

# Comparison of pathogenicity of the *Fusarium* crown rot (FCR) complex (*F. culmorum*, *F. pseudograminearum* and *F. graminearum*) on hard red spring and durum wheat

Alan T. Dyer · Robert H. Johnston ·  
Andrew C. Hogg · Jeffrey A. Johnston

Received: 9 January 2009 / Accepted: 7 May 2009 / Published online: 21 May 2009  
© KNPV 2009

**Abstract** *Fusarium* species involved in the *Fusarium* crown rot (FCR) complex affect wheat in every stage of development from seedling to grain fill. This study was designed to compare the aggressiveness of the FCR complex members including *F. culmorum*, *F. pseudograminearum* and *F. graminearum* in causing seedling blight, decreased plant vigour and crown rot. To assess their relative pathogenicity, two hard red spring wheat cultivars and two durum wheat cultivars were inoculated in the field with five isolates from each of the three species for two years. Significant differences in patterns of pathogenicity were identified. In particular, *F. culmorum* caused greater seedling blight while *F. pseudograminearum* and *F. graminearum* caused greater crown rot. Greatest yield reductions were caused by *F. pseudograminearum*. Cultivar differences were identified with respect to seedling disease and late season crown rot. No interactions were identified between cultivar performance and isolates or species with which they were challenged.

**Keywords** *Gibberella coronicola* · *G. zeae* · Foot rot · Seedling blight · Root pathogens

## Introduction

In Montana and the Pacific Northwest, *Fusarium* crown rot (FCR) of small grains is primarily caused by *F. culmorum*, *F. pseudograminearum* (*Gibberella coronicola*) and *F. graminearum* (*G. zeae*) (Paulitz et al. 2002). Initial infections occur early in the growing season and may cause pre-emergent and post-emergent damping-off of small grains. They may also enhance winter-kill in winter wheat (*Triticum aestivum* L.) by reducing seedling vigour (Dyer et al. 2007). If these early infections are not lethal, they become restricted in size by the plant's defences (Cook and Papendick 1970; Cook and Christen 1976). Under drought stress, defences weaken and the previously restricted *Fusarium* infections expand into the crowns and stems of the plants causing a brown discolouration (Cook and Christen 1976; Hare and Parry 1996). In severe cases, the pathogen invades the vascular tissue disrupting water movement, causing tillers to abort.

In the semi-arid regions of the Pacific Northwest, winter wheat losses due to FCR have been estimated at 9% of total yield in 1994 (Paulitz et al. 2002; Smiley et al. 2005b). For Montana, losses in spring wheat due to FCR in Hill, Judith Basin and Roosevelt counties were estimated at 8% or \$4.45 million in 2002 (Lenssen et al. 2004). Similar losses are thought to occur throughout most of the Pacific Northwest, Northern Great Plains and Canadian Prairie Provinces (Cook 1981). The effectiveness of chemical seed

---

A. T. Dyer (✉) · R. H. Johnston · A. C. Hogg ·  
J. A. Johnston  
Department of Plant Sciences and Plant Pathology,  
Montana State University,  
Bozeman, MT 59717-3150, USA  
e-mail: adyer@montana.edu

treatments and cultivar resistance is limited. Therefore, disease management has focused on cultural practices. Because FCR primarily develops during periods of drought stress, cultural controls are often related to moisture management (Papendick and Cook 1974; Cook 1980). In regions of low rainfall, this has involved limiting the foliage and plant biomass through reduced seeding densities and nitrogen rates (Cook 1980; Paulitz et al. 2002; Smiley et al. 1996).

In recent years, an increase in FCR severity has been linked to an increased adoption of conservation tillage practices (Smiley et al. 1996; Paulitz et al. 2002; Bailey et al. 2001). This increase in disease severity is contrary to expectations as soil water recharge is enhanced by conservation tillage practices (Bailey 1996). In response, many have speculated that the increase in FCR severity is the result of increased survival of the pathogens brought about by conservation tillage and/or an associated transition in predominant *Fusarium* species from *F. culmorum* to *F. pseudograminearum* (Sitton and Cook 1981, Paulitz et al. 2002). In addition, a dramatic increase in *F. graminearum* populations have likely occurred in many wheat-growing areas where *Fusarium* head blight (FHB) epidemics are common (Windels 2000). How this change may have impacted FCR severity is unknown.

Given the speculation, interests in the relative aggressiveness of *Fusarium* species and other common crown rot pathogens are being explored. Recent studies have shown that among the common wheat pathogens, *F. culmorum*, *F. pseudograminearum* and *F. graminearum* are the most aggressive pathogens of crown and root tissues (Kane et al. 1987; Fernandez and Chen 2005; Smiley et al. 2005a). In addition, a comparison between *F. pseudograminearum* and *F. culmorum* has shown *F. pseudograminearum* causes more severe late season disease (Smiley et al. 2005a) while a similar comparison between *F. culmorum* and *F. graminearum* showed no differences (Fernandez and Chen 2005). Besides interspecies comparisons, studies have identified significant differences among isolates within species, differences that appear to be affected by yearly variation in climate (Smiley et al. 2005a). For Montana, little information is available on the relative aggressiveness of *F. culmorum*, *F. pseudograminearum* and *F. graminearum* populations within the state. Given the documented differences in aggressiveness among isolates within species of the

FCR complex and changing population dynamics among species, it is important for the semi-arid climate of Montana that we understand the relative aggressiveness of the three species and how their variation relates to moderate tolerances found in some of our current wheat varieties.

The primary objectives of this study were to (1) compare virulence and aggressiveness of *F. culmorum*, *F. pseudograminearum* and *F. graminearum* on spring and durum wheat (*Triticum turgidum* var. *durum*) (2) determine if isolates within species vary in their patterns of pathogenicity and (3) determine whether variation in tolerance among cultivars is dependent on isolates and/or species with which they are challenged. To address these objectives, inoculated field trials were conducted during the summers of 2005 and 2006 using fifteen *Fusarium* isolates and two popular cultivars of hard red spring and durum wheat.

## Materials and methods

Field plots were planted in Bozeman, Montana in 2005 and 2006 with two hard red spring wheat cultivars ('Outlook' and 'Choteau') and two durum wheat cultivars ('Mountrail' and 'Kyle'). In previous trials, Outlook displayed moderate tolerance to FCR while Choteau displayed moderate susceptibility (Hogg et al. 2007). The field plots were seeded at a rate of 66 seeds m<sup>-1</sup> of row, which reflects recommended plant densities for this growing area. Individual plots were 3 m long by four rows wide with 30 cm row spacing. Plots were planted at ~2.5 cm depth and either inoculated in furrow with ~3.3 g of oat-based inoculum m<sup>-1</sup> row prepared according to Mathre and Johnston (1975) or left un-inoculated for the controls. The experiments were planted on May 2, 2005 and April 27, 2006. Experiments in both years were replicated four times in a split-plot design with the main plots being the four cultivars and subplots consisting of the 15 *Fusarium* isolates and the un-inoculated control. The 15 *Fusarium* isolates, five for each species, were randomly chosen from our culture collection (Table 1). All *F. culmorum* and *F. pseudograminearum* cultures were isolated from wheat crown tissues. The *F. graminearum* cultures were isolated from wheat crown tissues for those dated prior to the year 2000 and

**Table 1** Average performance of 15 *Fusarium* isolates across two hard red spring ('Choteau' and 'Outlook') and durum wheat ('Mountrail' and 'Kyle') cultivars and two years

Isolate	Year collected	Species	% Stand		Vigour <sup>a</sup>		DSI		% Yield	
	–	–	Y05 <sup>b</sup>	Y06	Y05	Y06	Y05	Y06	Y05	Y06
	–	<i>Uninoculated</i>	100	100	4.8	4.5	0.556	0.516	100	100
2103	2001	<i>F. culmorum</i>	84.4	63.1	3.9	2.5	0.521	0.440	102.7	91.5
2223	2002	<i>F. culmorum</i>	80.7	86.3	3.6	3.6	0.548	0.517	100.6	101.1
2230	2002	<i>F. culmorum</i>	90.7	91.9	4.2	3.7	0.486	0.447	99.9	100.7
2279	2003	<i>F. culmorum</i>	86.3	70.6	4.1	3.1	0.570	0.408	100.9	97.1
2286	2003	<i>F. culmorum</i>	93.9	96.3	4.5	4.0	0.505	0.469	99.4	99.5
423	1981	<i>F. graminearum</i>	91.1	94.1	4.3	3.9	0.521	0.510	100.4	100.8
468	1983	<i>F. graminearum</i>	95.7	82.6	4.5	3.1	0.918	0.531	94.7	94.5
2225	2002	<i>F. graminearum</i>	92.0	82.4	4.5	3.1	0.545	0.458	96.3	94.5
2318	2004	<i>F. graminearum</i>	92.1	97.6	4.2	3.9	0.631	0.437	99.5	101.8
2319	2004	<i>F. graminearum</i>	94.1	97.6	4.3	3.8	0.671	0.498	97.3	99.6
2100	2001	<i>F. pseudograminearum</i>	96.6	98.0	4.7	3.8	0.661	0.408	98.4	101.9
2228	2002	<i>F. pseudograminearum</i>	95.6	89.9	4.6	3.5	0.649	0.538	97.6	83.7
2234	2002	<i>F. pseudograminearum</i>	97.1	50.8	4.5	2.2	0.554	0.518	101.9	76.0
2278	2003	<i>F. pseudograminearum</i>	96.4	88.8	4.4	3.4	0.862	0.494	88.1	95.2
2317	2004	<i>F. pseudograminearum</i>	96.0	89.6	4.6	3.4	0.573	0.471	103.0	93.3
		Inoculated Mean	92.2	85.3	4.3	3.4	0.614	0.476	98.7	95.4
		Fisher's LSD <sup>c</sup> (α = 0.05)	6.2		0.36		0.102		6.90	

<sup>a</sup> Vigour ratings were taken on June 15 and May 25 for years 2005 and 2006, respectively

<sup>b</sup> Indicates the year from which the data was collected (Y05=2005; Y06=2006)

<sup>c</sup> Fisher's LSD is calculated for the isolate  $\times$  year interaction. Reported LSD values may be applied to make separations across all year  $\times$  isolate combinations

from grain for those isolated after 2000 (Table 1). Species designations were determined following the guidelines of Nelson et al. (1983) and by PCR (Hogg et al. 2007). During both years, weed control was achieved by hand cultivation to prevent plant stress that may occur with herbicide application. Different fields were used for each year and these were chisel-ploughed and disked prior to planting. Both fields were fallowed in the previous year and were planted to spring wheat two years prior. Past experience in these fields showed low levels of FCR with native populations being primarily *F. pseudograminearum*.

For each year, plots were examined throughout the growing season for stand densities, vigour, plant height, tiller density, disease severity, and yield. For seedling stands, plants were counted at the two-leaf stage for 2.4 m of one middle row in each plot. For vigour ratings, individual plots were

rated on a 1–5 scale with 1 being severe stunting and 5 being completely healthy and a vigorous stand. Plant heights were measured as the general height of each plot. For 2005, stand, vigour and plant heights were measured on May 18, June 15, and June 19, respectively. For 2006, stand, vigour and plant heights were measured on May 16, May 25, and June 6, respectively. For each year, a 60 cm portion of a middle row from each plot was removed just prior to harvest to measure tiller density and make disease evaluations. On average 60 cm of row produced 25 plants with three tillers per plant. The first internode of each collected tiller was rated for disease on a three-point scale with 1 being healthy to slight discolouration, 2 being moderately discoloured (light brown) and 3 being severely discoloured (dark brown). A disease severity index (DSI) was then generated using the

following equation based on the number of tillers in each of the three categories:

$$\text{DSI} = (\text{Number of disease severity class 1 tillers}) \\ + (2 \times \text{Number of tillers of disease severity class 2}) \\ + (4 \times \text{Number of tillers of disease severity class 3}) / (4 \times \text{Total number of tillers}).$$

The resulting DSI spans from 0.25–1.0 and takes into consideration that relatively clean stems have significant *Fusarium* populations (Hogg et al. 2007) and the highest rating disproportionally affects yield (Smiley et al. 2005b). For Montana, observations made at the first node have correlated well with yields and *Fusarium* populations (Hogg et al. 2007). Yields were taken from the middle two rows of each plot minus the 60 cm of row taken for tiller and disease severity ratings. For both years, rows were harvested in the first week of August. In order to correct for differences in genetic potential among cultivars and germination rates among seed lots, measures of stand, plant height and yield for each plot were transformed into a percentage of the respective control plots for purposes of comparisons.

For each response variable, a multi-factor analysis of variance was conducted with isolates, cultivars, years, and their interactions using the programme MacAnova v. 5.05 (Oehlert and Bingham 1997). While the isolates were selected randomly from a culture collection, they were assumed to be a non-random sampling of the natural populations for purposes of statistical analyses and therefore the data were analysed using a fixed effect model. For all analyses, residue plots were examined for normality (plots of residuals vs normal scores) and homogeneity of variances (plots of residuals vs treatment means). If the analysis found a significant difference among isolates, three two-tailed statistical contrasts were conducted to provide all pair-wise comparisons among the *Fusarium* species in question.

## Results

In 2005, weather was relatively cool and dry. Precipitation was 5.7, 2.9, 7.5 and 2.7 cm and average temperatures were 6.8, 9.8, 12.6 and 20.0°C for April, May, June and July, respectively. For 2005, there were notable differences among isolates and species in their

ability to cause disease (Table 1). In particular, *F. culmorum* reduced stands to 87.2% of the uninoculated controls, which was significantly lower than both *F. pseudograminearum* at 96.3% and *F. graminearum* at 93.0% ( $\alpha < 0.05$ ). These differences seemed to translate into significantly lower mid-season vigour ratings for *F. culmorum* (mean = 4.06) relative to *F. pseudograminearum* (mean = 4.56) and *F. graminearum* (mean = 4.36), which were significantly different from each other ( $\alpha < 0.05$ ). The number of tillers for *F. culmorum* (mean = 77.6 tillers/ 60 cm of row) was similar to those of *F. pseudograminearum* (mean = 81.8) and *F. graminearum* (mean = 78.5). Isolates and species showed little differences in their impacts on plant height. Late season disease was most severe with *F. pseudograminearum* and *F. graminearum* (mean DSI = 0.659 and 0.657 respectively), which were significantly greater than *F. culmorum* (mean DSI = 0.526,  $\alpha < 0.05$ ). Similar yield losses resulted from *F. pseudograminearum* (97.8% of controls) and *F. graminearum* inoculations (97.6%). These yield losses were significantly greater than those for *F. culmorum* (100.7%,  $\alpha < 0.05$ ). There were differences among cultivars for plant height, yield, vigour, FCR severity and tillers/ 60 cm of row (Tables 2,  $\alpha < 0.05$ ). The most notable difference attributable to wheat type (durum vs hard red spring wheat) was for tillers where the hard red spring wheat had on average 89.7 tillers/ 60 cm of row and the durum wheat had on average 69 tillers/ 60 cm of row (Table 2).

In comparison with 2005, weather in 2006 was wetter and warmer. Precipitation was 7.5, 4.3, 1.3 and 8.5 cm and average temperatures were 7.6, 11.5, 15.3 and 21.5°C for April, May, June, and July, respectively. For 2006, notable differences were seen in stand, vigour and yield among isolates and species tested (Table 1). In particular, *F. culmorum* and *F. pseudograminearum* caused the greatest stand reductions with means of 81.6% and 83.4% of the un-inoculated controls, respectively. These were significantly lower than the stands for *F. graminearum* (mean = 90.8%,  $\alpha < 0.05$ ).

**Table 2** Performance of four wheat cultivars when challenged with 15 isolates from the FCR complex including *F. culmorum*, *F. graminearum* and *F. pseudograminearum*

Cultivar	Type <sup>a</sup>	% Stand		Vigour <sup>b</sup>	% Tillering		% Plant height		DSI		% Yield	
		Y05 <sup>c</sup>	Y06	Y05–06	Y05	Y06	Y05	Y06	Y05	Y06	Y05	Y06
‘Choteau’	H. Red	90.3	82.9	4.0	88.0	67.0	98.9	103.7	0.658	0.436	98.8	100.4
‘Outlook’	H. Red	92.1	83.3	3.6	91.4	75.2	100.3	97.9	0.547	0.486	99.9	92.1
‘Mountrail’	Durum	93.6	92.1	3.8	71.4	67.6	99.5	101.0	0.631	0.464	95.4	93.6
‘Kyle’	Durum	92.7	82.9	4.0	66.6	67.5	97.9	97.3	0.622	0.519	100.9	95.5
	Yearly Means	92.2	85.3	3.9	79.4	69.3	99.2	100.0	0.614	0.476	98.7	95.4
	Fisher’s LSDd (α = 0.05)	3.21		0.13	5.08		2.27		0.052		3.56	

<sup>a</sup> Indicates wheat type; either hard red spring wheat (H. Red) or durum wheat (Durum)

<sup>b</sup> Vigour ratings were taken on June 15 and May 25 for years 2005 and 2006, respectively

<sup>c</sup> Indicates year; either 2005 (Y05), 2006 (Y06) or combined years (Y05–06)

<sup>d</sup> LSD values are for the cultivar  $\times$  year interaction except for vigour ratings where that interaction was non-significant

This early season disease seemed to translate into decreased vigour, with *F. culmorum* and *F. pseudograminearum* having similar vigour ratings (means = 3.3 and 3.2 respectively), which were significantly lower than vigour ratings for *F. graminearum* (mean = 3.5,  $\alpha < 0.05$ ). Mean DSI for plots inoculated with both *F. pseudograminearum* (mean = 0.486) and *F. graminearum* (mean = 0.485) were greater than that of *F. culmorum* (mean = 0.456) but not significantly ( $\alpha < 0.05$ ). The lowest average yield was for *F.*

*pseudograminearum* (mean = 90.0%). This was significantly lower than the yields of both *F. culmorum* (mean = 97.9%) and *F. graminearum* (mean = 98.2%,  $\alpha < 0.05$ ). Differences among cultivars were detected for percent stand, number of tillers, percent plant height, and percent yield (Table 2).

When combining data across years, significant differences among fungal species were identified for percent stand, vigour, DSI, and percent yield (Tables 1 and 3). Isolates of *F. culmorum* had the greatest

**Table 3** Results of analysis of variance and three statistical contrasts for six response variables across two years, five isolates from each of three *Fusarium* species and two cultivars for each hard red spring (‘Choteau’ and ‘Outlook’) and durum wheat (‘Mountrail’ and ‘Kyle’)

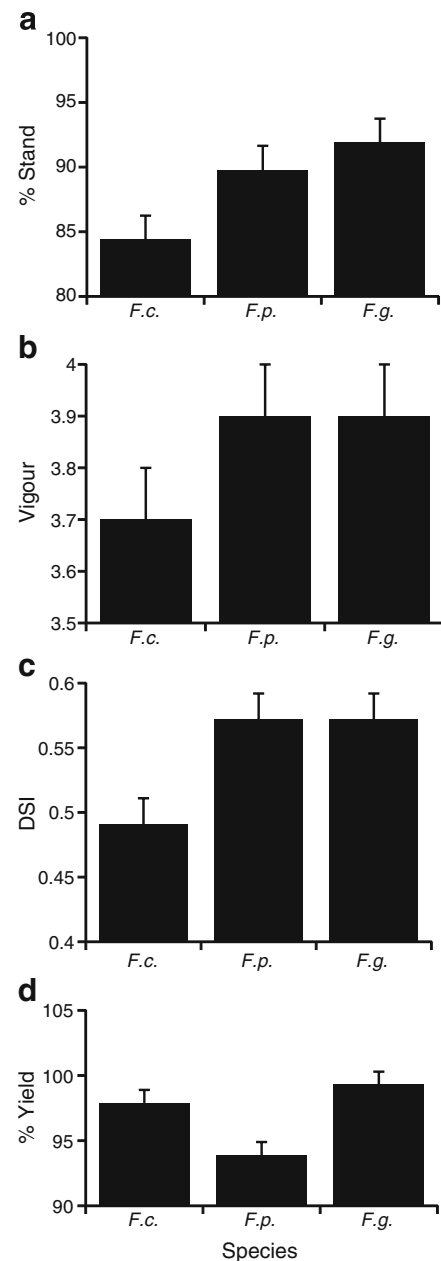
	% Stand		Vigour		Tiller		% Plant height		DSI		% Yield	
Independent variables:	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Cultivars	11.60	<0.001	11.72	<0.001	33.21	<0.001	7.63	<0.001	2.71	0.044	6.22	<0.001
Isolates	24.11	<0.001	11.48	<0.001	1.31	0.195	0.57	0.886	7.80	<0.001	4.99	<0.001
Year	70.25	<0.001	383.0	<0.001	59.78	<0.001	1.95	0.163	105.1	<0.001	13.2	<0.001
Interactions:												
Cultivar $\times$ Isolate	0.72	0.896	0.89	0.660	0.49	0.996	0.23	1	0.89	0.658	0.47	0.997
Cultivar $\times$ Year	5.21	0.001	2.02	0.110	15.69	<0.001	7.02	<0.001	6.92	<0.001	5.12	0.001
Isolate $\times$ Year	18.57	<0.001	10.17	<0.001	0.97	0.480	0.68	0.793	5.23	<0.001	5.80	<0.001
Cultivar $\times$ Isolate $\times$ Year	0.69	0.924	0.88	0.671	0.62	0.966	0.19	1	0.703	0.917	0.66	0.948
Contrasts (Two-tailed):												
<i>F. culmorum</i> vs <i>F. pseudograminearum</i>	–	<0.001	–	<0.001	–	–	–	–	–	<0.001	–	<0.001
<i>F. culmorum</i> vs <i>F. graminearum</i>	–	<0.001	–	<0.001	–	–	–	–	–	<0.001	–	0.208
<i>F. pseudograminearum</i> vs <i>F. graminearum</i>	–	0.042	–	0.517	–	–	–	–	–	0.966	–	<0.001



detrimental effects on stand with a mean stand of 84.4%, which was significantly lower than that of *F. pseudograminearum* at 89.8%, which in turn was significantly lower than *F. graminearum* at 91.9% of the un-inoculated controls (Fig. 1 a, Table 3). The impact of inoculations on seedlings translated into differences in mid-season disease as measured by vigour ratings where *F. culmorum* had significantly lower vigour ratings (mean = 3.7) relative to *F. pseudograminearum* and *F. graminearum*, both of which were not significantly different from each other (both means = 3.9, Fig. 1 b, Table 3). Spearman rank correlation showed a positive relationship between stand and vigour measures across years ( $R=0.86$ ,  $P < 0.001$ ,  $n=30$ ). In terms of late season disease, both *F. pseudograminearum* and *F. graminearum* had similar DSIs (means for both=0.572) which were significantly greater than the DSI for *F. culmorum* (mean DSI = 0.491, Fig. 1 c, Table 3). Contrasts showed *F. pseudograminearum* significantly reduced yield (mean = 93.9%) relative to *F. culmorum* and *F. graminearum*, which were not significantly different from each other at 97.9% and 99.3%, respectively (Fig. 1 d, Table 3). Notable among isolates, the most common impacts of inoculations were on stand and early season vigour relative to controls (Table 1). How yield related to disease was year-specific. Yield correlated with DSI across both years (Spearman rank correlation;  $R=-0.49$ ,  $P=0.005$ ,  $n=30$ ); while stand and vigour ratings correlated with yield in 2006 only (Spearman rank correlation;  $R=-0.70$ ,  $P=0.002$  and  $R=-0.75$ ,  $P < 0.001$ , respectively). Impacts of specific isolates on yield and disease severity were highly specific to year and isolate (Table 1).

## Discussion

This paper represents the first comparison of seedling blight and crown rot aggressiveness among three species in the FCR complex including *F. culmorum*, *F. pseudograminearum* and *F. graminearum*. The comparisons among these *Fusarium* species show that they have different patterns of pathogenicity. In particular, *F. culmorum* is the most consistent seedling pathogen causing significant stand losses in both years; while less consistent, *F. pseudograminearum* may also cause significant stand losses. Impacts on stand were also reflected in vigour ratings, where plots inoculated with



**Fig. 1** Impacts of *Fusarium culmorum* (F.c.), *F. pseudograminearum* (F.p.) and *F. graminearum* (F.g.) on disease in wheat for years 2005 and 2006 including **a** percent stand relative to controls, **b** plant vigour, **c** disease severity (indicated by disease severity index (DSI)) and **d** percent yield relative to controls. Trials were performed in Bozeman, Montana. Bars indicate standard error

*F. culmorum* isolates also had the lowest vigour ratings. For crown rot, both *F. graminearum* and *F. pseudograminearum* performed similarly with the highest disease severity indices. The aggressiveness

of *F. graminearum* isolates suggests that FCR severity may increase in areas where FHB is common. For Montana and the USA, FHB is caused primarily by *F. graminearum*, while in Europe, it is primarily caused by *F. culmorum* (Stack 2000). Given these documented differences and the high genetic diversity within the three species, the patterns of pathogenicity described by this study should be considered a local phenomenon until proven otherwise (Miedaner et al. 2008).

The patterns of pathogenicity described by this study may reflect species biology where *F. graminearum* and *F. pseudograminearum* are strictly residue-borne pathogens that depend on infesting late season tillers for survival between cropping cycles, while *F. culmorum* is capable of surviving between cycles as durable chlamydospores in the soil as well as in plant residue (Sitton and Cook 1981; Pereyra and Dill-Macky 2004). Not requiring residues for survival may allow *F. culmorum* to be a more aggressive seedling pathogen and preclude it from causing severe crown rot as lower plant stands generally decrease crown rot severity later in the season due to decreased water stress (Cook, 1980). Previous work has indicated that *F. pseudograminearum* is more active in warmer (Cook 1981) and wetter environments (Smiley and Patterson 1996). This seems partially confirmed in this study where *F. pseudograminearum* showed it was capable of aggressively attacking seedlings in the warmer, wetter spring of 2006 but not in 2005.

The practical implications of these findings are that selecting specific species for trials involving specific disease phases may be justified. In other words if an evaluation for resistance to seedling blight is desired, one may wish to preferentially select among isolates of *F. culmorum*, as this species shows the most consistent effect on stand and mid-season vigour. In contrast, if late season disease is the focus, *F. pseudograminearum* or *F. graminearum* may be preferred. With that said, stand losses due to *F. pseudograminearum* seem to impact on yield more than those of *F. culmorum*. Whether *F. pseudograminearum*, being an aggressive late season pathogen, possibly prevents neighbouring plants from compensating for missing stand is something worth exploring further. With this in mind, it is worth noting that despite differences in seedling blight and late season disease, tiller densities did not differ significantly among isolates and were therefore probably not the source of yield differences described.

Similar to the results of others (Smiley et al. 2005a), patterns of pathogenicity and aggressiveness among isolates varied according to trial year. Why this occurs is unknown. For this study, assessment of inoculum, seed quality and cultural practices has not identified significant sources of this variation. Whether uncontrolled factors like climate interact with isolate variability to create these yearly differences needs to be addressed. Populations of *F. culmorum*, *F. pseudograminearum* and *F. graminearum* are diverse and largely non-clonal (Miedaner et al. 2008). In exploring this subject, it would be interesting to further study how the phenotypic variation described here relates to the genetic variability of the species.

Results from this study suggest that the transition in *Fusarium* species from primarily *F. culmorum* to *F. pseudograminearum* and *F. graminearum* may be at least partly responsible for the increase in FCR severity in no-till and conservation tillage systems (Paulitz et al. 2002). The adoption of conservation tillage increases inoculum pressures, cropping intensity, crown depths, and early season moisture. All of these factors have been shown to increase crown rot severity and together with species differences may explain much of the recent increases in FCR severity (Cook 1980, Swan et al. 2000; Wildermuth et al. 2001).

Significant differences were identified among cultivars for every response variable measured. While differences among cultivars appear modest, this is partly due to results from more aggressive isolates being masked by the less virulent isolates that poorly separate cultivar performance. Also, differences in resistance may become more dramatic in annual cropping systems where small differences may be amplified as greater disease severity in one-year results in greater *Fusarium* populations (Hogg et al. 2007) and greater disease pressure for next year (Backhouse, 2006). Differences noted in stand among cultivars appears to be the result of differential resistance to *Fusarium* and not the result of differences in seed quality as stands for un-inoculated plots were similar across cultivars (data not presented). This study did not identify any species or isolate-specific resistance as no interactions between cultivar performance and isolates were identified.

Significant interactions occurred between yield and other response variables including DSI, stand, and vigour ratings. The strongest of these was the

interaction between DSI and yield, where a significant correlation was detected across both years of this study. This correlation was not surprising as crown rot primarily affects plants during grain fill. In contrast to crown rot, stand and vigour ratings only correlated with yield in the second year of this trial when large stand losses were experienced. Yield losses due to reductions in stand are often minimised by the ability of neighbouring wheat plants to compensate for losses in stand. Both vigour and percent stand reflect the impacts of relatively early season infections and correlated well with each other in this study.

In conclusion, this study identified significant differences in pathogenicity among three members of the FCR complex and in particular that *F. culmorum* excels as a seedling pathogen, while *F. pseudograminearum* and *F. graminearum* cause significant late season disease. This work agrees with previous suggestions that the recent increase in FCR severity may be at least partially due to an increase in populations of *F. pseudograminearum*. This work also shows that *F. graminearum*, the cause of FHB in the USA, is an aggressive crown rot pathogen. Differences in performance of cultivars challenged with these pathogens were identified but these differences did not vary according to species or isolates with which they were challenged. Similar to past reports (Smiley et al. 2005a), the performance of isolates varied according to year suggesting the influence of uncontrolled and unidentified factors.

**Acknowledgements** This project was supported by the National Research Initiative of the United States Department of Agriculture Cooperative State Research, Education and Extension Service, grant number 2005-35319-16193, the Montana Wheat and Barley Committee and by the Montana Agriculture Experiment Station. We thank J. Martin, W. Grey and M. Burrows for their excellent technical support.

## References

- Backhouse, D. (2006). Forecasting the risk of crown rot between successive wheat crops. *Australian Journal of Experimental Agriculture*, 46, 1499–1506.
- Bailey, K. L. (1996). Diseases under conservation tillage systems. *Canadian Journal of Plant Science*, 76, 635–639.
- Bailey, K. L., Mortensen, K., Lafond, G. P., Watson, P. R., & Derksen, D. A. (2001). Effect of tillage and crop rotation on root and foliar disease of wheat and pea in Saskatchewan from 1991–1990: univariate and multivariate analyses. *Canadian Journal of Plant Science*, 81, 789–803.
- Cook, R. J. (1980). *Fusarium* foot rot of wheat and its control in the Pacific Northwest. *Plant Disease*, 64, 1061–1066.
- Cook, R. J. (1981). *Fusarium* diseases of wheat and other small grains in North America. In P. E. Nelson, T. A. Toussoun & R. J. Cook (Eds.), *Fusarium: diseases, biology, and taxonomy* (pp. 39–52). University Park: Pennsylvania State University Press.
- Cook, R. J., & Christen, A. A. (1976). Growth of cereal root rot fungi as affected by temperature–water potential interactions. *Phytopathology*, 66, 193–197.
- Cook, R. J., & Papendick, R. I. (1970). Soil water potential as a factor in the ecology of *Fusarium roseum* f.sp. *cerealis* 'culmorum'. *Plant and Soil*, 32, 131–145.
- Dyer, A. T., Burrows, M., Johnston, B. & Tharp, C. (2007). Small grain treatment guide. *MontGuide*: MT 199608 AG.
- Fernandez, M. R., & Chen, Y. (2005). Pathogenicity of *Fusarium* species on different plant parts of spring wheat under controlled conditions. *Plant Disease*, 89, 164–169.
- Hare, M. C., & Parry, D. W. (1996). Observations on the maintenance and measurement of soil water in simple pot experiments and its effects on the seed-borne *Fusarium culmorum* seedling blight of winter wheat. *Annals of Applied Biology*, 129, 227–235.
- Hogg, A. C., Johnston, R. H., & Dyer, A. T. (2007). Applying real-time quantitative PCR to *Fusarium* crown rot of wheat. *Plant Disease*, 91, 1021–1028.
- Kane, R. T., Smiley, R. W., & Sorrels, M. E. (1987). Relative pathogenicity of select *Fusarium* species and *Microdochium bolleyi* to winter wheat in New York. *Plant Disease*, 71, 177–181.
- Lenzsen, A. W., Johnson, G. D., Grey, W. R., Hatfield, P. G. & Blodgett, S. L. (2004). U.S.D.A Special Grant, 2003 Annual Report: Sustainable pest management in dryland wheat pp. 107.
- Mathre, D. E., & Johnston, R. H. (1975). Cephalosporium stripe of winter wheat: procedures for determining host response. *Crop Science*, 15, 591–594.
- Miedaner, T., Cumagun, C. J. R., & Chakraborty, S. (2008). Population genetics of three important head blight pathogens, *Fusarium graminearum*, *F. pseudograminearum*, and *F. culmorum*. *Journal of Phytopathology*, 156, 129–139.
- Nelson, P. E., Toussoun, T. A., & Marasas, W. F. (1983). *Fusarium species: An illustrative manual for identification*. University Park: The Pennsylvania State University Press.
- Oehlert, G. W. & Bingham, C. (1997) *MacAnova User's Guide*. Technical Report No. 617, School of Statistics, University of Minnesota.
- Papendick, R. I., & Cook, R. J. (1974). Plant water stress and development of *Fusarium* foot rot in wheat subjected to different cultural practices. *Phytopathology*, 64, 358–363.
- Paulitz, T. C., Smiley, R. W., & Cook, R. J. (2002). Insights into the prevalence and management of soilborne cereal pathogens under direct seeding in the Pacific Northwest, U.S.A. *Canadian Journal of Plant Pathology*, 24, 416–428.
- Pereyra, S. A., & Dill-Macky, R. (2004). Survival and inoculum production of *Gibberella zeae* in wheat residue. *Plant Disease*, 88, 724–730.



- Sitton, J. W., & Cook, R. J. (1981). Comparative morphology and survival of chlamydospores of *Fusarium roseum* 'culmorum' and 'graminearum'. *Phytopathology*, 71, 85–90.
- Smiley, R. W., & Patterson, L. M. (1996). Pathogenic fungi associated with Fusarium foot rot of winter wheat in the semi-arid Pacific Northwest. *Plant Disease*, 80, 944–949.
- Smiley, R. W., Collins, H. P., & Rasmussen, P. E. (1996). Diseases of wheat in long-term agronomic experiments at Pendleton, Oregon. *Plant Disease*, 80, 813–820.
- Smiley, R. W., Gourlie, J. A., Easley, S. A., & Patterson, L. M. (2005a). Pathogenicity of fungi associated with the wheat crown rot complex in Oregon and Washington. *Plant Disease*, 89, 949–957.
- Smiley, R. W., Gourlie, J. A., Easley, S. A., Patterson, L. M., & Whittaker, R. G. (2005b). Crop damage estimates for crown rot of wheat and barley in the Pacific Northwest. *Plant Disease*, 89, 595–604.
- Stack, R. W. (2000). Return of an old problem: Fusarium head blight of small grains. *Plant Health Progress*, . doi:[10.1094/PHP-2000-622-01-RV](https://doi.org/10.1094/PHP-2000-622-01-RV).
- Swan, L. J., Backhouse, D., & Burgess, L. W. (2000). Surface soil moisture and stubble management practice effects on progress of infection of wheat by *Fusarium pseudograminearum*. *Australian Journal of Experimental Agriculture*, 40, 693–698.
- Wildermuth, G. B., MacNamara, R. B., & Quick, J. S. (2001). Crown depth and susceptibility to crown rot in wheat. *Euphytica*, 122, 397–405.
- Windels, C. E. (2000). Economic and social impacts of *Fusarium* head blight: changing farms and rural communities in the Northern Great Plains. *Phytopathology*, 90, 17–21.