1 # The role of conidia in the dispersal of *Ascochyta rabiei*

2 **Ihsanul Khaliq**[1,*]**, Joshua Fanning**[2]**, Paul Melloy**[1]**, Jean Galloway**[3]**, Kevin Moore**[4]**, Daniel**
3 **Burrell**[1]**, Adam H Sparks**[1]

4 [1]University of Southern Queensland, Centre for Crop Health, Toowoomba, Queensland 4350,
5 Australia

6 [2]Agriculture Victoria, Horsham, Victoria, 3401, Australia

7 [3]Department of Primary Industries and Regional Development (DPIRD), Northam, WA, 6401,
8 Australia

9 [4]New South Wales Department of Primary Industries, 4 Marsden Park Rd, Tamworth, NSW,
10 2340, Australia

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* **Corresponding author**:
E-mail address: Ihsan.Khaliq@usq.edu.au
Phone: +61 7 4631 1877

Abstract

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30   *Ascochyta rabiei* asexual spores (conidia) were assumed to spread over short distances

31   (~10 m) in a combination of rain and strong wind. The potential distance of conidial spread

32   was investigated 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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61   **Keywords:** Ascochyta blight, epidemiology, conidial spread, wind-driven rain, chickpea,
62   sprinkler irrigation.

Introduction

Chickpea (*Cicer arietinum* L.) is the second most important legume crop globally and is the most widely grown legume grain crop in Australia with >1,060,000 ha harvested in 2018 (FAOSTAT 2020). Ascochyta blight caused by *Ascochyta rabiei* (syn. *Phoma rabiei*) is one of the most devastating chickpea diseases worldwide (Pande et al. 2005). With the exception of the Ord region in northern Western Australia, *A. rabiei* is the major biotic constraint to chickpea production in Australia with almost all chickpea growing areas affected (Bretag et al. 2008). *Ascochyta rabiei* survives on infected seed, volunteer chickpea plants and infested stubble, forming conidia that initiate primary infection. *Ascochyta rabiei* survives for up to two years on infested stubble at the ground surface but loses viability in up to five months when infested stubble are 5–40 cm deep in soil (W. J. Kaiser 1973; Navas‑Cortés et al. 1995). Conidia are hyaline, oval to oblong in shape, none to one septate, slightly bent at one or both ends and occasionally bicelled with size range from 8.2 to 10 x 4.2 to 4.5 μm (Nene 1982). The optimum range for the fungus growth, pycnidial production and conidial germination is 20 °C ; temperatures below 10 °C and above 30 °C have been found unfavourable for the fungus (Nene 1982; W. J. Kaiser 1973). Although there is no information on the effect of natural ultra violet light on *A. rabiei* conidia survival (Coventry 2012), exposure of cultures to wavelengths in the near ultra violet and blue range increased the rate of mycelial growth, pycnidial formation and conidial production in all isolates (W. J. Kaiser 1973).

Infected seed gives rise to infected seedlings through transmission from germinating seeds. Conidia are spread by rain splash or wind driven rain. Pycnidial formation, conidial production, host infection and disease development are favoured by temperatures between 5 and 30 °C (optimum 20 °C), relative humidity > 95 % (Nene 1982), and wetness period of 10 h or more (Khan 1999). A longer wetness period is required for spore germination at sub-optimal temperatures, and infection is rare in hot and dry conditions (Jhorar et al. 1998). Relative humidity is more important than temperature, thus *A. rabiei* development is very limited at lower humidity (e.g. 86 %) irrespective of temperature (Navas‑Cortés et al. 1998). Symptoms develop within 5–6 days after infection in cool and moist (20 °C and over 90 % humidity) conditions (Khan 1999). Pycnidia develop on the infected tissues, producing conidia that are responsible for the secondary spread of the pathogen (Pande et al. 2005). Conidia are the only spore type to have been reported in Australia. Putative ascospores have been reported only once in Australia (Galloway and MacLeod 2003), however, only one mating type has been detected and detailed molecular studies have shown Australian *A. rabiei* populations to be asexually reproducing (Leo et al. 2016; Bruvo et al. 2004; Mehmood et al. 2017), thus both primary and secondary infections are attributed to conidial infection.

98   Rain is needed for *A. rabiei* to infect and spread within a crop; dew alone will not

99   result in significant spread (Moore et al. 2016). During a rain event, pycnidia imbibe water

100   and hydrostatic pressure forces conidia in the pycnidia to exude through the ostiole in a

101   cirrhus. When a raindrop strikes the cirrhus, the kinetic energy breaks up the spore mass and

102   disperses the conidia to nearby healthy plants, thus spreading the disease (W. Kaiser 1992;

103   Nene and Reddy 1987; Coventry 2012). *Ascochyta rabiei* conidia have been reported to

104   spread over 1 m by splash dispersal (Kimber 2002). The amount of kinetic energy in

105   raindrops varies with the rainfall intensity, duration and size distribution with small drops

106   having less kinetic energy and thus remove fewer spores (Sache 2000). Splash dispersal by

107   large raindrops is considered more destructive because they tend to carry more spores

108   (Sache 2000). Spores can also be washed from upper leaves to lower leaves (Sache 2000).

109   Thunderstorms cause rapid spore dispersal from pycnidia and can result in diminution of

110   inoculum (Coventry 2012). Low intensity, intermittent rains combined with high wind have

111   been found to disperse spores more efficiently without diminishing the spore supply

112   (Coventry 2012).

113   Irrigation is the principal mechanism for increasing grain yield, supplementing rainfall

114   in drought seasons, or in areas receiving low rainfalls. Compared with furrow or flood

115   irrigation, sprinkler irrigation results in the wetting of the entire crop canopy and constitutes a

116   major source of moisture on all plant parts during dry conditions, thus increasing the risk of

117   foliar diseases (Rotem and Palti 1969). Sprinkler irrigation plays an important role in the

118   epidemiology of splash dispersed pathogens because spores are dispersed to their host

119   under moist conditions and their germination is practically ensured (Lomas 1991). Unlike

120   other forms of irrigation, water droplets generated by overhead sprinkler irrigation have the

121   impact energy to dislodge spores (Lomas 1991). This makes it likely to play an important role

122   in conidial spread for Ascochyta blight, *as A. rabiei* requires the impact energy of falling drops

123   to disperse its conidia from pycnidia. Despite this, there is no study on the distance and

124   quantity of *A. rabiei* conidia disperse during sprinkler irrigation events. Moreover, an

125   assumption exists that conidia disperse over short distances during sprinkler irrigation

126   events. Kimber et al. (2007) studied the spread of *A. rabiei* from primary infection foci

127   (infected seedlings) in small plots (15 m x 9 m) in Israel. Sprinkler irrigation was used to

128   irrigate plots, but only during dry periods, to provide conditions conducive to disease spread.

129   Moreover, the number of sprinkler irrigation events and amount of water applied during each

130   irrigation event were not recorded; therefore, any quantifiable relationship between irrigation,

131   disease and the pathogen spread (via conidia) was not established.

132   It has been reported that *A. rabiei* conidia spread over short distances (~1 m) via

133   splash dispersal, and up to 10 m in the presence of rain and strong wind (in the direction of

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134 wind) (Kimber 2002; Kimber et al. 2007). However, the actual distance and number of conidia

135 spread via wind driven rain have not been determined systematically (Coventry 2012).

136 Kimber et al. (2007) showed Ascochyta blight spread over short distances (< 10 m) from

137 primary infection foci (infected seedlings) in the direction of the prevailing winds. However,

138 this was spread from a rather limited quantity of inoculum (a single infected seedling). The

139 potential spread is likely to be greater when inoculum is plentiful. Previous studies have

140 considered the spread of *A. rabiei* in biological rather than epidemiological terms, focusing on

141 disease development and spread in the paddock and not on the spread of the pathogen via

142 conidia (Coventry 2012). However, the presence of a pathogen does not automatically lead

143 to disease development. Disease occurs due to complex interactions between a virulent

144 pathogen, a susceptible host(s) and an environment favorable for long enough for the

145 pathogen to cause disease (Agrios 2005).

146   Trapping spores on 'trap plants' distributed at various distances from the source of

147 infection for a short period of time is an excellent way to investigate the distance of conidial

148 spread. Trap plants are distributed at various distances from a source of infection for a

149 relatively short period of time to trap spores, and then transferred to a glasshouse to allow

150 lesion development (Salam et al. 2011). The numbers of lesions give an estimate of the

151 number of spores released and the distance travelled. Lesion development indicates that the

152 dispersed conidia are viable. The actual distance *A. rabiei* conidia travel from a standing crop

153 has not been determined in such a systematic manner on a large scale. Based on

154 preliminary work aimed to determine the distance of *A. rabiei* conidia dispersal from previous

155 year's infested stubble (Galloway, unpublished), we propose the pathogen is likely to spread

156 over longer distances, than reported in the literature, in wind driven rain. Experiments

157 conducted on plant pathogens, in a wind tunnel and rain tower, have shown that spores

158 released by rain splash and then transported by wind are likely to be important in long-

159 distance dispersal of pathogens (Fitt et al. 1989). Improving our understanding on how *A.*

160 *rabiei* may spread in wind driven rain can help in predicting spatial patterns of conidial spread

161 during rainfall events, and subsequent disease epidemics through modelling techniques

162 (Coventry 2012). Models are required to predict disease risk and spread for varying

163 environmental conditions, beyond their domain of study, as it is impractical to investigate

164 pathogens' epidemiology in all growing environments (Diggle et al. 2002).

165   To investigate *A. rabiei* conidial spread in epidemiological rather than biological terms,

166 focusing on the pathogen spread via conidia rather than the disease development and

167 subsequent spread in the paddock, the present study asked the following questions: (1) can

168 conidia spread over longer distances than previously reported, and (2) do conidia spread

169 over the same distances in rainfall and sprinkler irrigation events?

Methods

Study areas description

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

Experimental design

A method used by Salam et al. (2011) was modified for this study. At each location, 2–3 weeks old chickpea trap plants (variety PBA striker) were distributed at the distances of 0, 10, 25, 50 and 75 m from the control plots downwind of the prevailing wind direction. Downwind directions for the control plots were determined based on previous years' weather data. Trap plants were placed at the distances of 0–75 m along radial transects (there were no other chickpea crops downwind of the control plots where chickpea trap plants were distributed). There were 10 transects separated by 10-degree increments for a total of 90 degrees between the first and the last transect. There were four trap plant stations (trap plants units) at both 0 and 10 m, and 10 trap plant stations at the distances of 25, 50 and 75 m (Table 1, Fig. S1). At the distances 0–25 m, each trap plant station consisted of 10 chickpea seedlings in two pots (five seedlings per pot). At the distances 50 and 75 m, each trap plant station consisted of three chickpea seedlings in a single pot. The distances between individual trap plant stations at each distance (0, 10, 25, 50 and 75 m) were determined using the Law of Cosine (Table 1). As there were only 4 trap plant stations at the distances of 0 and 10 m, they were placed along transects 1, 4, 7 and 10, with 30 degrees

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205 difference (space) between each trap plant stations, to increase the chances of trapping

206 conidia. At distances of 25–75 m: all 10-trap plant stations were placed along 10 transects

207 with 10 degrees space between the individual trap plant stations (Table 1). The locations of

208 trap plant stations across transects were marked with flags to ensure trap plants were always

209 exchanged in the same spot for the entire duration of the experiment (Table S1). No

210 fungicides were applied over the duration trap plants were deployed in the paddock (Table 2).

211 *Spore trapping*

212 The distance of conidial spread was determined from September through to

213 December 2019. Spores were trapped in two rainfall events (event one ~ 4. 6 mm, and event

214 two ~ 18.6 mm) in Horsham, and a single rainfall event of 0.8 mm in Curyo (Table 2). A

215 sprinkler irrigation system (Hunter ®: Model MP300090210) located in a paddock just outside

216 Horsham was used to determine the distance of conidial spread for three irrigation events.

217 Sprinklers were set 110 cm above ground and were operated at 3.5 bar pressure. Each

218 sprinkler irrigation event was equivalent to 10–12 mm of simulated rain over approximately

219 90 minutes (a small rain shower of ~0.6 mm occurred during sprinkler irrigation event 3)

220 (Table 2).

221 In order to determine the distance of conidial spread in rainfall and sprinkler irrigation

222 events, trap plants were distributed in the paddock at the distances of 0–75 m from control

223 plots before forecast rainfall and scheduled irrigation events, respectively. Trap plants were

224 transferred to a controlled temperature room set at 20 °C for 48 hours (100 % humidity) after

225 being exposed in the field for 2–6 days for rainfall events, and for one day for irrigation

226 events (Table 2). The exposure period in paddock for the irrigation events was shorter for two

227 reasons. Firstly, each irrigation event was a single continuous controlled event as opposed to

228 natural rainfall events that fell in multiple showers over several days. Secondly, only the

229 infected plot was being irrigated (trap plants at the distances of 10–75 m were not getting

230 wet), therefore longer exposure period may have led to conidial desiccation on trap plants at

231 the distances of 10–75 m. After 48 hours incubation period, the trap plants were transferred

232 to a glasshouse (20 °C) to allow lesion development. Plants were watered daily via trays to

233 prevent splash dispersal to nearby plants. The numbers of lesions were counted on all plant

234 parts after two weeks giving an estimate of the number of conidia released and the distance

235 travelled.

236 Weather data was recorded by an automated weather station (Measurement

237 Engineering Australia, Adelaide, Australia). The data collected composed of date and time,

238 air temperature (° C), dew point (˚ C), rainfall (mm), relative humidity (%), wind speed (ms^{-1}),

239 and average wind direction (˚) recorded at 10-minutes intervals. The wind vane was not

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240 properly calibrated for the weather station at Curyo. Therefore, Birchip Cropping Group's

241 (BCG) agriculture farm (located 10 km away from the experimental location) weather

242 station's (Davis Australia) wind direction data was used for the interpretation of results (wind

243 direction data was not included in the analysis, as wind direction is highly unstable and

244 constantly changes). Wind direction data, recorded by Australia Bureau of Meteorology, at

245 two locations (Hopetoun Airport 39 km, and Charlton 75 km; located in the same area as

246 BCG and Curyo) were retrieved using the R programming language (R Core Development

247 Team 2019) contributed packages 'bomrang' v0.7.0 (Sparks et al. 2017) and 'stationaRy'

248 v0.5.1 (Iannone 2020) and compared with the BCG's weather station data to ensure the

249 BCG's weather station wind direction data was valid (Fig. S2).

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

251 A preliminary linear mixed model analysis was conducted in the R programming language,

252 using the lmer() function from the contributed package 'lme4' v1.1-1.23 (Bates et al. 2015), to

253 investigate the influence of 'spread event' (as a random variable: any spread event

254 regardless of sprinkler irrigation or rainfall events) and 'experimental location' on the number

255 of lesions recorded. A reductive approach was used to investigate the significance of the

256 random variables 'spread event' and 'experimental location' before modelling spatial patterns

257 of conidial spread. Preliminary analysis showed the influence of 'experimental location' to be

258 non- significant implying conidial spread patterns were consistent between experimental

259 locations. This result allowed generalised additive model (GAM) to compare the influence of

260 weather variables without the need to include experimental location as a dependant factor.

261 Generalised additive models were used because they have been reported to efficiently

262 describe the effect of various environmental variables on plant pathogen interactions (Sparks

263 et al. 2011; Yee and Mitchell 1991). The GAM for conidial dispersion, based on the pooled

264 data across all experimental locations for all six spread events, was fitted using the R

265 programming language via the gam() function from the contributed package 'mgcv' v1.8-31

266 (Wood 2011). Standard information criterion, such as Akaike's Information Criterion (AIC)

267 (Akaike 1974), the Bayesian Information Criterion (BIC) (Gideon 1978), as well as adjusted

268 R-squared values were compared across models to select the best fitting model.

269 Letting the mean number of lesions for pot i (pooled across all experimental locations

270 for all six spread events) be the response variable Y_i, and $\boldsymbol{x_i}$ be the associated covariate

271 vector with the distance of pot i from the infected plot being x_{i1}, the mean wind speed being

272 x_{i2} and the amount of irrigation or rainfall being x_{i3}, during spread events, the GAM model

273 that achieved best fit was of the form:

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

274   where the f_j are independent "thin-plate splines" which are the default smoother used by the

275   gam() function. For details about the mathematical specification of these and other

276   smoothing splines, see Wood (2017). The use of the Tweedie distribution family to model the

277   response data is now standard in the case of interval scale measurements with substantial

278   zero-inflation, i.e., a positive probability mass at zero will indicate no lesions were observed

279   (Dunn 2004; Hasan and Dunn 2010). As it is implemented in the tw() function passed to the

280   family parameter in the gam() function, the power parameter p – which relates the Tweedie

281   variance to its mean – is estimated from the data (Wood 2011). The chosen link function for

282   this family was the logarithm link; the canonical or natural link function for Tweedie

283   distributions, and the default supplied to the gam() function. The gam() function also allowed

284   the dimension of the basis for smoothed terms to be manually selected via the parameter k,

285   which controls the "wiggliness" of the resultant curve. The value of k was chosen to be 5

286   ($i.e. k = 5$) for all three predictors due to rather limited data.

287   *Data cleaning and visualisation*

288   Data were processed and visualised in R using the contributed packages 'tidyverse' v1.3.0

289   (Wickham et al. 2019), 'lubridate' v1.7.8 (Grolemund and Wickham 2011) and` 'clifro' (Seers

290   and Shears 2015) for wind roses. The best fitting GAM was visualised using a custom

291   function created for this work that uses the contributed package 'mgcViz' v0.1.6 (Fasiolo et

292   al. 2019). Mean wind speed was calculated using a circular averaging function from

293   'SDMTools' v1.1-221.2 (VanDerWal et al. 2014).

294   **Results**

295   *Model fit*

296   The linear mixed model analysis indicated that experimental location had no significant effect

297   on the number of conidia trapped and distance travelled during each spread event, thus

298   experimental location was not used when fitting the GAMs. Thirteen GAM models were

299   evaluated to describe spatial patterns of conidial spread. The model selected as the best

300   fitting had an adjusted R-squared value of 0.674, AIC value of 663 and a BIC value of 709.

301   The smooth terms for distance (D) and precipitation (P) were significant terms ($p < 0.05$). The

302   smooth term for wind speed (W) was not significant. However, including this term only as a

303   linear predictor reduced the fitness of the model, R-squared value of 0.657, AIC value of 689

304   and BIC value of 729, so the smoothed term was included in the final model (Fig. 1).

305   *Dispersal in rainfall events*

306   Trap plants at all distances (0–75 m) were infected in all 3-rainfall events, indicating conidia

307   spread to 75 m in each rainfall event. There was a strong relationship (R^2 = 0.657) between

308   mean wind speed, rainfall intensity, distance from the infected plot, and the number of

309   conidia trapped (counted as lesions). The highest number of lesions on trap plants were

310   recorded closest to the control plot at 0 m in each rainfall event - the numbers decreased as

311   the distance from the control plots increased (Fig. 2). The number of lesions recorded

312   increased with increasing rainfall. At Horsham, a total of 159 lesions were recorded at all

313   distances in rainfall event 1 (~ 4.8 mm), and 275 lesions were recorded in rainfall event 2

314   (~18.6 mm) (Table 2). In rainfall event 1 (Horsham Rain 1), a uniform conidial spread pattern

315   across transects was observed at the distances of 0–25 m (i.e., all trap plant stations at the

316   distances of 0–25 m were infected), whereas a non-uniform conidial spread pattern across

317   transects was observed at the distances of 50 and 75 m (Fig. 3). Uniform conidial spread

318   pattern across transects at all distances was observed in rainfall event 2 (Horsham Rain 2).

319   Mean wind speed and direction varied during rainfall events 1 and 2 (Fig. 4). Mean wind

320   direction was predominantly in the direction of trap plants (NE, SE) during both spread

321   events (Fig. 4)

322   At Curyo, a total of 193 lesions were recorded in a single rainfall event (Curyo Rain 1) of 0.8

323   mm (Table 2). Conidial spread pattern was almost uniform across transects at the distances

324   of 0–50 m, while a non-uniform conidial spread pattern across transects was observed at 75

325   m (Fig. 3). Mean wind speed and direction varied during the spread event (Fig. S2). Mean

326   wind direction was not in the direction of trap plants (Fig. S2) but, compared to rainfall

327   events-1 and 2, wind direction appeared to have limited influence on the number of lesions

328   recorded (Table 2), and the spatial patterns of conidial spread at Curyo (Fig. 3).

329   *Dispersal with sprinkler irrigation*

330   Trap plants at all distances (0–75 m) were infected in all three irrigation events. There was a

331   strong correlation between mean wind speed, irrigation, distance from the infested plot and

332   the number of conidia trapped (counted as lesions). The highest numbers of lesions on trap

333   plants were recorded closest to the control plot in each irrigation event - the numbers

334   decreased as the distance from the control plot increased (Fig. 2). The total number of

335   lesions recorded on trap plants varied greatly between all three irrigation events, with a total

336   of 250 lesions recorded in event 1 (~10–12 mm), 368 lesions in event 2 (~10–12 mm) and

337   477 lesions in event 3 (~10–12 mm irrigation event and a small rain shower of 0.6 mm)

338   (Table 2). In event 1 and 3 (Horsham Irrg1 and Horsham Mxd1), a uniform conidial spread

339   pattern across almost all transects was observed at the distances of 0–50 m, whereas

340   conidial spread pattern across transects was not uniform at 75 m (Fig. 3). In event 2: conidial

341   spread pattern across transects was uniform at the distances of 0–25 m, whereas a non-

342   uniform conidial spread pattern across transects was observed at the distances of 50 and 75

343   m (Fig. 3). Mean wind speed and direction varied between each spread event (Fig. 4).

344   Maximum mean wind speed (6.5 ms^{-1}) (Table 2) and maximum gust (11.2 ms^{-1}) were

345   recorded was recorded during irrigation event 3. Mean wind direction was predominantly in

346   the direction of trap plants (NE, SE) during all spread events (Fig. 4).

Discussion

348   Conidia were shown to distribute *A. rabiei* over longer distances than previously reported.

349   Conidia dispersed 75 m from infected plots in all sprinkler irrigation and rainfall events. The

350   mean number of lesions recorded on trap plants decreased as the distance from infected

351   plots increased. There was a strong relationship ($R^2 = 0.657$) between mean wind speed, the

352   amount of precipitation (rainfall and/or sprinkler irrigation) and the number of conidia trapped.

353   The experimental location had no significant effect on the number of conidia trapped and

354   distance travelled during each spread event (P>0.01). A model was developed that efficiently

355   described spatial patterns of conidial spread under field conditions. Given more data and

356   further development, this model can be used to predict the spread of *A. rabiei*.

357   The highest mean number of lesions on trap plants were recorded closest to the

358   control plots in all spread events – the numbers decreased as the distance from the control

359   plots increased. These results support the findings from previous studies (Coventry 2012;

360   Kimber et al. 2007) who showed *A. rabiei* inoculum density decreased as the distance from

361   infected foci increased. A similar dispersal pattern has been observed for other splash

362   dispersed pathogens, such as *Colletotrichum acutatum* (Yang et al. 1990),

363   *Parastagonospora nodorum* (previously known as *Septoria nodorum*) (Griffiths and Ao 1976),

364   and *Ascochyta fabae* (Pedersen et al. 1994). For splash dispersed pathogens, plants close

365   to the source of infection are more exposed to spore load due to localised splash dispersal

366   and become infected quickly, resulting in more lesions (Coventry 2012). More lesions were

367   recorded on trap plants with increased rainfall and in an event with a combination of a small

368   rain shower and a sprinkler irrigation event compared to a sprinkler irrigation event alone (in

369   case of sprinkler irrigation event 3, i.e., Horsham Mixd), suggesting that increased

370   precipitation dislodged more conidia, which were dispersed by wind driven rain. The amount

371   of rainfall has been reported to have a major influence on Ascochyta blight severity and the

372   distance disease spreads (Coventry 2012).

373   Wind speed and direction coinciding with increased rainfall influenced the spatial

374   patterns of conidial spread. Uniform conidial spread across transects at all distances was

375   observed in rainfall event 2 (Horsham Rain 2), which indicates strong winds from NW

376   directions coincided with increased rainfall and dispersed conidia across all transects

377   downwind (SE, NE) from the infected plot. Although trap plants were located downwind in

378   rainfall event 1 (Horsham Rain 1), uniform conidial spread across all transects was not

379   observed at 50–75 m, which reflects the influence of reduced rainfall and rather low wind

380   speed (compared to rainfall event 2) during the spread event. Compared to rainfall event 1 at

381   Horsham, the amount of rainfall and wind direction appeared to have limited influence on the

382   number of conidia trapped and the spatial patterns of conidial spread for rainfall event 3

383   (Curyo Rain 1) at Curyo. More lesions (193 lesions) were recorded in a single rainfall event

384   of 0.8 mm at Curyo, although mean wind direction was not in the direction of trap plants. In

385   addition, conidial spread pattern was almost uniform at the distances of 0–50 m. Conversely,

386   fewer lesions (159) were recorded in a rainfall event of 4.8 mm at Horsham when trap plants

387   were located downwind; and conidial spread pattern was uniform at the distances of 0–25 m

388   only. However, a direct comparison between these two rainfall events is not possible due to a

389   location difference and rather limited data. Furthermore, our model does not consider

390   continuously changing wind direction and dynamics associated with turbulence, which may

391   assist in explaining variation in spatial patterns of conidial spread. Conidia dispersed 75 m

392   and spatial pattern of conidial spread was uniform across transects at the distances of 0–50

393   m, when the amount of rainfall was as low as 0.8 mm (Curyo Rain 1 event with mean wind

394   speed of 3.6 ms^{-1}); and mean wind direction was not predominantly in the direction of trap

395   plants. This suggests that only a small amount of rain is required to dislodge a large number

396   of conidia. A similar dispersal pattern has been reported for the sexual spores (ascospores)

397   of *A. rabiei*, where ascospores discharge depended more on the occurrence of rain than the

398   amount (Trapero-Casas et al. 1996).

399   More conidia (368) were trapped in sprinkler irrigation event 2, compared to sprinkler

400   irrigation event 1, but conidial spread pattern across transects was not uniform at the

401   distances of 50–75 m. Conversely, fewer conidia (250) were trapped in sprinkler irrigation

402   event 1, but conidial spread pattern was almost uniform across transects at all distances.

403   The lower number of spores and non-uniform spatial spread pattern for sprinkler irrigation

404   event 2 is rather surprising because an equal amount (~10–12 mm) of irrigation was applied

405   in both sprinkler irrigation events. Moreover, stronger mean wind speed was recorded for

406   sprinkler irrigation event 2 and the non-infected trap plants were located downwind (the

407   mean wind direction was from the west, therefore trap plants placed at the distances of 50–

408   75 m east of the infected plot were expected to be uniformly infected). The reasons for this

409   dispersal pattern are not clear, and our analysis is limited by rather limited data. Detailed

410   studies are needed to get a more complete picture of spatial patterns of conidial spread

411   during sprinkler irrigation events.

412   Above canopy irrigation reduces mean ambient air temperature by 7–9 °C and

413   increases humidity up to 30 % during the irrigation period (Rotem and Palti 1969). This has

414   implications for Ascochyta blight development within an irrigated chickpea paddock, as *A.*

415   *rabiei* only requires 3–10 h leaf wetness for host penetration and infection at the optimum

416   temperature (Khan 1999; Moore et al. 2016). Therefore, extended periods of sprinkler

417   irrigation events may not be required for disease development, especially in a cool and moist

418   season. In the laboratory; more than 50 % of conidia, incubated on membrane filters,

419   germinated after four days at relative humidity as low as 12.5 % (temperature 20 °C)

420   (Coventry 2012). *Ascochyta rabiei* conidia have been shown to survive and remain infective,

421   when inoculated on chickpea seedlings in a growth chamber, during dry periods lasting 24 h

422   (Armstrong-Cho et al. 2004). However, conidia are unlikely to withstand dry conditions for

423   extended periods of time under field conditions, especially at sub-optimal temperatures. For

424   conidial spread with sprinkler irrigation, this implies that even though conidia may spread to

425   equal distances (75 m in this case) during sprinkler irrigation and rainfall events, leaf wetness

426   provided by dew and/or humidity over 90% to facilitate conidial penetration and infection will

427   be important in establishing disease on chickpea outside the irrigated paddock in the

428   absence of rain (if temperature requirement is met). Conversely; rainfall usually occurs over

429   a large area, and only a few mm of rain later in the day or at night satisfies the leaf wetness

430   requirement (Moore et al. 2016). Therefore, leaf wetness provided by dew and/or high

431   relative humidity is not necessary to facilitate conidial penetration and infection at longer

432   distances for conidia dispersed in rainfall events. This further implies that rainfall might be

433   more important than sprinkler irrigation for conidial spread and subsequent disease

434   development at farther distances. Future work determining the viability of conidia after

435   exposure to different duration of dry periods, under field conditions, is necessary to

436   understand the duration of dry period over which *A. rabiei* conidia can survive when

437   dispersed outside the irrigated paddock. To the best of our knowledge, this is the first

438   systematic study to determine conidia dispersal with sprinkler irrigation.

439   The finding that conidia travelled 75 m during all rainfall and sprinkler irrigation events

440   suggests that conidia can potentially play a role in the long-distance dispersal of *A. rabiei.*

441   Conidia dispersed 50 m from naturally infested stubble from the previous year (there were no

442   trap plants farther than 50 m to test long-distance dispersal) (Galloway, unpublished). The

443   sexual spores of the fungus (ascospores) have been reported to travel up to hundreds of

444   metres to several kilometres from the source of infection (Trapero-Casas et al. 1996; W.

445   Kaiser and Küsmenoglu 1997; Trapero-Casas and Kaiser 1992). The present study did not

446   have trap plants farther than 75 m from the infected plot and wind speed during spread

447   events was rather low with a maximum mean wind speed of 6.5 ms^{-1} and maximum gust of

448   11.2 ms^{-1}. It is likely that conidia could dispersed farther than 75 m, especially when wind

449   speed is high and there are strong wind gusts. It has been hypothesized that if conidial

450   dispersal is aided by turbulent winds and conidia enter the turbulent boundary layer, they

451   could be dispersed to distances that are associated with ascospores only (McCartney and

452   West 2007; Coventry 2012). While the role of conidia in long-distance dispersal has not been

453   recognized, it has been hypothesized that liquid suspensions in air (aerosols) can

454   incorporate a large number of conidia in heavy rain that can be transported over longer

455   distances by wind (Coventry 2012). A severe Ascochyta blight epidemic developed across

456   the southern region of Australia in 1998. It is speculated that aerosols developed during

457   heavy rains, which travelled over hundreds of meters to kilometers and contributed to the

458   epidemic development (Coventry 2012). This suggests that role of conidia in the long-

459   distance dispersal has been underestimated. Further work distributing trap plants at

460   distances farther than 75 m is necessary to determine the potential distance conidia can

461   travel.

462   When fitting observed data to logistic models, the known biology of pathogens needs

463   to be considered rather than simply considering the shape of the curve (Sparks et al. 2008).

464   Generalised additive models are data-driven not model-driven, as they allow the data to

465   determine the shape of the response curves rather than being limited by the shapes

466   attainable through some parametric specification. The inability to control environmental

467   factors, such as wind speed, amount of rainfall, temperature and humidity makes it difficult to

468   use parametric statistical models e.g., generalised linear models (GLMs) to make inferential

469   comparisons across sites without a high risk of the presence of confounding variables.

470   Generalised additive models offer a flexible modelling approach that provides a good

471   balance between highly interpretable linear models that have undesirable predictive

472   capabilities and black-box machine learning approaches, such as neural networks, which

473   have excellent predictive performance but low interpretability (Hastie and Tibsbirani 1990).

474   This capacity to achieve interpretable separation of covariate contributions in a strong

475   descriptive model is the main reason that GAMs were chosen to model spatial patterns of

476   conidial spread. A model was developed that efficiently described spatial patterns of conidial

477   spread under field conditions. The model will be useful for chickpea growers in identifying the

478   scale of potential damage and could be used to predict the spread of *A. rabiei* with further

479   development. When further developed, this model can also be used to inform chickpea

480   growers how far to grow chickpea from the neighbouring paddocks.

481   A comparison of conidial spatial dispersal patterns in identical amount of irrigation
482   and rainfall events would have been beneficial, but constantly changing wind speed and
483   direction makes a direct comparison difficult under field conditions. Conidial spread was
484   investigated in the late stage of plant growth with 90–100 % plants in plots being infected.
485   Detailed studies at different plant growth stages and disease incidence levels are now
486   needed to provide a more complete picture of distance conidia disperse and their spatial
487   dispersal patterns. It should be noted that counting lesions on trap plants gave an estimate of
488   only viable conidia dispersed (not the total number of conidia dispersed), which could cause
489   disease under field conditions if conditions are favourable for disease development. This
490   study was primarily conducted to get an estimate of the distance conidia travel and remain
491   viable. Future studies should consider using trap plants, spore traps and molecular
492   approaches (e.g. trapping spores sticky tapes and subsequent spore count using quantitative
493   PCR) to get an accurate estimate on the number of conidia dispersed. Spore trapping
494   coupled with quantitative PCR has been demonstrated to be a useful tool for epidemiological
495   studies and biosecurity surveillance (Vogelzang 2012). More work is required to establish the
496   equivalency of number of lesions to the number of conidia. Many other factors are involved in
497   the spore dispersal, including changing wind directions, turbulence and topographic factors
498   (Coventry 2012), which add complexity to the model and were not considered in the present
499   model. These factors need to be addressed in future models.

500   Acknowledgements

507   *Conflict of interest*

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

509   *Ethical approval*

510   This study did not involve working with animals or humans

511   *Consent to participate*

512   Not applicable

513   *Consent for publication*

514   Not applicable

515   *Availability of data and material*

516   The raw data are documented and available from https://doi.org/10.5281/zenodo.3842293.

517   All raw and generated data and further associated materials have been made further

518   available as a part of a research compendium available from

519   https://doi.org/10.5281/zenodo.3810826.

520   *Code availability*

521   All code used in the analyses and data visualisation have been made available as

522   a research compendium, available from https://doi.org/10.5281/zenodo.3810826.

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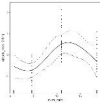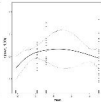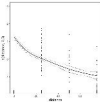685   *of Vegetation Science, 2*(5), 587-602.
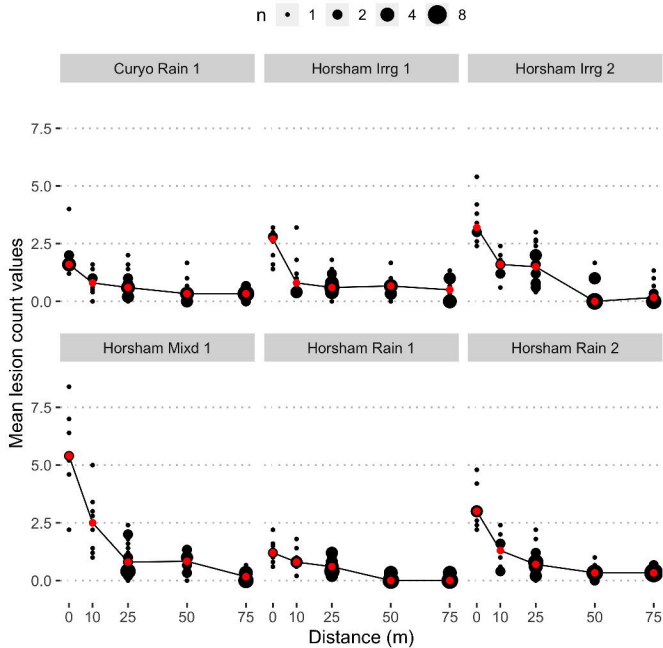
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689 ## Figure captions

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

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

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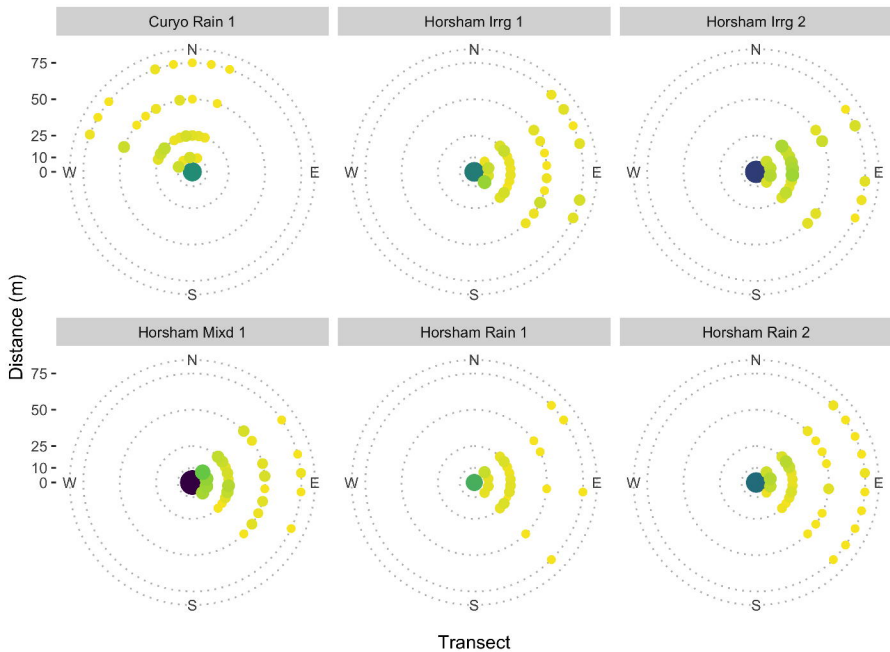703 dotted line represents 75 m distance from the infected plot

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

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Wind Speed (m/s) — [0,2.25] (2.25,4.5] (4.5,6.74] (6.74,8.99] (8.99,11.2]

Horsham Irrg 1 · Horsham Irrg 2 · Horsham Mixd 1 · Horsham Rain 1 · Horsham Rain 2

Wind Speed (m/s): [0,2.16] (2.16,4.32] (4.32,6.48] (6.48,8.64] (8.64,10.8]

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