Neth. J. Pl. Path. 92 (1986) 163-174

Rain-induced dispersal in Puccinia arachidis, studied by means of a rainfall simulator

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Accepted 23 May 1986

Abstract

A rainfall simulator was used on groundnut *(Arachis hypogaea)* plots artificially infected with *Puccinia arachidis* in order to study urediniospore dispersal caused by various amounts of rainfall. Several trapping methods were used to compare dry, splash and drip dispersal caused by rain. The spore liberation mechanisms activated by rain and the flows of spores which they generate can be studied at the infected canopy or at the sporulating lesion scales. Two systems referring to these scales were considered to discuss the results. Dry dispersal seemed preponderant. The spore content of the lesions in the canopy was strongly reduced by rain. The results indicated that light rain showers may promote disease dispersal, whereas it may be hampered by heavy showers.

Additional keywords: spore liberation mechanisms, dry dispersal, splash dispersal, drip dispersal, rainfall intensity, spore trapping methods.

Introduction

Studies on spore dispersal in pathogenic fungi, especially rusts, are described in various environmental conditions by several authors, Ingold (1971), Gregory (1973), Meredith (1973), and Zadoks and Schein (1979). In the case of groundnut rust *(Puccinia arachidis* Speg.), some information is available (Mallaiah and Rao, 1982; Savary, 1986). However, the effects of rain on spore dispersal in *P. arachidis* were not studied yet.

When a groundnut *(Arachis hypogaea* L.) crop infected by rust is hit by a rain shower, several spore dispersal processes may take place in the canopy. The aim of this study is to provide some insight into these processes and to estimate their relative importance, using simulated rainfalls on inoculated plots.

Material and methods

Experimental plots and inoculations. Five square plots (5 m × 5 m) were sown on 11 November, 1984, with a highly susceptible, short-cycle and erect local groundnut cultivar at a density of 150 000 seeds ha^{-1}. When necessary, replacements were made ten days after sowing with seedlings grown in pots to obtain a final density of 150 000 plants ha^{-1}. In the evening of 10 December (at flowering stage), field inoculations were performed by the application of dry *Puccinia arachidis* urediniospores mixed with kaolin (Savary, 1985a). Hundred mg of such a mixture, containing 380 spores mg^{-1}, were powdered on each plot to be inoculated. Fifteen plants at the center of each plot were inoculated and immediately covered by a small (1.0 × 1.0 × 0.3 m) plastic tent which was removed early in the following morning.

Rust assessment. Three plants were selected at random from the inoculated and from the non-inoculated plants in each of the five plots (thirty plants in total). They were rated for rust intensity (non-destructive sampling) on 7 January (Savary 1986), i.e. approximately 1.5 to 1.8 latency period after inoculation (Savary 1985b).

Rain simulation. The rain simulator (Asseline and Valentin, 1978) consists of a telescopic tower on which one single nozzle is mounted (Fig. 1). Moved by an adapted windscreen wiper motor, the nozzle oscillates across the plot at a height of 3.5 m. The angle of oscillation, altered by adjusting the angle of the drive shaft, can be rapidly modified from the ground to obtain the required rain intensity (from 30 to 140 mm h^{-1}).

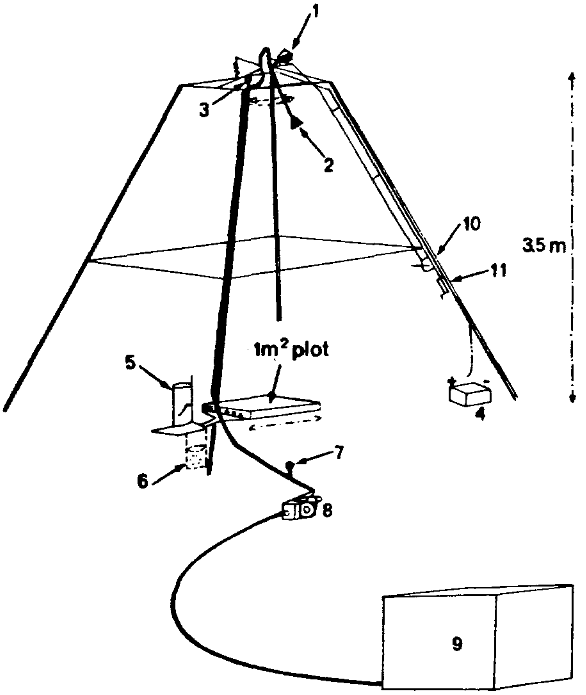

Fig. 1. The rainfall simulator (after Asseline and Valentin, 1978) used to study rain-induced dispersal of *Puccinia arachidis.*
1) Windscreen wiper motor; 2) Oscillating nozzle; 3)Water pressure gauge; 4) Battery (12 V); 5) Water level recorder; 6) Water run-off tank; 7) Gate valve; 8) Motor pump; 9)Water tank; 10) Adjusting handle for the verticality of the nozzle; 11) Adjusting handle for regulating intensities.

Table 1. Rain induced dispersal of *Puccinia arachidis*. Amount, duration and intensity of simulated rain showers.

Plot no.	Rust severity[1] (%)	Simulated rains				
		amount (mm)	duration (min)	intensity (mm h^{-1})	diameter of drops[2] (mm)	kinetic energy[3] (J $mm^{-1}m^{-2}$)
1 (reference)	16.9	0	0	0	0	0
2	15.8	2.5	5	30	0.84 (0.47-1.22)	14.7
3	22.2	5.0	10	30	0.84 (0.47-1.22)	14.7
4	16.1	10.0	10	60	1.49 (1.03-2.10)	19.0
5	20.2	20.0	10	120	1.35 (0.79-2.16)	23.0

[1] Differences between focal centers of plots are not significant (F(3,4) = 0.88).

[2] The mean diameter of the drops is followed by the diameters of the 25th and the 75th percentile of the drop population.

[3] The kinetic energy of the rain is expressed in joules per mm of rainfall per m^2 of soil hit by the rain.

The average size of drops produced by the rain simulator is small when compared to that employed by Gregory et al. (1959) (2-5 mm) and Hirst and Stedman (1963) (3.4 mm). The size distribution of the droplets produced by the simulator is strongly asymmetric, as is the case with natural raindrops. For an intensity of 60 mm h^{-1}, the mean droplet size is 1.5 mm, but about 70% of the droplets have a diameter within the size bracket of 1.0 to 4.0 mm (Valentin, 1981). A rain simulator producing a range of droplet sizes, instead of single-sized drops, probably provides a realistic approach of field conditions. The apparatus was designed to mimmick the effect of tropical rain showers on soil surfaces. Special attention was given to the kinetic energy of the artificial rain which should approximate that of natural rain (Valentin, 1981).

On four plots, different rainfall events were simulated on 8 January; the fifth plot was used as a reference. Amounts, durations and intensities of the artificial rains are shown in Table 1. The experimental conditions are representative of natural showers observed in Ivory Coast (Asseline and Valentin, 1978). No rainfall had occurred on the plots during the week before the rain simulation experiment.

Spore counts. Three different methods of spore counting were used before and during rain simulation.

In each plot (Fig. 2), four rain gauges were placed, two with their funnel openings at canopy top level (approximately 0.2 m above the ground), and two at ground level. After the rain shower, their contents were filtered through a twin (20 and 40 mesh) wire gauze filter and deposited on a paper filter, which was then dried, cut into pieces and agitated in 2 ml water with 0.01 % (v/v) Triton X-100. The spore contents of the suspen-

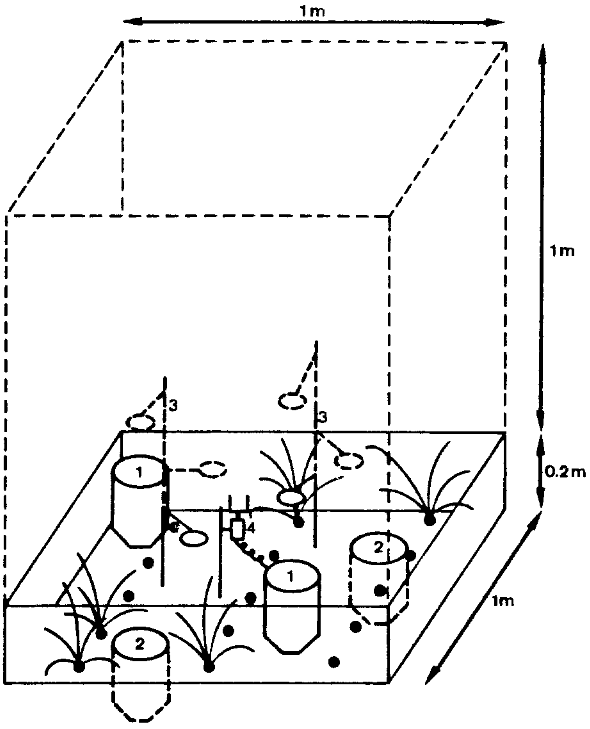

Fig. 2. Rain-induced of *Puccinia arachidis*. Lay-out of sampling devices. Objects contained within the volume of the canopy (approx.: 0.2 × 1 × 1 m) are represented in drawn lines. Objects above or under this volume are shown in broken lines. Plant position are indicated by dots and a few plants are drawn schematically.

1. Rain gauges (opening at canopy top level = 0.2 m).
2. Rain gauges (opening at ground level = 0.0 m).
3. Inverted petri dishes at 0.2, 0.3, and 0.5 m height.
4. Rotorod sampler at 0.2 m height.

sions obtained from the rain gauges were assessed by counting (five counts per sample), using a Nageotte hemocytometer, as described by Roelfs et al. (1970).

Two sets of inverted plastic petri dishes, 8.8 cm in diameter, their bottom covered with a filter paper disk, were placed in the four plots submitted to simulated rains at three heights above the ground: 0.2, 0.3 and 0.5 m (Fig. 2). The spores caught on the paper surface were recovered and their numbers were estimated as mentioned before.

Before and during each simulated rain, aerial spore densities were estimated by means of rotating impaction (Rotorod) samplers. Sampling duration was 10 min in each case, except for the 2.5 mm rain simulation, when the duration was 5 min.

Before and after each rain, one leaflet of the 6th or the 7th leaf (from the apex) was taken away from each of five inoculated plants chosen at random in every plot. Each leaflet was cut into pieces and shaken in 5 ml water with 0.01 % (v/v) Triton X-100 before counting. The number of spores per leaflet was divided by the number of lesions observed on the leaflet, so that the final result could be expressed as number of spores per lesion.

Results

Rust assessment. The average rust severity in the inoculated areas of the plots was estimated at 18.4% versus 3.4% in the non-inoculated areas. A two-way analysis of variance indicated a significant ($p < 0.0005$) effect of inoculation on rust severity, but did not indicate plot or plot × inoculation effects.

Rain simulation. The rain simulator worked according to the above specifications. Specified and measured rain catches are mentioned in Table 2.

Spore counts. There was a significant difference ($p < 0.05$) between the contents of lesions before (Table 2,A) and after (B) each rain shower. Their depletion increased between 2.5 and 10.0 mm of rain, as can be seen from the percent values (relative depletion). Rotorod spore captures (Table 2, C and D) increased significantly with increasing rainfall amounts. High variation (least significant difference at $p < 0.05$: 8500 spores m^{-2}) was noticed in the data obtained from the petri dish counts (Table 2, E, F, G). The amounts of trapped spores were usually higher at canopy top level ($z = 0.2$ m) than at other heights. Table 2 indicates a trend; spore counts increased with rainfall amounts and intensities at all heights. In rain gauges the spore counts were higher ($p < 0.05$) at ground level (Table 2, I) than at canopy level (H). Higher spore catches were usually obtained with higher rainfall amounts with all methods of spore catching.

Discussion

Physical processes. When a rain shower hits a groundnut canopy infected by rust, several spore liberation mechanisms can be activated : (a) mechanical momentum shedding off the spores (Zadoks and Schein, 1979), (b) microgusts of air, caused by rain drop impaction (Hirst and Stedman, 1963), blowing the spores away, and (c) raindrop backsplash (Gregory et al., 1959), carrying the spores away in microdroplets. These mechanisms can be superimposed on the spore liberation caused by the wind (mechanical momentum, gustiness). They generate flows of spores above and within the canopy: (a) a flow of dry spores, (b) a flow of water-borne spores in splash droplets, (c) a horizontal flow of spores (dry or droplet-borne) abducted by wind, (d) a downward flow of spores caught by rain droplets, (e) a flow of spores suspended in water dripping from the leaves, and (f) a flow of spores suspended in water running off the petioles and stems.

Spore flows. The system studied in these experiments is, in a first approach (System 1), limited to a canopy space with a surface of one square meter and a height of 0.2 m, topped by one cubic meter of air. In this system, the number of spores in the pustules increases by spore formation and decreases by spore liberation. For the duration of each rainfall experiment, spore formation is negligible. Considering the systems at equilibrium, and following an approach similar to that of Rijsdijk and Rappolt (1978), we write:

$$A = B + C + D, \tag{1}$$

where A represents the outflow from the spore source (the lesions), and B, C and D, the inflows into three sinks, the canopy space (lesion excepted), the air space above

Table 2. Rain-induced dispersal of *Puccinia arachidis*. Spore counts from a rain simulation experiment with various methods of spore sampling.

Rainfall (mm)			Lesions counts[2] (10^3spores lesion^{-1})		Rotorod counts[3] (spores m^{-3})		Petri dish counts[4] (10^3 spores m^{-2})			Rain-gauge counts[5] (10^3 spores m^{-2})	
specified	measured[1]		A	B	C	D	E	F	G	H	I
	canopy	ground	before rain	after rain	before rain	after rain	$z=0.2$	$z=0.3$	$z=0.5$	canopy	ground
2.5	2.48	2.58	3.4 a	2.4 bcd (−29%)	15 (0-30)	690 (640-740)	21.2 a	2.4 e	3.7 e	50 c	420 b
5.0	5.15	4.80	2.7 abc	1.6 def (−41%)	23 (13-32)	1120 (1060-1170)	18.7 abc	7.4 de	2.5 e	90 c	710 a
10.0	10.3	10.5	3.0 ab	1.4 ef (−53%)	28 (17-39)	3580 (3400-3760)	16.2 bc	14.5 bcd	2.5 e	90 c	970 a
20.0	19.4	21.5	2.1 cde	1.0 f (−52%)	40 (38-52)	3830 (3640-4020)	25.0 a	24.9 a	12.4 cd	200 bc	770 a

[1] Each entry corresponds to the mean of two rain catches.

[2] Each entry is the mean of five counts on each of five sampled leaflets.
Entries followed by different letters are significantly different at 95% level: *LSD* (p = 0.95) = 0.90. Numbers between brackets are the relative depletions of lesions in percentages.

[3] Calculations according to the manufacturer's specification; each entry is followed by its confidence interval at p = 95% level.

[4] Each entry is the mean of five counts on each of two petri dishes. Data followed by different letters are significantly different at 95% level; *LSD* (p = 0.95) = 8.5. z is the trapping height in m.

[5] Each entry is the mean of five counts for each of two rain gauges. Data followed by different letters are significantly different at 95% level: *LSD* (p = 0.95) = 260.

the canopy, and the soil, respectively.

The outflow from source A was measured as the difference between the contents of the lesions before and after the rain experiments.

Two of the variables measured help to quantify the inflow into the canopy space (B). (1) The number of spores m^{-2} trapped by inverted petri dishes at canopy top level represents splash dispersal; (2) the difference between the number of spores m^{-2} caught in the rain gauges at canopy top level and the number of spores m^{-2} trapped by the petri dishes, also at canopy top level, represents rain scrubbing.

The Rotorod catches are assumed to estimate the density of dry spores in the air, i.e. the content of sink C. It is assumed that dry spores suspended in droplets cannot be trapped with this device because the droplets do not adhere to the silicone grease covering the rods.

The counts from the rain gauges at ground level are taken to represent the inflow to sink D (the soil), run-off being disregarded here.

Calculation of spore flows (System 1). The number of lesions k in the canopy was estimated as:

$k = d \times l \times L = 15 \times 84 \times 47.7 = 6.0 \times 10^4$ lesions m^{-2}.

where d is the number of plants m^{-2}, l is the number of leaflets plant^{-1}, and L the number of lesions leaflet^{-1} (derived from disease assessment). Multiplication of k by the number of spores lesions^{-1} leads to values of 1.3 to 2.0 $\times$ 10^8 spores m^{-2}, which is within the range of results obtained for other rusts. Ingold (1953), for instance, quoted an amount of 2.5 $\times$ 10^9 spores m^{-2} for *Puccinia graminis.* These values are also consistent with previous observations on groundnut rust under laboratory conditions (Savary, 1985 b) and field conditions (unpublished data).

The rate of depletion of the lesions during rain (Table 3, A2) was calculated from the difference between lesion content before (Table 2, A) and after (Table 2, B) rain. The average aerial spore density (Table 2, C), calculated over the duration of the experiment (8.20 a.m. till 10.50 a.m.), was 26.5 spores m^{-3}.

During the experimental period, the average depletion of the lesions (calculated from counts before rain, Table 2, A) was $3390 - 2130 = 1260$ spores lesion $^{-1}$. During such a period (150 min), at optimal temperature conditions, spore production cannot exceed 191 spores lesion^{-1} (Savary, 1985 b). Thus, the maximum depletion which could have been caused by wind only is $1260 + 191 = 1451$ spores lesion^{-1}. This result corresponds to an average depletion rate of $1451/150 = 9.71$ spores lesion^{-1} min^{-1}. The ratio of the average depletion rate to the mean aerial density before rain is: $9.7/26.5 = 0.37$. This ratio was used to estimate the lesion depletion rate corresponding to the dry dispersal represented by the aerial densities during rain (Table 2, D). Using the coefficient k, these lesion depletion rates were transformed into rates of outflow from the source, expressed in spores m^{-2} min^{-1} (Table 3, B2).

The numbers of water-borne spores dispersed by splashing (Table 3, C1) and dripping (Table 3, D1) were derived from the figures of Table 2, columns E and I. The number of water-borne spores scrubbed from the air is listed in Table 3, E1. The rates of the various spore flows are obtained by dividing the numbers calculated as above by the respective durations of the rain showers (Table 3, C2, D2, and E2).

Table 3. Rain-induced dispersal of *Puccinia arachidis* . Estimates of some spore flows above and within a groundnut canopy at variable amounts of rainfall.

Rainfall amount (mm)	Duration (min)	A Spores released from pustules		B Dry spores dispersed during rain		C Splash dispersed spores		D Spores leached from the canopy		E Spores washed out from the air		F Dry spore dispersal by wind	
		1 amount[1]	2 rate[2]	1 amount[1]	2 rate[2,3]	1 amount[1]	2 rate[2,3]	1 amount[1]	2 rate[2,3]	1 amount[1]	2 rate[2,3]	1 amount	2 rate[4]
0	0	–	0.56-10^{6}	0	0	0	0	0	0	0	0	–	0.56-10^{6}
2.5	5	6.0-10^{7}	12.0-10^{7}	0.7-10^{8}	1.5-10^{7}	2.1-10^{4}	4.2-10^{3}	4.2-10^{5}	8.4-10^{4}	2.9-10^{4}	5.8-10^{3}	–	–
5	10	6.6-10^{7}	6.6-10^{7}	2.4-10^{8}	2.4-10^{7}	1.9-10^{4}	1.9-10^{3}	7.1-10^{5}	7.1-10^{4}	7.1-10^{4}	7.1-10^{3}	–	–
10	10	9.6-10^{7}	9.7-10^{7}	7.5-10^{8}	7.5-10^{7}	1.6-10^{4}	1.6-10^{3}	9.7-10^{5}	9.7-10^{4}	7.4-10^{4}	7.4-10^{3}	–	–
20	10	6.6-10^{7}	6.6-10^{7}	8.1-10^{8}	8.1-10^{7}	2.5-10^{4}	2.5-10^{3}	7.7-10^{5}	7.7-10^{4}	17.5-10^{4}	17.5-10^{3}	–	–

[1] Per m^2 of crop.

[2] Per m^2 of crop and per min, averaged over rainfall duration.

[3] Estimated under the assumption that spore take-off is constant throughout rain duration.

[4] Per m^2 of crop and per min.

Time constants of the dispersal processes. The various transport processes should not be considered as constant throughout the rain duration. On the contrary, they involve different scales of time, different time constants. For instance, Rapilly et al. (1970) showed that the number of urediniospores of *P. striiformis* dispersed by splashing decreases exponentially with time, the time constant being approximately 17 min. The time constant of dry spore dispersal by rain-drop impact at the onset of a rain shower is much shorter, as follows from the study by Hirst and Stedman (1963).

Therefore, the use of the rain duration to estimate the rate of depletion (Table 3, A2) and the rates of flow due to splash dispersal (Table 3, C2), dripp-off (Table 3, D2), and rain scrubbing (Table 3, E2) is incorrect. For these flows, only the numbers of dispersed spores should be considered.

Comparison of flows. The equilibrium equation (1) implies that the outflow from the source (A, lesions) cannot be smaller than any of the considered inflows (B, C, and D) into the sinks. The highest amount (and rate) of the estimates listed in Table 3 is that of dry dispersal (B1), which usually exceeds that of the depletion of the source (Table 3, A1). Apparently, the amount of dry spores were over-estimated in the calculation for System 1. This result indicated that dry spore dispersal has the shortest time constant among the processes considered. Indeed, Hirst and Stedman (1963) showed that rain-induced dry spore dispersal of several fungi nearly instantaneously led to a strong increase of the aerial spore density, followed rapidly by a decrease.

The amounts of spores scrubbed from the air are equivalent to those dispersed by splashing (Table 3, E1 and C1). Many of the spores scrubbed from the air must have been dry-dispersed.

Calculation of flows (System 2). Another approach to the handling of the data in Table 2 is to focus on the spore liberation mechanisms. System 2 can be defined as a single lesion, with its spores allocated to the various take-off mechanisms. To reduce calculations and to allow comparisons, this single-lesion-system will be multiplied by the total amount of lesions m^{-2} *(k)*. The equilibrium equation is:

$$A = S + W + I + E, \text{ or}$$
$$I = A - S - W - E, \qquad (2)$$

where A has the same meaning as in equation (1), i.e., the amount of spores lesion^{-1}; S, W and I are the amounts allocated to splash, wind and dry-spore dispersal, respectively. E represents the error, i.e. the amounts which cannot be allocated to any of the considered mechanisms. It can be taken, for instance, as the number of spores per lesion washed away by water running over the leaf surface. A and S were estimated for each rainfall amount (Table 3, A1 and C1, respectively). The values for W (Table 4) were estimated as the product of the ratio:

rate of depletion / aerial density = 0.37,

and the aerial spore densities measured before rain (Table 2, C). The resulting depletion rates, multiplied by the duration of the rains, provided estimates of what the depletion of lesions would have been without rain. With equation (2), I can be estimateds if E is negligible.

The comparison of the estimates for I in System 2 (Table 4) with those obtained in System 1 (Table 3, B1) shows that the discrepancy between the estimates of dry dispersal increased with rain intensity. In other words, increasing rain intensities appeared

Table 4. Rain-induced dispersal of *Puccinia arachidis*.Calculation of spore flows in System 2 and comparison of estimates for dry spore dispersal following System 1 and 2.

System 2					Discrepancy between System 1 and System 2 for dry dispersal: (Table 3, B1)-*I* (spores m^{-2})
P (mm)	*A* (spores m^{-2})	*S* (spores m^{-2})	*W* (spores m^{-2})	$I=A\text{-}S\text{-}W$ (spores m^{-2})	
2.5	$6.0\text{-}10^{7}$	$2.1\text{-}10^{4}$	$1.6\text{-}10^{6}$	$5.8\text{-}10^{7}$	$0.7\text{-}10^{8} - 5.8\text{-}10^{7} = 1.2\text{-}10^{7}$
5	$6.6\text{-}10^{7}$	$1.9\text{-}10^{4}$	$4.8\text{-}10^{6}$	$6.1\text{-}10^{7}$	$2.4\text{-}10^{8} - 6.1\text{-}10^{7} = 1.8\text{-}10^{7}$
10	$9.6\text{-}10^{7}$	$1.6\text{-}10^{4}$	$5.9\text{-}10^{6}$	$9.0\text{-}10^{7}$	$7.5\text{-}10^{8} - 9.0\text{-}10^{7} = 6.6\text{-}10^{7}$
20	$6.6\text{-}10^{7}$	$2.5\text{-}10^{4}$	$8.4\text{-}10^{6}$	$5.8\text{-}10^{7}$	$8.1\text{-}10^{8} - 5.8\text{-}10^{7} = 7.5\text{-}10^{7}$

P: Rainfall in mm
A: Depletion of lesions, from leaflet counts
S: Splash dispersal, from petri dish counts
W: Wind dispersal (momentum and microgusts), estimated from pre-rain Rotorod counts.
I: Dry dispersal due to rain impaction, estimated using equation for *I*.

to be associated with diminishing time constants of the process. The value for *E* was not considered in this discussion. If *E* were important, it would reduce the value for *I* in equation (2), and thus increase the discrepancy between the two estimates for dry dispersal, and so suggest an even shorter time constant of this process.

Contributions of System 1 and System 2 to the analysis of results. In a first attempt (System 1) to estimate the flows of spores, the assumption of constant spore take-off throughout time, i.e. the use of rain duration in calculations, produces an obviously higher error in the case of dry spore dispersal. According to Table 3, the dry spore flow (B) seems to be higher than the depletion flow (A) which, in turn, is higher than flows due to other transport processes (C, D, E and F). Therefore, the shortest time-constant of the considered processes must be assigned to dry spore flow. The difference between the range of variation of the outflow from the source (Table 3, A), and that of the flow of spores, except dry dispersal (Table 3, C, D, and F), is very high: the corresponding sampling techniques did not account for a large proportion of liberated spores, suggesting a substantial abduction of spores from the observation area. In other words, these experiments only considered dispersal at short mesoscale (Zadoks and Schein, 1979), while an important transport probably occured at larger scales as well.

Conclusion. The use of a rain simulator over a canopy of a groundnut crop infected by rust allowed a comparison between different spore flows caused by rain. The spore content of pustules decreased rapidly during rainfall even at small amounts of rain. Among the types of dispersal processes caused by rain, three types were considered in more detail: dry dispersal, splash dispersal and drip dispersal. The first of these processes seems preponderant. Dry dispersal increases rapidly with the amount and the intensity of a rain shower, but it appears to come to a quick stop after the onset of rain.

Not all possible spore flows were investigated, among which abduction by wind (Rijsdijk and Rappolt, 1978) and spore run-off.

Our results indicate that short-lasting showers could contribute to the build-up of an epidemic, due to an intensification of spore dispersal. The overall effect of heavy and prolonged showers on the retardation of an epidemic (Zadoks and Leemans, 1984) depends on the efficacy of dispersal and on subsequent infection conditions. This overall effect was not measured. Resumption of sporulation by depleted lesions was not yet studied. According to Rapilly et al. (1970) sporulation may resume within few hours in yellow rust of wheat.

In conclusion, this experiment with simulated rains indicates that a small rain shower may be favourable and that strong showers may be quite unfavourable to the progress of an epidemic of groundnut rust.

Acknowledgements

The authors are indebted to Professor J.C. Zadoks (Department of Phytopathology, Wageningen, the Netherlands), for constructive criticism of this work and linguistic assistance. Thanks are due to Mr M. Zawolek (temporarily at the above adress) for suggestions in analysis of physical processes.

Samenvatting

Verspreiding van Puccinia arachidis door regen, bestudeerd met behulp van een regensimulator

Een regensimulator, een krachtig beregeningsapparaat, werd ingezet boven een aantal aardnoot- *(Arachis hypogaea)* veldjes geïnoculeerd met de aardnootroest *(Puccinia arachidis)* om de uredosporenverspreiding te bestuderen bij verschillende hoeveelheden regenval. Diverse vangtechnieken werden toegepast om droge verspreiding, spatverspreiding en druipverspreiding ten gevolge van regen te vergelijken. De sporeninhoud van de sporenhoopjes op het gewas werd door regen sterk verminderd. De resultaten, verkregen in twee verschillende, maar elkaar aanvullende analyses, geven aan dat lichte regenbuien de ziekteverspreiding bevorderen, terwijl zware buien deze zouden afremmen.

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