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Short Communication

Fusarium pseudograminearum and *F. culmorum* affect the root system architecture of bread wheat

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ABSTRACT

Yield losses of bread wheat due to crown rot can be more severe when drought conditions occur during the grain-filling period. Root architecture characteristics are important for soil exploration and below-ground resource acquisition and are essential for adaptation to water-limited environments. Traits such as root angle, length and density have been strongly associated with acquisition efficiency and contribute to yield stability of the crop. The impact of crown rot pathogens on wheat root architecture is poorly understood. We examined differences in root angle, length and number, as well as dry root weight of the crown rot-susceptible bread wheat cultivar, Livingston inoculated with one of two crown rot pathogens *Fusarium culmorum* or *Fusarium pseudograminearum* in a transparent-sided root observation chamber. Significant adverse impacts on plant health and growth were revealed by visual discolouration of the leaf sheaths; fresh and dry shoot weight; leaf area of the oldest and the youngest fully expanded leaf and leaf number. Values of most recorded root system measurements were reduced when inoculated with either *F. culmorum* or *F. pseudograminearum*. In contrast, root angle was increased in the presence of *F. culmorum* but was not significantly changed by *F. pseudograminearum*. The development of whiteheads and grain losses in bread wheat caused by crown rot have previously been associated with blockages of the vascular systems. The method employed here was able to identify differences in the pathogen impacts on roots, which were not detected using previous systems. This research indicates that in the presence of *F. culmorum* and *F. pseudograminearum* infection, not only reductions in the size and biomass of the shoot system but also changes in the length, biomass and architecture of the root system could play an important role in yield loss.

1. Introduction

Fusarium culmorum and *Fusarium pseudograminearum* are the most common and globally important causal agents of crown rot of grain cereals [1–4]. *Fusarium pseudograminearum* is the most widely spread and has been reported in all soil types found in all cereal growing regions in Australia [2,5]. *Fusarium culmorum* also occurs in all cropping regions of Australia, however, it is more widely distributed in high rainfall temperate regions of Victoria and South Australia, and the eastern Darling Downs in southern Queensland [5,6]. In some areas of the southern cropping region of Australia, rainfall can occur relatively uniformly during the year but in many areas, with a Mediterranean climate, rainfall is winter dominant [5,7–9]. Many different soils occur in the southern cropping regions while soils in the western region are generally sandy with less water holding capacity [8,9]. However, it has been reported that the severity of the disease is greater in the northern grain region where deep clay soils with high water holding capacity predominate. In this, region, rainfall is summer dominant and cereals such as wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) are grown during winter and spring often relying heavily on the sub-soil moisture accumulated during the summer [2,10]. Significant yield losses, due to crown rot, can occur particularly in areas with water stress where minimum tillage, stubble maintenance and similar conservation agricultural procedures are practised [2,11].

Infected stubble is the main source of crown rot inoculum in the field [2,3,11]. Infection of the plant can occur at any growth stage and has been reported to occur from the seedling stage right through to maturity [2,12]. During the growing season, the fungus develops progressively through the plant post-infection. Soil

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moisture can have a major impact on infection levels in the field, as new infections can only occur in relatively moist soils [2,3]. The disease becomes more severe when soil moisture levels are high early in the season, which can cause a high incidence of infection and rapid plant growth. However, late in the season depletion of the sub-soil moisture, makes the plant more susceptible to water stress and more likely to suffer damage due to infection. Yield losses due to crown rot pathogens are intensified by limited rainfall during grain-fill [13,14].

The first symptoms of crown rot in winter cereals manifest as necrotic lesions on the coleoptile, sub-crown internode, root emergence points and the basal portion of the leaf sheaths [12,15,16]. At the flowering stage, extensive colonisation of the fungus has been reported up to the fifth internode of the stem of very susceptible cultivars [17,18]. Under conditions of water deficiency, prematurely senescing stems can form whiteheads during grain-fill, which contain shrivelled or no grain [2,12,19,20]. The fungus present in the crown and the sub-crown internode tends to occlude the transport of water from the seminal root system. Thus, compromising the function of the xylem and phloem causing hyphal disruption of water transport from the root system to the head [2,20].

Visual above-ground symptoms and yield have been used extensively [1,2,18,19,21] to evaluate genetic material for resistance and tolerance to crown rot. However, there appears to be limited published information on the effects of *F. culmorum* and *F. pseudograminearum* on the root system architecture of bread wheat.

Genotypic variation in root system characteristics of bread wheat cultivars has been identified [7–9,22–24]. Such characteristics include root depth [25], root elongation rate, root distribution at depth [23], xylem vessel diameter [26] as well as root angle and overall root system architecture [8,9,22]. The usefulness of each root characteristic for increasing grain yield under water stress is affected by the level and timing of moisture stress during the crop development cycle [9].

Studies that have reported the effect of crown rot pathogens on the root system of wheat [27–30], did not report details of changes to root architecture past the very early seedling stages. Root dry and fresh weight, root number and root length were used to test the plant growth parameters. However, the limited soil volumes, limited growth period and different research aims of each of these studies meant that either the expression of root architectural differences induced by crown rot infection was limited or that any changes in root architecture were not reported in detail [27–29].

Root physiology during crown rot infection is poorly understood compared to the shoot-related characteristics. It is important to understand the impacts of this disease on the root system that are likely to lead to changes in soil exploration and the ability to access water. Thus, the objectives of this study were to determine whether *F. culmorum* or *F. pseudograminearum* effect the root system of a susceptible bread wheat and whether any effects on the root system architecture of bread wheat are similar between these two important crown rot pathogens. To achieve this aim, a system to observe the roots of crown rot infected plants using transparent-sided root observation chambers was developed.

2. Materials and methods

2.1. Strains and inoculum preparation

Experiments were performed using *F. pseudograminearum* strain A09#04 collected in Emerald, Queensland [21], Australia, and *F. culmorum* strain, Fc 13–195 collected in the Wimmera region of Victoria, Australia. Both were isolated from crown rot infected wheat stems. Each isolate was cultured to produce colonised grain inoculum as described by Saad et al. [21]. Individual inocula were ground using an electric Laboratory Mill (Christy and Norris Ltd., Ipswich, UK) until they were small enough to pass through a 2 mm sieve. Sterilised and ground un-inoculated wheat grain was used as a non-inoculated control. Inoculum was stored at 4 °C until required.

2.2. Root chamber, plant growth and inoculation

The bread wheat cv. Livingston used in all experiments is classified as a susceptible cultivar to both crown rot pathogens [21,30]. Root chamber tests were conducted as a series of six experiments. Three experiments were conducted for each *Fusarium* species. One experiment with *F. pseudograminearum* consisted of six inoculated replicates with six replicates of the non-inoculated control. All other experiments consisted of eight inoculated replicates and four replicates of the non-inoculated control. Each experiment was designed as a randomised complete block design, where each treatment (inoculated or uninoculated) was randomly allocated to a chamber within each replicate block. All experiments were performed in a growth chamber at the Leslie Research Facility, Department of Agriculture and Fisheries, Toowoomba, (27°31′58″S, 151°56′8″E), Queensland, Australia. The plant growth medium consisted of self-mulching black Vertosol of the Irving clay soil association, obtained from the Darling Downs in Queensland, Australia [31], mixed with river sand (50% sand to 50% soil by volume). The soil mixture was pasteurised at 75 °C for 45 min and air-dried for seven days. No fertiliser was added to the mix. The root chambers were similar to those described by Manschadi et al. [9]. Briefly, the dimensions of the chambers were 38 cm wide, 65 cm long and 3.2 cm deep and were constructed using steel frames with transparent polycarbonate sheeting on the front and back (0.8 cm thick).

The plant growth and inoculation methods were based on the layer pot design described by Wildermuth and McNamara [32]. Prior to planting, 6.3 kg (52 cm depth) of soil mix was added to each chamber and saturated using deionised water then allowed to drain overnight. The following day all chambers were covered with one side of polycarbonate sides and two seeds were placed on top of the soil, using forceps. The seeds were covered with 365 g (4 cm depth) of dry soil. Ground inoculum (0.30 g) was applied in an even layer on top of the soil surface. Sterilised ground grain was applied to each of the negative control treatments. The inoculum was covered with 120 g of dry soil (2 cm depth). Polycarbonate sides of the chambers were covered with black vinyl sheeting to exclude light from the root system and placed in a growth cabinet at 20 °C with a 12 h day/12 h night cycle. One week after planting, where two seeds had germinated the smallest plant was removed. Chambers were watered 1 week after planting to activate the inoculum, and then once weekly to saturation before they again were allowed to drain.

After 30 days of growth, one side of each chamber was removed to expose the entire soil profile in the chamber. A nail board was used to retain the root system architecture as the entire contents of each chamber were inverted and the chamber removed from above. The soil was then washed from the roots held in place on the nail board. A picture of each plant root system was taken using a Canon EOS 80D DSLR 26 MP camera (Fig. 1).

2.3. Root, shoot, and visual discolouration assessment

The severity of symptoms on the first three leaf sheaths was assessed using a 0 to 100% rating scale based on the visual brown to black discolouration where 0 = no discolouration and 100% = discolouration of 100% of the sheath tissue. The percentage of visual

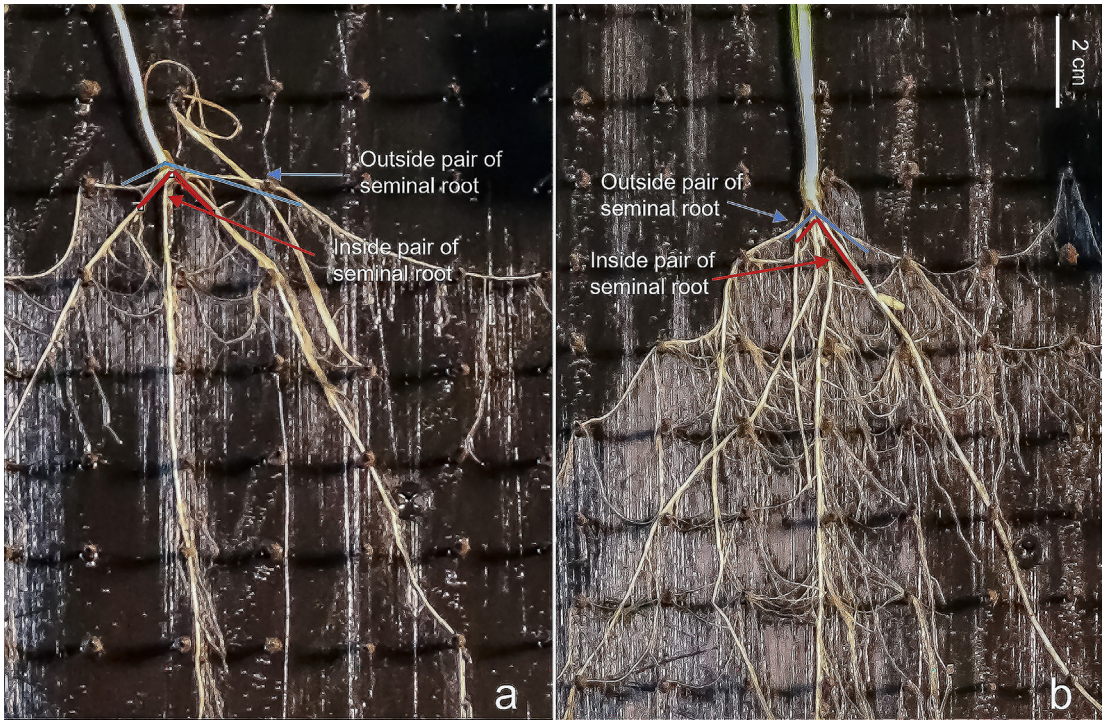

Fig. 1. Example of the root angle of the outside pair of seminal roots (blue) and the inside pair (red) of bread wheat cv. Livingston inoculated with *Fusarium culmorum* (a) and the non-inoculated control (b) on the nail board 30 days after emergence. Scale bar, 2 cm.

discolouration on the sheaths of the first three leaves was averaged. The intact root system of each plant was removed from the nail board and placed individually into a water bath containing Tetrasodium Pyrophosphate (TSPP) ($Na_4P_2O_7$) (Albright & Wilson Limited, Australia) overnight to clean off any clay adhering to the roots.

The leaf area of the oldest and the youngest fully-expanded leaf for each plant was measured using a leaf area meter (LI-3100C Area Meter, LI-COR Biosciences, Lincoln, NE, USA). Shoots and roots were placed in a separate paper bag and were dried in a 60 °C oven for 36 h, after which dry weights were recorded.

ImageJ software (https://imagej.nih.gov/ij/) was used to analyse the root angle of the first-pair of seminal roots (inside pair), which are the first pair to emerge after the primary seminal root [9], and the outside-pair of seminal roots, which is usually the last pair of seminal roots developed (Fig. 1). Each image was also used to score the root number and the length of the longest root.

2.4. Data analyses

The analysis of each variable was performed using a one-way ANOVA model, which included fixed effects for inoculum, experiment and their interactions. There were no significant differences between the three *F. culmorum* experiments nor between the three *F. pseudograminearum* experiments in any of the traits measured. Therefore, the experiments for each pathogen were combined and analysed together. Terms to account for replicate blocks, chambers, and plant within chamber were included as random effects, with variances estimated separately for each experiment. To test the distributions for normality, Kolmogorov-Smirnov [33] and Shapiro-Wilk [34] tests were applied.

$$SED = \sqrt{SE_1^2 + SE_2^2}$$

where, SED is the standard error of difference; SE_1 and SE_2 are the standard errors for the inoculated and the uninoculated treatments, respectively. All analyses were performed in Genstat 18th Edition (VSN International Limited, Hemel Hempstead, UK), using a significance level of 0.05.

3. Results

Infection with *F. culmorum* and *F. pseudograminearum* significantly reduced root length and number as well as dry weight of the root system (Table 1). Percentage reductions due to infection with *F. pseudograminearum* were slightly higher for all these parameters when compared to reductions caused by *F. culmorum*. The root angle measurements of *F. culmorum* inoculated plants exhibited a significant increase for both the inside and the outside pair. In contrast, there was no significant effect of *F. pseudograminearum* on the root angle of either the inside or outside pair of seminal roots compared to the non-inoculated control although the mean angle of treated plants was generally less compared to that of the non-inoculated control plants for both root types.

The averaged leaf sheath visual discolouration of cv. Livingston was significantly higher when infected with *F. culmorum* and *F. pseudograminearum* compared to the non-inoculated controls (Table 1). As anticipated, there was little or no visual discolouration in any of the non-inoculated controls. There was a significant reduction in the leaf area of the oldest leaf, youngest fully-expanded leaf, shoot fresh and dry weights as well as the number of the leaves when infected with *F. culmorum* and *F. pseudograminearum* compared to the non-inoculated control. The proportional reduction due to *F. pseudograminearum* was greater than *F. culmorum* treatments for all shoot measurements.

4. Discussion

A clear root chamber system was developed to study the effects of crown rot pathogens *F. culmorum* and *F. pseudograminearum* on the root system architecture of bread wheat. This has provided the

Table 1
Comparison in traits of wheat with and without inoculating *Fusarium culmorum* or *F. pseudograminearum*.

Trait	*F. culmorum*				*F. pseudograminearum*			
	Control	Inoculated	Diff. (%)	*P*-value	Control	Inoculated	Diff. (%)	*P*-value
Root angle (inside, °)	64.86 b	73.43 a	13.21	0.029	81.31 ns	78.11 ns	3.93	0.422
Root angle (outside, °)	78.63 b	92.45 a	17.58	0.028	106.37 ns	91.63 ns	13.86	0.076
Root length (cm)	63.73 a	56.65 b	11.11	0.004	58.14 a	49.10 b	15.56	0.01
Root dry weight (g)	0.043 a	0.029 b	32.61	0.006	0.036 a	0.014 b	60.86	< 0.001
Root number	6.95 a	5.37 b	22.75	0.002	5.99 a	3.78 b	36.86	< 0.001
Leaf sheath disease rating (%)	0.16 b	30.07 a	99.50	< 0.001	0 b	20.33 a	100	< 0.001
Leaf area (oldest, cm^2)	1.65 a	0.98 b	40.56	0.01	1.07 a	0.36 b	66.17	< 0.001
Leaf area (youngest, cm^2)	13.30 a	7.07 b	46.89	< 0.001	10.64 a	3.49 b	67.16	< 0.001
Shoot fresh weight (g)	1.62 a	0.94 b	41.95	< 0.001	1.87 a	0.68 b	63.51	< 0.001
Shoot dry weight (g)	0.15 a	0.11 b	29.34	< 0.001	0.20 a	0.093 b	53.92	< 0.001
Leaf number	5.22 a	4.50 b	13.74	0.027	6.22 a	4.28 b	31.19	< 0.001

Inside and outside root pairs are defined as shown in Fig. 1. Control was the non-inoculated treatment. Different letters indicate significant difference ($P < 0.05$) between means of the control and the inoculated treatment while "ns" indicates that means were not significantly different.

clearest evidence to date that infection with these pathogens affects not only the overall growth of the root system but also the detailed root architecture. The phenotyping system using root observation chambers provided a repeatable root characterisation method that could help researchers to identify genetic variation in root system response to infection by *F. culmorum* and *F. pseudograminearum*. It could also assist breeders to select lines tolerant to be used as parents in breeding programs aiming to develop tolerant cultivars. This method was able to identify differences in the pathogen effects on roots, which were not observed using previous systems [27–29].

The levels of plant damage observed in shoots in our study were similar to those reported for infected susceptible plants in the field [13,14,18,20]. Thus, the effects of infection appeared to be in an agronomically relevant range. This gives some confidence that the root system effects observed are relevant in the target environment. Additionally, non-limiting water and temperature conditions were chosen while establishing the method to reduce possible confounding effects of introducing more variables such as water or heat stress, for example. However, it would be of interest in future studies to investigate any effects on root architecture arising from the effects of different soil types and other environmental stresses relevant to important cropping regions where pathogens cause yield losses. The *F. culmorum* and *F. pseudograminearum* strains tested in this study significantly reduced the root biomass, length and number compared to the non-inoculated controls. A large and deep root system can contribute to the improved adaptation of wheat cultivars in dry seasons [35]. Thus, reduced root growth due to infection may further contribute to limiting plant growth by reducing the capacity of the root systems to effectively extract water and nutrition from the soil during the seedling stage. Two quantitative trait loci (QTL) studies in durum wheat infected with *F. pseudograminearum* [36] and bread wheat infected with *F. graminearum* [37], have indicated that genotypes with higher seminal root number and total root biomass were more tolerant to disease infection [36,37]. This could be due to the higher lignin/fibre content of root tissues with different morphological compositions [37]. Alahmad et al. [36] identified QTL on chromosome 6B (*qCR-6B*) associated with *F. pseudograminearum* tolerance, stay-green and root biomass in durum wheat. Manschadi et al. [8] reported that greater root length or density at depth resulted in increased water extraction late in the season, hence, improved wheat grain yields. Further research is required to determine the effect of crown rot pathogens on the root systems of bread wheat and the role of root development in the ability of the plant to tolerate crown rot infection during drought conditions.

A significant increase in the root angles of *F. culmorum* inoculated plants was observed. The bread wheat cv. Livingston is grown in the northern region of Australia. The cultivars grown in this region vary in root angle and root number, with the angle of roots reported to be an important characteristic, influencing the root architecture and thus the amount of water uptake at depth late in the season [9]. A narrower seminal root angle was associated with a greater proportion of roots at depth late in the season leading to greater soil water uptake and yield [38].

Water availability is critical during the life cycle of crops of wheat in rain-fed agricultural systems worldwide [39–41]. Deep and dense root systems can play a fundamental role in the adaptation of grain crops to a dry environment [7,9]. The deleterious impact of the two pathogens on the root system of cv. Livingston in our study suggests the vulnerability of wheat seedlings to water stress under crown rot disease was increased. Reduced water uptake due to infection is likely to impede the growth of the plant which may cause premature senescence leading to the death of grains (whiteheads).

Previously, the development of whiteheads and grain losses have been thought to be due to a blockage of the vascular systems [18,20]. This research indicates that a reduction in the length and size of the root systems under both *F. culmorum* and *F. pseudograminearum* infection could also play an important role in yield loss in bread wheat as could change in root angle induced by *F. culmorum*.

Plant biomass is an important factor in the study of functional plant biology and growth analysis. It is associated with grain yield and growth rate [42]. In our study, there was a significant reduction in the shoot fresh and dry weight as well as the leaf areas of both the oldest and the most recent growing leaf of cv. Livingston when infected with either *F. culmorum* or *F. pseudograminearum*. Infection with both crown rot pathogens had a negative impact on plant growth, which in field grown plants, would be expected to lead to reduced water use efficiency under early infection and a negative impact on the light interception capacity adversely affecting the plants capability for photosynthesis and carbon fixation resulting in the reduction of the plant total biomass and yield [43–45].

The use of a single susceptible genotype allows clear demonstration of the negative effects of more than one pathogen using a constant genetic background. However, the system could be used in future to test for any differences in responses between tolerant and intolerant genotypes.

CRediT authorship contribution statement

Ahmed Saad: Conceptualization, Methodology, Investigation, Data Curation, Formal analysis, Writing – Original Draft, Writing

– Review & Editing. **Jack Christopher:** Conceptualization, Resources, Methodology, Validation, Supervision, Writing – Review & Editing. **Anke Martin:** Validation, Supervision, Writing - Review & Editing. **Stephen McDonald:** Validation, Methodology, Writing – Review & Editing. **Cassandra Percy:** Conceptualization, Methodology, Validation, Resources, Supervision, Project Administration, Writing – Review & Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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