

1      **The role of conidia in the dispersal of *Ascochyta rabiei***  
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29    **Abstract**

30    *Ascochyta rabiei* asexual spores (conidia) were assumed to spread over short distances  
31    (~10 m) in a combination of rain and strong wind. We investigated the potential distance of  
32    conidial spread in three rainfall and three sprinkler irrigation events. Chickpea trap plants  
33    were distributed at the distances of 0, 10, 25, 50 and 75 m from infected chickpea plots  
34    before scheduled irrigation and forecast rainfall events. Trap plants were transferred to a  
35    controlled temperature room (20 °C) for 48 h (100% humidity) after being exposed in the field  
36    for 2–6 days for rainfall events, and for one day for irrigation events. After a 48 h incubation  
37    period, trap plants were transferred to a glasshouse (20 °C) to allow lesion development.  
38    Lesions on all plant parts were counted after two weeks, which gave an estimate of the  
39    number of conidia released and the distance travelled. Trap plants at all distances were  
40    infected in all sprinkler irrigation and rainfall events. The highest number of lesions on trap  
41    plants were recorded closest to the infected plots – the numbers decreased as the distance  
42    from the infected plots increased. There was a positive relationship between the amount of  
43    rainfall and the number of lesions recorded. A generalised additive model was developed that  
44    efficiently described spatial patterns of conidial spread. With further development, the model  
45    can be used to predict the spread of *A. rabiei*. This is the first systematic study to show that  
46    conidia distribute *A. rabiei* over longer distances than previously reported.

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62    **Keywords:** Ascochyta blight, epidemiology, conidial spread, wind-driven rain, chickpea,  
63    sprinkler irrigation.

64 **Introduction**

65 Chickpea (*Cicer arietinum* L.) is the second most important legume crop globally and is the  
66 most widely grown legume grain crop in Australia with >1,060,000 ha harvested in 2018  
67 (FAOSTAT 2020). Ascochyta blight caused by *Ascochyta rabiei* (syn. *Phoma rabiei*) is one of  
68 the most devastating chickpea diseases worldwide (Pande et al. 2005). With the exception of  
69 the Ord region in northern Western Australia, *A. rabiei* is the major biotic constraint to  
70 chickpea production in Australia with almost all chickpea growing areas affected (Bretag et  
71 al. 2008). *Ascochyta rabiei* survives on infected seed, volunteer chickpea plants and infested  
72 stubble, forming conidia that initiate primary infection. Infected seed gives rise to infected  
73 seedlings through transmission from germinating seeds. Conidia are spread by rain splash or  
74 wind driven rain. Pycnidial formation, conidial production, host infection and disease  
75 development are favoured by temperatures between 5 and 30 °C (optimum 20 °C), relative  
76 humidity > 95 % (Nene 1982), and wetness period of 10 h or more (Khan 1999). A longer  
77 wetness period is required for spore germination at sub-optimal temperatures, and infection  
78 is rare in hot and dry conditions (Jhorar et al. 1998). Symptoms develop within 5–6 days after  
79 infection in cool and moist conditions (Khan 1999). Pycnidia develop on the infected tissues,  
80 producing conidia that are responsible for the secondary spread of the pathogen (Pande et  
81 al. 2005). Conidia are the only spore type to have been reported in Australia. Putative  
82 ascospores have been reported only once in Australia (Galloway and MacLeod 2003),  
83 however, only one mating type has been detected and detailed molecular studies have  
84 shown Australian *A. rabiei* populations to be asexually reproducing (Leo et al. 2016; Bruvo et  
85 al. 2004; Mahmood et al. 2017), thus both primary and secondary infections are attributed to  
86 conidial infection.

87 Rain is needed for *A. rabiei* to infect and spread within a crop; dew alone will not  
88 result in significant spread (Moore et al. 2016). During a rain event, pycnidia imbibe water  
89 and hydrostatic pressure forces conidia in the pycnidia to exude through the ostiole in a  
90 cirrus. When a raindrop strikes the cirrus, the kinetic energy breaks up the spore mass and  
91 disperses the conidia to nearby healthy plants, thus spreading the disease (Kaiser 1992;  
92 Nene and Reddy 1987; Coventry 2012). The amount of kinetic energy in raindrops varies  
93 with the rainfall intensity, duration and size distribution with small drops having less kinetic  
94 energy and thus remove fewer spores (Sache 2000). Splash dispersal by large raindrops is  
95 considered more destructive because they tend to carry more spores (Sache 2000). Spores  
96 can also be washed from upper leaves to lower leaves (Sache 2000). Thunderstorms cause  
97 rapid spore dispersal from pycnidia and can result in diminution of inoculum (Coventry 2012).  
98 Low intensity, intermittent rains combined with high wind have been found to disperse spores  
99 more efficiently without diminishing the spore supply (Coventry 2012).

100            Irrigation is the principal mechanism for increasing grain yields where water is  
101 abundant, supplementing rainfall in drought seasons, or in areas receiving low rainfalls.  
102 Compared with furrow or flood irrigation, sprinkler irrigation results in the wetting of the entire  
103 crop canopy and constitutes a major source of moisture on all plant parts during dry  
104 conditions, thus increasing the risk of foliar diseases (Rotem and Palti 1969). Sprinkler  
105 irrigation plays an important role in the epidemiology of splash dispersed pathogens because  
106 spores are dispersed to their host under moist conditions and their germination is practically  
107 ensured (Lomas 1991). Unlike other forms of irrigation, water droplets generated by  
108 overhead sprinkler irrigation have the impact energy to dislodge spores (Lomas 1991). This  
109 makes it likely to play an important role in conidial spread for Ascochyta blight, as *A. rabiei*  
110 requires the impact energy of falling drops to disperse its conidia from pycnidia. Despite this,  
111 there is no study on the distance and quantity of *A. rabiei* conidia disperse during sprinkler  
112 irrigation events. Moreover, an assumption exists that conidia disperse over short distances  
113 during sprinkler irrigation events. Kimber et al. (2007) studied the spread of *A. rabiei* from  
114 primary infection foci (infected seedlings) in small plots (15 m x 9 m) in Israel. Sprinkler  
115 irrigation was used to irrigate plots, but only during dry periods, to provide conditions  
116 conducive to disease spread. Moreover, the number of sprinkler irrigation events and amount  
117 of water applied during each irrigation event were not recorded; therefore, any quantifiable  
118 relationship between irrigation, disease and the pathogen spread (via conidia) was not  
119 established.

120            It has been reported that *A. rabiei* conidia spread over short distances (~1 m) via  
121 splash dispersal, and up to 10 m in the presence of rain and strong wind (in the direction of  
122 wind) (Kimber 2002). However, the actual distance and number of conidia spread via wind  
123 driven rain have not been determined systematically (Coventry 2012). Kimber et al. (2007)  
124 showed Ascochyta blight spread over short distances (< 10 m) from primary infection foci  
125 (infected seedlings) in the direction of the prevailing winds. However, this was spread from a  
126 rather limited quantity of inoculum (a single infected seedling). The potential spread is likely  
127 to be greater when inoculum is plentiful. Previous studies have considered the spread of *A.*  
128 *rabiei* in biological rather than epidemiological terms, focusing on disease development and  
129 spread in the paddock and not on the spread of the pathogen via conidia (Coventry 2012).  
130 However, the presence of a pathogen does not automatically lead to disease development.  
131 Disease occurs due to complex interactions between a virulent pathogen, a susceptible  
132 host(s) and an environment favorable for long enough for the pathogen to cause disease  
133 (Agrios 2005).

134            Trapping spores on ‘trap plants’ distributed at various distances from the source of  
135 infection for a short period of time is an excellent way to investigate the distance of conidial

136 spread. Trap plants are distributed at various distances from a source of infection for a  
137 relatively short period of time to trap spores, and then transferred to a glasshouse to allow  
138 lesion development (Salam et al. 2011). The numbers of lesions give an estimate of the  
139 number of spores released and the distance travelled. Lesion development indicates that the  
140 dispersed conidia are viable. The actual distance *A. rabiei* conidia travel from a standing crop  
141 has not been determined in such a systematic manner on a large scale. Based on  
142 preliminary work aimed to determine the distance of *A. rabiei* conidia dispersal from previous  
143 year's infested stubble (Galloway, unpublished), we propose the pathogen is likely to spread  
144 over longer distances, than reported in the literature, in wind driven rain. Experiments  
145 conducted on plant pathogens, in a wind tunnel and rain tower, have shown that spores  
146 released by rain splash and then transported by wind are likely to be important in long-  
147 distance dispersal of pathogens (Fitt et al. 1989). Improving our understanding on how *A.*  
148 *rabiei* may spread in wind driven rain can help in predicting spatial patterns of conidial spread  
149 during rainfall events, and subsequent disease epidemics through modelling techniques  
150 (Coventry 2012). Models are required to predict disease risk and spread for varying  
151 environmental conditions, beyond their domain of study, as it is impractical to investigate  
152 pathogens' epidemiology in all growing environments (Diggle et al. 2002).

153 To investigate *A. rabiei* conidial spread in epidemiological rather than biological terms,  
154 focusing on the pathogen spread via conidia rather than the disease development and  
155 subsequent spread in the paddock, the present study asked the following questions: (1) can  
156 conidia spread over longer distances than previously reported, and (2) do conidia spread  
157 over the same distances in rainfall and sprinkler irrigation events?

158 **Methods**

159 *Study areas description*

160 This study was conducted at three different locations, Horsham (-36.728879, 142.157311), a  
161 paddock just outside Horsham (-36.745871, 142.115969) and Curyo (-35.779312,  
162 142.778332), in Victoria, Australia. All three sites had not had chickpea planted on them for  
163 at least 4 years. Trials established by Agriculture Victoria to assess the efficacy of fungicides  
164 against Ascochyta blight in chickpea were used to determine the distance of conidial spread  
165 in rainfall and sprinkler irrigation events. Genetically pure chickpea seed (variety PBA Striker)  
166 was sourced from the previous year's disease free seed-increase plots. Chickpea plots were  
167 sown to dimension 10 m x 2 m on 13 May 2019. A handful (~300 mL) of naturally infested  
168 stubble inoculum was evenly scattered across each plot at three to four nodes plant growth  
169 stage on 26 June 2019 to initiate infection. Infested residues were collected, after passing  
170 through the back of the header, from the previous year's trial of similar nature. A domestic  
171 mulcher was used to breakdown residues into smaller pieces, and inoculum was mixed  
172 thoroughly before inoculating plots. Disease incidence for each plot was recorded as the  
173 percentage of plot with stem infections (with 0 % being no stem infections; 50 % being half  
174 the plot having stem infections; and 100 % being plot completely dead). Control plots (that  
175 received no fungicide treatments) had 90–100 % plants dead when the experiments were  
176 conducted.

177 *Experimental design*

178 A method used by Salam et al. (2011) was modified for this study. At each location, 2–3  
179 weeks old chickpea trap plants (variety PBA striker) were distributed at the distances of 0,  
180 10, 25, 50 and 75 m from the control plots downwind of the prevailing wind direction.  
181 Downwind directions for the control plots were determined based on previous years' weather  
182 data. Trap plants were placed at the distances of 0–75 m along radial transects (there were  
183 no other chickpea crops downwind of the control plots where chickpea trap plants were  
184 distributed). There were 10 transects separated by 10-degree increments for a total of 90  
185 degrees between the first and the last transect. There were four trap plant stations (trap  
186 plants units) at both 0 and 10 m, and 10 trap plant stations at the distances of 25, 50 and  
187 75 m ([Table 1](#)). At the distances 0–25 m, each trap plant station consisted of 10 chickpea  
188 seedlings in two pots (five seedlings per pot). At the distances 50 and 75 m, each trap plant  
189 station consisted of three chickpea seedlings in a single pot. The distances between  
190 individual trap plant stations at each distance (0, 10, 25, 50 and 75 m) were determined  
191 using the Law of Cosine ([Table 1](#)). As there were only 4 trap plant stations at the distances of  
192 0 and 10 m, they were placed along transects 1, 4, 7 and 10, with 30 degrees difference

193 (space) between each trap plant stations, to increase the chances of trapping conidia. At  
194 distances of 25–75 m: all 10-trap plant stations were placed along 10 transects with 10  
195 degrees space between the individual trap plant stations ([Table 1](#)). The locations of trap plant  
196 stations across transects were marked with flags to ensure trap plants were always  
197 exchanged in the same spot for the entire duration of the experiment ([Table S1](#)). No  
198 fungicides were applied over the duration trap plants were deployed in the paddock ([Table 2](#)).

199 *Spore trapping*

200 The distance of conidial spread was determined from September through to  
201 December 2019. Spores were trapped in two rainfall events (event one ~ 4.6 mm, and event  
202 two ~ 18.6 mm) in Horsham, and a single rainfall event of 0.8 mm in Curyo ([Table 2](#)). A  
203 sprinkler irrigation system (Hunter ®: Model MP300090210) located in a paddock just outside  
204 Horsham was used to determine the distance of conidial spread for three irrigation events.  
205 Sprinklers were set 110 cm above ground and were operated at 3.5 bar pressure. Each  
206 sprinkler irrigation event was equivalent to 10–12 mm of simulated rain over approximately  
207 90 minutes (a small rain shower of ~0.6 mm occurred during sprinkler irrigation event 3)  
208 ([Table 2](#)).

209 In order to determine the distance of conidial spread in rainfall and sprinkler irrigation  
210 events, trap plants were distributed in the paddock at the distances of 0–75 m from control  
211 plots before forecast rainfall and scheduled irrigation events, respectively. Trap plants were  
212 transferred to a controlled temperature room set at 20 °C for 48 hours (100 % humidity) after  
213 being exposed in the field for 2–6 days for rainfall events, and for one day for irrigation  
214 events ([Table 2](#)). The exposure period in paddock for the irrigation events was shorter for two  
215 reasons. Firstly, each irrigation event was a single continuous controlled event as opposed to  
216 natural rainfall events that fell in multiple showers over several days. Secondly, only the  
217 infected plot was being irrigated (trap plants at the distances of 10–75 m were not getting  
218 wet), therefore longer exposure period may have led to conidial desiccation on trap plants at  
219 the distances of 10–75 m. After 48 hours incubation period, the trap plants were transferred  
220 to a glasshouse (20 °C) to allow lesion development. Plants were watered daily via trays to  
221 prevent splash dispersal to nearby plants. The numbers of lesions were counted on all plant  
222 parts after two weeks giving an estimate of the number of conidia released and the distance  
223 travelled.

224 Weather data was recorded by an automated weather station (Measurement  
225 Engineering Australia, Adelaide, Australia). The data collected composed of date and time,  
226 air temperature (° C), dew point (° C), rainfall (mm), relative humidity (%), wind speed (ms<sup>-1</sup>),  
227 and average wind direction (°) recorded at 10-minutes intervals. The wind vane was not

properly calibrated for the weather station at Curyo. Therefore, Birchip Cropping Group's (BCG) agriculture farm (located 10 km away from the experimental location) weather station's (Davis Australia) wind direction data was used for the interpretation of results (wind direction data was not included in the analysis, as wind direction is highly unstable and constantly changes). Wind direction data, recorded by Australia Bureau of Meteorology, at two locations (Hopetoun Airport 39 km, and Charlton 75 km; located in the same area as BCG and Curyo) were retrieved using the R programming language (R Core Development Team 2019) contributed packages 'bomrang' v0.7.0 (Sparks et al. 2017) and 'stationaRy' v0.5.1 (Iannone 2020) and compared with the BCG's weather station data to ensure the BCG's weather station wind direction data was valid (Fig. S1).

### ***Development of a model to describe spatial patterns of conidial spread***

A preliminary linear mixed model analysis was conducted in the R programming language, using the lmer() function from the contributed package 'lme4' v1.1-1.23 (Bates et al. 2015), to investigate the influence of 'spread event' (as a random variable: any spread event regardless of sprinkler irrigation or rainfall events) and 'experimental location' on the number of lesions recorded. A reductive approach was used to investigate the significance of the random variables 'spread event' and 'experimental location' before modelling spatial patterns of conidial spread. Preliminary analysis showed the influence of 'experimental location' to be non-significant implying conidial spread patterns were consistent between experimental locations. This result allowed generalised additive model (GAM) to compare the influence of weather variables without the need to include experimental location as a dependant factor. Generalised additive models were used because they have been reported to efficiently describe the effect of various environmental variables on plant pathogen interactions (Sparks et al. 2011; Yee and Mitchell 1991). The GAM for conidial dispersion, based on the pooled data across all experimental locations for all six spread events, was fitted using the R programming language via the gam() function from the contributed package 'mgcv' v1.8-31 (Wood 2011). Standard information criterion, such as Akaike's Information Criterion (AIC) (Akaike 1974), the Bayesian Information Criterion (BIC) (Gideon 1978), as well as adjusted R-squared values were compared across models to select the best fitting model.

Letting the mean number of lesions for pot  $i$  (pooled across all experimental locations for all six spread events) be the response variable  $Y_i$ , and  $x_i$  be the associated covariate vector with the distance of pot  $i$  from the infected plot being  $x_{i1}$ , the mean wind speed being  $x_{i2}$  and the amount of irrigation or rainfall being  $x_{i3}$ , during spread events, the GAM model that achieved best fit was of the form:

$$Y_i \sim \text{Tw}_p(\mu_i, \phi), \quad \log \mu_i = \alpha + \sum_{j=1}^3 f_j(x_{ij})$$

where the  $f_j$  are independent “thin-plate splines” which are the default smoother used by the `gam()` function. For details about the mathematical specification of these and other smoothing splines, see Wood (2017). The use of the Tweedie distribution family to model the response data is now standard in the case of interval scale measurements with substantial zero-inflation, i.e., a positive probability mass at zero will indicate no lesions were observed (Dunn 2004; Hasan and Dunn 2010). As it is implemented in the `tw()` function passed to the family parameter in the `gam()` function, the power parameter  $p$  – which relates the Tweedie variance to its mean – is estimated from the data (Wood 2011). The chosen link function for this family was the logarithm link; the canonical or natural link function for Tweedie distributions, and the default supplied to the `gam()` function. The `gam()` function also allowed the dimension of the basis for smoothed terms to be manually selected via the parameter  $k$ , which controls the “wigginess” of the resultant curve. The value of  $k$  was chosen to be 5 (*i.e.*  $k = 5$ ) for all three predictors due to rather limited data.

## 275 ***Data cleaning and visualisation***

276 Data were processed and visualised in R using the contributed packages ‘tidyverse’ v1.3.0  
 277 (Wickham et al. 2019), ‘lubridate’ v1.7.8 (Grolemund and Wickham 2011) and `‘clifro’ (Seers  
 278 and Shears 2015) for wind roses. The best fitting GAM was visualised using a custom  
 279 function created for this work that uses the contributed package ‘mgcViz’ v0.1.6 (Fasiolo et  
 280 al. 2019). Mean wind speed was calculated using a circular averaging function from  
 281 ‘SDMTools’ v1.1-221.2 (VanDerWal et al. 2014).

## 282 **Results**

### 283 ***Model fit***

284 The linear mixed model analysis indicated that experimental location had no significant effect  
 285 on the number of conidia trapped and distance travelled during each spread event, thus  
 286 experimental location was not used when fitting the GAMs. Thirteen GAM models were  
 287 evaluated to efficiently describe spatial patterns of conidial spread. The model selected as  
 288 the best fitting had an adjusted R-squared value of 0.674, AIC value of 663 and a BIC value  
 289 of 709. The smooth terms for distance (D) and precipitation (P) were significant terms ( $p <$   
 290 0.05). The smooth term for wind speed (W) was not significant. However, including this term  
 291 only as a linear predictor reduced the fitness of the model, R-squared value of 0.657, AIC  
 292 value of 689 and BIC value of 729, so the smoothed term was included in the final model  
 293 ([Fig. 1](#)).

294     *Dispersal in rainfall events*

295     Trap plants at all distances (0–75 m) were infected in all 3-rainfall events, indicating conidia  
296     spread to 75 m in each rainfall event. There was a strong correlation between mean wind  
297     speed, rainfall intensity, distance from the infected plot, and the number of conidia trapped  
298     (counted as lesions). The highest number of lesions on trap plants were recorded closest to  
299     the control plot at 0 m in each rainfall event - the numbers decreased as the distance from  
300     the control plots increased (Fig. 2). The number of lesions recorded increased with  
301     increasing rainfall. At Horsham, a total of 159 lesions were recorded at all distances in rainfall  
302     event 1 (~ 4.8 mm), and 275 lesions were recorded in rainfall event 2 (~18.6 mm) ([Table 2](#)).  
303     In rainfall event 1 (Horsham Rain 1), a uniform conidial spread pattern across transects was  
304     observed at the distances of 0–25 m (i.e., all trap plant stations at the distances of 0–25 m  
305     were infected), whereas a non-uniform conidial spread pattern across transects was  
306     observed at the distances of 50 and 75 m ([Fig. 3](#)). Uniform conidial spread pattern across  
307     transects at all distances was observed in rainfall event 2 (Horsham Rain 2). Mean wind  
308     speed and direction varied during rainfall events 1 and 2 ([Fig. 4](#)).

309           At Curyo, a total of 193 lesions were recorded in a single rainfall event (Curyo Rain 1)  
310     of 0.8 mm ([Table 2](#)). Conidial spread pattern was almost uniform across transects at the  
311     distances of 0–50 m, while a non-uniform conidial spread pattern across transects was  
312     observed at 75 m ([Fig. 3](#)). Mean wind speed and direction varied during the spread event  
313     ([Fig. S1](#)).

314     *Dispersal with sprinkler irrigation*

315     Trap plants at all distances (0–75 m) were infected in all three irrigation events. There was a  
316     strong correlation between mean wind speed, irrigation, distance from the infested plot and  
317     the number of conidia trapped (counted as lesions). The highest numbers of lesions on trap  
318     plants were recorded closest to the control plot in each irrigation event - the numbers  
319     decreased as the distance from the control plot increased (Fig. 2). The total number of  
320     lesions recorded on trap plants varied greatly between all three irrigation events, with a total  
321     of 250 lesions recorded in event 1 (~10–12 mm), 368 lesions in event 2 (~10–12 mm) and  
322     477 lesions in event 3 (~10–12 mm irrigation event and a small rain shower of 0.6 mm)  
323     ([Table 2](#)). In event 1 and 3 (Horsham Irrg1 and Horsham Mxd1), a uniform conidial spread  
324     pattern across almost all transects was observed at the distances of 0–50 m, whereas  
325     conidial spread pattern across transects was not uniform at 75 m ([Fig. 3](#)). In event 2: conidial  
326     spread pattern across transects was uniform at the distances of 0–25 m, whereas a non-  
327     uniform conidial spread pattern across transects was observed at the distances of 50 and 75  
328     m ([Fig. 3](#)). Mean wind speed and direction varied between each spread event ([Fig. 4](#)).

329 **Discussion**

330 Conidia were shown to distribute *A. rabiei* over longer distances than previously reported.  
331 Conidia dispersed 75 m from infected plots in all sprinkler irrigation and rainfall events. The  
332 mean number of lesions recorded on trap plants decreased as the distance from infected  
333 plots increased. There was a significant relationship between mean wind speed, the amount  
334 of precipitation (rainfall and/or sprinkler irrigation) and the number of conidia trapped. The  
335 experimental location had no significant effect on the number of conidia trapped and distance  
336 travelled during each spread event. A model was developed that efficiently described spatial  
337 patterns of conidial spread under field conditions. Given more data and further development,  
338 this model can be used to predict the spread of *A. rabiei*.

339 The highest mean number of lesions on trap plants were recorded closest to the  
340 control plots in all spread events – the numbers decreased as the distance from the control  
341 plots increased. These results support the findings from previous studies (Coventry 2012;  
342 Kimber et al. 2007) who showed *A. rabiei* inoculum density decreased as the distance from  
343 infected foci increased. A similar dispersal pattern has been observed for other splash  
344 dispersed pathogens, such as *Colletotrichum acutatum* (Yang et al. 1990),  
345 *Parastagonospora nodorum* (previously known as *Septoria nodorum*) (Griffiths and Ao 1976),  
346 and *Ascochyta fabae* (Pedersen et al. 1994). For splash dispersed pathogens, plants close  
347 to the source of infection are more exposed to spore load due to localised splash dispersal  
348 and become infected quickly, resulting in more lesions (Coventry 2012). More lesions were  
349 recorded on trap plants with increased rainfall and in an event with a combination of a small  
350 rain shower and a sprinkler irrigation event compared to a sprinkler irrigation event alone (in  
351 case of sprinkler irrigation event 3, i.e., Horsham Mixd), suggesting that increased  
352 precipitation dislodged more conidia, which were dispersed by wind driven rain. The amount  
353 of rainfall has been reported to have a major influence on Ascochyta blight severity and the  
354 distance disease spreads (Coventry 2012).

355 Wind speed and direction coinciding with increased rainfall influenced the spatial  
356 patterns of conidial spread. Uniform conidial spread across transects at all distances was  
357 observed in rainfall event 2 (Horsham Rain 2), which indicates strong winds from NW  
358 directions coincided with increased rainfall and dispersed conidia across all transects  
359 downwind (SE, NE) from the infected plot. Although trap plants were located downwind in  
360 rainfall event 1 (Horsham Rain 1), uniform conidial spread across all transects was not  
361 observed at 50–75 m, which reflects the influence of reduced rainfall and rather low wind  
362 speed (compared to rainfall event 2) during the spread event. Compared to rainfall event 1 at  
363 Horsham, the amount of rainfall and wind direction appeared to have limited influence on the  
364 number of conidia trapped and the spatial patterns of conidial spread for rainfall event 3

365 (Curyo Rain 1) at Curyo. More lesions (193 lesions) were recorded in a single rainfall event  
366 of 0.8 mm at Curyo, although trap plants were not located downwind. In addition, conidial  
367 spread pattern was almost uniform at the distances of 0–50 m. Conversely, fewer lesions  
368 (159) were recorded in a rainfall event of 4.8 mm at Horsham when trap plants were located  
369 downwind; and conidial spread pattern was uniform at the distances of 0–25 m only.  
370 However, a direct comparison between these two rainfall events is not possible due to a  
371 location difference and rather limited data. Furthermore, our model does not consider  
372 continuously changing wind direction and dynamics associated with turbulence, which may  
373 assist in explaining variation in spatial patterns of conidial spread. Conidia dispersed 75 m  
374 and spatial pattern of conidial spread was uniform across transects at the distances of 0–50  
375 m, when the amount of rainfall was as low as 0.8 mm (Curyo Rain 1). This suggests that only  
376 a small amount of rain is required to dislodge a large number of conidia. A similar dispersal  
377 pattern has been reported for the sexual spores (ascospores) of *A. rabiei*, where ascospores  
378 discharge depended more on the occurrence of rain than the amount (Trapero-Casas et al.  
379 1996).

380 More conidia (368) were trapped in sprinkler irrigation event 2, compared to sprinkler  
381 irrigation event 1, but conidial spread pattern across transects was not uniform at the  
382 distances of 50–75 m. Conversely, fewer conidia (250) were trapped in sprinkler irrigation  
383 event 1, but conidial spread pattern was almost uniform across transects at all distances.  
384 The lower number of spores and non-uniform spatial spread pattern for sprinkler irrigation  
385 event 2 is rather surprising because an equal amount (~10–12 mm) of irrigation was applied  
386 in both sprinkler irrigation events. Moreover, stronger mean wind speed was recorded for  
387 sprinkler irrigation event 2 and the non-infected trap plants were located downwind (the  
388 mean wind direction was from the west, therefore trap plants placed at the distances of 50–  
389 75 m east of the infected plot were expected to be uniformly infected). The reasons for this  
390 dispersal pattern are not clear, and our analysis is limited by rather limited data. Detailed  
391 studies are needed to get a more complete picture of spatial patterns of conidial spread  
392 during sprinkler irrigation events.

393 Above canopy irrigation reduces mean ambient air temperature by 7–9 °C and  
394 increases humidity up to 30 % during the irrigation period (Rotem and Palti 1969). This has  
395 implications for Ascochyta blight development within an irrigated chickpea paddock, as *A.*  
396 *rabiei* only requires 3–10 h leaf wetness for host penetration and infection at the optimum  
397 temperature (Khan 1999; Moore et al. 2016). Therefore, extended periods of sprinkler  
398 irrigation events may not be required for disease development, especially in a cool and moist  
399 season. In the laboratory; more than 50 % of conidia, incubated on membrane filters,  
400 germinated after four days at relative humidity as low as 12.5 % (temperature 20 °C)

401 (Coventry 2012). *Ascochyta rabiei* conidia have been shown to survive and remain infective,  
402 when inoculated on chickpea seedlings in a growth chamber, during dry periods lasting 24 h  
403 (Armstrong-Cho et al. 2004). However, conidia are unlikely to withstand dry conditions for  
404 extended periods of time under field conditions, especially at sub-optimal temperatures. For  
405 conidial spread with sprinkler irrigation, this implies that even though conidia may spread to  
406 equal distances (75 m in this case) during sprinkler irrigation and rainfall events, leaf wetness  
407 provided by dew and/or humidity over 90% to facilitate conidial penetration and infection will  
408 be important in establishing disease on chickpea outside the irrigated paddock in the  
409 absence of rain (if temperature requirement is met). Conversely; rainfall usually occurs over  
410 a large area, and only a few mm of rain later in the day or at night satisfies the leaf wetness  
411 requirement (Moore et al. 2016). Therefore, leaf wetness provided by dew and/or high  
412 relative humidity is not necessary to facilitate conidial penetration and infection at longer  
413 distances for conidia dispersed in rainfall events. This further implies that rainfall might be  
414 more important than sprinkler irrigation for conidial spread and subsequent disease  
415 development at farther distances. Future work determining the viability of conidia after  
416 exposure to different duration of dry periods, under field conditions, is necessary to  
417 understand the duration of dry period over which *A. rabiei* conidia can survive when  
418 dispersed outside the irrigated paddock. To the best of our knowledge, this is the first  
419 systematic study to determine conidia dispersal with sprinkler irrigation.

420 The finding that conidia travelled 75 m during all rainfall and sprinkler irrigation events  
421 suggests that conidia can potentially play a role in the long-distance dispersal of *A. rabiei*.  
422 Conidia dispersed 50 m from naturally infested stubble from the previous year (there were no  
423 trap plants farther than 50 m to test long-distance dispersal) (Galloway, unpublished). The  
424 sexual spores of the fungus (ascospores) have been reported to travel up to hundreds of  
425 meters to several kilometres from the source of infection (Trapero-Casas et al. 1996; Kaiser  
426 and Küsmenoglu 1997; Trapero-Casas and Kaiser 1992). The present study did not have  
427 trap plants farther than 75 m from the infected plot and wind speed during spread events was  
428 rather low with a maximum mean wind speed of  $6.5 \text{ ms}^{-1}$  and maximum gust of  $11.2 \text{ ms}^{-1}$ . It  
429 is likely that conidia could dispersed farther than 75 m, especially when wind speed is high  
430 and there are strong wind gusts. It has been hypothesized that if conidial dispersal is aided  
431 by turbulent winds and conidia enter the turbulent boundary layer, they could be dispersed to  
432 distances that are associated with ascospores only (McCartney and West 2007; Coventry  
433 2012). While the role of conidia in long-distance dispersal has not been recognized, it has  
434 been hypothesized that liquid suspensions in air (aerosols) can incorporate a large number  
435 of conidia in heavy rain that can be transported over longer distances by wind (Coventry  
436 2012). A severe *Ascochyta* blight epidemic developed across the southern region of Australia

437 in 1998. It is speculated that aerosols developed during heavy rains, which travelled over  
438 hundreds of meters to kilometers and contributed to the epidemic development (Coventry  
439 2012). This suggests that role of conidia in the long-distance dispersal has been  
440 underestimated. Further work distributing trap plants at distances farther than 75 m is  
441 necessary to determine the potential distance conidia can travel.

442 When fitting observed data to logistic models, the known biology of pathogens needs  
443 to be considered rather than simply considering the shape of the curve (Sparks et al. 2008).  
444 Generalised additive models are data-driven not model-driven, as they allow the data to  
445 determine the shape of the response curves rather than being limited by the shapes  
446 attainable through some parametric specification. The inability to control environmental  
447 factors, such as wind speed, amount of rainfall, temperature and humidity makes it difficult to  
448 use parametric statistical models e.g., generalised linear models (GLMs) to make inferential  
449 comparisons across sites without a high risk of the presence of confounding variables.  
450 Generalised additive models offer a flexible modelling approach that provides a good  
451 balance between highly interpretable linear models that have undesirable predictive  
452 capabilities and black-box machine learning approaches, such as neural networks, which  
453 have excellent predictive performance but low interpretability (Hastie and Tibshirani 1990).  
454 This capacity to achieve interpretable separation of covariate contributions in a strong  
455 descriptive model is the main reason that GAMs were chosen to model spatial patterns of  
456 conidial spread. A model was developed that efficiently described spatial patterns of conidial  
457 spread under field conditions. The model will be useful for chickpea growers in identifying the  
458 scale of potential damage and could be used to predict the spread of *A. rabiei* with further  
459 development. When further developed, this model can also be used to inform chickpea  
460 growers how far to grow chickpea from the neighbouring paddocks.

461 A comparison of conidial spatial dispersal patterns in identical amount of irrigation  
462 and rainfall events would have been beneficial, but constantly changing wind speed and  
463 direction makes a direct comparison difficult under field conditions. Conidial spread was  
464 investigated in the late stage of plant growth with 90–100 % plants in plots being infected.  
465 Detailed studies at different plant growth stages and disease incidence levels are now  
466 needed to provide a more complete picture of distance conidia disperse and their spatial  
467 dispersal patterns. It should be noted that counting lesions on trap plants gave an estimate of  
468 only viable conidia dispersed (not the total number of conidia dispersed), which could cause  
469 disease under field conditions if conditions are favourable for disease development. This  
470 study was primarily conducted to get an estimate of the distance conidia travel and remain  
471 viable. Future studies should consider using trap plants, spore traps and molecular  
472 approaches (e.g. trapping spores sticky tapes and subsequent spore count using quantitative

473 PCR) to get an accurate estimate on the number of conidia dispersed. Spore trapping  
474 coupled with quantitative PCR has been demonstrated to be a useful tool for epidemiological  
475 studies and biosecurity surveillance (Vogelzang 2012). More work is required to establish the  
476 equivalency of number of lesions to the number of conidia. Many other factors are involved in  
477 the spore dispersal, including changing wind directions, turbulence and topographic factors  
478 (Coventry 2012), which add complexity to the model and were not considered in the present  
479 model. These factors need to be addressed in future models.

480 **Declarations**

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484 GRDC provided financial assistance in this work through their co-investment project  
485 DAV00150.

486 **Conflict of interest**

487 We confirm that we have no conflict to interest to disclose.

488 **Ethical approval**

489 This study did not involve working with animals or humans

490 **Consent to participate**

491 Not applicable

492 **Consent for publication**

493 Not applicable

494 **Availability of data and material**

495 All raw and generated data and further associated materials have been made available as a  
496 research compendium available from <https://doi.org/10.5281/zenodo.3810826>

497 **Code availability**

498 All code used in the analysis and data visualisation of this manuscript has been made  
499 available as a research compendium available from  
500 <https://doi.org/10.5281/zenodo.3810826>.

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648 **Figure captions**

649 **Fig. 1** Generalised additive model fit for smoothed terms of three predictors: distance, mean  
650 windspeed (mws) and total precipitation (sum\_rain)

651 **Fig. 2** Mean number of conidia dispersed (counted as lesions) during each spread event at  
652 each distance, where 'n' (indicated by the point size) represents the number of pots that  
653 shared the same mean number of lesions counted per trap plant per pot. The mean count  
654 values are shown on the y-axis and distance conidia dispersed is shown on the x-axis. Red  
655 dots indicate median lesions counted per trap plant. Conidia dispersed 75 m in all irrigation  
656 and rainfall event

657 **Fig. 3** Heatmaps showing spatial patterns of conidial spread during each spread event.  
658 Spatial spread patterns were determined by counting lesions on trap plants (placed along  
659 radial transects at the distances of 0–75 m from infected plots), where 'n' represents mean  
660 number of lesions per trap plant per pot. Concentric circles show distance of trap plants from  
661 the infected plots: the inner single solid dot represents 0 m distance and the outer most  
662 dotted line represents 75 m distance from the infected plot

663 **Fig. 4** Wind roses, for all spread events except Curyo Rain 1, showing wind speed and  
664 direction recorded at 10 minutes interval

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679      Table 1 Distances from infected plot, number of trap plants stations and distances between  
 680      each station.

Distance from infected plot (m)	Number of trap plants stations	Length of an arc (m)	Distance between each trap plant station (m)	Degrees between each trap plant station
0	4	NA*	NA*	NA*
10	4	14.14	5.18	30 °
25	10	35.36	4.36	30 °
50	10	70.71	8.72	10 °
75	10	106	13.07	10 °

681      \* NA means trap plants were placed together (0 degrees) at 0 m distance.

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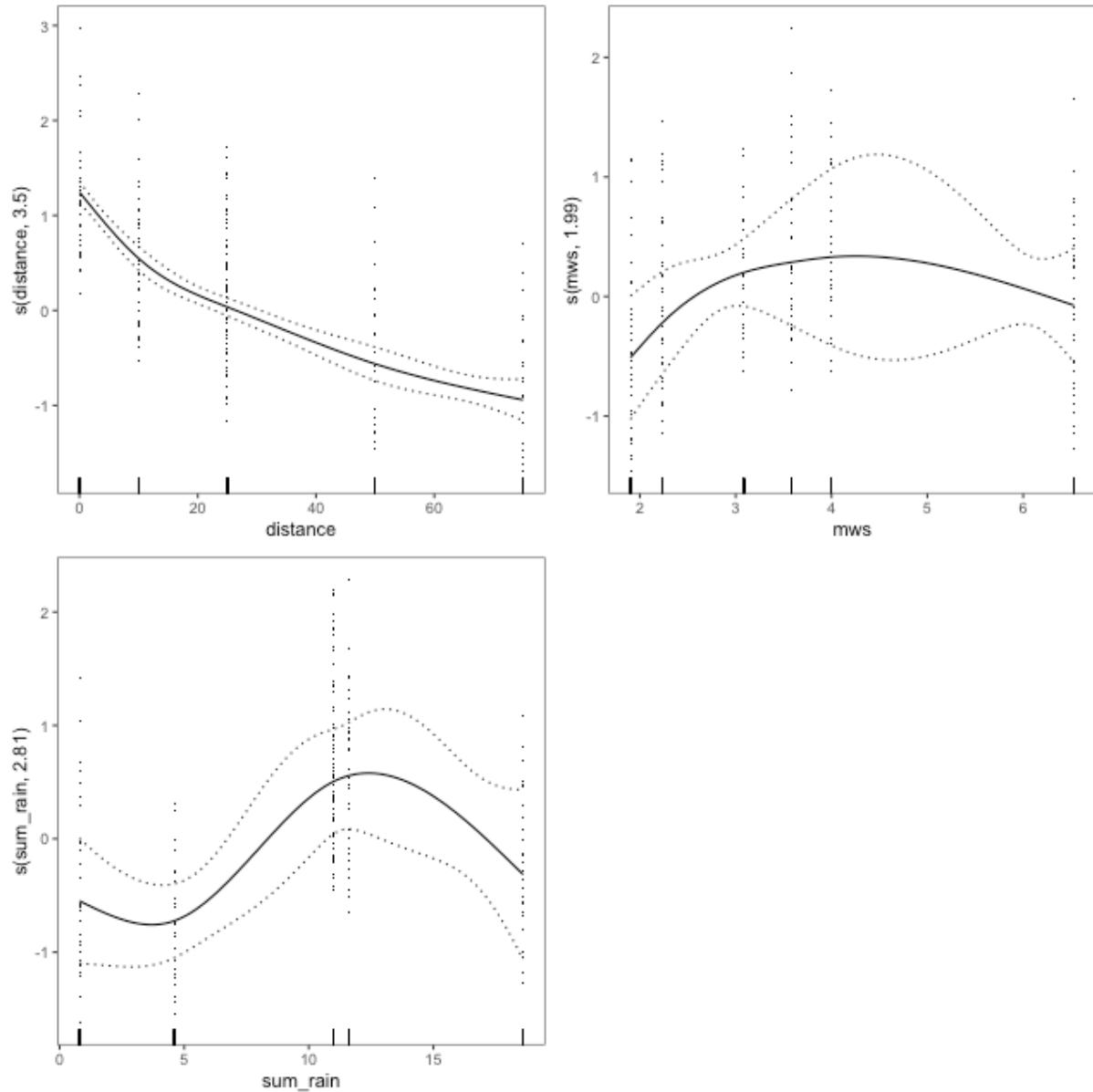
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695      Table 2 Amount and duration of precipitation (rain and/or sprinkler irrigation), mean wind  
 696      speed, hours trap plants deployed in the paddock and total lesions recorded on trap plants  
 697      during each spread event. A small rain shower of 0.6 mm occurred during sprinkler irrigation  
 698      event 3 (Horsham Mixd 1)

Spread event	Precipitation (mm)	Precipitation duration (minutes)	Mean wind speed	Hours trap plants deployed in the paddock	Total lesions recorded
Horsham Irrg 1	10 - 12 *	90*	1.9	24	250
Horsham Irrg 2	10 - 12 *	90*	2.2	24	368
Horsham Mixd 1	10 - 12 * and 0.6	90* and 30	6.5	24	477
Horsham Rain 1	4.8	170	3.1	48	159
Horsham Rain 2	18.6	510	4	144	275
Curyo Rain 1	0.8	40	3.6	48	193

699      \* Indicates values for sprinkler irrigation events

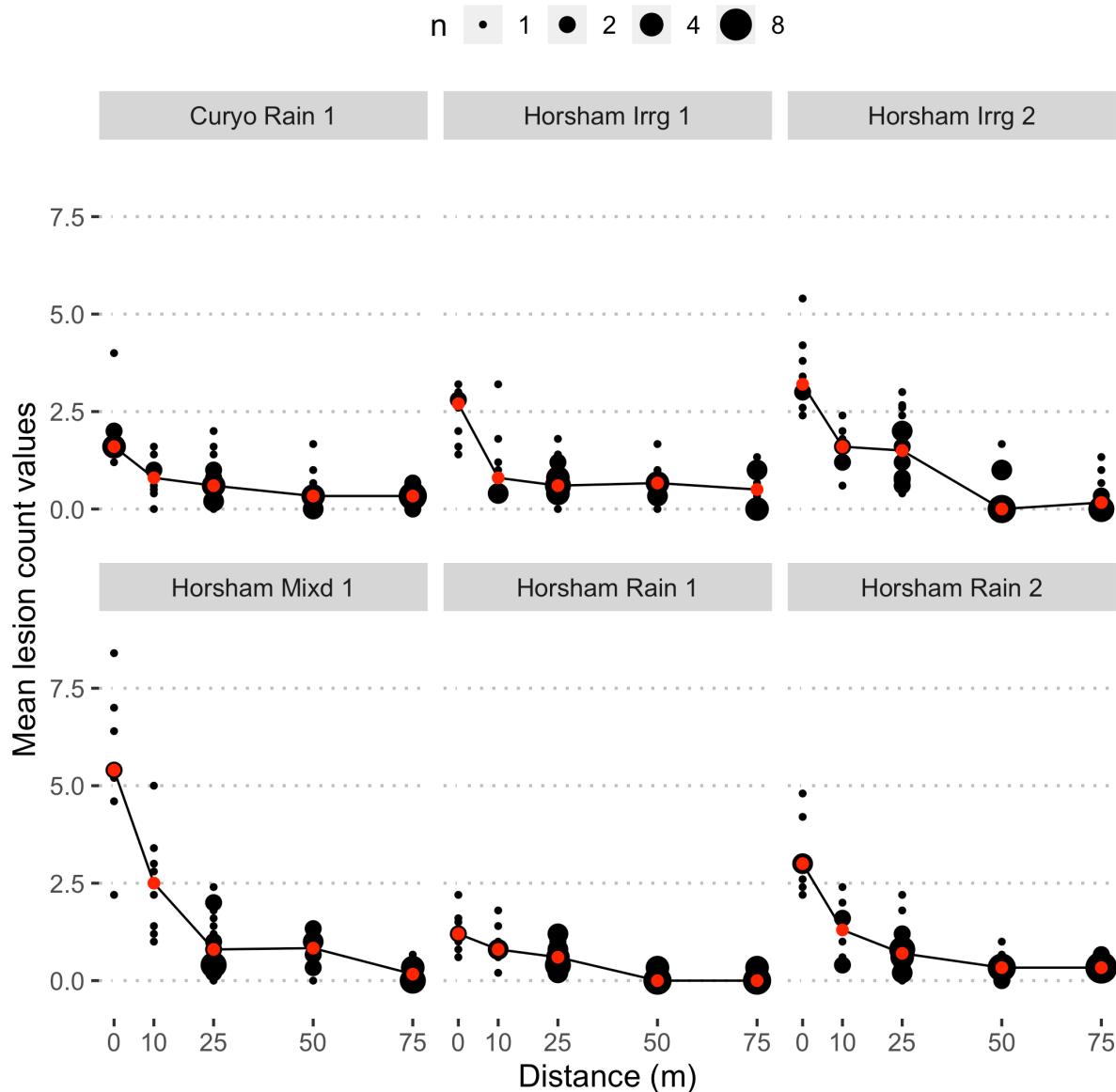
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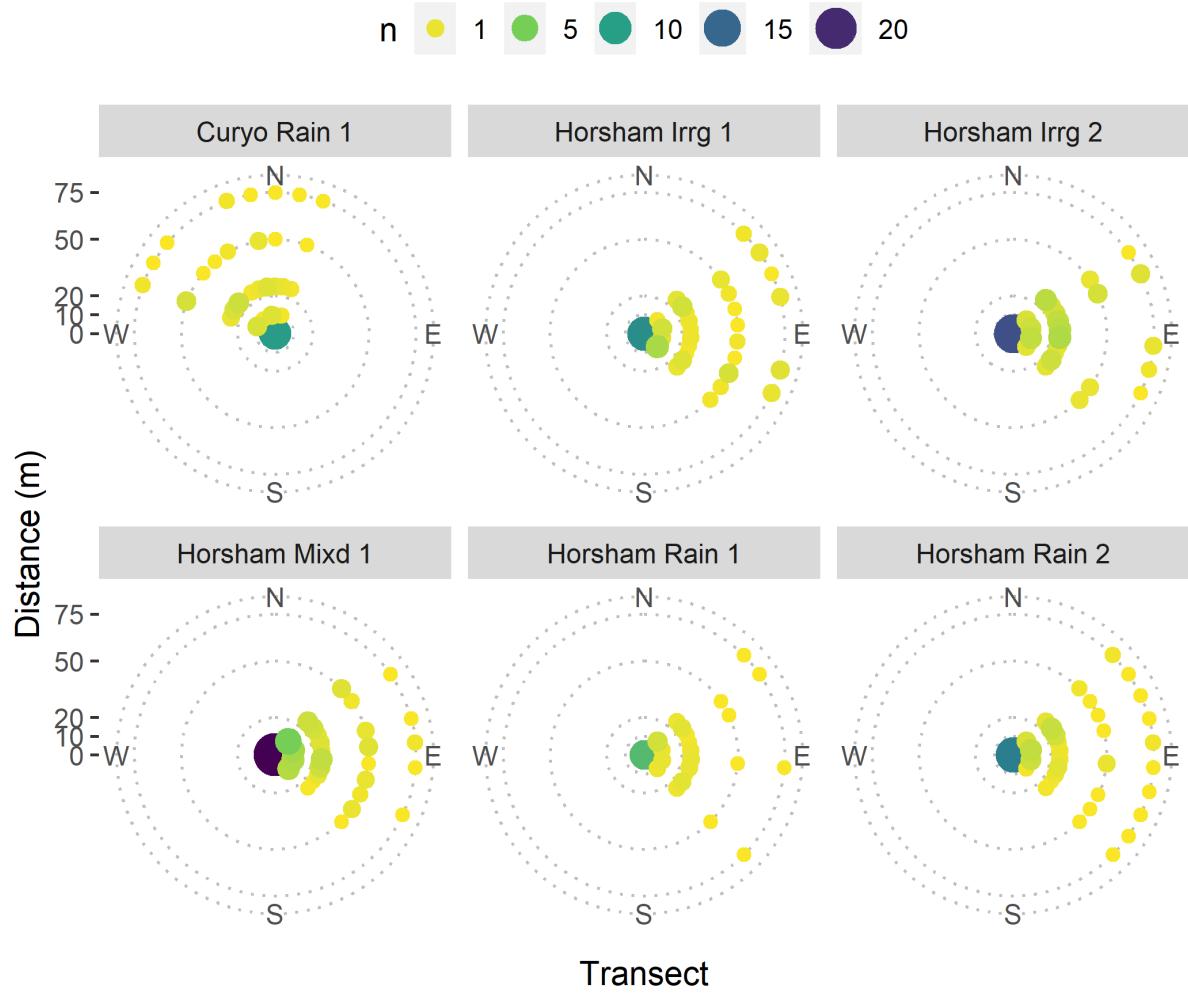


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**Fig. 1** Generalised additive model fit for smoothed terms of three predictors: distance, mean windspeed (mws) and total precipitation (sum\_rain)



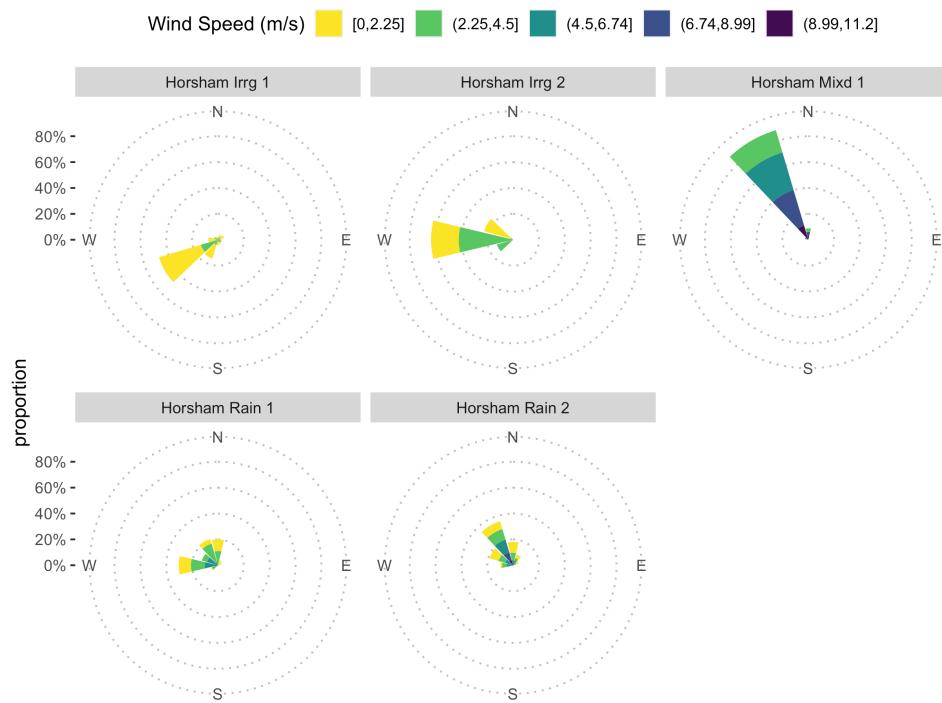


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712 **Fig. 3** Heatmaps showing spatial patterns of conidial spread during each spread event.  
 713 Spatial spread patterns were determined by counting lesions on trap plants (placed along  
 714 radial transects at the distances of 0–75 m from infected plots), where 'n' represents mean  
 715 number of lesions per trap plant per pot. Concentric circles show distance of trap plants from  
 716 the infected plots: the inner single solid dot represents 0 m distance and the outer most  
 717 dotted line represents 75 m distance from the infected plot

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721 **Fig. 4** Wind roses, for all spread events except Curyo Rain 1, showing wind speed and  
722 direction recorded at 10 minutes interval

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## Supplementary material

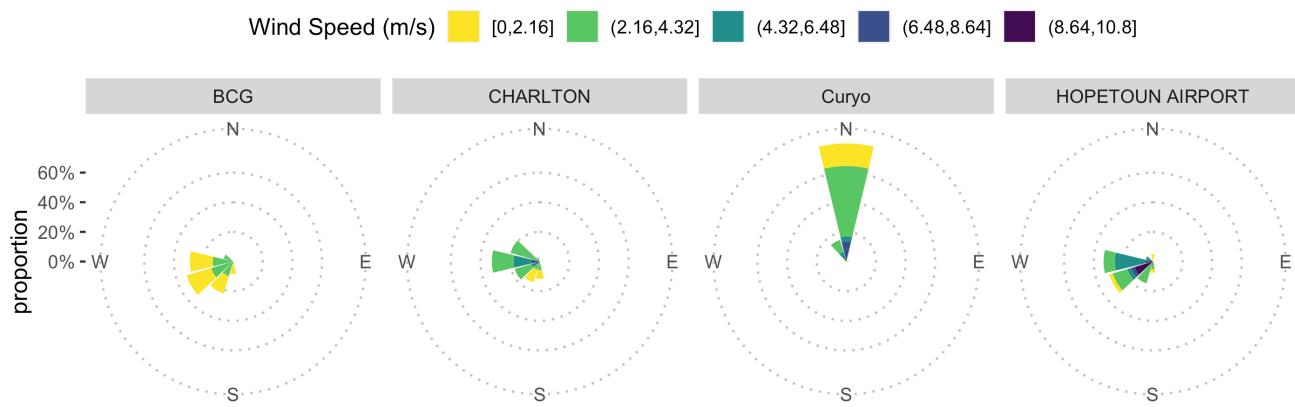
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739 **Table S1** Transects location detail for each experimental location. Plant Breeding Centre  
 740 (PBC) represents the irrigated plot where conidial spread in sprinkler irrigation events was  
 741 investigated. Trap plant stations were placed along transects-1, 4, 7 and 10 (shaded) at the  
 742 distances of 0 and 10 m; and across all transects 10 at the distances of 25 – 75 m

<b>Experimental location</b>	<b>Transect number</b>	<b>Transect location (degrees)</b>
Horsham	1	45
Horsham	2	55
Horsham	3	65
Horsham	4	75
Horsham	5	85
Horsham	6	95
Horsham	7	105
Horsham	8	115
Horsham	9	125
Horsham	10	135
Curyo	1	290
Curyo	2	300
Curyo	3	310
Curyo	4	320
Curyo	5	330
Curyo	6	340
Curyo	7	350
Curyo	8	360
Curyo	9	10
Curyo	10	20
PBC	1	45
PBC	2	55
PBC	3	65
PBC	4	75
PBC	5	85
PBC	6	95
PBC	7	105
PBC	8	115
PBC	9	125
PBC	10	135

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746 **Fig. S1** Comparison of wind direction data for Curyo Rain 1 spread event. Wind direction  
747 data was collected from Birchip Cropping Group's (BCG) agriculture farm (10 kilometres  
748 away from the trial location), Hopetoun Airport (39 kilometres), and Charlton (75 kilometres).  
749 Birchip Cropping Group's agriculture farm weather station's wind direction data were used for  
750 the interpretation of spatial patterns of conidial spread for Curyo Rain 1 spread event, as  
751 Curyo's weather station wind vane was not calibrated

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