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Accounting for periods of wetness in displacement of *Fusarium pseudograminearum* from cereal straw

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Key words

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Abstract

Displacement of pathogenic *Fusarium* species from cereal residues by other fungi is an important mechanism for the effectiveness of fallows and crop rotations on disease management, as well as in potential biological control. The effect of fluctuating environmental conditions on the rate of displacement was assessed using two different approaches. In the first, wetness durations between 4 and 10 h were simulated by spraying water onto straw inoculated with *F. pseudograminearum* and antagonists in a greenhouse. For a given cumulative period of wetness, displacement of *F. pseudograminearum* was generally higher for short (4 h) wetting durations than longer (10 h), indicating that it was the number of wetting events, rather than their individual durations, that determined rate of displacement.

In the second approach, exponential decay models using thermal time adjusted for rainfall were fitted to published data on survival of *Fusarium* species in residues. Heat sums calculated from the mean temperature of days on which rain fell, or rainday-degrees (RDD) gave good fits to data from short-term experiments on displacement of *F. pseudograminearum* by antagonists under natural conditions. RDD and two other indices, decomposition days (DCD) and corrected degree-days (CDD) were equally satisfactory for modelling straw decomposition and mortality of *Fusarium* in longer-term data sets. Such models could be useful for predicting the effects of environmental variation on rotations and biocontrol for *Fusarium* management in cereals.

Keywords

Fusarium graminearum, biological control, straw decomposition, wetness periods, environmental variability, thermal time

Introduction

The fungi *Fusarium graminearum* Schw. (teleomorph *Gibberella zeae* (Schwein.) Petch) and *F. pseudograminearum* Aoki & O'Donnell (*G. coronicola* Aoki & O'Donnell) are important pathogens of wheat and other small grain cereals in most parts of the world. They cause head blight when inflorescences are infected at flowering, and crown rot when roots or stems are infected (Chakraborty *et al*., 2006). Regardless of the mode of infection or symptoms, these fungi survive in the absence of living hosts in infested residues, especially stem tissue. The mycelium aggressively colonizes the stems during senescence so that it has prior occupancy of the tissue at the time before the host plant dies (Trail *et al*., 2005). The amount of inoculum in a field, whether as spores or as mycelium capable of direct infection of plants, depends on the quantity of infested residues (Pereyra *et al*., 2004; Backhouse, 2006).

Crop rotation is an effective tool for management of *Fusarium* diseases in cereals. It is presumed to work by allowing time for a natural decline in inoculum to below economic threshold level. Summerell & Burgess (1988) and Pereyra *et al*. (2004) studied the survival of *F. pseudograminearum* and *F. graminearum* respectively in wheat residues in the field. They found that both the dry weight of the residue, and the proportion of pieces from which each pathogen could be isolated, declined over a period of two years. The decline in recovery of *F. graminearum* from residue pieces was accompanied by an increase in recovery of saprotrophic *Fusarium* species (Pereyra *et al*., 2004). This is consistent with the hypothesis that a major cause of mortality of pathogenic *Fusarium* species in straw is through displacement by non-pathogenic fungi, against which they are poor competitors. Displacement from residues by antagonistic fungi has been suggested as a means of biological control of diseases in cereals caused by *Fusarium* species (Luongo *et al*., 2005).

Effective biological control, and forecasting the effects of rotations and long fallows, requires knowledge of how the environment affects survival of *Fusarium* inoculum in cereal residues. In previous work (Singh *et al*., 2009) we identified fungi from straw that were representative of the range of interaction types with *F. pseudograminearum*, and examined the effects of temperature and water potential under constant conditions on displacement of *F. pseudograminearum* from cereal straw. In general, high displacement occurred at water potentials greater than -2 MPa, and displacement was faster at higher temperatures. The implications of this are that the most significant displacement in the field will occur when the straw is wet after periods of rain or dew, and there will be a strong temperature interaction as well. In the field, temperature and moisture availability fluctuates over time scales of hours or days, which means that rates of displacement under field conditions cannot be predicted directly from this type of laboratory experiment.

Two types of approaches have been undertaken by researchers for studying the effects of fluctuating environmental conditions on systems analogous to the displacement of *Fusarium* from straw. The first is exemplified by the work of Zhang & Pfender (1992, 1993) on wheat residues infested with *Pyrenophora tritici-repentis* (Died.) Drechsler. Pathogen-infested straw was inoculated with antagonists and subjected to repeated periods of wetness durations ranging from 6 to 48 hours, using a misting system in a greenhouse. They found that some antagonists suppressed the production of ascospores of *P. tritci-repentis* in wheat straw only when the straw remained wet for longer than 12 hours at a time (Zhang & Pfender 1993). The frequency of these long-period wetness events in the field was greatest in straw close to the soil surface, and this was correlated with reduced ascocarp production (Zhang & Pfender 1992). There do not appear to have been any similar studies on the effects of wetness duration or frequency of wetness on displacement of other pathogens from cereal residues.

The second approach is the modelling of straw decomposition rates using time scales adjusted for temperature and moisture. Most such models assume an exponential decay function, and use variants of thermal time (degree-days) that are corrected for rainfall or other indices of moisture availability (Steiner *et al.*, 1999; Quemada, 2004). Displacement of *Fusarium* species from straw is strongly correlated with decomposition (Pereyra *et al*. 2004), so it is most likely that similar models could be applied to this pathogen.

The aim of this study was to evaluate methods for predicting displacement of *Fusarium* species from cereal residues under fluctuating environmental conditions. The methods of Zhang & Pfender (1993) were used to investigate the effects of wetting periods on displacement of *F. pseudograminearum* from stubble by antagonists. Models for environmental effects on residue decomposition were tested against published data of Summerell & Burgess (1988) and Pereyra *et al*. (2004), in which both stubble weight and survival of *Fusarium* were monitored over two-year periods. The expected outcome was

identification of the best approach to account for environmental effects in biocontrol or rotation treatments.

Materials and Methods

Inoculation of barley straw substrate with *F. pseudograminearum* and antagonists

Barley straw pieces free of soil were chopped into pieces of about 5 cm length including one node. Straw pieces were soaked in distilled water overnight, and then drained. The straw was placed into autoclavable plastic bags (polyester oven bags). Non-absorbent cotton wool was used to plug the mouth of the plastic bags, and the mouths of these bags were covered with aluminium foil. The bags were autoclaved for 15 min on each of two successive days.

Ten plugs of 5 mm diameter were cut from 4-5 d old cultures of *F. pseudograminearum* grown on ¼ strength potato dextrose agar (PDA) and placed on the straw pieces in the bags. The inoculated straw pieces were incubated for two weeks at 25°C with occasional mixing so that *F. pseudograminearum* inoculum could spread uniformly on all stubble pieces. Stubble pieces were then dried under laminar flow for 2 d.

Four fungi isolated from wheat stubble by Singh *et al*. (2009) were used: *Trichoderma harzianum* (*Th*), *Fusarium equiseti* (*Fe*), *F. nygamai* (*Fn*) and *Alternaria infectoria* (*Ai*). Inoculum was prepared by growing each of the four fungi on wheat bran. Fresh wheat bran (15 mL) was combined with 12 mL of water in a glass Petri plate and autoclaved twice on successive days at 121°C for 20 min (Zhang & Pfender, 1993). After sterilization, 3 mL antibiotic solution (streptomycin sulphate 0.1 g L^{-1} and penicillin G 0.03 g L^{-1}) was added. The moistened bran in each plate was inoculated with four agar plugs of one of the four fungal cultures from ¼ PDA plates and incubated at room temperature until the fungi had completely colonized the bran. After 5-10 d depending on fungal growth rate, the colonized

bran was air-dried overnight and ground in a sterile mortar with a pestle. For the control treatments, uninoculated bran was incubated and ground similarly.

Bran inoculum of the antagonists was placed on one end of the precolonized straw pieces. A drop of autoclaved 1.3% methylcellulose solution was applied first in a narrow band to one end of the straw to serve as adhesive, and 5 mg of bran inoculum was immediately applied to this (Zhang & Pfender, 1993). The straw pieces were then placed vertically with the bran inoculum uppermost on truss nail plates with 32 teeth approximately 6 mm apart (Pryda SN5 Strapnail, Pryda Australia, Melbourne). The plates of inoculated straw pieces were supported 5 cm above the base of a rectangular plastic bin (597 mm long × 362 mm wide × 381 mm deep) with holes drilled in the base at one end to drain excess water. For the control, straw pieces were placed in the same way as other treatments. The position of the plates with each treatment was randomized within each bin.

Misting treatments under green house conditions

The bins containing the plates of inoculated straw were placed on a bench in a greenhouse, and the inoculated straw was exposed to alternating wet and dry treatments to simulate rain and drying events. The irrigation system was controlled electronically (Sterling Mist Master; Superior Controls, Valencia, CA, USA). Filtered tap water was run through full circle fan microspray nozzles delivering 0.3 L min^{-1} each with two nozzles suspended 15 cm above the straw pieces in each bin.

A misting frequency of 3 s every 10 min was used within the misting period. The misting period was scheduled to end before midday, to allow the straw to dry during the afternoon. There were three replicates of each misting period in each experiment laid out in a randomised complete block design.

An intial experiment with misting durations of 8, 16 and 24 h gave high displacement of *F. pseudograminearum* by antagonists with all misting schedules. Two experiments were therefore done with shorter misting durations of 4, 7 and 10 h in each 24 h period. One experiment was run in March-April (autumn) and one in June-July (winter). Mean daily minimum and maximum temperatures in the greenhouse during the experiments were 12.6°C and 29.8°C (March-April) and 8.7°C and 20.7°C (June-July).

At weekly intervals during each experiment, 8 straw pieces per replicate were removed and surface sterilized for 1 min in 1% NaOCl in 10% ethanol. The straw pieces were then placed on ¼ PDA for scoring displacement after 4-5 d (Singh *et al.*, 2009). The degree of displacement of *F. pseudograminearum* was recorded on a 0-4 scale based on proportion of the length of each straw piece from which either *F. pseudograminearum* or the antagonist grew, where 0, *F. pseudograminearum* only; 1, predominantly *F. pseudograminearum*; 2, equally *F. pseudograminearum* and the antagonist; 3, predominantly the antagonist; and 4, antagonist only. The scores for the eight pieces were summed to give a displacement index with a maximum value of 32 (Singh *et al*., 2009). Data were analysed by ANOVA in SPSS version 17 software (SPSS Inc, Chicago, Ill., USA). No transformation of the data was necessary.

Experiment under natural conditions

An experiment was set up in natural conditions of rainfall, dew and temperature for recording displacement of *F. pseudograminearum* by antagonists. Washed river sand was placed in rectangular plastic seedling trays (33 × 28 × 5 cm) to provide a free-draining base. Barley straw pieces were inoculated with *F. pseudograminearum* and antagonists as described above and placed in 5 × 10 cm litter bags made of 2 mm mesh size aluminium insect screen. The litter bags were placed on top of the sand in the trays which were placed in the open at

Armidale, Australia (30° 29' S, 151° 38' E, 1035 m). The experiment was run four times in autumn, winter and spring 2007 (Table 1). In each experiment, straw was exposed for four weeks. Displacement of *F. pseudograminearum* by antagonists was measured as for the green house experiment. During the experimental period data was collected for hourly temperature, wetness and rainfall using TA1 thermistor air temperature and LW01 leaf wetness sensors (Monitor Sensors, Caboolture, Qld, Australia) a tipping-bucket rain gauge. A completely randomised experimental design was used with five replications. The results were analyzed using ANOVA after log transformation to ensure homogeneity of variance.

Modelling of published data

Relationships between weather variables and pathogen displacement suggested by the experiment under natural conditions were tested against published data of Summerell & Burgess (1998) and Pereyra *et al.* (2004).

Summerell & Burgess (1988) measured recovery of *F. pseudograminearum*, and loss of weight, of naturally infested stubble of two wheat varieties at Moree, NSW, Australia. The data chosen were the means of the two varieties for percent recovery from crowns and stems, and percent stubble weight remaining, for a treatment where the stubble was retained on the soil surface at 3.2 t ha^{-1}. The stubble was exposed for 24 months. Daily weather data were obtained from the Bureau of Meteorology for the Moree weather station, approximately 5 km from the experimental site.

Pereyra *et al*. (2004) measured recovery of *F. graminearum* and weight loss of naturally infested wheat straw at Crookston, MN, USA. The data chosen were for a treatment where plots were chisel ploughed, and the residue was placed in residue bags on the surface. The residue was exposed for 24 months. Daily weather data for the site were obtained from the University of Minnesota (2007).

Three climate indices that adjust thermal time for the effects of moisture were calculated. All indices assumed a base temperature of 0°C for straw decomposition and displacement of *Fusarium*. The first index was the heat sum in degree-days, calculated from the mean daily temperature, for days on which rainfall was recorded, referred to here as rainday-degrees (RDD).

The decomposition day (DCD) index of Steiner *et al*. (1999) was calculated according to Ruffo & Bollero (2003). This index compares a moisture coefficient (MC) and a temperature coefficient (TC). Each coefficient varies between 0 and 1, with conditions most favorable for decomposition equal to 1. The DCD for any day is the minimum value of the TC or the MC, on the assumption that the most limiting factor controls the rate of decomposition. The moisture coefficient is calculated assuming that surface residue is completely wet by rainfall of 4 mm. If rainfall for the day is 4mm or greater, MC is set to 1. If rain is less than 4 mm, MC is calculated as the rainfall divided by 4. If no rain falls, MC is set to half of the MC for the previous day.

The temperature coefficient is calculated as follows:

$$TC = \frac{2.Tmean^2.Topt^2 - Tmean^4}{Topt^4}$$

where *Tmean* is the average of the daily maximum (*Tmax*) and minimum (*Tmin*) temperatures, and *Topt* is the optimum temperature for residue decomposition (32° C).

The corrected degree days (CDD) of Quemada (2004) were calculated as:

$$CDD = \frac{Tmean}{(Tmax - Tmean)}$$

This index assumes that moisture, either rain or high humidity, will be more available on days with low daily temperature ranges Quemada (2004).

Nonlinear regression in SPSS was used to fit first-order exponential decay functions to the residue and *Fusarium* recovery data of Pereyra *et al*. (2004) and Summerell & Burgess (1988), with RDD, DCD and CDD as the independent variables.

Results

Effect of wetness duration on *F. pseudograminearum* displacement under greenhouse conditions

Displacement of *F. pseudograminearum* in stubble by *Ai* was very low and not significantly different from controls at all the misting durations of 4, 7and 10 h in both experiments. No difference between misting durations was observed in either experiment (Fig. 1 A, E). The other three fungi gave moderate levels of displacement over the course of the experiment, with *Th* (Fig 1 D, H) showing significantly ($P < 0.05$) higher displacement than the *Fn* (Fig 1 C, G) or *Fe* (Fig. 1 B, F).

Figure 1 shows displacement plotted against cumulative hours of misting. If there is a minimum threshold time for displacement activity to occur, and the rate of displacement depends on the length of time for which straws are misted, then the curves for misting durations longer than the threshold should be collinear, and curves for misting durations shorter than the threshold should be below those for longer durations. However, the displacement values for the shortest duration of misting (4 h) were generally higher than for longer durations at a given cumulative duration of misting (Fig. 1). When displacement was plotted against number of misting events, the curve for each misting duration became more collinear for each antagonist in both the experiments (not shown).

Displacement of *F. pseudograminearum* from straw under natural conditions

There were highly significant ($P < 0.01$) effects of experiment and antagonist on displacement of *F. pseudograminearum* from straw under natural conditions and a highly significant ($P < 0.01$) interaction between antagonist and experiment. In all experiments *Th* displaced *F. pseudograminearum* from straw pieces significantly more than did *Fe* and *Fn*, with displacement by *Ai* being significantly lower (Fig. 2). Overall displacement declined from April-May to June-July and was highest in September-October (Fig. 2).

A range of weather variables were recorded to find those which correlated with displacement by each antagonist. Variables derived from the leaf wetness sensor, such as heat sums when the wetness was above a threshold value, gave poor fits (data not shown). This was probably because of dew, which would wet the surface of the sensor but not provide enough moisture to wet the interior of the straw. Variables or indices based on rainfall gave more satisfactory results.

Heat sums for days on which rain fell (RDD) gave significant positive correlations with displacement for all treatments and the control (Table 2). Scatter plots suggested a linear relationship and correlations were not improved by transforming the data. Decomposition days (DCD) also gave positive correlations for all treatments, although these were not significant for the control or *Fn*. Corrected degree-days (CDD) gave inconsistent results, with low correlations for most treatments and a highly significant negative correlation with *Fn* (Table 2).

Modelling of published data

The indices RDD, DCD and CDD all gave good fits when used as the time term in exponential decay models fitted to residue decomposition at Moree (Summerell & Burgess (1988) and Crookston (Pereyra *et al*., 2004). More than 94% of the variance was explained by the models for all three indices at both sites (Table 3). The R^2 values were lower when

models were fitted to displacement of *F. pseudograminearum* (Moree) or *F. graminearum* (Crookston) (Table 3). When goodness of fit of models using each index were compared using *F* ratios of error sums of squares from the nonlinear regressions, there were no significant differences between the indices for any of the variables being modelled. Decay coefficients (*k*) for Crookston were generally higher than those for Moree (Table 3).

Plots of the exponential decay models for residue dry weight and survival of *F. pseudograminearum* or *F. graminearum* against RDD gave good descriptions of the measured changes over two year periods (Fig. 3). Plots for DCD and CDD were similar (not shown).

Discussion

Interactions between antagonists and *F. pseudograminearum* in these experiments were done by displacement scoring in culture (Singh et al., 2009). Real-time PCR was evaluated as an alternative for quantifying *F. pseudograminearum* in the straw, but preliminary results suggested that the efficiency of DNA extraction changed with the state of decomposition. Because there was nothing that could be used as an internal reference for quantification, the culture-based method was considered more reliable for the particular experiments described here.

The initial experiment used 8, 16 and 24 hr misting periods to determine the threshold period of wetness for displacement of *F. pseudograminearum* because this was the range of times that Zhang & Pfender (1993) had found critical for antagonism of *P. tritici-repentis* in straw. However, high displacement by antagonists was found at all misting cycles of 8, 16 and 24 h wetting. Therefore, later studies used shorter times of 4, 7 and 10 h misting cycles.

At 4, 7 and 10 h misting duration, the minimum wetness duration for displacement could not be determined. The level of displacement appeared to be related to the number of

wetting events rather than their duration. This is contrary to the findings of Zhang & Pfender (1993) for suppression of ascocarp production by *P. tritici-repentis*, in which wetness durations of at least 24 h were required. However, the most antagonistic fungi used by Zhang & Pfender (1993), *Limonomyces roseipellis* Stalpers & Loerakker and *Laetisaria arvalis* Burdsall, were unable to antagonize *P. tritici-repentis* at water potentials of -0.5 MPa or below (Pfender *et al*., 1991). The antagonists in this study, *Fe*, *Fn* and *Th*, all showed considerable ability to displace *F. pseudograminearum* from straw at water potentials below -2 MPa at optimum temperature (Singh *et al*., 2009). This suggests that the straw does not need to be kept wet for displacement of *F. pseudograminearum* to occur. Antagonistic activity could continue for longer periods as the straw dries out after having been wet. The implication for modelling processes in the field is that it is the occurrence of wetness events, such as rainfall, rather than their duration that needs to be accounted for.

The effect of environment on rate of decomposition of plant residues on or above the soil surface has been modelled satisfactorily using a range of indices based on heat sums adjusted for moisture availability (Steiner *et al.*, 1999; Ruffo & Bollero, 2003; Quemada, 2004). However, this approach does not seem to have been used previously for modelling effects on antagonism of pathogens in straw. In short-term experiments, heat sums of days on which rain fell (RDD) gave significant positive correlations with displacement of *F. pseudograminearum* by antagonists in straw, indicating the potential for indices of this type to be used for calculating displacement rates.

DCD gave a low correlation with displacement of *F. pseudograminearum* by *F. nygamai*. This index has the most assumptions built into its calculation, including an optimum temperature and a nonlinear relationship between temperature and the temperature index. While DCD may give good results with residue decomposition (Steiner *et al.*, 1999; Ruffo & Bollero, 2003) which is presumably due to the activity of a suite of microorganisms,

it may not work well with individual fungi if their temperature relations differ from those assumed in the model. Further research investigating the effect of combinations of the antagonist test species on *F. pseudograminearum* displacement may indicate whether certain antagonist combinations are better able to displace *F. pseudograminearum* under less favourable environmental conditions.

CDD gave poor correlations with displacement of *F. pseudograminearum* in short term experiments. This index assumes that rainy days will have small ranges between minimum and maximum temperatures (Quemada, 2004). In the experiment conducted in September-October (spring), most of the rain fell in afternoon thunderstorms on days with large diurnal temperature ranges. This meant that CDD was not correlated with rainfall under this set of weather conditions, limiting its usefulness in short term experiments and indicating that it may be more suited to temperate conditions, rather than sub-tropical or tropical conditions.

All three indices tested (RDD, DCD, CDD) performed equally well on the residue decomposition and *Fusarium* displacement data of Summerell & Burgess (1988) and Pereyra *et al*. (2004). RDD and DCD take both rainfall and temperature into account, and would be expected to be highly correlated. CDD has the advantage of being calculated solely from daily maximum and minimum temperatures. Although it performed poorly in short term experiments when its assumptions were violated by a run of unusual weather, over longer periods its performance appears satisfactory, at least in continental climates (Quemada, 2004).

The indices used here considered only moisture that came from rain or dew. The moisture content of cereal straw could also be influenced by soil moisture. Zhang & Pfender (1992) showed that straw remained wet for longer after rainfall events if it was in contact

with the soil. The effect of soil type on retention of moisture may need to be considered in more precise modelling.

Decomposition rates calculated for Crookston were higher than those for Moree. Several factors affect decomposition rates, including density of residues and N content (Steiner *et al*., 1999). It is also possible that differences in microflora may affect decomposition rates. The fits of regression models to *Fusarium* survival data were less good than fits to decomposition data. The most likely reason for this is the greater variance associated with estimates of *Fusarium* recovery based on isolation in culture, compared with measurement of residue weight. Despite this, exponential decay functions appeared to be appropriate models for survival of different *Fusarium* species in straw under contrasting climatic conditions.

Backhouse (2006) found that inoculum potential of *F. pseudograminearum* could be estimated from the square root of the product of incidence of infection and crop yield, which was a surrogate for biomass. Since both the mass of residue, and the proportion of pieces from which the pathogen can be isolated, declined exponentially relative to RDD, DCD or CDD, then inoculum potential, or the capacity to infect plants, should decline in the same way. This means that models of the type fitted here could be used to predict and understand the behavior of crown rot during long fallow and rotations in relation to weather conditions during those periods.

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Table 1. Weather conditions during four field experiments in conducted in Armidale in 2007 for displacement of *Fusarium pseudograminearum* from barley straw by antagonists. Each experiment ran for 4 weeks.

Starting date	Mean temperatures (° C)		Rainfall	
	Maximum	Minimum	Total (mm)	Raindays
20 April	19.3	6.4	51	7
18 May	15.1	0.6	35	6
15 June	10.2	0.8	30	13
29 September	23.5	5.2	71	7

Table 2. Pearson's correlation coefficient (*r*) between displacement of *Fusarium pseudograminearum* from straw by antagonists and rainday-degrees (RDD), decomposition days (DCD) and corrected degree-days (CDD). Significance of correlation shown by * $P < 0.05$; ** $P < 0.01$ (18 df).

Treatment	RDD	DCD	CDD
Control	0.478*	0.411	-0.206
A. infectoria	0.658**	0.776**	0.162
F. equiseti	0.568*	0.574*	-0.237
F. nygamai	0.558*	0.219	-0.693**
T. harzianum	0.671**	0.694**	-0.110

Table 3. Decay coefficients (k) and proportion of variance (R^2) accounted for exponential decay models for residue dry weight and displacement of *Fusarium* species from wheat residues at two locations as a function of rainday-degrees (RDD), decomposition days (DCD) and corrected degree-days (CDD). Calculated from data for Moree (NSW, Australia) from Summerell and Burgess (1988) and for Crookston (MN, USA) from Pereyra *et al*. (2004).

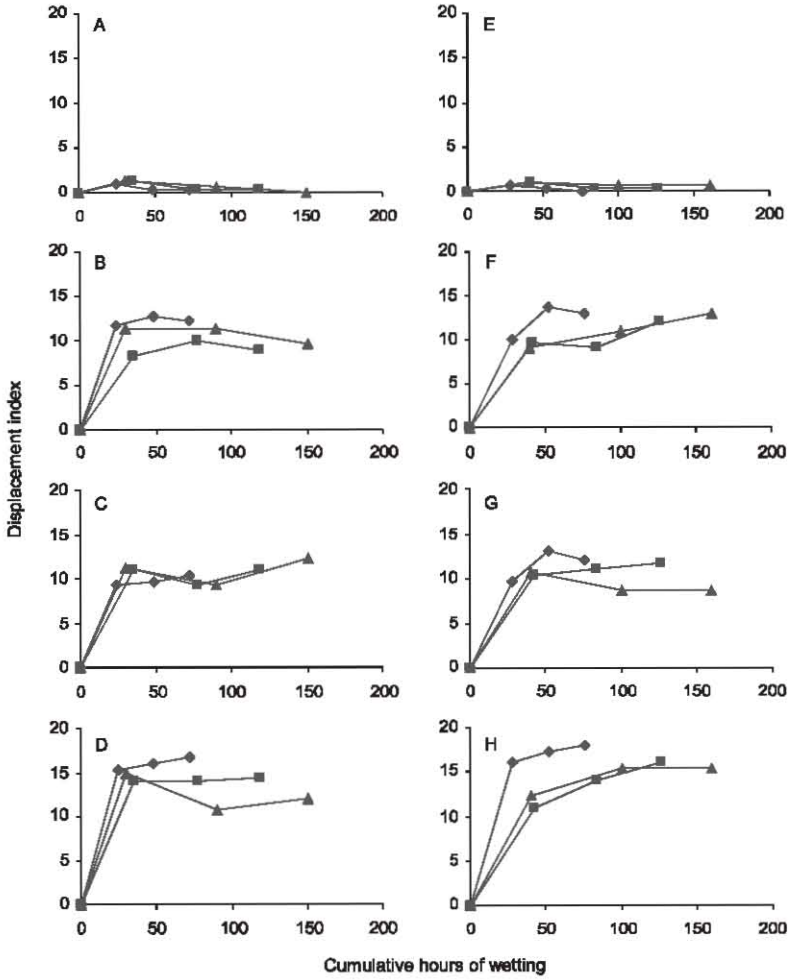
Location	Parameter	RDD		DCD		CDD	
		$k \times 10^3$	R^2	k	R^2	$k \times 10^3$	R^2
Moree	Residue dry weight	0.24	0.944	0.0108	0.938	0.62	0.981
	Fusarium (crowns)	0.25	0.670	0.0112	0.676	0.65	0.701
	Fusarium (stems)	0.42	0.431	0.0208	0.476	1.05	0.439
Crookston	Residue dry weight	0.91	0.982	0.0227	0.966	2.30	0.980
	Fusarium (nodes)	0.62	0.870	0.0157	0.833	1.59	0.860

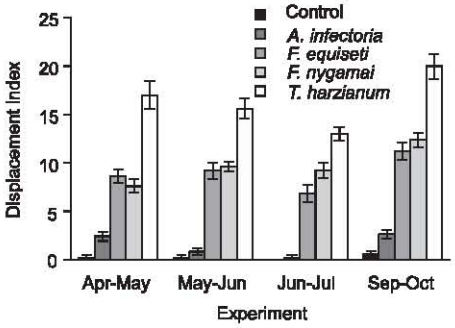
Figure legends

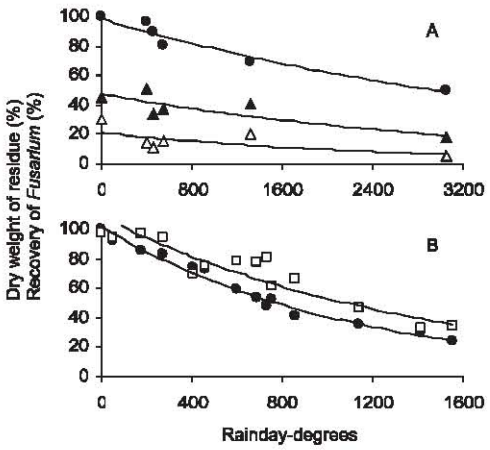
Figure 1 Effect of total duration of barley residue misting on displacement of *Fusarium pseudograminearum* by *Alternaria infectoria* (A, E), *F. equiseti* (B, F), *F. nygamai* (C, G) and *Trichoderma harzianum* (D, H) at 4 (◆), 7 (■) and 10 (▲) hour misting periods, in experiments conducted in March-April (A-D) and June-July (E-H). Standard errors of means 0.74 (experiment 1), 0.72 (experiment 2), 2 df.

Figure 2 Displacement of *Fusarium pseudograminearum* from barley straw pieces by antagonists in four experiments under natural conditions. Error bars show standard errors of means (4 df).

Figure 3 Effect of rainday-degrees on dry weight of residue (●) and recovery of *Fusarium* species from crowns (▲), stems (△) or nodes (□) of residues at Moree (NSW Australia) (A) and Crookston (MN, USA) (B). Lines are exponential decay curves fitted by nonlinear regression. Calculated from data for Moree from Summerell and Burgess (1988) and for Crookston from Pereyra *et al*. (2004).


A
B
C
D
E
F
G
H
Displacement index
Cumulative hours of wetting
0
5
10
15
20
50
100
150
200


Control
A. infectoria
F. equiseti
F. nygamai
T. harzianum
Displacement Index
25
20
15
10
5
0
Apr-May
May-Jun
Jun-Jul
Sep-Oct
Experiment


A
B
100
80
60
40
20
0
0
800
1600
2400
3200
400
1200
Dry weight of residue (%)
Recovery of Fusarium (%)
Rainday-degrees