Australasian Plant Pathology (2022) 51:363–368
https://doi.org/10.1007/s13313-022-00860-1

RESEARCH NOTE

Stubble trouble! Moisture, pathogen fitness and cereal type drive colonisation of cereal stubble by three fungal pathogens

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Received: 26 August 2021 / Accepted: 11 March 2022 / Published online: 24 March 2022

Abstract

Stubble-borne cereal diseases are a major constraint to production in Australia, with associated costs rising as a result of increased adoption of conservation agriculture systems. The fungal pathogens that cause these diseases can saprotrophically colonise retained cereal residues, which may further increase inoculum levels post-harvest. Hence, saprotrophic colonisation by the stubble-borne fungal pathogens *Fusarium pseudograminearum*, *Pyrenophora tritici-repentis* and *Bipolaris sorokiniana* were compared under a range of moisture conditions for stubble of six cereal varieties (two bread wheat, two barley, one durum wheat and one oat). Sterile cereal stubble was inoculated separately with two isolates of each pathogen and placed, standing, under constant relative humidity conditions (90, 92.5, 95, 97.5 and 100%) for 7 days at 25 °C. Stubble was then cultured in increments of 1 cm to determine the percentage colonisation height of each tiller. *Fusarium pseudograminearum* colonised farther within tillers, leaving a greater proportion of the standing stubble colonised compared with *B. sorokiniana* and *P. tritici-repentis*, suggesting *F. pseudograminearum* has higher saprotrophic fitness. Saprotrophic colonisation also increased with increasing relative humidity for all pathogens and varied by cereal type. Disease management strategies, such as reduced cereal harvest height, may limit saprotrophic colonisation and improve stubble-borne disease management in conservation agriculture systems.

Keywords Fusarium crown rot · Yellow leaf spot · Common root rot · Epidemiology · Broadacre · Fallow

Fusarium crown rot (caused primarily by *Fusarium pseudograminearum*), yellow leaf (tan) spot (caused by *Pyrenophora tritici-repentis*) and common root rot (caused by *Bipolaris sorokiniana*) are significant stubble-borne diseases of cereal crops in Australia. The causal fungal pathogens can survive across seasons in cereal stubble, making them difficult to control in conservation agriculture systems (Simpfendorfer et al. 2019). In Australia, the economic impact to the wheat industry alone is valued at AUD 90 million for Fusarium crown rot, AUD 52 million for yellow leaf spot and AUD 30 million for common root rot (Murray and Brennan 2009).

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Genetic resistance is one of the main strategies used to manage stubble-borne diseases in Australia (Simpfendorfer et al. 2019). In a living host, the colonisation of tissue by the pathogen is slowed as host resistance increases, limiting infection and disease development (Knight and Sutherland 2017). But these pathogens are also capable of saprotrophic (post-harvest) growth in cereal stubble (Malaker et al. 2007; Summerell and Burgess 1988a, b). This means inoculum levels may increase after harvest in resistant crops as host resistance is unlikely to continue to suppress the pathogen after senescence (Percy et al. 2012; Summerell and Burgess 1988a).

Infection by multiple pathogens is also common, especially in the northern grains region of Australia (NGR), with co-infections by *F. pseudograminearum* and *B. sorokiniana* occurring in approximately 50% of wheat crops (Simpfendorfer and McKay 2019). Differences in biology between stubble-borne pathogens means their individual requirements for saprotrophic colonisation are likely to differ between species (Magan and Lynch 1986). This may affect how rapidly each pathogen colonises stubble and may

determine which one dominates in a following season. For example, pathogens which can colonise stubble under lower moisture conditions may dominate the substrate, as moisture is a major limiting factor for saprotrophic colonisation (Magan and Lynch 1986; Summerell and Burgess 1989). Three hypotheses were tested using cultivars relevant to the NGR: (1) when moisture is increased, saprotrophic colonisation by pathogens will also increase, (2) different pathogens have varying rates of saprotrophic colonisation as influenced by individual isolate or species fitness, and (3) saprotrophic colonisation will not be affected by the genetic resistance traits of cereal crop types or varieties.

Two isolates each of *F. pseudograminearum* (DAR 84148 and DAR 84149), *P. tritici-repentis* (DAR 84971 and DAR 84972) and *B. sorokiniana* (DAR 84145 and DAR 84144) were collected from bread wheat (*Triticum aestivum*) or durum wheat (*Triticum durum*) crops in New South Wales (NSW), Australia between 2017 and 2019. Isolates were cultured on 1/4 strength Potato Dextrose Agar (PDA) + novobiocin (10 g PDA, 15 g technical agar plus 0.1 g novobiocin/L water) and incubated under alternating white and near ultraviolet lights for a 12 h photoperiod of 66.6% alternating fluorescent (FL36W/865, Sylvania, East Sussex, United Kingdom) and 33.3% blacklight blue (F36T8 BLB, Crompton lighting, Bradford, United Kingdom) light for 7 days at 25 °C.

Cereal stubble with no visible sign of disease was collected post-harvest from experimental plots grown in 2019 at Narrabri and Tamworth in NSW, Australia (Table 1). Two varieties each of bread wheat and barley were selected to provide a range of disease susceptibilities, and oat and durum wheat varieties were selected based on industry relevance. Plants were broken down into individual tillers of all types with leaf sheath removed. Tillers were randomly selected and cut at the first internode (between the roots and first node) into 10 cm lengths (determined in pilot experiment to be practical length for 7-day study). Tillers were soaked in sterile distilled water for 24 h, then sterilised by autoclaving twice (on successive days) at 120 °C for 20 min. Three tillers of each variety were cut into 1 cm segments and cultured as specified above for 4 days at 25 °C to verify sterility.

Each tiller was inoculated with a single fungal isolate (one tiller for each isolate by variety combination) by pressing the hollow base of each tiller into the actively growing edge of the selected culture, embedding an agar plug (3 mm deep) inside the tiller base. The inoculated end of the tiller was inserted onto a tooth of a 2 × 2 galvanised steel nail plate (21 mm Pryda Foil Fix, Pryda Australia, Melbourne, Australia) with one tiller per nail plate to avoid touching of nearby tillers. Nail plates were attached to a corflute base that was fitted inside each humidity chamber to simulate standing stubble.

Custom-built humidity chambers were used to impose five different humidity treatments. These were set to an average of 90% RH, 92.5% RH, 95% RH, 97.5% RH and approximately 99.9% RH (referred to throughout as nominal 100% RH), as the greatest difference in colonisation rate was expected to occur between 90 and 100% RH (Magan and Lynch 1986). Humidity chambers contained a misting unit (Humidi Mist from Reptile One, Ingleburn, NSW) connected to a humidistat (Humidity controller IHC-200 from Inkbird Tech C.L., Shenzen, China) which automatically regulated misting when RH was ± 1% of the set RH. A data logger (Tinytag View 2 TV-4500, Gemini Data Loggers, Chinchester, United Kingdom) measured temperature and RH every 1 min. The experiment was run for 7 days at constant temperature (25 ˚C) and exposed to a 12 h photoperiod (as specified above).

After 7 days, tillers were trimmed into 1 cm sections and cultured for 4 days at 25 °C as specified above. Vertical saprotrophic colonisation was measured by presence of distinctive colonies of the inoculated pathogen emerging from each tiller section. Percentage of tiller section vertically colonised by each pathogen was then calculated where each 1 cm section colonised equals 10%.

The experiment was repeated twice over time, with treatments arranged according to a split-plot design. The

Table 1 Cereal crop type (species and variety), collection location and disease ratings for Fusarium crown rot (FCR), common root rot (CRR) and yellow leaf spot (YLS) of the selected cereal varieties used in the experiment. Rating information sourced from Winter Crop Variety Sowing Guide 2021 (Matthews et al. 2021)

Cereal species	Variety	Collection location	FCR rating	CRR rating	YLS rating
Bread wheat	EGA Gregory	Narrabri	S	MS-S	S
	LongReach Lancer	Narrabri	MS-S	S	MR-MS
Barley	Compass	Narrabri	S	MS	NA
	Rosalind	Narrabri	MS-S	S	NA
Durum wheat	DBA Lillaroi	Tamworth	S-VS	MS-S	MR-MS
Oat	Eurrabie	Narrabri	NA	NA	NA

Not applicable (NA) as resistance level unknown or considered a non-host, moderately resistant (MR), moderately susceptible (MS), susceptible (S), very susceptible (VS)

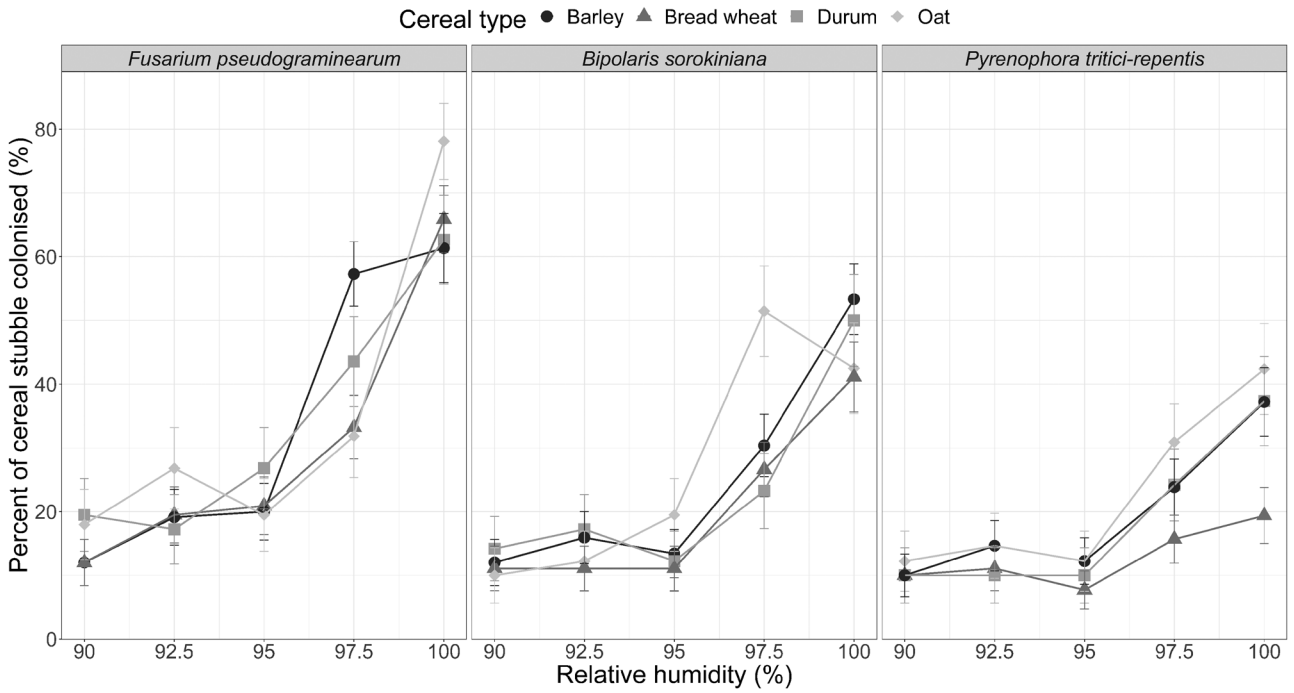

Fig. 1 Colonisation of stubble from four cereal species by three cereal pathogens, as a percentage (%) of cereal stubble height colonised after seven days, under differing relative humidity regimes. Error bars represent approximate standard error of the mean

RH treatments were randomly assigned to humidity chambers within each replicate run, while individual tillers corresponding to different cereal types and varieties, inoculated with different pathogens and isolates, were randomly assigned to individual nail plates within each humidity chamber.

Percentage vertical colonisation was analysed using a linear mixed model framework and required an arcsine square root transformation to meet model assumptions. The treatment structure, with all terms fitted as fixed effects, was specified using the notation of Wilkinson and Rogers (1973) as:

$$RH\ Treatment * (Cereal\ Type/Variety) * (Pathogen/Isolate),$$

where the operators * and / correspond to the crossing and nesting operators respectively. Terms corresponding to the experimental design structure were fitted as random effects. Predictions of the fixed effects were provided as empirical best linear unbiased estimates (eBLUEs), and back-transformed to the original scale for presentation. Approximate standard errors of the back-transformed eBLUEs were obtained using a Taylor series approximation (Butler et al. 2017). Models were fitted using the ASReml-R package (Butler et al. 2017) in R (R Core Team 2019). Variance components were estimated using residual maximum likelihood (Patterson and Thompson 1971). A Fisher's least significant difference test was used to compare significant fixed effects at the 5% level.

Saprotrophic colonisation of cereal stubble by *F. pseudograminearum, B. sorokiniana* and *P. tritici-repentis* was affected by RH, pathogen species and cereal type, evident by a significant three-way interaction between these treatments (Fig. 1 and Supplementary Table 1, $P = 0.03$). The differences between isolates of the same species were not significantly different ($P = 0.20$) so the mean colonisation results of both isolates for each species are presented (Fig. 1). Similarly, there were no significant differences in percentage vertical colonisation between two varieties of the same cereal type ($P = 0.18$). As such, the mean colonisation results of the bread wheat and barley varieties are presented (Fig. 1). Percentage vertical colonisation by all pathogens increased with increasing RH, supporting Hypothesis (1) (Fig. 1). Saprotrophic colonisation increased with increasing moisture, which is likely due to a decrease in fungal metabolic demand for osmoregulation (Liddell and Burgess 1988). This relationship is consistent with different fungal pathogen species on a range of substrates (Magan and Lynch 1986) and reinforces the importance of moisture to saprotrophic colonisation of cereal stubble by pathogenic fungi.

Saprotrophic colonisation by *B. sorokiniana* and *P. tritici-repentis* was possible at 90% to 95% RH but required 97.5% RH to colonise beyond 20% of tiller length (Fig. 1 and Supplementary Table 1). This suggests *P. tritici-repentis* has a wider moisture range for colonising stubble than previous

reports of 0.0 to -2.5 MPa (equivalent to 98–100% RH at 25 °C) (Summerell and Burgess 1989). Wet conditions are also required for production of primary inoculum on stubble; conidia for *B. sorokiniana* (Chand et al. 2002) and pseudothecia, which release ascospores, for *P. tritici-repentis* (Pfender et al. 1988). Although wet conditions are more conducive to mycelial growth and inoculum production, they also favour cereal stubble decomposition, which can ultimately reduce pathogen survival (Lakhesar et al. 2010). A combination of wet conditions to promote saprotrophic growth within cereal stubble early post-harvest, followed by cool and dry conditions to promote survival of inoculum (Summerell and Burgess 1989; Zhang and Pfender 1992), is likely to be ideal for survival of these pathogens.

Saprotrophic colonisation of cereal stubble by *F. pseudograminearum* was generally more extensive compared with *B. sorokiniana* and *P. tritici-repentis* under moisture conditions of 92.5% RH and above. At 100% RH, *F. pseudograminearum* had the highest percentage vertical colonisation (61 to 78% colonised) for every cereal type compared to *B. sorokiniana* (41 to 53% colonised) and *P. tritici-repentis* (19 to 42% colonised) (Fig. 1 and Supplementary Table 1). This supports Hypothesis (2) that the different fungal pathogens have varying rates of vertical colonisation of cereal stubble, due to differences in saprotrophic fitness (Magan and Lynch 1986). As such, *F. pseudograminearum* could more rapidly saprotrophically colonise infected cereal stubble making it more likely to dominate in following seasons. *Fusarium pseudograminearum* has been shown to suppress *B. sorokiniana* during the pathogenic phase (Moya-Elizondo et al. 2011), and our results suggest *F. pseudograminearum* may outcompete both *B. sorokiniana* and *P. tritici-repentis* in the saprotrophic phase, but mixed-inoculation studies are needed to verify.

Colonisation of the different crop types and varieties by each pathogen did not align with existing disease susceptibility ratings. This partially supports Hypothesis (3), although crop type did affect saprotrophic colonisation in some cases. Oat stubble, for example, allowed higher saprotrophic colonisation for several pathogen by RH combinations (Fig. 1 and Supplementary Table 1). For instance, the percentage of tiller length colonised by *B. sorokiniana* at 97.5% RH was significantly higher in oat compared to other stubble types.

All three pathogens colonised further in oat and barley stubble compared with bread wheat, even though oat exhibits lower incidence and severity of Fusarium crown rot (Knight and Sutherland 2017), common root rot (Wildermuth and McNamara 1987) and yellow leaf spot (Hosford et al. 1987; Rees and Platz 1979), and barley is not a recognised host of *P. tritici-repentis*. The barley and oat stubble had larger and hollow tillers which may allow pathogens to colonise more freely than in bread wheat. This may explain why *P. tritici-repentis* was slowest to colonise bread wheat stubble at 100% RH (Fig. 1 and Supplementary Table 1) despite bread wheat being the main host of *P. tritici-repentis* (Summerell and Burgess 1988a). Saprotrophic growth may, in this case, be influenced by structural factors such as the anatomy (e.g. culm density) and morphology (e.g. stem diameter or thickness) of cereal stubble, which is unlikely to be related to metabolic disease resistance traits of the crop. Further effects on saprotrophic colonisation of stubble may include the nutritional composition and decomposition rates, which can vary by cereal type and growing conditions (Garrett 1972; Pfender and Wootke 1987; Smith and Peckenpaugh 1986).

These findings have potential implications for NGR crop rotation sequences, particularly if oat or barley are commonly grown following wheat. Even a low-level of infection could result in high levels of saprotrophic mycelial growth in retained standing cereal stubble, especially following extended periods of wet weather. Although crop selection cannot further slow or prevent saprotrophic colonisation of pathogens in post-harvest stubble (Summerell and Burgess 1988a), it remains a useful tool for limiting infection and disease severity in-crop (Simpfendorfer et al. 2019). The most effective approach for preventing saprotrophic colonisation is to avoid infection altogether, through inoculum avoidance, sowing of highly resistant varieties or fungicide applications where effective. This, however, may not be a realistic goal for pathogens like *F. pseudograminearum*, where only partial genetic resistance is available and current fungicides have limited efficacy (Simpfendorfer et al. 2019). Disease management strategies such as reducing cereal harvest height could therefore limit further inoculum production in infected crops by (1) removing pathogen inoculum residing in the upper canopy (*P. tritici-repentis*) (Zhang and Pfender 1992) and/or (2) removal of excess upper-canopy substrate which would otherwise allow fungal pathogens such as *F. pseudograminearum* and *B. sorokiniana* to saprotrophically colonise vertically within post-harvest stubble.

Saprotrophic growth of fungal pathogens is likley to depend on moisture, stubble characteristics and the individual different species requirements, plus additional factors like temperature and competition between microbes (Pfender et al. 1988). In susceptible crops, significant mycelial growth may have already occurred prior to senescence (Knight et al. 2021, 2017; Petronaitis et al. 2020), so the infection status of a crop at maturity should also be considered. Linking the pathogenic (in-crop) colonisation with saprotrophic (post-harvest) colonisation of cereal stubble is therefore needed under field conditions to fully illustrate the effect of host susceptibility on pathogen inoculum dynamics within and between seasons.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s13313-022-00860-1.

Acknowledgements This research was made possible by the significant contributions of growers through their support of the Grains Research and Development Corporation (GRDC). Ms Petronaitis thanks the GRDC and New South Wales Department of Primary Industries for co-funding her Grains Agronomy and Pathology Partnership PhD scholarship (BLG211). Rick Graham and Gururaj Kadkol are thanked for providing cereal stubble. Technical assistance provided by Chrystal Fensbo and Jason McCulloch is gratefully acknowledged. The authors also thank Dr Narelle Moore, Hayley Wilson, Nicole Dron, Kerry Bell and Emily Plant who reviewed the manuscript.

Author contributions This article is based primarily on a student thesis prepared by PhD candidate Toni Petronaitis. All authors contributed to the study conception. Material preparation and data collection was performed by Toni Petronaitis and data analysis conducted by Clayton Forknall. The first draft of the manuscript was written by Toni Petronaitis and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions.

Declarations

Conflicts of Interest The authors declare that they have no conflict of interest.

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