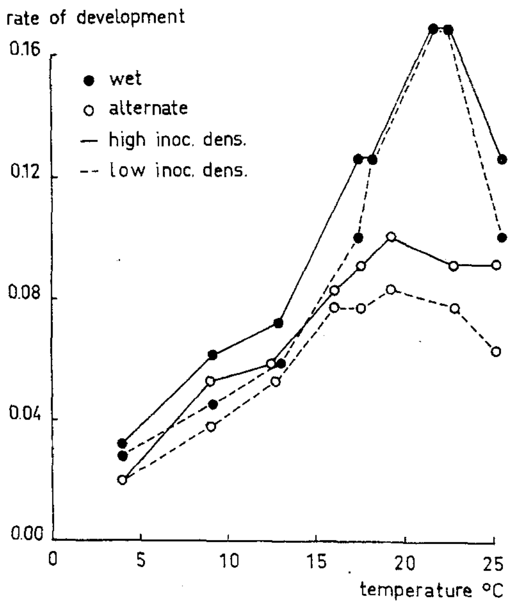


Fig. 5. The effect of temperature and moisture treatments, and of inoculum densities on the 'rate of development' in units.day^{-1} (see text) of *Septoria nodorum* in seedlings of wheat 'Felix', under controlled conditions. For moisture treatments (wet and alternate) and inoculum densities (high and low), see under 'Materials and methods'.

Fig. 5. De invloed van temperatuur- en vochtbehandelingen, en van inoculumdichtheden op de 'ontwikkelingssnelheid' van Septoria nodorum in kiemplanten van tarwe 'Felix', in klimaatkamers.

The latent period as defined in 'materials and methods' is the shortest latent period observed in plant samples of a given size, treated with a given inoculum density. This conforms to the latent period as defined for *Puccinia striiformis* on wheat by Zadoks (1961). The larger the sample size, the greater the chance to find the very shortest latent period under the given conditions. This is partly due to the 'law of the large numbers', assuming that there are variations in susceptibility between plants within one cultivar. The effect of inoculum density may also be attributed in part to the 'law of the large numbers', the higher the inoculum density, the greater the chance to find the very shortest latent period, but there is certainly also a physiological effect. The greater the number of infections per leaf, the faster the leaf is exhausted. This conforms with observations on *Puccinia recondita* on wheat (Mehta and Zadoks, 1970). Apart from the variance between leaves in the time of the appearance of the first sporulating pycnidium, there is also a variance within leaves in the time of appearance of successive sporulating pycnidia. These variances have been conveniently neglected in this paper, but the point is raised to demonstrate the complications encountered in the study of the latent period.

Differences in light treatment (see materials and methods) may have influenced the results to some extent. This influence has been ignored because identical light intensities at different temperatures have different physiological effects.

Acknowledgments

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Samenvatting

De latente periode van Septoria nodorum in tarwe. 1. Het effect van temperatuur- en vochtbehandelingen onder gecontroleerde omstandigheden

De proeven werden gedaan in klimaatkamers met kiemplanten van het cv. 'Felix'. De onafhankelijke variabelen waren temperatuur, vocht, en inoculumdichtheid. De afhankelijke variabele was de latente periode, dit is de kortst waarneembare periode in dagen vanaf de inoculatie tot de eerste sporulatie van de resulterende pycnidien. Voor de temperaturen zie Tabel 1. De vochtbehandelingen waren 'droog', 'nat' en 'afwisselend nat en droog'. Op planten van de 'droge' behandeling, met RV van 85 tot 90%, sporuleerde de schimmel niet. Op planten van de 'natte' behandeling, met water verzadigde lucht, sporuleerde de schimmel goed. Op planten met een wisselbehandeling, 's nachts in verzadigde lucht en overdag bij 85 tot 90% RV, sporuleerde de schimmel vertraagd.

Bij inoculatie met 5×10^5 pycnidiosporen.ml^{-1} sporuleerde de schimmel eerder dan bij inoculatie met 5×10^4 sporen.ml^{-1}. De gesignaleerde verschillen waren systematisch (Fig. 1, 3 en 4) en additief (Tabel 3). Latente periode en temperatuur (van laagste waarde tot optimum) waren omgekeerd evenredig aan elkaar (hyperbolisch verband, Tabel 2, Fig. 1 en 2).

Gebruikmakend van de gesignaleerde regelmatigheden, n.l. het hyperbolisch verband tussen latente periode en temperatuur, de systematische verschillen ten gevolge van onderbreking van de natte behandeling en van de verlaging van de inoculumdichtheid, kon met enkele hulpaannamen een wiskundig verband afgeleid worden tussen latente periode, temperatuur, onderbrekingsduur van de natte behandeling en inoculumdichtheid.

Dit verband werd in een in FORTRAN geschreven formule vastgelegd. Voor de symbolen zie Tabel 4. De ontwikkelingssnelheid kan worden gedefinieerd als de inverse van de latente periode. De ontwikkelingssnelheid wordt uitgedrukt in eenheden per dag, waarbij de totale ontwikkeling vanaf inoculatie tot en met het eerste sporulerende pycnidium de waarde 1 krijgt. De curve van de ontwikkelingssnelheid tegen de temperatuur (Fig. 5) is een typische optimumcurve.

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