Neth. J. Pl. Path. 92 (1986) 57-69

Postponed germination of Puccinia recondita urediospores deposited on wheat seedlings. I. Ripening and longevity of urediospores with postponed germination

J.C. ZADOKS and E.M. VAN HEES-BOUKEMA

Laboratory of Phytopathology, Binnenhaven 9, 6709 PD Wageningen, the Netherlands

Accepted 25 October 1985

Abstract

Urediospores of *Puccinia recondita* f.sp. *tritici* were applied to wheat seedlings. Inoculated plants were placed in a growth chamber to expose the spores to dry periods from zero to nine days at near-optimal temperatures. The dry period was followed by a wet period varying from 2 to 24 hours for spore germination. Results were subjected to analysis of variance. The effects of dry period, wet period, and temperature on germination were highly significant. The dry period × wet period interaction was significant at $P < 0.1$. The interaction implies that germinability of spores increased (ripening) or decreased (dying) according to the conditions. Post-detachment ripening of urediospores of *P. recondita* is a real but erratic phenomenon, which is difficult to predict. The magnitude of the ripening phenomenon varied considerably, but on average it was small. Longevity of urediospores on dry wheat leaves at near-optimal temperatures was at least nine days. The epidemiological relevance of these indoor results is discussed.

Additional keywords: brown rust, germinability, infectivity, maturation.

Introduction

Wheat infected by brown rust *(Puccinia recondita* Rob. ex Desm. f.sp. *tritici)* can produce large amounts of urediospores which are deposited in part on wheat leaves. Sometimes, such deposits can be seen with the naked eye. In the absence of free water these urediospores may lie idle. But for how long? How fast do they loose their germinability and infectivity? How well is the brown rust adapted to such occasional idleness? If the absence of free water causes a delay of germination, what are the epidemiological effects of postponed germination? The phenomenon of postponed germination was studied in growth chambers, using fresh urediospores deposited on primary leaves of wheat seedlings.

Material and methods

Experimental conditions. The experiments (Table 1) are indicated by a two-digit code, of which the first digit refers to the experimenter and the second digit to the serial number of the experiment. Conditions in the walk-in growth chamber are indicated in Table 1. Light came from fluorescent tubes (Philips TL-F, 40 W, colour 33). The

Table 1. General information on the spore germination experiments.

A[1]	B	C	D	E	F	G	H	I	J
1.1	1037	Flamingo	16	16[2]	20	90	[3]	—	13649
2.2	1034	Flamingo	2 × 15	20[2]	20	88	12	—	49071
3.1	C	Felix	2 × 10	11.3	18	65	6.1	0.18	18323
3.2	C	Felix	2 × 7	7.9	15	72	6.6	0.09	8096
					18	65	6.1		9740
					20	87	5.8		9828

[1] A = Experiment code number: B = Registration code of isolate; C = Cultivar to which isolate is specifically virulent; D = Spores applied in mg; E = Spore deposit in spores mm^{-2}; F = Temperature in °C during the dry period DP; G = relative humidity in % during dry period DP; H = Light intensity in klux during dry period DP; I = Coefficient of variation for residuals in ANOVA of GTR; J = Total number of spores considered.
[2] Counts on vaselined slides.
[3] 40 W m^{-2}.

light intensity at soil level was about 6 klux, as measured by a flat lux meter. Day length was 16 h. Material and methods were approximately equal in all three experiments; those described here refer to Experiment 3.

Plants. Seeds of the winter wheat cv. Rubis were sown in square pots (5×5×5 cm) with steamed pot soil at a rate of 8 to 12 plants per pot. Per pot 15 ml of chlormequat (diluted with water to 0.5 % v/v) was added to keep plants short. Plants were grown at 15, 18 or 20 °C, according to the postinoculation test temperatures, up to inoculation which was performed at development stage DC 1.1 (Zadoks et al., 1974). Before inoculation, plants were thinned so that six good and equal plants per pot remained.

Urediospores had been stored in liquid nitrogen. For inoculation, fresh spores were grown on cv. Rubis at 18 °C and 65 % RH. One day before inoculation, ripe and old spores were blown off the sporulating leaves by means of a cyclone collector and compressed air. Twenty four hours later, recently formed spores were collected using the same cyclone collector attached to a vacuum pump (Mehta and Zadoks, 1971).

Inoculation. Wheat seedlings were inoculated in a settling tower, into which the spores were shot by means of a CO_2 gun. Spores were allowed to sediment for five minutes onto the seedling leaves which had been placed in a horizontal position. Between two shots, each with half of the spore lot, the leaves were inverted. The uniformity of the spore deposit was checked by exposing vaselined microscope slides among the leaves.

Dry period. Postponement of germination was obtained by exposing the inoculated plants to the current growth chamber environment(s) (see above and Table 1) during a varying number of days. The period of delay, called dry period (DP), is measured in days. The shortest dry period was 0 days, which means that inoculated leaves were exposed to leaf wetness immediately after inoculation. The longest dry period was nine days.

Wet period. Following the dry period, leaf wetness was applied for germination of the spores. The duration of the leaf wetness period, here called wet period (WP), was measured in hours. It varied from 2 to 24 hours. The 24 hours values were used as a reference, as after 24 hours at near-optimal temperatures no further germination can be expected. Leaf wetness was obtained by placing the pots with inoculated plants in improvised dew chambers, one for each pot, after spraying them lightly with tap water. Leaf wetness was applied at current growth chamber temperatures.

Spore germination. Following the wet period, spore germination was determined. From two leaves per pot some 2 cm length was sampled by means of collodion strips. The strips were mounted in lactophenol with cotton blue and examined under the microscope at 80 or 100 × magnification. Spores were considered germinated when the germ tube length surpassed the smallest spore diameter. Per strip at least 10 views of 1.25 mm were examined. The numbers of germinated and ungerminated spores, and sometimes the numbers of stomata, per view were determined. The results are expressed as the fraction of germinated spores relative to the total number of spores (GTR according to Zadoks and Schein, 1979). Subscripts of GTR refer to the duration of the wet period in hours (i = variable; m = mean).

Statistical considerations. In view of the wet period treatment, in which each pot was treated individually and – maybe – differently, the pot was used as the basic statistical unit. Data collected at sub-pot level (plant, view) were compacted into one statistic per pot. Standard techniques for the analysis of variance (ANOVA) were applied. Experiment 3.2 was handled as a split plot experiment, with temperatures as plots and dry period * wet period combinations as sub-plots.

Results

Only Experiment 3.2 is discussed in detail, as the other experiments followed the same pattern.

Spore deposit. The regularity of the spore deposit in the settling tower was checked in Experiment 3.2. As only 20 pots could be handled at a time, the inoculation had to be repeated 11 times with two shots per inoculation. Spores per microscope view were counted and averaged per shot for two positions in the settling area. The main effects of inoculation and position were significant at $P < 0.1$. The mean deposit was 7.9 spores per mm^2. The coefficient of variation of the experiment was 0.08.

Wet period duration. The increase of GTR with time follows a sigmoid curve (Mehta and Zadoks, 1970). With brown rust of wheat at near-optimal temperature, germination begins after one or two hours of leaf wetness and germination is nearly completed after 6 to 8 hours. The results of the present experiments (Fig. 1) were in accordance with these facts. The terminal germination (GTR_{24}), varied from 0.65 to 0.85. The effect of the wet period on germination was highly significant in Experiments 3.1 and 3.2 (Tables 1 to 4).

Dry period duration. Fig. 2 gives an overview of all experiments for GTR_{24} after dry

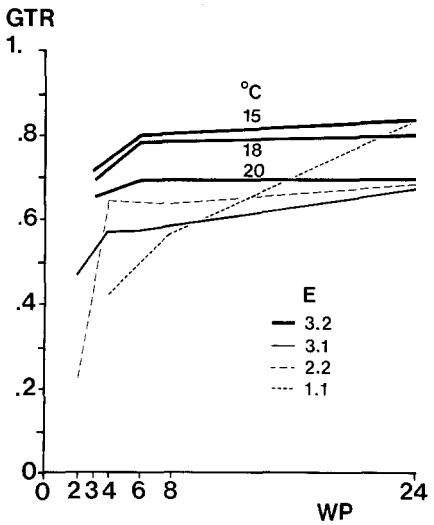

Fig. 1. Summary of all experiments. Germination (GTR) is plotted versus wet period (WP) duration. For every WP, GTR was averaged over all available dry periods. E = experiment number. Spore germination temperature of E 1.1 = 20 °C, of E 2.2 = 20 °C and of E 3.1 = 18 °C.

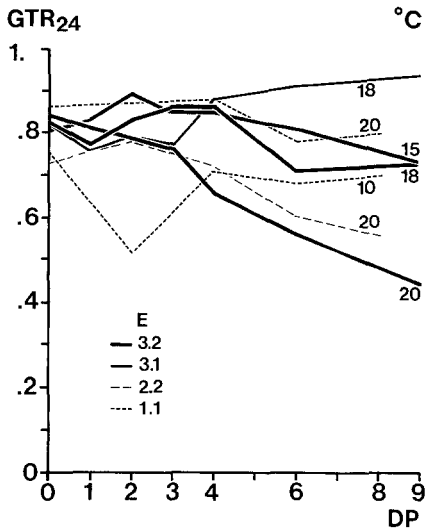

Fig. 2. Summary over all experiments. Terminal germination (GTR_{24}) is plotted against dry period (DP) duration. E = experiment number. For E 1.1 the 10 °C line is added.

periods of varying durations. The quality of the spores used was satisfactory, as indicated by a GTR_{24} of about 0.8 at DP = 0. The results varied according to experiments. A slight and usually temporary increase in GTR_{24} can be seen at 15 and 18 °C. At 20 °C, a more or less regular and strong decrease of GTR_{24} with increasing DP was the rule.

Fig. 3 gives the same information as Fig. 2, but now GTR is averaged over all available leaf wetness periods (GTR_m). The general tendency of the curves in Fig. 3 is the same as in Fig. 2, but the differences between experiments become more pronounced. At 15 °C there was a minor and temporary increase in GTR_m. At 18 °C the temporary increase at DP = 2 was pronounced in one experiment, whereas in another experiment there was a continuous increase of GTR_m over the whole range of dry periods. At 20 °C, all GTR_m curves show an initial increase and a later decrease with increasing DP. The position of the maximum GTR_m at 20 °C varied according to the experiment from one to four days DP. Whereas in Experiment 1.1 the increase of GTR_m was most conspicuous, Experiment 3.2 predominantly showed a decrease of GTR_m. In Experiment 2.2 GTR had an intermediate position. The effect of dry period was highly significant in Experiment 3.1 (Tables 2 and 3) and Experiment 3.2 (Tables 4 and 5).

Interaction between dry period and wet period. More information is obtained when data are plotted according to leaf wetness period. Experiment 3.1 (Fig. 4) shows that the increase of GTR_i with DP was more pronounced when WP was shorter. Except for an unexplained anomaly at the dry periods of 0 and/or 1 day, there was no decrease in GTR_i over the whole range of dry periods.

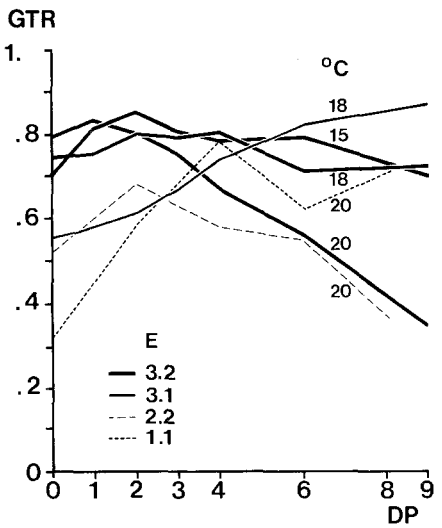

Fig. 3. Summary over all experiments. Mean germination (GTR) is plotted against dry period (DP) duration. For every DP, GTR was averaged over all available wet periods. E = experiment number.

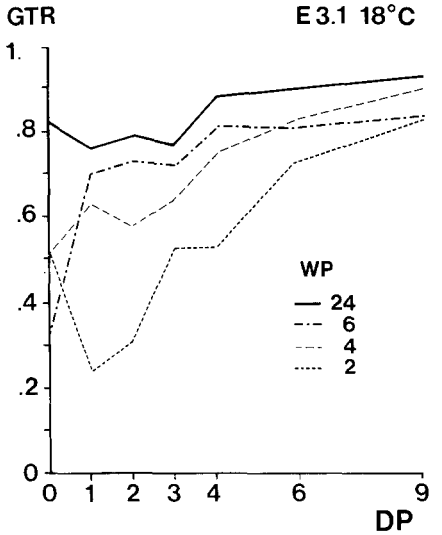

Fig. 4. Experiment 3.1. Germination (GTR) plotted against dry period (DP) duration for different wet periods (WP).

Table 2. Experiment 3.1. Germination fractions (GTR, multiplied by 100).

DP[1]	WP[1]				Mean
	2	4	6	24	
0	54	51	32	82	55 a[2]
1	24	63	70	76	58 a
2	31	58	73	79	61 a
3	53	64	72	77	67 ab
4	53	75	81	88	74 b
6	73	83	81	91	82 bc
9	83	90	84	93	87 c
Mean	53	69	71	84	—
	p	q	q	r	

[1] Dry period (DP) in days, wet period (WP) in hours.

[2] Means of rows and columns characterized by the same letter do not differ significantly according to Duncan's test at $P = 0.05$. Critical difference for row means = 12.7, for column means 8.9 at $P = 0.05$.

Table 3. Data from Table 2, analysis of variance.

Effect	Sum of squares	Degrees of freedom	Mean square	F	*P*
Level	400559	1			
Main effects					
dry period	11049	6	1842	11.8	< 0.005
wet period	9967	3	3322	21.2	< 0.005
Interaction					
dry × wet	6550	18	364	2.3	0.05
Residual	8765	56	156		
Total	436891	84			

Table 4. Experiment 3.2. Germination fractions (GTR, multiplied by 100).

DP[1]	WP[1]			T[1]			Mean
	3	6	24	15	18	20	
0	69	72	82	70 a[2]	74 ab	79 de	74
1	74	83	81	81 b	75 ab	83 e	79
2	78	82	84	85 b	80 b	80 de	82
3	72	80	82	80 b	79 b	75 d	78
4	68	78	79	78 b	80 b	67 c	75
6	63	74	69	79 b	71 a	56 b	69
9	53	59	64	70 a	72 a	35 a	59
Mean	68	76	77	78	76	68	74

T[1]	WP[1]			Mean
	3	6	24	
15	71 a[2]	79 b	83 c	78
18	69 a	78 b	80 b	76
20	65 a	69 b	69 b	68
Mean	68	76	77	74

[1] Dry period (DP) in days, wet period (WP) in hours, temperature (T) in centigrades.
[2] Values within columns (upper table) or within rows (lower table) characterized by the same letter do not differ significantly according to Duncan's test at $P = 0.05$.

Table 5. Experiment 3.2. Analysis of variance of germination fractions (GTR).

Effect[1]	Sum of squares	Df	Mean square	F	*P*
Level	1028964	1			
Main effects					
T = Temperature	3335	2	1668	42	< 0.005
DP = Dry period	9602	6	1600	40	< 0.005
WP = Wet period	2782	2	1391	35	< 0.005
1-way interactions					
T × DP	8604	12	717	18	< 0.05
T × WP	331	4	83	2	0.1
DP × WP	761	12	63	1.6	0.1
2-way interaction					
T × DP × WP	994	24	41	1.0	> 0.1
Residual	5016	126	40		
Total	1060389	1899			

[1] Note that the ANOVA table presents data as if treatments were completely randomized; in fact, the experimental design was a double split plot design with temperature as blocks, dry period as plots and wet periods as sub-plots. The coefficient of variation of residuals is 40/7379 = 0.09.

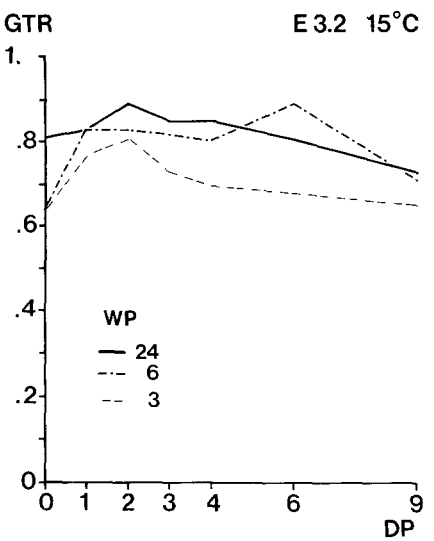

Fig. 5. Experiment 3.2, 15 °C. Germination (GTR) plotted against dry period (DP) duration for different wet periods (WP).

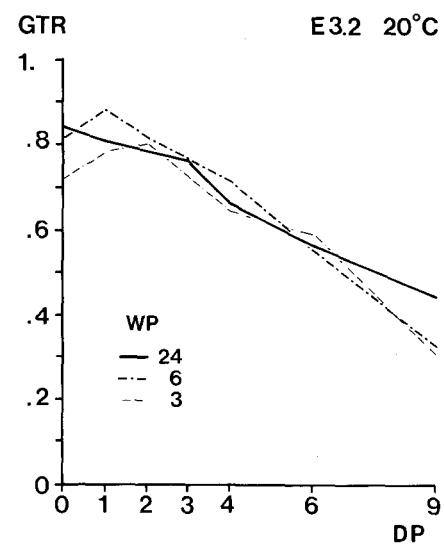

Fig. 6. Experiment 3.2, 20 °C. Germination (GTR) plotted against dry period (DP) duration for different wet periods (WP).

The results of Experiment 3.2 at 15 °C (Fig. 5) approximate those of 18 °C, but each of the three curves seemed to have an optimum. The optimum was most pronounced at DP = 2. At 20 °C (Experiment 3.2, Fig. 6) GTR_i generally decreased with DP, but at short WP's there seemed to be an optimum at a dry period of one or two days.

The interaction was highly significant in Experiment 3.1 (Table 3) but it depended largely on the anomaly mentioned above. If DP = 0 was omitted from the analysis, the interaction was significant at $P < 0.1$, as in Experiment 3.2.

Temperature. In Experiment 3.2 the dry period effect was tested at three near-optimal temperatures, viz. 15, 18 and 20 °C. To avoid temperature shocks, the plants had been grown at the same temperatures before inoculation. The effect of temperature was highly significant (Table 5), as was the interaction between temperature and dry period. When the effect of temperature was tested against this interaction, it was significant again. The interaction between temperature and wet period was significant only at $P = 0.1$.

Discussion

Leaf wetness period. The effect of the wet period on germination was as usual. As it was not the objective of this study it wil not be discussed here.

Variability of results. Spore germination studies are notoriously difficult because of their poor reproducibility. They can only be successful when large numbers of spores are counted, and when experiments are repeated several times. Sharp et al. (1958) observed at least 900 urediospores per treatment in a study of *Puccinia graminis.* Sharp (1965) observed about 3000 urediospores of *P. striiformis* per treatment. Similar numbers were used in the present study (Table 1), and experiments were repeated by different persons in different years.

The present study emphasizes once more the problem of reproducibility, even when large spore numbers are used. The coefficients of variation of the residual effect in the ANOVA's (Table 1) confirm this statement; they are relatively high. The reasons are unknown. The differences in situational factors (Zadoks and Schein, 1979) between experiments do not explain the differences in germination behaviour between experiments. Sharp (1967) pointed to variation in heavy ion content of the air as one cause of poor reproducibility in urediospore germination studies with *P. striiformis,* but similar information for *P. recondita* is not available. Several authors point to the conditions under which the spores were formed, the age and condition of the host plant, and the age of the uredinia as a cause of variation (Chester, 1946; Lehmann et al., 1937; Melhus and Durrell, 1919; Schaffnit, 1909; Sharp, 1965; Sussmann and Halvorson, 1966); these factors were reasonably standardized in the present experiments. For the present time, poor reproducibility in urediospore germination studies has to be accepted.

The homogeneous spore sample. De Weille (1961, 1963) strongly emphasized the necessity to produce a homogeneous spore sample, that is a spore sample with spores all of the same age, as a prerequisite for spore germination studies. In the Experiments 3.1 and 3.2, all spores were formed within a 24 hour period. As spore collection by cy-

clone is a rough method, a certain amount of incompletely ripened spores may have been incorporated in the spore sample. Notwithstanding this objection, the spore samples used were considered to comply with De Weille's requirement of homogeneity.

Decline of germinability. Germinative capacity, germinative power (De Weille, 1961, 1963, 1964) or germinability is the capacity to germinate. In the experiments discussed above, germinability of urediospores obviously declines gradually at 20 °C, which is a supra-optimal temperature for *P. recondita.* At sub-optimal temperature (15 °C) and near-optimal temperature (18 °C) the decline is negligible for one week or more. Apparently, the germinability of healthy urediospores is conserved when they are situated on wheat leaves at (sub-)optimal temperatures. The spores were exposed to a relatively dry atmosphere, but the drying effect of the air may have been moderated due to the water vapour produced by evapotranspiration of the leaves. Wind speed in the growth chambers was 0.5 m s^{-1} on average; it must have been far less at the leaf surface, where the spores were situated. The light intensity was modest (about 6 klux); it may have contributed to the conservation of germinability as it is known that light, even at relatively low intensities, inhibits urediospore germination in *P. recondita* (Zadoks, 1967; Zadoks and Groenewegen, 1967). The effect of heat radiation concurrent with light radiation was minimized by using fluorescent tubes and by maintaining a minimum distance of 10 cm between inoculated leaves and lamps. Temperature seems to be the major factor in the decline of germinability over the period studied. If an extrapolation of the curves of Fig. 2 is allowed, at least some germinable spores remain on the wheat leaves after a fortnight at 20 °C. Within the temperature range of 15 to 20 °C, the minimum survival period seems to be 14 days. This result agrees with that of Eversmeyer and Burleigh (1968).

Increase of germinability. Far more interesting than its decline is the increase of germinability found repeatedly. At 15 °C, germinability increased during the first two days of the dry period. In Experiment 3.2 (Fig. 5) this increase was small but significant. At 18 °C, the increase in germinability was pronounced in Experiment 3.1, but negligible in Experiment 3.2. At 20 °C, the increase of germinability was very pronounced in Experiment 1.1, small and hardly significant in Experiment 3.2, and intermediate in Experiment 2.2. The shorter the leaf wetness period was, the more pronounced the increase in germinability was. This interaction between wet period and dry period was consistent throughout the experiments. It was most obvious in Experiments 1.1 and 2.2 at 20 °C and in Experiment 3.1. at 18 °C. The interaction lead to a typical optimum curve in Experiment 2.2 only.

Spore ripening. Sussman and Halvorson (1966) defined 'maturation', here equated to 'ripening', as 'the complex of changes associated with... the germinable stage...'. To them, spore detachment was not a criterium. De Weille (1964) stated 'maturation is the phenomenon of the germinative power increasing with time', disregarding the moment of detachment. Arthur (1929, p.219) and Gottlieb (1978), however, considered spores to be 'ripe', that is ready to germinate, when they are 'spontaneously detachable' from their support. De Weille (1961, 1963, 1964), working with peronosporaceous fungi, in a way solved the problem by distinguishing pre-detachment ripening and post-detachment ripening. With urediospores, the moment of detachment is not clear. In

the present experiments, the urediospores having left the uredinia were obviously detached. To detached and displaced urediospores the term after-ripening was applied by Chester (1946, p. 108).

Post-detachment ripening has been reported repeatedly in the literature. De Weille (1961, 1963, 1964) found post-detachment ripening under the influence of UV radiation in *Peronospora arborescens, P. destructor* and *Phytophthora infestans.* Other examples are *Myrothecium verrucaria* (quoted in Gottlieb, 1978), *Puccinia coronata* (Melhus and Durrell, 1919, *Puccinia 'dispersa'* (Marshall Ward, 1903, Table 1), and oospores of *Phytophthora cactorum* (quoted in Gottlieb, 1978). Schaffnit (1909, p. 514) extensively studied urediospore ripening in wheat rusts. He did not equate ripeness of the spore with its detachment from the sporogenous cell. To him, darkness of urediospore colour was correlated with pre-detachment spore ripening. He found no post-detachment ripening of urediospores in *P. graminis* and *P. striiformis,* possibly because he worked at relatively high temperatures. The literature is rather silent on post-detachment urediospore ripening. Several authoritative reviews do not mention it (Allen, 1965; Burnett and Trinci, 1979; Bushnell and Roelfs, 1984; Madelin, 1966; Scott and Chakravorty, 1982; Weber and Hess, 1976).

The present experiments demonstrate the existence of post-detachment spore ripening in *P. recondita.* They also show the erratic behaviour of the penomenon. It seems that spore ripening is induced either way, by short exposure to leaf wetness and/or by prolonged exposure to drought. The experiments do not give a clue as to the physiological or biochemical background of spore ripening. 'In nature, the balance between inhibitors and stimulants probably serves as a regulatory factor in germination' (Allen, 1965). It seems, that some of these regulatory substances can be metabolized during germination (Woodbury and Stahmann, 1970) and, possibly, also during ripening.

Lipid and volatile spore germination inhibitors exist (Allen, 1955, 1965; Woodbury and Stahmann, 1970). Mutual inhibition of urediniospores may be expected at spore densities of 20 spores mm^{-2} or more, densities which were avoided in the present experiments. Self-inhibition of spores cannot be excluded. If so. spore ripening may be due to loss of self-inhibiting substances by metabolization and/or volatilization. Volatilization might proceed rapidly in the presence of free water and slowly without. An alternative hypothesis is that the presence of free water induces germination, a process in which the active and rapid elimination of self-inhibitor(s) is an early step, whereas dry spores passively and slowly loose their self-inhibitor(s).

Hydration of urediniospores improves germinability (Allen, 1965; Sharp, 1965; Sharp et al. 1958; Woodbury and Stahmann, 1970; J.C. Zadoks, unpublished). Small liquid droplets may form around isolated urediniospores by local condensation of water vapour (Woodbury & Stahmann, 1970). No specific observations were made during the experiments reported here. Though the water vapour pressure at the site of the spores on the leaf surface is not known, the authors do not believe that hydration-like processes were involved in the spore ripening during the dry delay of germination.

Decrease of germinability could be due just to death of spores, but this explanation may be too simplistic. Oxidation of the lipid film-forming materials associated with uredospores leads to toxic substances that reduce germination (Woodbury and Stahmann, 1970).

Longevity of urediospores. The longevity of *P. recondita* urediospores can be impressive under artificial conditions (Chester, 1946, p. 115; Hollier, 1985). The results of the present study fall well within the range specified by Eversmeyer and Burleigh (1968). Urediospore survival, expressed as GTR after nine days on dry wheat leaves, was between 0.35 and 0.87 at temperatures from 15 to 20 °C.

Epidemiological relevance of the results. The usual comparisons of spore germination on leaves with spore germination on agar or on glass slides have been omitted, as nature does provide neither agar nor glass as a substrate. Such data are epidemiologically irrelevant. Even so, the question arises whether data on the effects of 'postproduction-pregermination environment' (Hollier, 1985) are epidemiologically relevant. The situational factors of importance to this question are seedlings, near-optimal temperature range, and 'mild' environmental conditions. During an epidemic, we deal with adult plants, temperatures with strong upward and downward deviations from the optimum temperature, and strong radiation.

In the Netherlands, prolonged periods without leaf wetness are rare. Even when there is no rain, at least some dew is present during most nights. A relevant result is that appreciable spore germination does not occur even after two hours of leaf wetness at near-optimal temperatures. Another relevant result probably is that spores may maintain their germinability after deposition on wheat leaves for several days at least, when they are not exposed to leaf wetness nor to extreme environmental conditions. This proviso might be realized in dense crops at the undersides of leaves and at the lower leaf layers. The phenomenon of urediospore ripening is a real one, but its epidemiological relevance cannot be assessed, because it is too erratic.

An indirect assessment could be made by inverting the argument. As long as the urediospores stay within the uredinia, their germination is delayed due to special germination inhibitors. As soon as urediospores are 'turned loose', their germinability increases in a few days when dry and in a few hours when wet.

Samenvatting

Uitgestelde kieming van uredosporen van Puccinia recondita afgezet op tarwekiemplanten. I. Rijping en levensduur van uredosporen met uitgestelde kieming

Uredosporen van de bruine roest van tarwe *(Puccinia recondita* f.sp. *tritici)* werden over het eerste blad van tarwekiemplanten verstoven. De aldus geïnoculeerde planten werden in een klimaatkamer geplaatst bij vrijwel optimale temperatuur gedurende nul tot negen dagen, teneinde de sporen aan een droge periode bloot te stellen. Deze werd gevolgd door een natte periode (met bladnat) variërend van 2 tot 24 uur om de sporen te laten kiemen. De kiemingsresultaten werden onderworpen aan een variantieanalyse. De effecten van droge periode, natte periode en temperatuur op de kieming waren zeer significant. De interactie tussen de droge periode en de natte periode was weinig significant ($P < 0.1$). Deze interactie geeft aan dat de kiemkracht van de sporen stijgt (sporenrijping) of daalt (sporendood) al naar gelang de combinatie van uitwendige omstandigheden. Sporenrijping na losmaking uit het sporenhoopje is bij uredosporen van bruine roest een reëel maar grillig verschijnsel, dat zich moeilijk laat meten en voorspellen. De sporenrijping, uitgedrukt als toename van het kiempercentage,

wisselt maar is meestal niet omvangrijk. De levensduur van uredosporen, droog en bij ongeveer optimale temperatuur bewaard op tarwebladeren, was ten minste negen dagen. De epidemiologische betekenis van deze resultaten, verkregen uit proeven in klimaatkamers, wordt besproken.

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