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## Short-distance dispersal of wheat rust spores by wind and rain

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**Abstract** – After a brief description of the biophysical environment of diseased plants, mechanisms of short-distance dispersal of wheat rust spores by wind and rain are reviewed. Wind, and especially intermittent gusts, is the main agent of removal and transport of spores. Whereas wind does not seem to limit the process of short-distance dispersal, the effect of rain events is more complex. Laboratory and field experiments have shown that rain events enhance spore removal from sporulating lesions. Rain events also scrub airborne spores and deposit them onto susceptible plants. Extended or violent rain events, however, may finally wash off spores already deposited on leaves and be detrimental to the spread of disease.

**wheat / rust / rain / wind / epidemiology**

**Résumé** – Dissémination à courte distance des spores des rouilles du blé par le vent et la pluie. Après une brève description de l'environnement biophysique des plantes malades, les mécanismes de dispersion à courte distance des spores des rouilles du blé par le vent et par la pluie sont discutés. Le vent, surtout lorsqu'il est intermittent, est l'agent principal de libération et de transport des spores. Alors que le vent ne semble jamais avoir d'action limitante sur la dispersion des spores à courte distance, l'influence des épisodes pluvieux est plus complexe. Des expérimentations au champ et en laboratoire ont montré que les épisodes pluvieux favorisent la libération des spores à partir des lésions sporulantes. Les épisodes pluvieux lessivent également les spores contenues dans l'air et les déposent sur les plantes sensibles. Cependant, des épisodes pluvieux prolongés ou violents peuvent entraîner le lessivage des spores déjà déposées sur les feuilles, et être ainsi défavorables à la progression de la maladie.

**blé / rouille / pluie / vent / épidémiologie**

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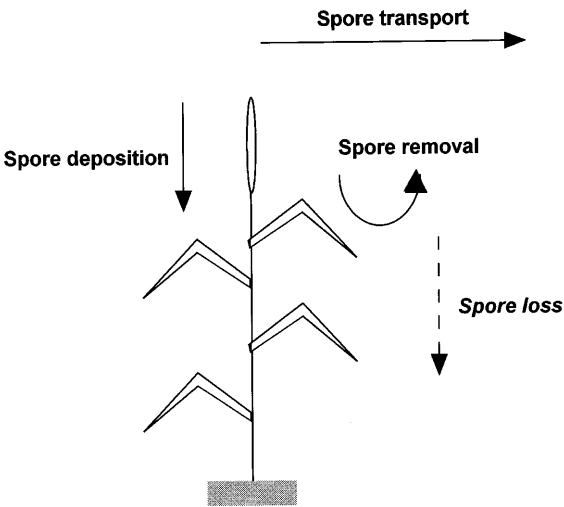
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1. Introduction

Rusts of wheat (Tab. I) cause significant yield loss in all wheat-growing areas of the world when proper control methods, i.e. combination of resistant cultivars and fungicide sprays, are not available or incorrectly applied [29]. Rusts are able to spread over large areas during very short time periods because they are mainly dispersed by way of numerous microscopic spores. Epidemic spread during the crop season is caused by the asexual urediniospores (sometimes called uredospores or urediospores, and hereafter called spores for the sake of simplicity), which are repeatedly produced during successive infection cycles occurring on the cereal host only. Environmental conditions during spring and early summer are in most cases conducive to spore production, and enormous quantities of spores are ready to be removed from the host plant and transported on a scale ranging from a few centimetres to thousands of kilometres, before being eventually deposited on a suitable host plant [39]. Liberation (meaning removal, or take-off), transport, and deposition are widely recognised as the three subprocesses involved in aerial spore dispersal [3, 22]. This distinction is rather artificial, especially on the smaller scales, but provides a convenient framework for analytical studies of the mechanisms involved in spore dispersal.

The rust spores are aerodynamically adapted to wind removal and transport (*anemochory*, Fig. 1)



**Figure 1.** Schematic representation of the effects of wind on dispersal of cereal rust spores. Solid arrows: positive effects on dispersal; dashed arrows: negative effects on dispersal.

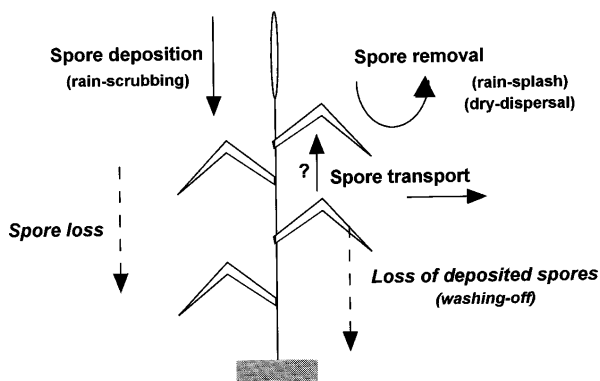
[33]. Historical records of coloured spore clouds observed over heavily infected fields and able to stain clothes and other objects were reviewed by Chester [6]. On a much larger scale, continental wind patterns have been advocated to explain the so-called ‘*Puccinia* paths’ followed every year by the epidemics in Northern America [39], India [30] and China [25].

Dispersal of rust spores by rain (*ombrochory*, Fig. 2) earned much less attention, because the hydrophobic rust spores were assumed not to be

**Table I.** Nomenclature of wheat rust diseases and their causal fungi.

Disease common name		Fungus nomenclature <sup>a</sup>
Europe	America	
Black rust	Stem rust	<i>Puccinia graminis</i> Pers.: Pers. f. sp. <i>tritici</i> Eriks. and E. Henn.
Brown rust	Leaf rust	<i>Puccinia recondita</i> Roberge ex Desmaz. f. sp. <i>tritici</i> (Eriks. and E. Henn.) D.M. Henderson (= <i>Puccinia triticina</i> Eriks.) [formerly <i>Puccinia rubigo-vera</i> (DC) Winter]
Yellow rust	Stripe rust	<i>Puccinia striiformis</i> Westend.f. sp. <i>tritici</i> Eriks. [formerly <i>Puccinia glumarum</i> Eriks. and E. Henn.]

<sup>a</sup> After [8] and [53].



**Figure 2.** Schematic representation of the effects of rain on dispersal of cereal rust spores. Solid arrows: positive effects on dispersal; dashed arrows: negative effects on dispersal. Vertical spore transport, although highly probable, has not been experimentally demonstrated yet.

easily caught and carried away by rain drops. Regarding their dispersal mechanism, rust spores have often been opposed to 'true' splash-dispersed, hydrophilic spores produced for instance by *Septoria* spp. [13] or *Colletotrichum* spp. [26]. Early reports of the detrimental effect of rain on cereal rust dispersal [6, 43] were mainly based on circumstantial evidence and can be considered as 'educated guesses' only. Whereas wind dispersal has been extensively studied on a wide range of spatio-temporal scales in several cereal rust pathosystems [19], quantitative information on rain dispersal is rather sparse [21, 38, 41]. Specific methods and devices devoted to the study of rain-dispersed fungi [11] have been only recently applied to cereal rust fungi [15–18].

This paper aims to review our current knowledge of the dispersal of rust spores by wind and rain. Although other factors such as relative humidity, wetness and solar radiation may influence spore dispersal, this review will concentrate on wind and rain as the two main dispersal agents of cereal rust spores. Rain will be highlighted as a hitherto neglected dispersal agent, but wind needs also to be considered since both usually occur together in field situations. Large-scale dispersal of rust diseases [30] is comparatively better described than local dispersal, so this review will focus on

the short-dispersal events occurring on a field-scale during and shortly after spore removal. These events are responsible for primary disease outbreaks and the build-up of disease foci within a field.

In the following, the biophysical environment of the rust spores on the surface of cereal leaves is briefly discussed. Next, the mechanisms of spore dispersal by wind and rain, as they have been studied in laboratory conditions, are described. The third part of the review assesses the importance of these mechanisms in field conditions and their effect on the spread of disease. Finally, the possible use of these results for improving disease control is discussed in relation to meteorological predictions. In this review, the effect of rain is emphasised due to the recent findings on this topic [14–18].

## 2. Characterisation of the environment of spores

Since this review focuses on within-field dispersal, only 'local' characteristics of wind and rain, i.e. at the canopy level, will be summarised hereafter.

### 2.1. Wind

Wind is usually characterised by its mean speed [m/s] measured by standard weather stations, but this characteristic is of little relevance for processes occurring at the leaf level during very short time periods. Turbulent movements, i.e. change in speed and direction of the wind, can be of mechanical (friction of air parcels on surfaces) or thermic (ascending movements of heated air parcels) origin [5]. Distribution of wind speed near leaves is even more complex [28], and is also influenced by canopy density, height, and roughness [3]. Wind profiles within crops are characterised by a higher intermittence [3]. Average wind speed is lower than above the canopy but turbulence may increase with increasing depth. Relatively large eddies that penetrate the canopy cause gusts of high wind speed and low frequency [45].

## 2.2. Rain

Whereas wind is a continuous factor varying in intensity, atmospheric rain occurs as discrete rain events. A rain event is usually characterised by its duration and the amount of fallen rain [mm/h], with great variation in each rain event just as with a wind event. The distribution of drop diameters, depending on the number of drops per unit volume and the rain intensity, has been characterised for different types of rain events [51] and can be assessed in field conditions using a spectropluviometer. The total drop momentum or kinetic energy of a rain event can be calculated using numerical integration methods [17, 18] or directly measured using a specific calibrated sensor [27]. Formation of splash droplets after impaction depends on several factors including the diameter and the terminal velocity of incident drops and the physical characteristics of the target [26]. A variable proportion of the incident drops and splash droplets are not intercepted by the uppermost leaves and their kinetic attributes may be dramatically altered during their travel through the lower leaf layers [1].

## 2.3. Morphology of spore producing structures and dispersal units

Rust spores accumulate in a sorus that erupts through the host plant cuticle. The spores are borne singly on a pedicel, but they abscise at a very early development stage and are presented to dispersal as a floccose powder of detached spores [21]. Therefore, removal of spores is entirely passive and does not involve the specialised morphological structures required for discharge or ejection of other types of fungal spores (e.g. ascospores and ballistospores). Spore removal only requires an aerodynamic or mechanical force sufficient to overcome the forces of adhesion holding the spore to the surface [28]. Spores of the different cereal rust species have a common ovoid to elliptical shape and do not differ in size (average diameter range 15–30 µm). However, the average size of the dispersal unit, defined as the smallest fungal entity able to propagate disease [37], differs among

species. Spores of yellow (stripe) rust (*Puccinia striiformis*) are embedded in a mucilaginous layer and are mostly removed in clusters (2–>10 spores per cluster, average 3.5). Conversely, spores of black (stem) rust (*Puccinia graminis* f. sp. *tritici*) and brown (leaf) rust (*Puccinia recondita* f. sp. *tritici*) are more often removed as singlets [27, 46]. Centrifugation of leaf fragments bearing sporulating rust lesions shows that the minimal force required to remove spores is about five times larger in yellow than in brown rust, reflecting the difference in the size of dispersal units [16]. Both forces are one order of magnitude smaller than those required to remove the stalkborne conidia in Southern corn leaf blight (*Helminthosporium turcicum*) [2], and two to three orders of magnitude smaller than those required to remove the conidial chains of barley powdery mildew (*Erysiphe graminis* f. sp. *hordei*) [4]. There seems to be a good agreement between the removal mechanism and the force required to remove the spores, the less firmly attached spores requiring the smallest force to be removed.

## 3. Laboratory studies of the dispersal mechanisms

### 3.1. Removal of spores by wind

The effects of wind on spore dispersal are outlined in Figure 1. Due to the large spatio-temporal scales involved in spore transport and deposition, removal is the only spore dispersal subprocess suitable for laboratory experiments. Foliar surfaces are embedded within a laminar boundary layer of relatively slow-moving air that protects spores from removal. Turbulence breaks this boundary layer and allows wind to blow with ambient speed close to the leaf surfaces, where the spores are ready to be removed [3].

Miniaturised wind tunnels are a convenient means to study spore removal from infected leaf fragments submitted to simulated wind of various velocity and duration, even if the flow characteristics in the tunnel are quite different from wind

flows occurring over and within canopies. In such studies, no removed rust spore could be detected until a minimal threshold wind velocity had been reached. Measured threshold values range from 0.5 to 1.5 m/s for black [46], brown [16, 47, 48] and yellow [16, 38] rusts. When compared in strictly similar conditions, yellow rust spores required a higher minimum wind velocity threshold for removal than brown rust spores, another probable consequence of the difference in dispersal unit size [16]. For both rusts, duration as well as intensity (velocity) of the applied stress (wind) is of importance [16, 48]. A pioneer study of spore movement by Laser Doppler Velocimetry [36] gave minimum wind velocity thresholds larger than those obtained from conventional wind-tunnel studies.

Recently, spore removal in wheat brown rust was studied in a large wind-tunnel (length 12 m, cross section 1 m<sup>2</sup> [11]) mimicking more realistically wind patterns observed over a crop. Spore accumulation prior to the experiment was standardized by harvesting all available spores 24 hours before the start of the experiment. There was no minimum wind velocity threshold and the quantity of removed spores was found to increase linearly with increasing wind velocity [18]. Anyway, studies with constant wind velocity do not reproduce the brief wind gusts that are able to remove most of the spores present [3]. Although not attempted experimentally, simulated wind gusts will probably enhance spore removal.

Results obtained in miniaturised wind-tunnels must therefore be considered with caution, but are of primary interest to calculate aerodynamical forces required to remove spores [2, 4, 16] and to characterise the duration and intensity of stress required to remove spores from leaves.

### 3.2. Removal, transport and deposition of spores by rain

Rain as a dispersal agent usually acts on a much smaller scale than wind, and the subprocesses of spore removal, transport and deposition (Fig. 2) can be studied altogether.

Rain can remove fungal spores by at least two mechanisms, rain-splash and dry-dispersal (Fig. 2). In rain-splash, the incident drop breaks into smaller splash droplets when hitting the sporulating lesions, and each of the droplets may incorporate one or several spores and carry them away. The mechanism has been studied in detail for fungi that produce their spores in mucilaginous, hydrophilic structures [13, 26]. The travel distance of spores incorporated in droplets is usually very small unless wind gusts carry them farther away, and spore and disease dispersal gradients of typically rainborne diseases are usually very steep [12]. Dry-dispersal occurs when a raindrop hits a non-sporulating part of the leaf and transfers its motion energy to the leaf, detaching spores that remain dry [23]. Deposition occurs when spores in suspension in the atmosphere are scrubbed by incident water drops and reach leaf surfaces [9].

#### 3.2.1. Single-drop experiments

In laboratory experiments, splash- and dry-dispersed spores can be counted separately when trapped on glass slides coated with the Naphtol Green B dye [21]. Early studies with black rust [21, 23] and yellow rust [38] of wheat have confirmed the dry-dispersal of spores caused by rain, but failed to show significant splash-dispersal. It was hypothesised that hydrophobic, non-wettable rust spores could not be incorporated in splash droplets as it occurs for wettable spores of typically splash-dispersed pathogens [26]. It seems, however, that the hydrophobic rust spores are trapped on the droplet surface, as reported for other non-wettable fungal spores [9] and coffee rust (*Hemileia vastatrix*) spores [32]. Recent experiments using a range of rain drop diameters matching a real rain event (2.5–4.9 mm) and falling from 5 to 100 cm showed that spores of brown and yellow rusts of wheat are splash- and dry-dispersed, both mechanisms having comparable removal efficiency [17]. Both mechanisms of dispersal had the same characteristics in both rusts: the first three released drops removed 50–80% of the total spores removed, and the number of removed spores as well as their flight distance increased with drop diameter and height of fall. Both spore splash- and

dry-dispersal gradients were very steep and no spore could be collected beyond 9 cm from the target [17]. These conclusions are qualitatively equivalent to those obtained with typically splash-dispersed pathogens [13, 26, 28].

### 3.2.2. Rain simulator experiments

Single drops released from a height of 1 m [17] or 2.1 m [38] do not reach the terminal velocity they would have reached in natural rain conditions. Their spore dispersal efficiency is therefore probably underestimated. A vertical tower 11 m high is required to approximately simulate a natural rain [11]. Using such a large device also allows collecting the removed spores on trap plants rather than slides. The infectious potential of the removed spores is then expressed by incubating the trap plants in suitable conditions and counting the resulting sporulating lesions, but splash- and dry-dispersal mechanisms cannot be separated anymore. Dry-dispersal was shown to be preponderant in groundnut rust (*Puccinia arachidis*), studied with another type of simulator that mimicked tropical showers [42]. In cereal rusts, rain simulation seems to have been used only recently [18], whereas it has been widely used for several rain-splashed pathogens [13, 26]. Infection of trap plants (not directly exposed to simulated rain) following exposure of infected source plants to simulated rain events had the same qualitative characteristics as collection of removed spores on slides described above [18]: maximum disease severity was reached after 10 minutes of rain exposure, and increased with the rain drop diameter. Disease gradients were steeper for yellow rust than for brown rust, and a few lesions of both rusts could be detected up to 84 cm from the source plants. Exhaustion of sporulating lesions occurred after 20 minutes of continuous simulated rain, as shown by the lack of infection of trap plants and visual observation of source plants. Restoration of the sporulation capacity after a prolonged rain event, as shown by infection of trap plants, needed a dry period of 2 hours for brown rust and up to 5–6 hours for yellow rust, as already observed in the latter case [38].

The above studies did not address the question of possible wash-off of spores already deposited on

healthy leaves, which could also have been studied by exposing both source and trap plants to incident rains.

### 3.2.3. Kinetic energy and spore removal

In the case of brown and yellow rusts, both single-drop and rain simulation experiments were summarised by a linear relationship between the number of spores removed (by single drops) or disease severity on trap plants (after rain simulation) and total kinetic energy of incident rain [17, 18]. Based on these relationships, some qualitative predictions of the 'dispersal ability' of different types of rain events were made, using the rain drop size distribution and the experimental relationships between kinetic energy of drops and disease severity [18]. The very numerous small drops have a reduced kinetic energy and their contribution to spore removal is marginal compared to the rare large drops of high kinetic energy [24, 26]. Therefore, thunderstorms have probably a much higher potential for spore removal than showers or widespread rains.

### 3.3. Dispersal of spores by concomitant wind and rain

Since the pioneer experiments of Faulwetter [10] on the dispersal of bacterial cotton angular leaf spot by 'wind-blown rain', dispersal by simultaneous wind and rain has received relatively little attention. Simulating both wind and rain in laboratory conditions requires highly specialised equipment such as the rain tower / wind tunnel (already mentioned in Sect. 3.1) complex at Rothamsted Experimental Station [11]. The complex was used to submit for 20 minutes brown rust sporulating lesions to a simulated rain with a drop diameter of 4.9 mm and a simulated wind of either 1 or 4 m/s. For the highest wind velocity, the number of removed spores linearly decreased with duration of exposure (by successive steps of 5 minutes each). With the lowest wind velocity, the number of spores removed after the first 5 minutes was significantly lower than for the highest wind velocity, but both types of simulated wind released the same number of spores for the further exposure periods.

The spore traps were located 5 m downwind of the spore source. Wind therefore increased the travel distance of spores primarily released by rain impaction from less than one meter [18] to at least 5 meters.

#### **4. Dispersal of spores and spread of disease in field conditions**

Results of laboratory and simulation experiments cannot be directly extrapolated to real field situations, because only a few subprocesses of the whole dispersal process are accessible to experiment. Moreover, the combination of several meteorological and biological factors cannot be accounted for in the controlled conditions of experiments. Specific experiments must therefore be designed in order to validate the conclusions drawn indoors. The processes of spore liberation and its contribution to airborne spore load, scrubbing of the airborne spores and their deposition on leaves by incident raindrops, and finally possible wash off of the deposited spores by rain (Fig. 2) need to be addressed to better understand the global effect of rain on disease spread.

##### **4.1. Airborne spore concentrations**

Diurnal periodicity in spore liberation over infected fields has been shown for spores of several cereal rust species pooled together [20], and specifically for black, brown [34] and yellow rust [38]. Continuous sampling of spores of brown and yellow rust with a suction sampler operating in the middle of artificially inoculated fields confirmed these patterns, with a main concentration peak around 11 h UT for brown rust and around 15 h UT for yellow rust [49], associated to the period of maximal wind velocity rather than to a specific characteristic of the fungi [38]. The delayed peak in yellow rust can be attributed to the need of an extended warm period to dry off the mucilaginous layer embedding the spores and inhibiting their removal.

Rain events dramatically disturb the diurnal periodicity recorded during dry days. Rain events, often associated with a high level of turbulence, have been shown to cause brief but large increase in airborne spore concentrations in black [21, 34], brown [34] and yellow rusts [15, 38, 49] at the start of rain. A systematical analysis of individual rain events during one crop season [49] showed that rain events of short duration and/or low intensity had no noticeable effect on further spore removal. In contrast, extended or violent rain showers exhausted available spore stocks and inhibited further sporulation processes for hours, as observed in the rain simulation experiments (see Sect. 3.2.2) and in early field experiments [34, 38]. Further analysis of several rain events will be necessary to validate this dual pattern.

##### **4.2. Rainborne spore concentrations**

Detection of cereal rust spores in rain samples has already been performed in a few studies. Presence of rust spores in rain samples was used to predict the local onset of rust epidemics in India, but only qualitative results (presence or absence of spores in the samples) were published [31]. Using quantitative techniques [40], spore concentrations were assessed in rain samples collected in the north-central USA during two seasons, and related to the amount of rain [41]. Anyway, these studies did not attempt to relate the spore concentrations to the dynamics of rain (intensity and duration). To study the dynamics of rain scrubbing (Fig. 2) of the airborne spores, rain samples were collected during periods of 10 minutes in glass vials placed on the edges of experimental plots heavily infected with either brown or yellow rusts during two cultural seasons [15, 49]. All samples contained large amounts of spores (range 300–30000 spores/cm<sup>3</sup>). For the 14 rain events analysed, there was a positive correlation between the spore concentration in rain water collected during the first 10 minutes of a rain event and the peak in airborne concentration recorded during the same period, illustrating the rapid scrubbing of airborne spores by the incident raindrops. For a given rain event, the spore

concentration in the water collected decreased linearly with the rain duration, and nearly no spores were collected in water after 40 minutes of continuous rain [49]. The scrubbing of airborne spores by rain had often been postulated without experimental validation [34, 38, 54] to explain sharp decreases in airborne spore concentrations during rain events.

#### 4.3. Infection during rain events

Wash off by incident drops of rust spores already deposited on leaves (Fig. 2) has often been hypothesised [38, 54] but was apparently never reproduced in laboratory conditions. Indirect evidence can be obtained in field conditions by exposing susceptible trap plants during a rain event, with or without rain-shelter, in a heavily infected field [14]. Preliminary experiments showed that infection by yellow or brown rust was dramatically reduced when trap plants were not protected from incident rain [49]. If and only if confirmed for a greater number of rain events, this result would mean that rain is globally detrimental for rust infection, the wash-off of already deposited spores by rain being the definitive and cumulative effect of rain. The 'educated guesses' of early authors [6, 43] would therefore be validated by field experiments.

Vertical upward spore dispersal between successive leaf layers by the way of splash droplets (Fig. 2) has not been explicitly demonstrated in rust. Comparison of yellow rust severity on different layers at successive assessment times suggests the existence of such a mechanism [44]. The intensity and the frequency of this dispersal mechanism may depend on the redistribution of splashed droplets within the canopy [1]. Such a mechanism of vertical dispersal may be necessary to explain rust spread when new leaf layers appear in absence of significant airborne concentration of rust spores. Vertical spore dispersal, along with lateral wind dispersal, may contribute to the rapid contamination of newly emerged leaf layers.

## 5. Conclusions

From the results of laboratory and field experiments reviewed above, it is clear that wind (Fig. 1) is not a limiting factor for rust spore dispersal on a short-scale. Even at very low velocity, wind is able to remove spores from leaves, the efficiency of the removal being dramatically increased by local turbulence. Wind dispersal, therefore, will depend more on the quantity of available spores than wind characteristics.

Rain (Fig. 2) is often considered as a conducive factor for the spread of disease because rain events are followed by an extended period of leaf wetness, which is critical for rust infection (germination and penetration processes) [52]. The effect of rain is here indirect. This review has shown, however, that rain events also have a direct influence on the epidemic's spread. The laboratory experiments reported above provided evidence of removal of cereal rust spores by rain drops, but evaluation of the global effect of rain events on the spread of disease is much more complex than in the case of wind. Using the results of laboratory and field experiments, it is possible to attempt a typification of rain events according to their probable effect on disease dispersal. Thunderstorms remove most of the available spores in a very short time period and deposit them very quickly on leaves, but they also exhaust sporulating lesions, impair further sporulation and wash-off the deposited spores. Conversely, light rains, even if less efficient for initial spore removal, may be much more conducive for the spread of disease. Intermittent rain events of light intensity are probably the most efficient, especially if they are associated with high wind speeds. Wind, by increasing the dispersal distance of spores removed during rain events, may influence mainly the spread of disease on larger scales. The relative importance of wind and rain as dispersal agents remains unknown and difficult to assess since both agents operate on different temporal and spatial scales.

Individual characteristics of rain events and their mechanistic consequences on disease dispersal are not included in predictive models. Precipitation

frequency was only marginally related to yellow rust severity [7] in the Pacific Northwest (USA). Rainfall occurring in winter or early spring is only indirectly related to further epidemic spread because of its positive effect on crop development [35, 50]. Inclusion of rain in predictive models will be difficult in the near future because prediction of rain events cannot be done with great accuracy on a small scale.

To conclude, more field experiments are needed to assess if it is worth including rain effects in predictive models of disease spread. Whatever the answer to this question is, the detailed knowledge of the mechanisms by which rain affects epidemic spread of cereal rusts could be included in mechanistic models of crop-disease development, which are research tools rather than decision-aid systems.

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