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Uredospore production and sporulation period of Puccinia recondita f. sp. triticina on primary leaves of wheat

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Abstract

Uredospore production per day and per sporulation period was measured under near-optimal conditions. Pustule density influenced time and rate of pustule opening, size of pustules, time of maximum sporulation, length of the sporulation period and the time and rate of tissue necrotisation. Within limits total dry weight of spores per leaf per sporulation period was independent of pustule density; it roughly equalled the dry weight of the spore producing leaf. The longest sporulation period observed was 65 days; at low pustule densities secondary pustules replaced exhausted primary pustules. Infectivity of the spores was normal up to 46 days after inoculation. The long sporulation period was epidemiologically interpreted as a survival mechanism.

Introduction

Several workers such as Chester (1946), Yarwood (1961), and others have studied uredospore production by rust fungi. Relatively little information was available on the uredospore production by *Puccinia recondita* f. sp. *triticina*. Eyal and Peterson (1967) reported on the effect of light and temperature on the uredospore production by *P. recondita* f. sp. *triticina*. The present paper aims at a more detailed investigation of the uredospore production and the sporulation period of *P. recondita* f. sp. *triticina* on susceptible wheat seedlings under near-optimal conditions.

Materials and methods

Plants. Seedlings of cv. 'Rubis' were grown in sterilized compost soil in a conditioned greenhouse (Experiments 1 and 2) or in a walk-in growth chamber (Experiment 3). The environmental conditions are specified in Table 1. Only the primary leaves were used in this experiment; any growth beyond the primary leaf was cut away after every spore collection round.

Rust. One single-spore isolate of *P. recondita* f. sp. *triticina* ('Felix' race, isolate number 1035, from cv. 'Felix'. Wieringermeer, The Netherlands, 1961) was used (Zadoks, 1966).

Inoculation. Plants were inoculated with dry spores when the second leaf was just emerging. Inoculation was effected by gently rubbing sporulating leaves over the leaves to be inoculated. The inoculated plants were incubated for 18 hours in a

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Table 1. Environmental conditions during the experiments on sporulation as measured at plant height. During Experiment 1 conditions were similar to those in Experiment 2 but somewhat more variable and on the average slightly hotter and dryer during daytime.

	Experiment 2		Experiment 3			
	day	night	day		night	
			transition	constant	transition	constant
hours	16	8	3	13	3	5
temperature in °C	19	16	i[1]	15	i	11
relative humidity in %	68	85	i	49	i	91
light intensity[2]						
lux	8,500	—	17,500		—	
mgcal. cm^{-2} . min^{-1}	90.4	—	150		—	

[1] i = intermediate

[2] Measured by a spherical lightmeter; divide by 2 to approximate value given by flat light meter.

Table 1. Milieuomstandigheden tijdens de sporulatieproeven, gemeten op planthoogte.

completely dark moist chamber with a water-saturated atmosphere at 16 °C.

Time indication. Time was measured in days from inoculation. Day 10 means the tenth day after inoculation.

Spore deposit. Twenty-four hours after inoculation, spore counts were made on four upper and four lower leaf surfaces chosen at random. The number of germinated and ungerminated spores per microscope view field (4.71 mm^2) was determined in a great number of fields (27 to 112). At least 200 spores per leaf surface have been examined. From these data the spore deposit, defined as the average number of spores per cm^2, was calculated. Leaf area at the time of inoculation was measured with a planimeter and the average number of spores per leaf was calculated.

Pustule density. The number of primary and secondary pustules per leaf was counted separately for upper and lower surfaces, on 15 leaves chosen at random. A lesion sporulating on both sides of the leaf has been considered as two pustules.

Pustule opening. The number of open pustules was counted daily on 4 leaves chosen at random for this purpose. Separate counts were made for upper and lower leaf surfaces. After some time rings of secondary pustules appeared around the primary pustules. These secondary pustules were counted from time to time.

Sporulation. To determine the uredospore production 50 leaves were used. At regular intervals, spores were collected by a cyclone collector from the upper and lower surfaces. Naturally released spores which fell on butter paper dics covering the pots were also collected. Spore collection was started soon after the first open pustule was observed and continued as long as possible. Immediately after collection the fresh weights of the spore lots were determined.

Pustule size. Leaves were washed in diluted chloralhydrate and stained with acid fuchsin. Length and width of the sporulation area of the pustule were measured under the microscope (40 pustules on each of 4 upper and 4 lower leaf surfaces per treatment) The pustule area was estimated as average lenths times average width.

Conversion factor. Fresh spores have been collected using a cyclone collector, weighed immediately, and suspended in a small volume of a 'specific gravity solution'

with 5% Tween 40. This solution consisted of 43.1% glycerol by volume in tap water and had a specific gravity of 1.10, approximately equal to that of the rust spores. The suspension was treated in an ultrasonic vibrator for 1 minute at ca. 19,000 cycles per second. This suspension was diluted to 10 ml by adding 'specific gravity solution' and the concentration of the spores was determined using a Neubauer hemocytometer. On average 1 mg of fresh spores amounted to 274,000 spores. Assuming that the fresh weight of the spores was approximately constant throughout the experiments, this figure was used as the conversion factor.

Host injury. Host injury of the plants used in the spore collection experiments was recorded as the estimated percentage of necrotic leaf area, averaged over 50 leaves. The slight injury caused by the cyclone did not appreciably influence the necrosis caused by the rust

Infectivity tests. Spores collected at various times after inoculation were tested for infectivity by inoculation experiments conducted under the conditions specified above.

Leaf sheaths. Pustules appearing on leaf sheaths have been ignored.

Results

Experiments and treatments

Experiment 1 was a pilot experiment. Experiment 2 produced the longest sporulation period (Fig.1). In Experiment 3, which is reported in detail, four treatments (A to D) differing in spore deposit were applied (Table 2). The results from treatment B were so similar to those from treatment A that in general they are not mentioned separately.

Germination and pustule formation. The germination ratio is the fraction of the spores that formed recognisable germ tubes within one day. The colonization ratio is the fraction of germinated spores that produced pustules. The infection ratio is the fraction of spores (total of germinated and ungerminated) that produced pustules. The infection ratio is the product of germination ratio times colonization ratio.

The differences between upper and lower leaf surfaces in spore deposit, germination ratio, colonization ratio, and infection ratio are considered to be insignificant. The first pustules opened on day 6 or 7, according to the treatment, and the process of opening of the primary pustules was completed on day 9 or 10 (Table 3). Other experiments, under slightly different conditions, showed somewhat more variation. Pustule size was clearly related to pustule density (Fig. 2).

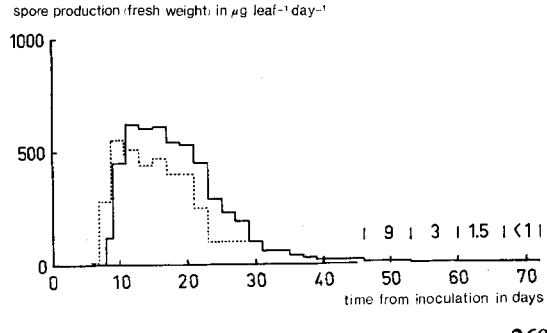

Fig. 1. Uredospore production by *Puccinia recondita* f. sp. *triticina* on primary leaves of the susceptible wheat cv. 'Rubis'.
.... Experiment 1
—— Experiment 2
Figures at the tail end of the drawn line are uredospore productions in µg per leaf per day.

Fig. 1. Uredosporenproduktie door P. recondita f. sp. triticina op kiembladeren van het vatbare tarwe cv. 'Rubis'. Proeven 1 en 2.

Table 2. Spore deposit, spore germination and pustule formation of *Puccinia recondita* f. sp. *triticina* on primary leaves of the susceptible wheat cv. 'Rubis': Experiment 3, explanation in text.

Treatment	Leaf surface	Spores[1] per cm²	Spores per leaf	Germinated spores per leaf	Pustules[2] per leaf	Germination ratio	Colonization ratio	Infection ratio
A	upper	1854	7972 ± 267[3]	6814 ± 89	895 ± 49	0.85	0.13	0.11
	lower	1549	6661 ± 356[3]	5566 ± 356	1022 ± 119	0.84	0.18	0.15
	total	3403	14633 ± 442[4]	12380 ± 341	1917 ± 129	0.85	0.15	0.13
B	upper	681	2928 ± 623	2423 ± 445	809 ± 86	0.83	0.33	0.28
	lower	673	2894 ± 534	2432 ± 267	658 ± 85	0.84	0.27	0.23
	total	1354	5822 ± 842	4855 ± 501	1468 ± 121	0.83	0.30	0.25
C	upper	397	1707 ± 178	1365 ± 116	482 ± 50	0.80	0.35	0.28
	lower	432	1858 ± 178	1443 ± 89	437 ± 75	0.78	0.30	0.23
	total	829	3565 ± 286	2808 ± 117	920 ± 90	0.80	0.33	0.26
D	upper	211	907 ± 36	642 ± 45	152 ± 47	0.71	0.24	0.17
	lower	204	877 ± 9	671 ± 27	153 ± 61	0.76	0.23	0.17
	total	415	1784 ± 39	1313 ± 48	305 ± 67	0.73	0.23	0.17

[1] Total number of spores examined 14,508.
[2] Total number of pustules counted 18,436.
[3] Variation is indicated by the standard error of the mean.
[4] Variation is indicated by the standard error of the sum of the mean values of upper and lower surfaces.
Tabel 2. Sporendepot, sporenkieming en uredosporenhoopjesvorming van P. recondita f. sp. triticina op kiembladeren van het vatbare tarwe cv. 'Rubis'; verklaring in de tekst.

Weight of spores produced Spore production in mg per leaf per day is represented in Fig. 1 and 3. At first, sporulation increased rapidly due to both an increase in the number of open pustules per leaf and to an increase in the number of spores produced per pustule. Maximum sporulation was found on day 9 to 13, according to pustule density. Eyal and Peterson obtained maximum sporulation from day 13 to 14, under comparable conditions. Sporulation continued up to 60 days in Experiment 3 and up to 72 days in Experiment 2.

In Treatments A, B, and C of Experiment 3 maximum sporulation was followed by a sharp but temporary decrease in sporulation. This decrease, which was not observed in Treatment D nor in the other experiments, cannot be explained.

Spore production per pustule The spore production per pustule can be calculated from the fresh weight of spores per leaf, the number of pustules per leaf, and the conversion factor (Fig. 4).

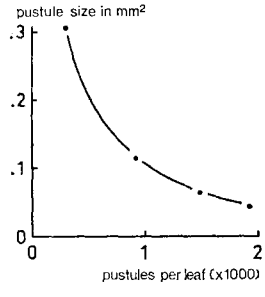

Fig. 2. Relation between pustule size and pustule density in *Puccinia recondita* f. sp. *triticina* on primary leaves of the susceptible wheat cv. 'Rubis'; Experiment 3. Pustule size is the average per pustule per treatment of actively sporulating pustule area.

Fig. 2. Verband tussen grootte en dichtheid van uredosporenhoopjes bij P. recondita f. sp. triticina op kiembladeren van het vatbare tarwe cv. 'Rubis'.

Table 3. *Puccinia recondita* f. sp. *triticina* on primary leaves of the susceptible wheat cv. 'Rubis'. Percentage of open pustules on successive days after inoculation, averaged over four randomly chosen leaves: Experiment 3.

Treatment	Leaf surface	Percentage of open pustules					Average number of pustules per leaf
		day 6	day 7	day 8	day 9	day 10	day 10
A	upper	0.48	7.50	93.2	100	–	895
	lower	0.42	5.40	91.4	100	–	1022
	total	0.44	6.40	92.3	100	–	1917
B	upper	0.59	3.61	91.4	100	–	809
	lower	0.49	3.23	84.7	99.9	100	658
	total	0.54	3.44	88.3	99.9	100	1468
C	upper	0.41	3.63	86.5	100	–	482
	lower	0.11	4.06	82.7	100	–	437
	total	0.26	3.84	84.6	100	–	920
D	upper	0	1.51	66.5	91.5	100	152
	lower	0	0.98	49.6	93.1	100	153
	total	0	1.20	58.0	92.3	100	305

Tabel 3. P. recondita f. sp. triticina op kiembladeren van het vatbare tarwe cv. 'Rubis'. Percentage open uredosporenhoopjes op opeenvolgende dagen na inoculatie.

The highest sporulation per pustule per day was found in Experiment 3, Treatment D; 854 μg spores per leaf per day were produced by 305 pustules, or 2.8 μg (ca. 767 spores) per pustule per day. Eyal and Peterson found 4 μg per infection site per day under comparable conditions (day: 14 hours at 16.5 °C and 2600 ft-c, night: 10 h at 16.5 °C). Chester (1946: p. 62) stated that a well developed pustule could, for a while, produce a 2000 spores per day. With *Uromyces phaseoli* Yarwood found a maximum sporulation of about 2000 spores per pustule per day at a comparable pustule density (50 to 100 pustules per cm^2).

Total spore production. The total fresh weight of all spores produced per leaf per sporulation period is given in Table 4. The dry weight/fresh weight ratio of five different spore batches averaged 0.88 (range 0.81 to 0.93). Assuming that this ratio

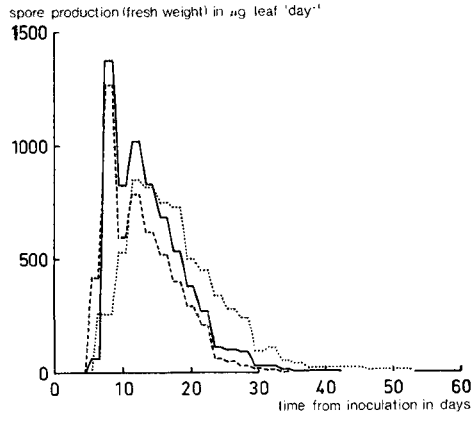

Fig. 3. Uredospore production by *Puccinia recondita* f. sp. *triticina* on primary leaves of the susceptible wheat cv. 'Rubis'; Experiment 3.
---- Treatment A, 1917 pustules per leaf.
—— Treatment C, 920 pustules per leaf.
.... Treatment D, 305 pustules per leaf.

Fig. 3. Uredosporenproduktie door P. recondita f. sp. triticina op kiembladeren van het vatbare tarwe cv. 'Rubis', Proef 3 – Sporenproduktie per blad per dag.

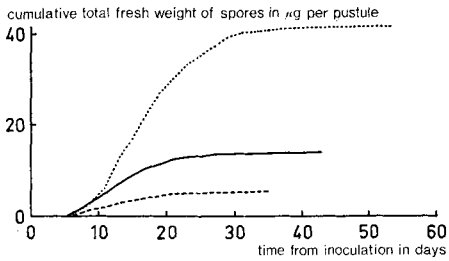

Fig. 4. Uredospore production by *Puccinia recondita* f. sp. *triticina* on primary leaves of the susceptible wheat cv. 'Rubis'; Experiment 3.
---- Treatment A, 1917 pustules per leaf.
—— Treatment C, 920 pustules per leaf.
. . . . Treatment D, 305 pustules per leaf.
For the conversion of fresh weights to numbers the following conversion factor can be used: 1 µg spores coresponds with ca. 274 spores.

Fig. 4. P. recondita f. sp. triticina op kiembladeren van het vatbare tarwe cv. 'Rubis', proef 3. Cumulatieve waarde van de sporenproduktie per sporenhoopje per dag.

was constant throughout the sporulation period, the dry weight of spores produced per leaf per sporulation period was approximately 10 mg. The ratio between the dry weight of the spores produced per leaf (the product) and the dry weight of the leaf (the producer) was about 1 (Table 4).

Table 4. Uredospore production by *Puccinia recondita* f. sp. *triticina* on the primary leaves of the susceptible wheat cv. 'Rubis'. Comparison between the dry weights of the product (estimated dry weight of all spores produced per leaf and per sporulation period) and the producer (dry weight per leaf at time of inoculation): Experiment 3.

Treatments	Fresh weight of all spores per leaf and per sporulation period in mg	Estimated dry weight of all spores per leaf sporulation period in mg	Average dry weight per leaf on day of inoculation in mg	Ratio product/ producer
		product	producer	
A	10.4	9.2	10.2	0.90
B	11.4	10.0	10.2	0.98
C	12.8	11.3	10.2	1.10
D	12.6	11.1	10.2	1.09

Tabel 4. Uredosporenproduktie door P. recondita f. sp. triticina op kiembladeren van het vatbare tarwe cv. 'Rubis'. Vergelijking van het drooggewicht van het produkt (drooggewicht der sporen geproduceerd per blad en per sporulatieperiode) met dat van de producent (drooggewicht per blad ten tijde van de inoculatie).

Secondary pustule formation. About twelve days after inoculation the first outbreak of pustules was completed. These pustules, which were scattered at random, are called primary pustules. When pustule density is not too high secondary pustules appear later (Chester, 1946, p. 62). The secondary pustules are usually organized in rings around the primary pustules, the innermost rings appearing earliest. A maximum number of eight more or less incomplete but concentric rings around a single primary pustule was observed.

Though in one case over 30 secondary pustules have been counted around one primary pustule, only few of the primary pustules produced rings of secondary pustules. In one case the ratio of secondary to primary pustules was about 2 at the end of the sporulation period (Table 5).

Table 5. Production of secondary pustules by *Puccinia recondita* f. sp. *triticina* on primary leaves of the susceptible cv. 'Rubis': Experiment 2.

	Days after inoculation					
	20			60		
pustules	primary	secondary	ratio[1]	primary	secondary	ratio
necrotic area of leaf in %	0	0	–	96	96	–
active pustules per leaf						
upper leaf surface	194	26	.13	8[2]	12	1.5
lower leaf surface	93	8	.08	4	11	2.7
total leaf surface	287	35	.12	11	23	2.1

[1] Number of secondary pustules per leaf divided by number of primary pustules per leaf.
[2] Calculated as the number of primary pustules per leaf on day 20 times fraction of non-necrotic leaf.
Tabel 5. Vorming van secundaire uredosporenhoopjes op kiembladeren van het vatbare tarwe cv. 'Rubis' door P. recondita f. sp. triticina.

In treatment D, the sporulation of the primary pustules ceased after 40 days, whereas formation of secondary pustules continued. The sporulation measured after day 40 was mainly due to the secondary pustules.

Host injury. Necrosis was first observed on day 15; the necrotic leaf area increased according to a sigmoid curve (Fig. 5). At high pustule density necrosis started earlier and extended faster than at low densities.

Infectivity of the spores produced. The results of an infectivity test of spores from Experiment 3, Treatments A and D, are given in Table 6. The germination ratio was normal but the germination ratio of spores from Treatment D was higher than of those from Treatment A. The colonization ratio and infection ratio in the infectivity experiments were unexpectedly high. There was no convincing evidence that infectivity decreased with time, though the colonization and infection ratios of day 30 were low. At this time the primary pustules were nearly exhausted.

Fig. 5. *Puccinia recondita* f. sp. *tricticina* on primary leaves of the susceptible wheat cv. 'Rubis'; opening of uredopustules, and host injury (necrosis) of rusted leaves; Experiment 3. The ordinate gives in the left hand pair of curves: open uredopustules as a percentage of total number of pustules, and in the right hand curves: necrotic leaf area as a percent age of total leaf area.
---- Treatment A, 1917 pustules per leaf.
—— Treatment C, 920 pustules per leaf.
. . . . Treatment D, 305 pustules per leaf.
.-.-. Healthy leaves.

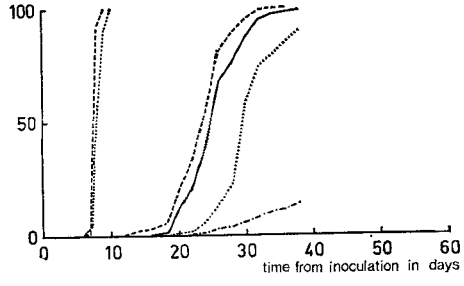

Fig. 5. P. recondita f. sp. triticina op kiembladeren van het vatbare tarwe cv. 'Rubis'. Links: opening van de uredosporenhoopjes. Rechts: necrose.

Table 6. Infectivity of the spores from Treatments A and D sampled on various days after inoculation: Experiment 3. Explanation in text.

Day after inoculation	Treatment	Spores per leaf[1]	Germinated spores per leaf[1]	Pustules per leaf[1]	Germination ratio	Colonization ratio	Infection ratio
10	A	3280	2688	1941	0.81	0.72	0.59
	D	2114	1825	1826	0.86	1.0	0.86
20	A	753	583	457	0.77	0.78	0.60
	D	1390	1241	1150	0.89	0.92	0.82
30	A	336	243	104	0.72	0.42	0.30
	D	649	560	189	0.86	0.33	0.29
46	D	573	503	321	0.87	0.63	0.56
53	D	–	–	65	–	–	–

[1] Entries are sums of counts from upper and lower leaf surfaces.

Tabel 6. Infektiositeit van de uredosporen van de Behandelingen A en D op diverse dagen na inoculatie. Verklaring in de tekst

Discussion

The sporulation pattern was similar in all experiments. The latent period, which is the period in days from inoculation to the opening of the first pustule, varied between six and nine days, according to pustule density and minor variations in environmental conditions. All the pustules do not open simultaneously. The number of opening pustules per day is low at first, increases rapidly, and then declines. Plotting of the total number or percentage of open pustules against time yields a typical sigmoid curve (Fig. 5) with a steep slope. The rate of pustule opening under near-optimal conditions shows a variation which depends on pustule density and minor differences in environmental conditions.

The amount of spores produced per day increases rapidly when the pustules open. Spore production reaches its maximum soon after its beginning and then gradually decreases. Sometimes spore production very gradually tapers off; in one case spores produced on day 72 could still be seen but could no longer be weighed. The general shape of the spore production curve, an asymmetrical dome shape, is the same as those found by Yarwood (1961) in *Uromyces phaseoli* and by Eyal and Peterson (1967) in *P. recondita*. In detail the shape of the spore production curve depends on environmental conditions and on pustule density. The dip in the curves of Fig. 3 may be an artefact. There is strong suspicion that the low values of the daily spore production have been underestimated because of the relative inefficiency of the cyclone collector at low spore amounts (Mehta and Zadoks, in prep.); therefore the sporulation figures presented are considered to be conservative estimates.

A high spore deposit leads to high pustule density. High pustule density causes a short latent period, a high rate of pustule opening, a steep increase of daily spore production, an early and high maximum of daily spore production, a relatively rapid decrease of daily spore production and a relatively short sporulation period.

Total spore production seems to be relatively independent of inoculum density and pustule density. This agrees with the far more elaborate data presented by

Yarwood (1961). Apparently, the main limiting factor is the photosynthetic apparatus. This hypothesis is confirmed by the observation that sporulation is more profuse when the second leaf is not cut away.

The leaf produced about its own dry weight in spores; this can also be calculated in the cases of *Uromyces appendiculatus* (= *U. phaseoli*) (data of Yarwood, 1961) and of *Puccinia striiformis* (Zadoks, unpubl.). The dry weight of an infected leaf roughly equals that of a healthy leaf of the same age. A drastic redistribution of the assimilates must have taken place in the infected plant. Indeed, the roots of infected plants had a lower dry weight than those of the uninoculated controls (Table 7); this is in accordance with data obtained a.o. by Martin and Hendrix (1967) using *P. striiformis*.

Table 7. The effect of *Puccinia recondita* f. sp. *triticina* on root development measured 40 days after inoculation. The rust was grown on the primary leaves of the susceptible wheat cv. 'Rubis'. Root length and root weight are slightly underestimated because not all smallest rootlets could be isolated from the pot soil. Experiment 3.

Treatment	Number of plants examined	Average maximum root length per plant in cm	Average dry weight of roots per plant in mg
Uninoculated	27	24.4	15.3
Treatment A	43	17.6	5.9

Tabel 7. Het effekt van P. recondita f. sp. triticina op de wortelontwikkeling gemeten 40 dagen na inoculatie. De roest groeide op kiembladeren van het vatbare tarwe cv. 'Rubis'.

The main purpose of this investigation was the sporulation period, which is the period during which an infected leaf produces a demonstrable amount of spores. Unfortunately the end of the sporulation period cannot be determined with great accuracy because of the asymptotic nature of the sporulation curve. At low pustule densities and near-optimal conditions for the rust the sporulation period was shown to exceed two months (65 days in Fig 1). This long sporulation period, according to the authors, must be interpreted as a survival mechanism. This interpretation is supported by model studies of epidemics (Zadoks, 1970). It is interesting to note that in this experiment spore infectivity decreased at the time when the primary pustules were nearly exhausted; however, infectivity was satisfactory up to 46 days.

It is not known whether sporulation periods of over two months also occur in nature under conditions favourable to the rust. A long sporulation period would enable the fungus to survive when the chances of infection are temporatily low, e.g. during the summer when there are only few wheat plants available as a host or when the meteorological conditions are unfavourable to infection. In the Netherlands, one or two rings of secondary pustules are frequently observed in the field on spring sown winter wheat during the summer and on volunteer wheat in early autumn.

Acknowledgments

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Samenvatting

Uredosporenproduktie en sporulatieperiode van Puccinia recondita f. sp. triticina op kiembladeren van tarwe

De uredosporenproduktie per dag en per sporulatieperiode werd bepaald onder voor de roest vrijwel optimale milieuomstandigheden (Tabel 1). De proeven werden gedaan met herkomst 1035 van het Felix-fysio van de bruine roest. Na twee inleidende proeven werden in Experiment 3 vier inoculatiedichtheden (A, B, C en D) onderling vergeleken (Tabel 2). Uit deze inoculatiedichtheden (aantal sporen per blad) resulteerden verschillende aantallen sporenhoopjes per blad (sporenhoopjesdichtheid). Hoge sporenhoopjesdichtheid bekort de latente periode (tijd in dagen van de inoculatie tot de opening van het eerste sporenhoopje), vergroot de snelheid van het openen der sporenhoopjes (Tabel 3), doet kleinere sporenhoopjes ontstaan (Fig. 2), veroorzaakt een snellere toename van de sporenproduktie per dag met een hoger maximum (Fig. 3), maar versnelt ook de geleidelijke afname van de dagelijkse sporenproduktie, het afsterven van het blad (Fig. 5) en bekort de sporulatieperiode (periode in dagen gedurende welke aantoonbare sporenproduktie plaatsvindt, Fig. 4). Binnen zekere grenzen is de totale hoeveelheid sporen per blad en per sporulatieperiode onafhankelijk van de sporenhoopjesdichtheid (Tabel 4). Het totale drooggewicht van de sporen per blad en per sporulatieperiode (produkt) is ongeveer gelijk aan het drooggewicht van het gezonde blad ten tijde van de inoculatie (producent). Bij lage sporenhoopjesdichtheden worden de primaire sporenhoopjes door secundaire sporenhoopjes vervangen. De infectiositeit der sporen bleef normaal tot ten minste 46 dagen na inoculatie (Tabel 6). De sporulatieperiode kan langer dan twee maanden duren; de hoogst waargenomen waarde is 65 dagen (Fig. 1). Een dergelijke lange sporulatieperiode wordt aangeduid als een overlevingsmechanisme; de vorming van secundaire sporenhoopjes wordt gezien als een wezenlijk bestanddeel van dit mechanisme.

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