Analysis of the *Fusarium graminearum* species complex from wheat, barley and maize in South Africa provides evidence of species-specific differences in host preference

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**A B S T R A C T**

Species identity and trichothecene toxin potential of 560 members of the *Fusarium graminearum* species complex (FGSC) collected from diseased wheat, barley and maize in South Africa was determined using a microsphere-based multilocus genotyping assay. Although three trichothecene types (3-ADON, 15-ADON and NIV) were represented among these isolates, strains with the 15-ADON type predominated on all three hosts. A significant difference, however, was identified in the composition of FGSC pathogens associated with Gibberella ear rot (GER) of maize as compared to *Fusarium head blight* (FHB) of wheat or barley (*P* < 0.001). *F. graminearum* accounted for more than 85% of the FGSC isolates associated with FHB of wheat and barley (*N* = 425), and was also the dominant species among isolates from maize roots (*N* = 35). However, with the exception of a single isolate identified as an interspecific hybrid between *Fusarium boothii* and *F. graminearum*, GER of maize (*N* = 100) was exclusively associated with *F. botheii*. The predominance of *F. graminearum* among FHB isolates, and the near exclusivity of *F. botheii* among GER isolates, was observed across all cultivars, collection dates, and provinces sampled. Because these results suggest a difference in host preference among species of the FGSC, we hypothesize that *F. graminearum* may be less well adapted to infect maize ears than other members of the FGSC.

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1. Introduction

Members of the *Fusarium graminearum* species complex (FGSC) infect wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), maize (*Zea mays* L.) and other cereal crops across the world, causing diseases such as Fusarium head blight (FHB) and Gibberella ear rot (GER). These diseases significantly reduce grain yield and quality. In addition, FHB and GER are significant food safety problems because infected grain is often contaminated with trichothecene mycotoxins that inhibit protein synthesis and can produce a variety of health problems in humans and other animals (Bennett and Klich, 2003; Pestka, 2010). Trichothecenes also are phytotoxic and act as virulence factors on sensitive plant hosts (Jansen et al., 2005; Proctor et al., 1995). In South Africa, GER has been reported on maize (Marasas et al., 1979) and FHB on irrigated wheat (Marasas et al., 1988; Scott et al., 1988). With the substantial increase in wheat, barley and maize production areas overlapping in recent years, FHB and GER have become important diseases, particularly in irrigated fields. As is the case in much of the world, mycotoxin contamination of maize and wheat is of great concern in South Africa because these cereals constitute the major staple food of South Africans and because they are used extensively as animal feed. Moreover, trichothecene contamination of barley is of concern to the malting and beer brewing industries of South Africa.

To date, 13 species have been identified and formally described within the FGSC (O'Donnell et al., 2000, 2004, 2008; Starkey et al., 2007; Vli-Mattila et al., 2009), with *F. graminearum sensu stricto* being the species most commonly associated with FHB worldwide. In addition, a putatively new species within the FGSC was recently identified from Nepal (Chandler et al., 2003; Desjardins and Proctor, 2011). FGSC species produce type B trichothecenes (Goswami and Kistler, 2005; O'Donnell et al., 2008; Starkey et al., 2007; Vli-Mattila et al., 2009) that include deoxynivalenol (DON) and its acetylated forms 3-acetyl-deoxynivalenol...
(3-ADON) and 15-acetyl-deoxynivalenol (15-ADON), as well as nivalenol (NIV) and its acetylated form 4-acetylNivalenol or fusar- enone X (FX). Among the type B trichothecene-producing Fusari- 
sium species, three strain-specific chemotypes have been identi- 
fied: the NIV chemotype produces NIV and its acetylated 
dervatives, the 3-ADON chemotype produces DON and 3-ADON, 
and the 15-ADON chemotype produces DON and 15-ADON (Mill-
er et al., 1991). Although a slight difference exists between these 
compounds in the pattern of hydroxylation and acetylation, the 
biological activities of these compounds can be different, indicat-

ing that chemotype differences may have important health con-
sequences (Kimura et al., 1998).

In recent years, numerous studies have been conducted to as-
sess species and trichothecene chemotype diversity among FGSC isolates infecting wheat, barley and maize around the world, 
including North America (Ward et al., 2008), South America (Ra-
mirez et al., 2006; Scoz et al., 2009), Europe (Láday et al., 2004; 
Tóth et al., 2005; Yli-Mattila et al., 2009), Asia (Chandler et al., 
2003; Desjardins and Proctor, 2011; Suga et al., 2008; Yang et al., 
2008; Yli-Mattila et al., 2009), and New Zealand (Monds et al., 
2005). However, very little information is available on FGSC diver-
sity in Africa, with limited surveys having been conducted in Ethio-
pia (O’Donnell et al., 2008) and Kenya (Wagacha et al., 2010). 
Moreover, few studies worldwide have investigated the diversity 
of the FGSC recovered from maize, with most of the research focusing 
on wheat and barley. In this context, the objective of this study 
was to determine the species identity and trichothecene toxin poten-
tial of FGSC isolates collected from wheat, barley and maize 
from South Africa using a recently described microsphere-based 
multilocus genotyping assay (MLGT) (Ward et al., 2008). Such 
information is critical for developing management strategies for 
FHB and GER in South Africa, since these crops are often produced 
in rotation on the same fields, and is also needed to improve under-
standing of the distribution and significance of FGSC diversity 
worldwide.

2. Materials and methods

2.1. Isolates

A total of 560 South African isolates tentatively identified as 
members of the FGSC were selected for this study (Supplemental 
Table 1). These included 277 isolates from FHB-infected heads 
of five different wheat cultivars collected from all wheat-growing 
areas (six provinces, 23 localities) in 2008 and 2009 (Fig. 1a). 
In addition, 100 isolates were recovered from GER-infected maize 
ears of nine different cultivars collected from all maize-growing 
areas (five provinces, 19 localities) in 2008 and 2010 (Fig. 1b). 
An additional 35 isolates were obtained from maize roots collected 
from one cultivar at one locality in the KwaZulu-Natal Province 
in 2006; those 35 isolates were provided by Dr. Sandra Lamprecht 
(Plant Protection Research Institute, South Africa). Finally, 148 iso-
lates were obtained from FHB-contaminated barley heads collected 
in 2008 and 2009 from two different cultivars at eight localities in 
the Northern Cape Province of South Africa, where barley cultiv-
a

2.2. Multilocus genotyping assay (MLGT)

After isolates were grown on PDA plates for 5 days, genomic 
DNA was extracted from harvested aerial mycelia using the Wiz-
ard® SV Genomic DNA purification System Kit (Promega, South 
Africa). Isolates were subjected to a multilocus genotyping assay 
(MLGT) for simultaneous determination of species identity and 
prediction of trichothecene chemotype as previously described 
(Ward et al., 2008). Briefly, multiplex amplifications were per-
formed targeting six genes. The loci targeted in this assay include 
housekeeping genes and genes responsible for trichothecene bio-
synthesis. PCR products were subjected to allele-specific primer 
extension (ASPE) reactions in multiplex reactions containing 45 
probes, with each species and B-trichothecene chemotype targeted 
by probes in two different genes. Probes are described by O’Don-
nell et al. (2008), Ward et al. (2008), and Yli-Mattila et al. (2009). 
ASPE probes were designed with a unique S’ sequence tag specific 
to individual sets of Luminex (Luminex Corporation, Austin, TX, 
USA) xMAP fluorescent polystyrene microspheres. Biotinylated 
extension products from ASPE reactions were sorted by hybridiza-
tion to polystyrene microsphere sets coated with antisense se-
quences specific to the unique sequence tags appended to each 
of the extension probes. Individual microsphere sets also were la-
abeled with a specific mix of fluorescent dyes creating a unique 
spectral address that enabled extension products from different 
probes to be evaluated individually. Hybridization and detection 
were performed using a Luminex 100 flow cytometer (Luminex 
Corporation). Significance of differences in species composition 
was assessed via chi-square or Fisher exact probability tests.

2.3. Sequence analysis

One isolate (M-0014), collected from a maize ear in Gauteng 
Province in 2008, that could not be typed to species based on MLGT 
analysis was further characterized by sequencing portions of the 
translation elongation factor 1α (TEF-1) gene, the trichothecene 
3-O-acetyltransferase (TRI101) gene, a putative reductase gene 
(RED), and the mating-type locus (MAT). Sequencing reactions 
were carried out according to the method of Platt et al. (2007). 
Sequencing reaction products were purified using BigDye XTermi-
nator (Applied Biosystems, Foster City, CA, USA) and analyzed 
with an ABI 3730 DNA Analyzer (Applied Biosystems). DNA sequences 
were edited and aligned with Sequencher (version 4.10, Gene 
Codes, Ann Arbor, MI). The resulting DNA sequences were com-
pared to previously published sequences (O’Donnell et al., 2000, 
2004, 2008; Starkey et al., 2007; Ward et al., 2002; Yli-Mattila 
et al., 2009) deposited in the NCBI database using the Basic Local 
Alignment Search Tool (BLAST) and were also analyzed phyloge-
netically by the neighbor-joining method with the Kimura two-
parameter model of molecular evolution implemented in MEGA 
(version 4.0; Tamura et al., 2007). Support for individual nodes 
was assessed by bootstrap analysis with 1000 replications.

3. Results

3.1. Species diversity

Six of the 13 previously described species within the FGSC were 
recovered in our survey of FHB and GER in South Africa. These 
included F. graminearum, Fusarium bohemicum, Fusarium meridionale, 
Fusarium cortaderiae, Fusarium acaciea-mearnsii, and Fusarium bra-
silicum (Table 1). Among the isolates collected from wheat 
(N=277), the vast majority were identified as F. graminearum 
(85.2%). However, F. bohemicum (8.3%), F. meridionale (3.6%), F. ac-
ciae-mearnsii (1.4%), F. cortaderiae (1.1%), and F. brasiliicum (0.4%)
also were isolated from wheat. *F. graminearum* (87.2%) and *F. boothii* (12.8%) were the only FGSC species isolated from barley (*N* = 148). However, the frequencies of these species among barley isolates was not significantly different (*P* = 0.28) from those observed for wheat isolates, indicating that the FGSC pathogen composition was similar between wheat and barley in South Africa. In contrast, the composition of FGSC pathogens associated with GER of maize was significantly different (*P* < 0.001) than was observed for wheat isolates, indicating that the FGSC pathogen composition was similar between wheat and barley in South Africa.

**Table 1**

Diversity of the *Fusarium graminearum* species complex within hosts in South Africa. Results are expressed as percentage of isolates relative to the total number of isolates (*N*).

<table>
<thead>
<tr>
<th>Host</th>
<th><em>F. graminearum</em></th>
<th><em>F. boothii</em></th>
<th><em>F. meridionale</em></th>
<th><em>F. cortaderiae</em></th>
<th><em>F. acacia-mearnsii</em></th>
<th><em>F. brasilicum</em></th>
<th><em>N</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Wheat</td>
<td>85.2</td>
<td>8.3</td>
<td>3.6</td>
<td>1.1</td>
<td>1.4</td>
<td>0.4</td>
<td>277</td>
</tr>
<tr>
<td>Barley</td>
<td>87.2</td>
<td>12.8</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>148</td>
</tr>
<tr>
<td>Maize</td>
<td>0</td>
<td>99</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Maize (roots)</td>
<td>74</td>
<td>12</td>
<td>14</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>35</td>
</tr>
</tbody>
</table>

**Fig. 1.** Localities in South Africa where isolates were collected from wheat kernels in 2008 and 2009 (a) and from maize ears in 2008 and 2010 (b).
for FHB of wheat and barley. Excluding one isolate that could not be typed to species based on MLGT (discussed below), *F. boehii* was the only FGSC pathogen collected from maize ears (*N* = 100). However, *F. graminearum* (74%), *F. boehii* (12%) and *F. meridionale* (14%) were isolated from maize roots (*N* = 35). All of the isolates from maize roots were collected in KwaZulu-Natal Province. Interestingly, the FGSC composition on maize roots was not significantly different (*P* = 0.25) than that observed among isolates collected from wheat in KwaZulu-Natal Province, but was significantly different from the FGSC composition on maize ears in KwaZulu-Natal Province and across South Africa (*P* < 0.001).

Wheat was the only host for which we could assess differences in FGSC composition across provinces (Table 2). *F. graminearum* was the predominant pathogen of wheat in all South African provinces sampled, and it was the only FGSC species identified from wheat in the North West and Limpopo provinces. The greatest species diversity was observed within the KwaZulu-Natal Province, given that five of the six FGSC species found in South Africa were represented. In addition, KwaZulu-Natal was the only province in which *F. acaciae-mearnsii* was identified. It is noteworthy that the Free State Province (*N* = 26), in which *F. boehii* represented a significantly (*P* < 0.001) greater percentage of the isolates from wheat (46%) than was true for all other provinces (average = 5.3%), was the only province in which the dominance of *F. graminearum* among wheat isolates was challenged. Lastly, two isolates of *F. cortaderiae* from wheat in the Western Cape Province, as well as one from KwaZulu Natal, and one isolate of *F. brasilicum* from wheat in the Northern Cape Province represent the first reports of these species from Africa.

3.2. Trichothecene toxin chemotypes

The 15-ADON chemotype was predominant among isolates collected from wheat (93.1%), barley (99.3%), maize ears (100%) and maize roots (86%) in South Africa (Table 3). The NIV chemotype was present in 6.1% (*N* = 17) of the isolates collected from wheat and in 14% (*N* = 5) of the isolates collected from maize roots, but was not observed among isolates from barley or maize ears. Only three FGSC isolates from the entire collection were predicted to produce the 3-ADON chemotype. These isolates were from the Northern Cape Province, and included two isolates from wheat (one *F. graminearum* and one *F. brasilicum*) and one *F. graminearum* isolate from barley. Trichothecene chemotype polymorphism within individual species was limited to *F. graminearum*, in which 389 isolates possessed the 15-ADON chemotype, whereas only two isolates were of the 3-ADON chemotype. All of the *F. boehii* isolates (*N* = 145) possessed the 15-ADON chemotype, while *F. meridionale* (*N* = 15), *F. cortaderiae* (*N* = 3) and *F. acaciae-mearnsii* (*N* = 4) isolates represented the NIV chemotype. The single isolate of *F. brasilicum* in this collection possessed the 3-ADON chemotype.

3.3. Characterization of an unusual FGSC isolate

Species identity of one of the 560 FGSC isolates could not be determined unambiguously from the MLGT results. Isolate M-0014 was collected from a maize ear in Gauteng Province in 2008. This isolate was unusual in that it produced positive results with both *F. boehii*-specific probes, and also was positive for probe EF7(28), which is specific to *F. graminearum*. Sequence analysis confirmed the MLGT results by demonstrating that sequences for the *F. boehii*-specific probes and the EF7(28) probe were present in M-0014. Interestingly, M-0014 possessed *F. boehii* alleles at *TRI101* (100% identity across 1306 bp; 100% of bootstrap replicates) and RED (one nucleotide difference across 896 bp; 99% of bootstrap replicates), but possessed *F. graminearum* alleles at *TEF1* (100% identity across 687 bp; 100% of bootstrap replicates) and the MAT locus (four nucleotide differences across 5889 bp; 99% of bootstrap replicates), indicating that this strain is the product of interspecific hybridization between *F. boehii* and *F. graminearum*.

4. Discussion

In the decade since the initial recognition of cryptic genealogically exclusive species within *F. graminearum* as it was previously morphologically defined (O’Donnell et al., 2000), substantial effort has been directed at determining the extent, distribution, and significance of diversity within the FGSC. Results of the present study extend understanding of FGSC diversity by demonstrating for the first time that at least six species within the FGSC are associated with cereal hosts in South Africa (Table 1 and Fig. 2). Moreover, herein we document only the second naturally-occurring hybrid between species of the FGSC, which was confirmed by DNA sequence analysis, and the first to be detected by MLGT analysis. O’Donnell et al. (2000) previously demonstrated that a strain from Nepal was the product of interspecific hybridization between *Fusarium asiaticum* and *F. meridionale*. However, phylogenetic analyses based on numerous independent loci have demonstrated that the frequency of such hybridization events has been insufficient to oppose isolation by genetic drift (O’Donnell et al., 2000, 2004, 2008; Starkey et al., 2007), and the stability of the species-specific variation targeted by the MLGT assay is consistent with this conclusion (Gale et al., 2011; O’Donnell et al., 2008; Sampietro et al., 2011; Ward et al., 2008; Yli-Mattila et al., 2009).

Previously, small surveys of isolates collected on the African continent from wheat in Kenya (Wagacha et al., 2010) and Ethiopia (O’Donnell et al., 2008) revealed the presence of *F. boehii*, *F. graminearum* across provinces (Table 2).

### Table 2

<table>
<thead>
<tr>
<th>Provinces</th>
<th><em>F. graminearum</em></th>
<th><em>F. boehii</em></th>
<th><em>F. meridionale</em></th>
<th><em>F. cortaderiae</em></th>
<th><em>F. acaciae-mearnsii</em></th>
<th><em>F. brasilicum</em></th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Western cape</td>
<td>75</td>
<td>0</td>
<td>0</td>
<td>25</td>
<td>0</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>Mpumalanga</td>
<td>88</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>0</td>
<td>0</td>
<td>34</td>
</tr>
<tr>
<td>North west</td>
<td>100</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>Limpopo</td>
<td>100</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>16</td>
</tr>
<tr>
<td>Northern cape</td>
<td>94.3</td>
<td>4.7</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>106</td>
</tr>
<tr>
<td>KwaZulu-natal</td>
<td>78.7</td>
<td>5.3</td>
<td>9.3</td>
<td>1.3</td>
<td>5.3</td>
<td>0</td>
<td>75</td>
</tr>
<tr>
<td>Free state</td>
<td>50</td>
<td>46</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>26</td>
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</table>

### Table 3

<table>
<thead>
<tr>
<th>Host</th>
<th>Chemotype</th>
<th>N</th>
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<tbody>
<tr>
<td>Wheat</td>
<td>15-ADON</td>
<td>93.1</td>
</tr>
<tr>
<td></td>
<td>NIV</td>
<td>6.1</td>
</tr>
<tr>
<td></td>
<td>3-ADON</td>
<td>0.7</td>
</tr>
<tr>
<td>Barley</td>
<td></td>
<td>99.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.7</td>
</tr>
<tr>
<td>Maize</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0</td>
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<tr>
<td>Maize (roots)</td>
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<td>86</td>
</tr>
<tr>
<td></td>
<td></td>
<td>14</td>
</tr>
<tr>
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<td>0</td>
</tr>
</tbody>
</table>

Diversity of the *Fusarium graminearum* species complex on wheat within provinces in South Africa. Results are expressed as percentage of isolates relative to the total number of isolates (*N*).
graminearum, and a novel species reported only from Ethiopia (F. aethiopicum). Although the present study represents the first extensive survey of FGSC diversity in Africa, our previous investigations of FHB species diversity included a total of eight South African isolates identified as F. boothii, F. meridionale, and F. acaciae-mearnsii (O’Donnell et al., 2000, 2004; Starkey et al., 2007). Of these, only F. boothii was previously isolated from a cereal host (maize) in South Africa. Accordingly, the present study provides an improved understanding of the prevalence, geographic distribution, and host range of these three species in South Africa, and also documents the contribution of F. graminearum, F. cortaderiae, and F. brasilicum to FGSC diversity in South Africa. Although not previously reported from limited analyses of FGSC diversity in South Africa, the prevalence of F. graminearum (sensu stricto) among the FHB isolates examined was consistent with previous reports documenting that F. graminearum has a global distribution and is the most common FHB pathogen worldwide (O’Donnell et al., 2000, 2004). By contrast, F. cortaderiae and F. brasilicum were previously reported only from South America (Argentina, Brazil) and New Zealand (Monds et al., 2005; O’Donnell et al., 2004). The presence in Africa of these two species, along with F. meridionale, indicates that members of the previously defined South American clade within the FGSC (O’Donnell et al., 2004) can be found across the Southern Hemisphere.

In addition to demonstrating that a diverse group of species from the FGSC were responsible for diseases of cereals in South Africa, our MLGT analyses documented a dramatic difference in the composition of FGSC pathogens associated with GER of maize, as compared to those responsible for FHB of wheat or barley (Table 1). F. graminearum was the dominant FGSC species in all provinces sampled, and accounted for more than 85% of the isolates associated with FHB of wheat and barley (N = 425). However, we found that with the exception of a single isolate derived from interspecific hybridization between F. boothii and F. graminearum, GER of maize (N = 100) was exclusively associated with F. boothii. The predominance of F. graminearum among FHB isolates, and the near exclusivity of F. boothii among GER isolates, was observed for all cultivars, collection dates (year), and provinces sampled. Wheat, barley and maize are sometimes grown in the same areas in South Africa, especially in the North West and Northern Cape provinces, and are rotated with each other. In four of the eight provinces sampled, FHB and GER isolates were both collected (Fig. 1), and some GER isolates from maize were collected in fields where the previous crop was wheat or barley, and vice versa. Therefore, our data indicate that the difference in pathogen composition among FHB and GER isolates was not due to the geographic distributions of hosts or pathogens, and suggest that in comparison to F. boothii, F. graminearum has a reduced ability to cause GER of maize in South Africa.

Investigations of FGSC diversity on maize worldwide have been limited. For example, in the initial analysis of species limits within the FGSC, O’Donnell et al. (2000) characterized a few isolates (N = 10) from maize, with F. graminearum identified in the USA (N = 2), and Iran (N = 1); Fusarium australamericanum in Brazil (N = 1); F. meridionale in Nepal (N = 1), F. boothii in South Africa (N = 2) and Nepal (N = 1) and F. asiaticum in Nepal (N = 2). In a small survey conducted in New Zealand, Monds et al. (2005) characterized 20 isolates collected from maize and found 7 F. graminearum and 13 F. cortaderiae. In a more extensive survey, represented by a collection of 251 isolates from maize in Nepal, Desjardins and
Proctor (2011) recovered four species from the FGSC, including *F. meridionale* (56%), *F. asiaticum* (39%), *F. bohthii* (rare) and a putative new species. Surprisingly, *F. graminearum* was absent from this collection. Similarly, GER isolates collected in Argentina were represented exclusively by *F. meridionale* (N = 56) or *F. bohthii* (N = 10) (Sampietro et al., 2011). By way of contrast, *F. graminearum* was the only species represented in an analysis of 113 FHB isolates from wheat in Argentina (Ramirez et al., 2007). These results suggest that in contrast to the situation with FHB of wheat and barley, *F. graminearum* may not be the predominant FGSC pathogen causing GER of maize worldwide. Considering the results of these previous studies in conjunction with the data presented here, we hypothesize that *F. graminearum* may be at a selective disadvantage on maize ears relative to other members of the FGSC, and that this phenomenon may not be specific to maize production in South Africa.

Evidence of potential host preference among members of the FGSC also was suggested by a recent analysis of FGSC species diversity on rice in Korea, which indicated that *F. asiaticum* may be more fit in a rice agro-ecosystem than either *F. graminearum* or *F. bohthii* (Lee et al., 2009). As noted by Lee et al. (2009) the apparent host preference could be due to ecological adaptations that are not directly related to pathogenicity. However, the overlapping nature of maize and wheat cultivation in certain areas in South Africa, combined with the significant differences in FGSC composition observed on maize roots and ears (Table 1), suggest a difference in competitive ability that is specific to colonization of ears, and is not simply the by-product of differences in competitive ability within the environment in which maize is cultivated in South Africa.

To our knowledge, the relative aggressiveness of species within the FGSC has not been studied on maize. However, it was previously suggested that differences in host preference between *Microdochium nivale* var. majus and *M. nivale* var. nivale could be related to their differential sensitivity to the hydroxamic acid compounds found in different host plants (Simpson et al., 2000). Cyclic hydroxamic acids and related benzoxazolinone compounds are an important group of allelochemicals in graminaceous plants, which are found in maize (Friebe et al., 1998). Because of their inhibitory activity toward some fungi and bacteria, benzoxazinone allelochemicals and related derivatives are thought to be involved in plant disease resistance. Some fungi have been found to have different sensitivity to hydroxamic acids (Dowd et al., 1997; Friebe et al., 1998). It would be of interest to discover whether *F. graminearum*, *F. bohthii*, and other species within the FGSC are equally sensitive to hydroxamic acids, related benzoxazolinone compounds, or other antimicrobial compounds produced by maize. In addition, it also would be useful to integrate knowledge of FGSC diversity into analyses of competitive interactions with other cereal pathogens or endophytes. For example, it has previously been suggested that initial kernel infection by *Fusarium verticillioides*, the major causal agent of Fusarium ear rot (FER) on maize in South Africa (Marasas, 1995; Marasas et al., 1979), could out-compete *F. graminearum* for subsequent kernel invasion (Reid et al., 1999; Rheeder et al., 1990; Xu et al., 2007). In a different study, Van Wyk et al. (1988) suggested that maize seedlings are protected by *F. verticillioides* against infection by *F. graminearum* in soil. In addition, fumonisin B1 produced by *F. verticillioides* has been shown in vitro to have an antifungal effect on *F. graminearum* (Keyser et al., 1999). However, the effect of *F. verticillioides* and fumonisins on *F. bohthii*, or other species of the FGSC, has not been investigated.

Despite the significant differences in FGSC species prevalence, FHB and GER in South Africa were almost exclusively associated with the 15-ADON chemotype (Table 3). Isolates with a NIV chemotype accounted for 14% of the collection from maize roots, but our data indicate that NIV contamination of grain derived from maize, wheat, and barley in South Africa should be rare. Previous studies reporting contamination levels for these toxins in South Africa reported that DON contamination levels were higher than NIV contamination levels in maize (Rheeder et al., 1995; Thiel et al., 1982) and wheat (Sydenham et al., 1989). This finding has important implications for food safety, as NIV appears to have higher toxicity than DON (Forsell and Peskta, 1985; Luongo et al., 2010). These results also are consistent with a recent compilation of global data in which DON contamination levels in food and feed were found to be much higher than observed for NIV, although NIV contamination was prevalent in many Asian countries, New Zealand, and Brazil (Placinta et al., 1999). However, additional monitoring will be important for early detection of changes in the distribution or prevalence of FHB and GER pathogens that could influence the type or amount of trichothecene mycotoxins present in grain. Analyses of the FGSC in North America unexpectedly revealed the presence of *F. asiaticum*, local predominance of *F. graminearum* with the NIV chemotype, and the recent spread of a novel *F. graminearum* population with a 3-ADON chemotype that accumulates significantly more trichothecene than the previously dominant 15-ADON population during infection of susceptible or moderately resistant wheat varieties (Gale et al., 2002, 2011; Gilbert et al., 2010; von der Ohe et al., 2010; Ward et al., 2008).

In conclusion, we characterized for the first time the diversity of the FGSC species and trichothecene toxin types on wheat, barley and maize in South Africa. Our results demonstrate that FGSC strains with a 15-ADON chemotype are predominant on all three hosts. However, we also identified significant differences in the pathogen communities associated with either GER of maize or FHB of wheat and barley. Although the basis for this difference is not clear, we hypothesize that *F. graminearum* may be at a selective disadvantage on maize ears relative to other members of the FGSC. Understanding host-specific differences in pathogen composition will be of critical importance in the development of pathogen and mycotoxin control strategies, and could lead to novel approaches to achieve improved resistance in commercial cultivars.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.fgb.2011.05.005.

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