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Recent population changes of Fusarium head blight pathogens: drivers and implications

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Abstract: Several *Fusarium* species cause Fusarium head blight (FHB), a devastating disease that affects wheat and other small grain cereals. Besides causing significant yield losses, FHB pathogens reduce the quality of the grain and may produce mycotoxins that are harmful to both humans and animals. The development of effective management strategies for this disease requires an understanding of the composition of the FHB pathogen populations, which is important because different populations could be affected selectively. Recent reports of shifts in populations of FHB pathogens have shown that these populations are dynamic and change continuously, often associated with increased yield losses or changes in the mycotoxins produced in the grain. These population shifts include: replacement of *F. graminearum* by *F. poae* in Italy, hypothesized to be due to variation in environmental conditions; replacement of *F. culmorum* by *F. graminearum* in Europe, associated with climate change and increased maize production; a more aggressive and toxigenic *F. asiaticum* 3-ADON population replacing the existing NIV population in China; and a highly toxigenic population composed mainly of *F. graminearum* 3-ADON isolates replacing the existing 15-ADON population in North America. Additionally, reports of recent introductions of foreign species or populations into new areas include: *F. asiaticum* outside of Asia, *F. graminearum* NIV isolates in the USA and Luxembourg, *F. graminearum* 15-ADON isolates in Norway, *F. graminearum* in South Korea, *F. boothii* in Europe and USA, *F. vorosii* in Hungary and *F. cortaderiae* in New Zealand and Europe.

Keywords: FHB, *Fusarium graminearum* species complex, mycotoxins, trichothecenes, wheat, wheat scab

Résumé: Plusieurs espèces de *Fusarium* causent la brûlure de l'épi (BEF), une maladie dévastatrice qui s'attaque au blé et à d'autres céréales à petits grains. En plus d'occasionner d'importantes pertes, les agents pathogènes de la BEF réduisent la qualité du grain et peuvent produire des mycotoxines nocives pour les humains et les animaux. L'élaboration de stratégies efficaces de gestion de cette maladie requiert la compréhension de la composition des populations d'agents pathogènes de la BEF, ce qui est important parce que différentes populations pourraient être touchées sélectivement. De récents rapports sur les changements chez les populations d'agents pathogènes de la BEF ont montré que ces populations sont dynamiques et qu'elles changent continuellement, ce qui est souvent associé à l'augmentation des pertes de rendement ou à des modifications des toxines produites dans le grain. Ces changements chez les populations incluent: le remplacement, en Italie, de *F. graminearum* par *F. poae*, phénomène pouvant être imputable aux variations des conditions environnementales; le remplacement, en Europe, de *F. culmorum* par *F. graminearum*, associé aux changements climatiques et à la production accrue de maïs; une population plus agressive et toxigène de *F. asiaticum* 3-ADON remplaçant la population NIV en Chine; et une population hautement toxigène composée principalement d'isolats de *F. graminearum* 3-ADON remplaçant la population15-ADON en Amérique du Nord. En outre, des rapports sur de récentes introductions d'espèces ou de populations exotiques dans de nouvelles régions incluent: *F. asiaticum* à l'extérieur d'Asie, des isolats de *F. graminearum* NIV aux États-Unis et au Luxembourg, des isolats de *F. graminearum* 15-ADON en Norvège, *F. graminearum* en Corée du Sud, *F. boothii* en Europe et aux États-Unis, *F. vorosii* en Hongrie et *F. cortaderiae* en Nouvelle-Zélande et en Europe.

Mots clés: blé, brûlure de l'épi, complexe de l'espèce *Fusarium graminearum*, Fusariose, mycotoxines, trichothécènes

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Introduction

Fusarium head blight (FHB) is a devastating and economically important disease that affects wheat, barley, oats and other small grain cereals. Even though epidemics of FHB tend to be sporadic, they can be devastating (McMullen et al. 1997). For instance, from 1998 to 2000 FHB epidemics caused losses of almost \$3 billion in the USA and Canada alone (Goswami and Kistler 2004), and all of the cereal-growing regions in the world have experienced FHB epidemics (Dean et al. 2012). Furthermore, losses caused by FHB are not limited to grain producers, as they also have an effect on other sectors of the regional economy such as retail trade, finance, insurance and real estate. It has been estimated that secondary impacts of FHB on the economy amount to more than twice the direct losses sustained by grain producers (Nganje et al. 2004).

Fusarium head blight infection causes premature bleaching of spikes that fail to produce seed or produce shrivelled and soft kernels with reduced weight and functional qualities (Trail 2009). Additionally, the grain may be contaminated with mycotoxins, which are harmful to both humans and animals. Grain contaminated with mycotoxins is unsafe for human and animal consumption or for malting (Dean et al. 2012). Mycotoxin contamination further reduces marketability and prices, in many instances forcing farmers to sell at animal feed prices or to be penalized with huge discounts (McMullen et al. 1997). Consequently, grain affected by FHB is difficult to market, export, process, and feed. Low commodity prices coupled with the difficulties inherent in avoiding FHB and the economic losses it represents can make wheat cultivation unattractive to farmers. This situation has forced many US farmers to shift to less risky crops (McMullen et al. 2012; Bianchini et al. 2015).

Fusarium head blight is caused by several *Fusarium* species. Most of the FHB pathogens are grouped within the *Fusarium graminearum* species complex (FGSC), which includes: *F. acaciae-mearnsii, F. aethiopicum, F. asiaticum, F. austroamericanum, F. boothii, F. brasilicum, F. cortaderiae, F. gerlachii, F. graminearum, F. louisianense, F. meridionale, F. mesoamericanum, F. nepalense, F. ussurianum* and *F. vorosii* (Aoki et al. 2012). Species within the FGSC show a significant biogeographic structure, which suggests that independent allopatric speciation occurred in different parts of the world (O'Donnell et al. 2004; Aoki et al. 2012). Additionally, some degree of host preference or adaptation has been reported for FGSC species. For example, *F. asiaticum* predominates in rice, while *F. boothii* and *F. meridionale* seem to prefer maize in some areas of the world (Lee et al. 2009; Boutigny et al. 2011; Sampietro

et al. 2011). The members of the FGSC are self-fertile (= homothallic) (O'Donnell et al. 2004) and can also cause Gibberella ear rot (GER) and Gibberella stalk rot (GSR) in maize (Gai et al. 2017). Morphological and phenotypic characters are not sufficient to distinguish most of the species within the FGSC due to their morphological simplicity and overlapping conidial features combined with within-species variability (O'Donnell et al. 2004). Hence, molecular methods are required for an accurate identification. In addition, *F. lunulosporum, F. pseudograminearum, F. cerealis* and *F. culmorum* are self-sterile (= heterothallic) FHB pathogens closely related to the FGSC. Three novel species outside of the FGSC that are able to cause FHB, namely *F. dactylidis* (Aoki et al. 2015), *F. praegraminearum* (Gräfenhan et al. 2016) and *F. subtropicale* (Pereira et al. 2018) have recently been described. *Fusarium avenaceum, F. langsethiae, F. poae, F. sporotrichioides* and the non-toxigenic species *Microdochium nivale* are also commonly associated with the disease in different parts of the world (van der Fels-Klerx et al. 2012).

Fusarium species have the ability to produce an array of harmful mycotoxins. The most common mycotoxins associated with FHB are trichothecenes, but most species can also produce oestrogenic mycotoxins including zearalenone (O'Donnell et al. 2000; Stępień and Chełkowski 2010). The trichothecene mycotoxins are eukaryotic protein synthesis inhibitors and the most important are type A and B trichothecenes (Pestka and Smolinski 2005; Foroud and Eudes 2009). Members of the FGSC usually produce type B trichothecenes, and isolates are classified on their particular toxigenic profile (chemotype). These chemotypes include: (i) 3-ADON, producing deoxynivalenol (DON) and 3-acetyldeoxynivalenol (3-ADON); (ii) 15-ADON, producing DON and 15-acetyldeoxynivalenol (15-ADON); and (iii) NIV, producing nivalenol (NIV) and its acetylated derivatives. PCR methods have been developed to predict the chemotype of isolates (Ward et al. 2002). Symptoms after acute exposure to DON in sensitive animal species can range from vomiting to diarrhoea and anorexia (Pestka and Smolinski 2005). Moreover, DON acts as a virulence factor in wheat, causing necrosis and facilitating the spread of the fungus (Trail 2009). On the other hand, type A trichothecenes are usually produced by non-FGSC species such as *F. poae, F. langsethiae* and *F. sporotrichioides*, and they include the highly toxic T-2 and HT-2 toxins (Stępień and Chełkowski 2010; O'Donnell et al. 2013). Surprisingly, isolates of *F. graminearum* capable of producing a novel type A trichothecene called NX-2 have recently been reported in the northern USA and

southern Canada (Varga et al. 2015; Kelly et al. 2016; Kelly and Ward 2018; Lofgren et al. 2018). This observation was unexpected, since *F. graminearum* is part of a diverse lineage of *Fusarium* species characterized by the production of B type trichothecenes and therefore initially called the B-clade (O'Donnell et al. 2013). Consequently, the B-clade is now referred to as the *Fusarium sambucinum* species complex lineage 1 (FSAMSC-1) in order to avoid assumptions about the type of trichothecene produced by this group (Kelly et al. 2016).

Multiple field surveys have reported changes in the populations of FHB pathogens over time, which have been associated with increased yield losses due to the introduction of more aggressive and toxigenic isolates, or to changes in the mycotoxins accumulated in the grain due to the introduction of isolates with different mycotoxin profiles (van der Lee et al. 2015). Climate change is expected to increase severity of FHB epidemics (Zhang et al. 2014), and global warming will likely create suitable conditions for additional population shifts in the future (van der Lee et al. 2015). Thus, active surveillance is pivotal in early detection of potential population changes. The current review aims to summarize recent changes in populations of FHB pathogens around the world, as well as reports of foreign species or populations introduced in an area, with particular focus on the drivers of change. Moreover, the implications of these population shifts for grain producers and management of the disease are also discussed.

Shifts in populations of FHB pathogens

Changes in populations of FHB pathogens can occur at the species level when a species with a selective advantage replaces another species. Additionally, a different population of the same species could replace the existing population in a region. The introduction of foreign pathogens could result in a displacement event if the conditions are advantageous for the invading population. The following are recent reports of changes in the composition of FHB pathogens in different regions.

Replacement of F. graminearum *by* F. poae

The main causal agents of FHB in Italy have fluctuated throughout the years. The most common pathogens isolated from wheat seed from 1999 to 2002 were *F. graminearum, F. poae* and *M. nivale* (Shah et al. 2005). The incidence of seed infection was higher in the north of the country, with *M. nivale* accounting for most of the infections in that region, followed by *F. graminearum* and *F. poae*. Conversely, the incidence of seed infection was lower in the central and southern regions of Italy, and *F. poae* was the predominant species isolated.

During 2004 to 2006, the most abundant species isolated from organic wheat seed, in decreasing order, were *F. poae, M. nivale, F. verticillioides* and *F. graminearum* (Infantino et al. 2012). Seed infection rates were low (<5% for all species) but *F. poae* was the most commonly isolated species in 2005 and 2006. Moreover, the mean seed infection rate by *F. graminearum* decreased from 0.55% in 2004 to 0.25% in 2006. The predominance of *F. poae* was speculated to be due to the weather in Italy being warmer and drier than other European countries, which favours *F. poae* over other species (Xu et al. 2008).

In another survey study conducted in northern Italy from 1995 to 2007, *F. graminearum* was the most common species causing FHB in durum wheat (Pancaldi et al. 2010). However, its frequency of isolation from affected heads peaked at 67.5% in 1996, then fluctuated with a gradual downward trend until 2007 when the frequency of isolation was only 15.7%. Conversely, isolation of *F. poae* had an upward trend, with a frequency of 5% in 1999 and 23.2% in 2007. The isolation frequency of *F. poae* was higher in years when *F. graminearum* had a lower frequency and vice versa. *Fusarium poae* was more frequent than *F. graminearum* in 1997, 2005 and 2007. The authors suggested that frequencies varied in response to environmental conditions.

A two-year study conducted in central Italy in 2009 and 2010 revealed that *F. graminearum* was the most commonly isolated species from durum and soft wheat kernels (Covarelli et al. 2015). However, its frequency of isolation, relative to the other species isolated, was lower in 2009 (27% and 16% in durum and soft wheat, respectively) than in 2010 (69% and 60%). In contrast, the isolation frequency of *F. poae* and *F. avenaceum* was higher in 2009 than in 2010. There was lower rainfall and relative humidity, as well as higher temperatures, during anthesis in 2009 than in 2010. The authors indicated that the drier and warmer conditions in 2009 were unfavourable for *F. graminearum*, allowing increased incidence of *F. poae* and *F. avenaceum*.

A similar pattern was reported in Italian barley by many studies. *Fusarium graminearum* was never the predominant species in a study conducted in central Italy from 2011 to 2013, whereas *F. avenaceum*, *F. tricinctum* and *F. poae* were the main species causing FHB in 2011, 2012 and 2013, respectively (Beccari et al. 2017). Another survey from the same region revealed

that 63% of the isolates causing FHB of barley in 2013 were identified as *F. avenaceum* (Beccari et al. 2016). However, its prevalence decreased to 23% in 2014 (Beccari et al. 2018). Additionally, the results from both studies showed that the prevalence of *F. poae* increased from 5% in 2013 to 37% in 2014.

There have been reports of *F. poae* becoming an important pathogen of cereals in other countries as well. *Fusarium poae* has been the main FHB pathogen isolated from wheat in the Czech Republic since 2012, replacing *F. graminearum*, which used to be the predominant species (Sumíková et al. 2017). The authors speculated that dry environmental conditions observed during anthesis in 2012 favoured *F. poae*, which in turn could produce large amounts of inoculum that boosted its frequency in the following years. In addition, a survey in Argentina revealed that *F. poae* was isolated from barley more frequently than *F. graminearum*, 54.7% and 39.5%, respectively (Nogueira et al. 2018).

Disease surveys in Manitoba, Canada have revealed that *F. poae* has been the main FHB pathogen infecting barley in the province in recent years (Tekauz et al. 2013; Banik et al. 2014, 2016; Beyene et al. 2015). However, *F. graminearum* was the predominant pathogen reported in 2016 after excessive moisture during the growing season, which could have favoured *F. graminearum* over *F. poae* (Banik et al. 2017). In 2017, dry conditions predominated in the province, and *F. poae* was once again the predominant pathogen species reported in barley (Banik et al. 2018).

Despite being reported as less aggressive FHB pathogens when compared with the FGSC (Xue et al. 2004; Cerón-Bustamante et al. 2018), the predominance of *F. avenaceum* or *F. poae* could cause a change in the mycotoxins accumulated in the grain. *Fusarium avenaceum* has been reported to produce moniliformin, enniatin analogues and beauvericin (Beccari et al. 2018), while *F. poae* is known to accumulate NIV and type A trichothecenes such as diacetoxyscirpenol and neosolaniol (Vanheule et al. 2017; O'Donnell et al. 2018). These examples show how changes in climatic conditions continuously shape not only the species composition of FHB pathogens, but also the mycotoxin contamination of the crops as a consequence.

Replacement of F. culmorum *by* F. graminearum *in Europe*

Early reports from many European countries show that FHB was caused predominantly by *F. culmorum* (Parry et al. 1995; Waalwijk et al. 2003). However, *F. graminearum* seems to have increased in importance in Europe. The first indication of *F. graminearum* replacing *F. culmorum* as the main FHB pathogen in Europe was from a two-year study in the Netherlands in the early 2000s, which revealed that *F. graminearum* accounted for 58.5% of the isolates, whereas only 24% were identified as *F. culmorum* (Waalwijk et al. 2003). The long-term nature of this shift was documented by another study in 2009 that found *F. graminearum* in 46.5% of the wheat samples analysed, while *F. culmorum* was detected in only 2.3% of the samples (van der Fels-Klerx et al. 2012).

Similar shifts have been noted in other European countries where *F. graminearum* is now the most abundant FHB pathogen. A five-fold increase in the frequency of *F. graminearum* from 1998 to 2006 in Poland was reported, accompanied by a decline in the frequency of *F. culmorum* (Stępień et al. 2008). More recently, surveys in 2009 and 2012–2014 showed that *F. graminearum* was still the predominant pathogen found in Poland (Chełkowski et al. 2012; Gorczyca et al. 2018). Moreover, the level of *F. graminearum* has risen in the UK and Ireland at the expense of *F. culmorum* (Jennings et al. 2004; Xu et al. 2005). This finding was unexpected as these countries tend to have cooler summers than the rest of Europe, which would favour *F. culmorum* (Xu et al. 2005).

In Belgium, *F. graminearum* and *F. culmorum* were the most important pathogens isolated from wheat during 2002 to 2005 (Isebaert et al. 2009). Additionally, Isebaert et al. (2009) found that *F. graminearum* was isolated at higher frequencies when wheat was grown after maize or in regions where maize was an important crop. Additional evidence for the decreased prevalence of *F. culmorum* in Belgium was provided by two separate surveys conducted during 2003–2009 and 2007–2008 (Audenaert et al. 2009; Chandelier et al. 2011).

In Denmark, analysis of historical data of wheat samples from 1957 to 2000 showed low levels of *F. graminearum*, while *F. culmorum* was predominant along with *F. avenaceum* and *M. nivale* (Nielsen et al. 2011). However, a rapid increase in the prevalence of *F. graminearum* was noted in samples obtained from 2003 to 2007. *Fusarium graminearum* has also become increasingly important in northern Germany (Klix et al. 2008), as well as in Finland (Hietaniemi et al. 2016) and Sweden (Karlsson et al. 2017).

Even though the underlying causes of the shift from *F. culmorum* to *F. graminearum* have not been unequivocally elucidated, several hypotheses have been proposed. First, *F. graminearum* is regarded as having been recently introduced to Europe along with maize production (Xu et al. 2005). In countries such as Denmark, maize was introduced in the 1980s and the agricultural area dedicated to the crop has

rapidly increased (Nielsen et al. 2011). Maize is often included in crop rotation systems with wheat (Xu et al. 2005), which along with reduced tillage practices favours *F. graminearum* due to its ability to infect maize and over-winter on crop residue (Waalwijk et al. 2003). The fact that *F. graminearum* was more common in wheat grown after maize or from areas where maize was the predominant crop supports this hypothesis (Isebaert et al. 2009). Second, higher mean temperatures caused by climate change could favour *F. graminearum*, as it prefers warmer temperatures than *F. culmorum* (Xu et al. 2005; Nielsen et al. 2011). Finally, certain characteristics give *F. graminearum* increased competitiveness over *F. culmorum*. *Fusarium graminearum* has usually been regarded as more aggressive than *F. culmorum* in terms of yield loss and mycotoxin production (Jennings et al. 2004). In addition, being a homothallic species, *F. graminearum* can produce ascospores that are very important epidemiologically, unlike *F. culmorum*, which depends on the spread of its macroconidia for dispersal (Audenaert et al. 2009). Additionally, sexual reproduction can be advantageous to *F. graminearum* in terms of generating variability for adaptation to new environments (Xu et al. 2005).

Climate change is expected to bring higher temperatures and more humid conditions, especially to northern Europe, which would favour *F. graminearum* over *F. culmorum* (Parikka et al. 2012). These conditions would also allow for an expansion in maize cultivation to areas where it is currently not grown, providing a suitable substrate for over-wintering *F. graminearum* (Parikka et al. 2012; West et al. 2012).

Outside of Europe, a similar shift in *Fusarium* spp. was recently documented in Idaho, USA (Bissonnette et al. 2018). The authors found that *F. graminearum* was causing most of the FHB in the state (87% of the isolates), as opposed to *F. culmorum* (13%), which had been the prevalent pathogen according to a survey from 1984. Increased maize cultivation in the state, as well as maize-wheat rotation systems, were linked to this change in composition.

Fusarium asiaticum 3-ADON replaces the NIV population in China

The predominant FHB pathogen in China is *F. asiaticum*. Initial studies on the diversity of trichothecene genotypes of *F. asiaticum* isolated from barley in China along the Yangtze river revealed that there were sharp differences in their distribution (Yang et al. 2008). Despite being unable to differentiate between 15-ADON and 3-ADON isolates, the authors noted that NIV isolates were much more common than DON isolates (91% and 8.2%, respectively) in the upper valleys of the river, a region surrounded by large mountain ridges, which might act as a geographic barrier. On the other hand, DON producers had higher frequencies in all other regions surveyed (>70%, middle and lower reaches of the river). Since there was no clear correlation between trichothecene genotype and cropping system or climate variables, it was hypothesized that DON isolates had been recently introduced and were replacing the NIV population, which still existed at higher frequencies in the south-west region because of the mountain barrier.

Subsequently, a study conducted by Zhang et al. (2010) provided greater insight into the population dynamics of FHB pathogens in China. The survey determined that most of the DON isolates in the middle and lower parts of the Yangtze river belonged to the 3-ADON genotype, while a small number of isolates were of the 15-ADON genotype (Zhang et al. 2010). The authors found significantly higher genetic diversity in the upper reaches, where NIV isolates were dominant. Moreover, pairwise population genetic differentiation (F_{ST}) values showed that NIV and 3-ADON isolates were significantly different and therefore represented separate populations. Finally, isolates with high admixture probabilities revealed that there was a bias in the gene flow from 3-ADON to NIV isolates. Based on these results, the authors concluded that the 3-ADON population was spreading from east to west, replacing the existing NIV population.

In order to determine the cause of the shift in the *F. asiaticum* population, Zhang et al. (2012) carried out another survey and evaluated the fitness and aggressiveness of the isolates from each trichothecene genotype. The results supported the previous hypothesis that the 3-ADON population was increasing in frequency from east to west. In addition, they obtained similar levels of genetic differentiation between the populations, as well as an increase in biased gene flow from 3-ADON to NIV isolates. As far as aggressiveness, the authors found that the 3-ADON isolates caused more disease in moderately resistant and susceptible winter wheat varieties than NIV isolates. *In vitro* tests showed that the 3-ADON producers were not only able to grow faster and produce more and larger conidia, but also accumulated more mycotoxins than the NIV isolates. Additionally, the 3-ADON isolates had a higher level of benzimidazole resistance than NIV isolates. Taken together, these studies show

that a population of more aggressive and toxigenic *F. asiaticum* of the 3-ADON genotype and possessing benzimidazole resistance is expanding from east to west, as well as changing the trichothecene genotype composition in China.

Fusarium graminearum *3-ADON replacing 15-ADON population in North America*

Previous studies on the population structure of *F. graminearum* in North America pointed towards the hypothesis that it consisted of a panmictic population with little differentiation, but with high genetic diversity due to frequent recombination events (Zeller et al. 2004). However, this hypothesis was rejected when two distinct populations were discovered in the upper Midwest (Gale et al. 2007). The dominant population (89%) was composed mostly of 15-ADON genotype isolates and it was named MW15ADON (MW = Midwest). The second population found in Minnesota and North Dakota was referred to as UMW3ADON (UMW = upper Midwest) because it contained most of the 3-ADON isolates. The MW15ADON population was more genetically diverse, consistent with the hypothesis that it is the native North American population. The UMW3ADON population not only had low genetic diversity, but also was genetically similar to an Italian population that was included for comparison. Thus, it was speculated that the UMW3ADON isolates were recently introduced into North America from Europe. The MW15ADON and UMW3ADON populations described by Gale et al. (2007) were later renamed as NA1 and NA2, respectively. The reasoning behind this decision was that in addition to the distribution of these populations throughout North America and not only in the Midwest, trichothecene genotype is gradually becoming an unreliable predictor of population due to admixture between individuals of different populations (Liang et al. 2014; Kelly et al. 2015).

Shortly thereafter, a dramatic shift in the FHB pathogen populations of North America was reported (Ward et al. 2008). Analysis of the trichothecene genotype of *F. graminearum* isolated from wheat in Canada during 1998 to 2004 revealed that 135 (27.4%) of the 492 isolates analysed had the 3-ADON genotype, whereas the rest had the 15-ADON genotype. Remarkably, there was a longitudinal cline in the frequency of 3-ADON isolates, being higher in the eastern provinces (100% in Prince Edward Island) and gradually decreasing in each province from east to west (50% in Quebec, 31% in

Manitoba, 10.7% in Saskatchewan and 5.9% in Alberta). It should be noted that no samples from the provinces of Ontario, Nova Scotia or New Brunswick were obtained. Additionally, the 3-ADON isolates had a 14-fold increase in frequency over time during 1998 to 2004 (from 2.6% to 37.6%) in the western provinces of Manitoba, Saskatchewan and Alberta, suggesting that the 3-ADON population was probably introduced recently and is quickly expanding from east to west. There was also significant differentiation between the 3-ADON and 15-ADON populations ($F_{ST} > 0.243$) based on variable number tandem repeat (VNTR) data, which indicated that the two populations had not been in the same geographic area for sufficient time to allow for significant genetic exchange. The 3-ADON population from Canada was not significantly different from the aforementioned UMW3ADON isolates from Minnesota and North Dakota (Gale et al. 2007). Analysis of isolates with a high probability of admixture showed a biased gene flow from the 3-ADON to the 15-ADON population (Ward et al. 2008).

The 3-ADON population in general is able to grow faster and produce more trichothecene, as well as more and larger conidia than the 15-ADON isolates, according to *in vitro* tests (Ward et al. 2008). The authors hypothesized that these characteristics, if expressed under field conditions, could enable the 3-ADON isolates to be more aggressive than the 15-ADON isolates. However, no difference was found in aggressiveness towards the susceptible wheat cultivar 'Roblin' or moderately resistant cultivar '5602 HR'. It has been reported that 3-ADON isolates are more resilient to extreme temperatures, and that in response to high or low temperatures they accumulated more DON and zearalenone than the 15-ADON isolates (Vujanovic et al. 2012). Subsequent studies reported that the 3-ADON isolates were not only more aggressive, but also more toxigenic in some wheat lines than their 15-ADON counterparts (Puri and Zhong 2010; Foroud et al. 2012).

Several surveys conducted in barley and wheat in the upper Midwest region of the United States also noted the same population subdivision in *F. graminearum*, with the frequency of 3-ADON isolates rapidly increasing and their distribution expanding. The incidence of 3-ADON isolates in barley from North Dakota and Minnesota increased dramatically from 3.5% in 1997–2000 to 38% in 2008 (Burlakoti et al. 2011). The frequency of isolates with the 3-ADON genotype in North Dakota, South Dakota and Minnesota was reported to gradually decrease from north to south

(49% in the northern, 40% in the central and 29% in the southern area sampled), which was consistent with a southward expansion (Liang et al. 2014, 2015). A similar latitudinal cline in the frequency of 3-ADON isolates in winter wheat was reported in the eastern USA from 15.4% in New York in the north, decreasing steadily to 0.5% in North Carolina in the south (Schmale et al. 2011).

Evidence that there were additional regional differences in the distribution of *F. graminearum* populations in North America was initially provided from a study that evaluated several features of *F. graminearum* isolates from New York, USA belonging to both the 15-ADON and 3-ADON genotypes (Spolti et al. 2014). This study investigated the differences between both genotypes in growth rate, temperature sensitivity, perithecia formation, ascospore discharge, and aggressiveness to the 'Norm' spring wheat cultivar, which is regarded as highly susceptible. There was no difference between genotypes for most of the attributes analysed, which was contradictory to previous studies (Ward et al. 2008; Puri and Zhong 2010; Foroud et al. 2012; Vujanovic et al. 2012).

Expanded sampling in the eastern provinces of Canada between 2005 and 2007 detected other regional differences in the *F. graminearum* populations that were not observed previously, and that these populations had also changed throughout the years depending on the region (Kelly et al. 2015). These regional differences in population dynamics were not reported previously due to small sample sizes from eastern Canadian provinces, as well as the lack of samples from other provinces in prior studies (Ward et al. 2008). Overall, the frequency of 3-ADON isolates grew to 37%, compared with the previous 27.4% reported by Ward et al. (2008). Instead of a large longitudinal cline, there were actually two separate longitudinal clines. The first gradient was between the Maritime provinces (Prince Edward Island, New Brunswick and Nova Scotia) and the eastern provinces (Quebec and Ontario). The frequency of 3-ADON isolates was significantly higher in the Maritime provinces (91%) than in the eastern provinces (22%). The 3-ADON frequencies gradually dropped in these two regions from 98% in Prince Edward Island to 11% in Ontario. The 3-ADON genotype also was dominant in Manitoba (55%), starting the second cline in the western Canadian provinces, which included Manitoba, Saskatchewan and Alberta. Once again, the occurrence of 3-ADON isolates declined from east to west, from 27% in Saskatchewan to 7% in Alberta. The trichothecene genotype composition of the *F. graminearum* population throughout the study was also variable from year to year depending on the region (Kelly et al. 2015). In the western provinces the 3-ADON frequency increased in the three years that surveys were conducted, except in Alberta where it remained consistently low. On the other hand, the frequency in the Maritimes and in eastern provinces remained stable, which indicated that they had population dynamics different from those in the rest of the country.

As far as population structure using VNTR data, the NA1 and NA2 populations mentioned above were observed in all Canadian regions studied (Kelly et al. 2015). The NA1 population was mainly composed of 15-ADON isolates, while most of the 3-ADON isolates belonged to the NA2 population. Differentiation within each population was low, which was indicative of population homogeneity and that the regional differences observed were not due to significant subdivision of the populations. Kelly et al. (2015) examined isolates with a high probability of genetic admixture and discovered that there were biases in gene flow, yet these also varied depending on the region. Whereas there was a biased gene flow favouring the NA2 over the NA1 population in the Maritimes and western provinces (significantly more isolates with 15-ADON genotypes assigned to the NA2 population, which is mainly composed of 3-ADON isolates), the opposite was observed in Ontario and Quebec where gene flow was biased from NA1 to NA2 (significantly more isolates with 3-ADON genotypes assigned to the NA1 population).

The contrasting results obtained among Canadian regions indicate that there are other factors such as climate and host distribution that may affect the population dynamics of FHB pathogens in Canada, and phenotypic and pathogenicity traits that could be potentially advantageous in the NA2 population (Ward et al. 2008; Puri and Zhong 2010; Foroud et al. 2012). Furthermore, the authors mentioned that it is possible that those attributes could have been transferred from the NA2 to the NA1 population through recombination, since they were not evaluated in the study (Kelly et al. 2015). Climate differences do not seem to affect the distribution of the populations, since regions with different climates like western and maritime provinces had similar compositions. Lastly, the authors speculated that host distribution could also have an effect, because most of the wheat grown in the western Canadian and Maritime provinces is spring wheat, whereas winter wheat predominates in Ontario. Nevertheless, the drivers of population dynamics across Canada are still unknown.

These results were corroborated by additional survey studies published later that reported a low frequency of 3-ADON isolates in Ontario. In 2010, *F. graminearum* of the 15-ADON genotype represented 97% of the isolates

obtained from Ontario wheat samples, while only 3% had the 3-ADON genotype (Tamburic-Ilincic et al. 2015). Similar results were obtained from wheat and maize in Ontario during 2010–2012, with only a small portion of isolates having the 3-ADON genotype (2% for wheat and 4% for maize), and the remaining isolates were of the 15-ADON genotype (Burlakoti et al. 2017).

In 2015, isolates capable of producing a newly discovered type A trichothecene named NX-2 were reported in Minnesota (Varga et al. 2015). Later, they were described as a separate population of *F. graminearum* named NA3 and restricted to the northern USA and southern Canada (Kelly et al. 2016; Kelly and Ward 2018). This further confirms the hypothesis that there are multiple populations of *F. graminearum* in North America and not just one single panmictic population.

Genome wide selection scans on isolates representing the three populations of *F. graminearum* in North America (NA1, NA2 and NA3) have shown that multiple regions in the genome have been the target of selection within each population (Kelly and Ward 2018). These regions contained the trichothecene gene cluster and other genes potentially related to plant infection. In addition, the authors found 121 genes across all three populations that were conserved in one population but absent or rare in the other populations, with predicted functions related to pathogenicity, secondary metabolism, and interactions with other microorganisms. These results showed that each sympatric *F. graminearum* population in North America has unique genomic features that contribute to pathogen specialization and could potentially represent a reservoir of adaptive abilities for this fungus (Kelly and Ward 2018).

Reports of new species/genotypes in a region

Fusarium asiaticum *outside of Asia. Fusarium asiaticum* is presumed to have originated and evolved in Asia, where it is composed of all type B trichothecene genotypes (3-ADON, 15-ADON and NIV) (O'Donnell et al. 2000, 2004; Aoki et al. 2012). This species is also the main FHB pathogen in Asia, especially in regions where rice is grown (van der Lee et al. 2015), and it is regarded to have rice as its preferred host (Desjardins and Proctor 2011). Indeed, it is well known that *F. asiaticum* is favoured in crop rotation systems that include rice (Qiu et al. 2016; Zhang et al. 2016; Yang et al. 2018). However, no difference was observed in pathogenicity towards rice between *F. graminearum, F. asiaticum* and *F. boothii* isolates from South Korea, which indicates

that the selective advantage *F. asiaticum* has in rice might not be due to pathogenicity (Lee et al. 2009).

Outside of Asia, *F. asiaticum* has been reported in several countries, mostly associated with rice production. When *F. asiaticum* was formally described as a separate species, it was known to be present in oats, rice, ryegrass and wheat from Brazil (O'Donnell et al. 2004; Del Ponte et al. 2013). There have been recent reports of *F. asiaticum* with the NIV genotype in Uruguay (Umpiérrez-Failache et al. 2013) as well as Brazil (Gomes et al. 2015; Castañares et al. 2016), always associated with rice. The fact that *F. asiaticum* was found at low levels in Brazilian regions that are distant from rice-growing fields supports the hypothesis that it has a host-preference for rice (Del Ponte et al. 2015; Gomes et al. 2015).

The first report of *F. asiaticum* in North America was from wheat in southern Louisiana, USA, representing 23.4% of the isolates obtained in that study (Gale et al. 2011). The low genetic diversity found in the isolates and the fact that all of them had the NIV genotype suggested that it was an introduced population. The authors also speculated that this species was probably introduced into the region along with rice, since its distribution overlapped areas where rice is a predominant crop.

Fusarium graminearum *'Gulf coast' and 'Southern Louisiana' populations in the USA*. In 2007, it was reported for the first time that a *F. graminearum* population in Louisiana and Florida included all three trichothecene genotypes, although the NIV genotype was the most common (Starkey et al. 2007). Two Florida isolates were obtained from commercially grown leatherleaf fern (*Rumohra adiantiformis*), whereas the six remaining isolates were from Louisiana wheat spikes. These isolates were genetically divergent based on polymorphisms detected in the *MAT* gene and three other loci. The authors named this newly discovered population the 'Gulf coast population' and hypothesized that it was indigenous to the region. Subsequently, after additional sampling and population analyses, 44 more isolates were added to the Gulf coast population (Gale et al. 2011). Even though most of the isolates in the Gulf coast population were from Louisiana, one isolate from Ohio and another from Indiana were also classified as members of this population. The 3-ADON genotype was dominant within this sample (65.9%), followed by NIV (25%) and 15-ADON (9.1%). In the same study, the authors also found a separate population of *F. graminearum* with a high frequency of NIV isolates (93.6%) that was named the 'Southern Louisiana population' because it was found mostly in Louisiana. The F_{ST} values between these two populations were very high (0.5), indicating that they were significantly different from each other. Furthermore, the

genetic diversity of these two populations was lower than in the NA1 population, which is widespread in North America, suggesting that they were recently introduced. The origin of both populations is still unknown. As with *F. asiaticum* from the same region, it was conjectured that they could have been introduced with rice or that perhaps the weather in the region could be favourable (Gale et al. 2011).

The introduction of NIV-producing isolates (of both *F. graminearum* and *F. asiaticum*) into the USA represents a food safety risk, since NIV is not currently tested in grain and it is regarded as more toxic to humans than DON (Minervini et al. 2004). Additionally, NIV is detected poorly by some of the rapid detection methods for mycotoxins approved by the United States Department of Agriculture's Grain Inspection, Packers and Stockyards Administration (Tangni et al. 2010).

Fusarium graminearum *NIV in Luxembourg.* The first reported observation of *F. graminearum* isolates of the NIV genotype in Luxembourg was in 2009 (Pasquali et al. 2009). The authors reported that the NIV isolates represented 2.5% of the isolates sampled in 2007 and 1% in 2008. Subsequently, Pasquali et al. (2010) went on to show that there was a positive correlation between growing wheat after maize and the presence of the NIV genotype. It was speculated that maize production favoured NIV isolates in Luxembourg, since NIV has been reported to be a virulence factor in maize (Pasquali et al. 2010). In France, Boutigny et al. (2014) reported that isolates of the NIV genotype had a higher frequency in the south of the country (21.2%), where most of the maize in the country is grown, than in the north (4.4%).

Fusarium graminearum *15-ADON in Norway.* Isolates of *F. graminearum* of the 15-ADON genotype were reported for the first time in Norway at low levels in samples from 2006 and 2007 as part of a study that characterized isolates from 1982–1998 and 2004–2007 (Aamot et al. 2015). Only four of 105 *F. graminearum* isolates were of the 15-ADON genotype (3.8%), while the remaining were the 3-ADON genotype (96.2%). This finding was unexpected, since the 15-ADON genotype, which is more common in western and southern Europe, had not been reported in Norway. The authors linked the introduction of 15-ADON isolates into Norway with the detection of 15-ADON producers in Denmark in 1997, which then could have been carried by the wind or imported with seed. The 15-ADON isolates were more aggressive to wheat than the 3-ADON isolates under greenhouse conditions, but additional studies are required to validate this observation due to the small number of 15-ADON isolates.

Fusarium graminearum *in South Korea.* Several studies have reported the presence of *F. graminearum* in South Korea, always in regions of the country where maize is an important crop, whereas *F. asiaticum* dominates in rice-growing regions (Lee et al. 2009, 2010, 2012; Shin et al. 2018). In 2002, *F. graminearum* represented 21.5% of the isolates from rice in eastern South Korea, a region where maize predominates, while the remaining isolates were identified as *F. asiaticum* (Lee et al. 2009). The same study found that all the isolates from southern South Korea, where little maize is grown, were identified as *F. asiaticum*. Additional surveys revealed that *F. graminearum* predominates in maize, whereas *F. asiaticum* is the most abundant species in rice (Lee et al. 2010, 2012).

Amplified fragment length polymorphism (AFLP) analyses have shown that the *F. graminearum* population in South Korea has a low genetic diversity (Lee et al. 2009, 2012). A recent introduction of *F. graminearum* to South Korea (possibly with imported maize seed) could explain this observation (Lee et al. 2012). The authors pointed out that most of the maize seed in South Korea is imported from the USA, where *F. graminearum* predominates, which supports this hypothesis.

Fusarium boothii *in Hungary, France, and the USA.* *Fusarium boothii* is believed to have evolved in Central America along with *F. mesoamericanum* (Aoki et al. 2012), but its origins are unclear due to its wide geographic distribution, which includes Mexico and multiple countries in Africa, Asia and South America (Boutigny et al. 2011; Desjardins and Proctor 2011; Sampietro et al. 2011; Malihipour et al. 2012; Duan et al. 2016; Zhang et al. 2016; Cerón-Bustamante et al. 2018). Recent surveys have expanded our knowledge of the distribution of this species. In Hungary, *F. boothii* was isolated from wheat at a low frequency (Láday et al. 2004; Tóth et al. 2005), which probably represents an unintentional introduction. Two *F. boothii* × *F. graminearum* hybrids were isolated from maize in France (Boutigny et al. 2014). Since *F. boothii* was not found in France, this suggests the hybrids were most likely introduced on seed, possibly from South Africa. *Fusarium boothii* is very common in South Africa, especially in maize, and hybrids between *F. graminearum* and *F. boothii* have been reported (Boutigny et al. 2011).

Most studies have isolated *F. boothii* from maize, and host-adaptation of *F. boothii* to maize has been suggested (Boutigny et al. 2011; Zhang et al. 2016; Beukes et al. 2018). *Fusarium boothii* was recently reported to cause FHB of wheat for the first time in Nebraska, USA (Wegulo et al. 2018). *Fusarium boothii* had been

previously isolated from maize in Texas (Aoki et al. 2012), but it had never been isolated from wheat in the USA. This finding could be associated with the fact that maize is one of the main crops in Nebraska and that maize and wheat are often included in crop rotation systems in the state. When compared to *F. graminearum*, *F. boothii* initially seemed to be restricted to warmer regions (Backhouse 2014). However, reports from cooler regions in China show that it can actually withstand −30° C temperatures during winter (Zhang et al. 2016). If the *F. boothii* isolates from Nebraska have a host-preference for maize, as do their South African counterparts (Boutigny et al. 2011), this could represent a threat to maize production in the state. However, comparative aggressiveness and population studies including both wheat and maize isolates will be required to evaluate this hypothesis.

Fusarium vorosii *in Hungary.* The discovery of an atypical *Fusarium* isolate in Hungary led to the description of *F. vorosii* (Tóth et al. 2005; Starkey et al. 2007). This isolate had unique randomly amplified polymorphic DNA (RAPD) and intergenic spacer region (IGS) restriction fragment length polymorphism (RFLP) haplotypes, as well as a divergent reductase (*RED*) gene sequence, but it was closely related to an *F. asiaticum* isolate (Tóth et al. 2005). Subsequently, Starkey et al. (2007) formally described *F. vorosii* as a novel species using genealogical concordance phylogenetic species recognition (GCPSR) on the Hungarian isolate and two additional isolates from Japan. Two additional isolates of *F. vorosii* were subsequently obtained from the Russian Far East (Yli-Mattila et al. 2009). Multilocus molecular phylogeny using 13 different genes showed that *F. vorosii* clustered with *F. asiaticum* and *F. ussurianum*, indicating very strong bootstrap support for an Asian clade (Yli-Mattila et al. 2009; Aoki et al. 2012). Thus, it appears that *F. vorosii* originated from Asia and was introduced to Hungary (Yli-Mattila et al. 2009).

Fusarium cortaderiae *in New Zealand, France and Italy.* The holotype of *F. cortaderiae* was isolated from pampas grass (*Cortaderia selloana*) in New Zealand, hence its name (O'Donnell et al. 2004). However, this species is believed to have originated from South America, along with *F. brasilicum, F. austroamericanum* and *F. meridionale* (O'Donnell et al. 2004; Yli-Mattila et al. 2009; Aoki et al. 2012). Pampas grass is not native to New Zealand, but was imported from South America as an ornamental plant, and at the same time may have introduced *F. cortaderiae*, which has now spread to cereal crops (Monds et al. 2005). Additionally, *F. cortaderiae* is believed to have been introduced to France (Boutigny et al. 2014). The authors reported three *F. cortaderiae* isolates that were obtained from maize in south-western France. The geographic restriction of these isolates and the fact that they were found at low frequency in maize, but not in wheat and barley, suggested that they were recently introduced. This species could have been introduced on seed, as France imports most of the maize seed it needs from South Africa where *F. cortaderiae* has been found (Boutigny et al. 2011, 2014). Survey studies from Italy found *F. cortaderiae* isolates in wheat samples from the Marche region (central Italy) and Sardinia (island in the Mediterranean Sea), which also appear to correspond to recent introductions (Somma et al. 2014; Balmas et al. 2015).

Implications of population changes and introduction of new species/genotypes

Changes in FHB populations in a region could have multiple consequences. New populations with a different chemotype would result in a change in the mycotoxin profile in the grain. It is vital to know what mycotoxins the current pathogen populations produce in order to evaluate the risk that they represent, and to use appropriate toxin detection methods to ensure the safety of the grain supply. Additionally, the introduction of more aggressive isolates can lead to greater economic losses due to reduction in yield and quality that would be worsened by the accumulation of mycotoxins.

The population changes discussed, the reports of recent introductions of exotic populations into new areas, and the fact that *Fusarium* spores can be dispersed long distances in air currents (Schmale et al. 2012; Keller et al. 2014) and through international grain export and germplasm exchange indicates increased effective vigilance and continuous global monitoring of FHB pathogens is needed in order to detect possible population shifts. From this perspective, the international grain trade may represent a risk, and each country should develop phytosanitary regulations to avoid the accidental introduction of more aggressive and toxigenic foreign pathogens. If not prevented, this can result in dramatic changes in the population composition and toxigenic profiles when local conditions are favourable to the introduced population. Phytosanitary regulations should not be limited to grain crops, as the introduction of non-native ornamental plants also represents a risk because they can also harbour FHB pathogens, such as the imported pampas grass hypothesized to introduce *F. cortaderiae* into New Zealand (Monds et al. 2005).

Accurate species and trichothecene genotype identification of isolates for surveillance is therefore critical. This represents a challenge regarding the species within the FGSC, because they are morphologically indistinguishable and the only methods currently available for identifying them are sequencing of informative genes. Currently, these are the translation elongation factor 1-α (*TEF1-α*) or the DNA-directed RNA polymerase II largest (*RPB1*) and second largest subunit (*RPB2*) genes (O'Donnell et al. 2015). Another alternative is the use of the multilocus genotyping (MLGT) assay developed by Ward et al. (2008). The MLGT assay has many advantages, including the ability to simultaneously identify most FHB pathogens and their trichothecene genotype in a high-throughput platform. However, it is not readily available to most labs and there is a need for simpler and more affordable assays, such as species-specific PCR-based methods.

Besides determining the species and trichothecene genotype of the pathogens in a region, it is also important to determine the genetic population structure and the population dynamics over time. This identifies changes at the population level, as well as fitness differences among populations (Ward et al. 2008; Kelly et al. 2015). Moreover, management strategies should be planned by taking into consideration population-level variation due to the fact that different populations could be affected selectively (Kelly et al. 2015). Furthermore, in the context of screening and breeding for FHB resistance, it is important to consider the pathogen populations to which the plants could be exposed, in order to ensure that the varieties developed have broad resistance to all pathogen populations (Ward et al. 2002).

The genomic diversity in *F. graminearum* suggests that this species has a very high potential for adaptation. It was noted that *F. graminearum* isolates have many polymorphisms within a 'two-speed' genome organization (Laurent et al. 2018). In plant pathogens with two-speed genomes, one of the subgenomes tends to evolve more rapidly and have more diversity than the rest of the genome, and genes that are important for infection are usually located in these high-diversity areas (Dong et al. 2015). Together with the ability to undergo sexual recombination, bipartite genome architecture allows for a prompt evolutionary response when faced with selective pressures (Laurent et al. 2017, 2018). This represents a challenge for the control of this economically important disease, because management practices should evolve constantly to keep up with the 'arms race' (Laurent et al. 2017). Attempts have been made to predict changes in populations of FHB pathogens, but this

has proven to be challenging due to the complexity and variability of the system and all of the factors that should be considered (Parikka et al. 2012; Vaughan et al. 2016). However, most studies point to the fact that severity and incidence of FHB will increase significantly due to climate change (Madgwick et al. 2011; West et al. 2012; Zhang et al. 2014).

Concluding remarks

The studies reviewed in this article clearly show that populations of FHB pathogens are dynamic and change continuously. The effect of climate and anthropogenic activities on FHB pathogens at the population level is evident; however, most of the causes of population shifts have not been completely elucidated and remain largely unexplored. The effects of climate change and the ability of these populations to travel long distances underscore the importance of ongoing surveillance and phytosanitary regulations. Understanding the composition of the FHB pathogen populations in an area is critical for developing effective management strategies.

With regard to future challenges, the development of alternative means of identifying FHB pathogens would be valuable in order to effectively monitor populations. Finally, additional studies are necessary to fully understand the drivers of population changes and population differences between regions, which, as was pointed out by Kelly et al. (2015), will result in new management strategies or improvement of the current tools available for the management of FHB.

Funding

References

Aamot HU, Ward TJ, Brodal G, Vrålstad T, Larsen GB, Klemsdal SS, Elameen A, Uhlig S, Hofgaard IS. 2015. Genetic and phenotypic diversity within the *Fusarium graminearum* species complex in Norway. Eur J Plant Pathol. 142(3):501–519.

Aoki T, Vaughan MM, McCormick SP, Busman M, Ward TJ, Kelly A, O'Donnell K, Johnston PR, Geiser DM. 2015. *Fusarium dactylidis* sp. nov., a novel nivalenol toxin-producing species sister to *F. pseudograminearum* isolated from orchard grass (*Dactylis glomerata*) in Oregon and New Zealand. Mycologia. 107(2):409–418.

Aoki T, Ward TJ, Kistler HC, O'Donnell K. 2012. Systematics, phylogeny and trichothecene mycotoxin potential of Fusarium head blight cereal pathogens. JSM Mycotoxins. 62(2):91–102.

Audenaert K, Van Broeck R, Bekaert B, De Witte F, Heremans B, Messens K, Höfte M, Haesaert G. 2009. Fusarium head blight (FHB) in Flanders: population diversity, inter-species associations and DON contamination in commercial winter wheat varieties. Eur J Plant Pathol. 125(3):445–458.

Backhouse D. 2014. Global distribution of Fusarium graminearum, F. asiaticum and F. boothii from wheat in relation to climate. Eur J Plant Pathol. 139(1):161–173.

Balmas V, Scherm B, Marcello A, Beyer M, Hoffmann L, Migheli Q, Pasquali M. 2015. Fusarium species and chemotypes associated with Fusarium head blight and Fusarium root rot on wheat in Sardinia. Plant Pathol. 64(4):972–979.

Banik M, Beyene M, Tekauz A. 2014. Fusarium head blight and leaf spot diseases of barley in Manitoba in 2013. Can Plant Dis Surv. 94:107–108. www.phytopath.ca/publication/cpds.

Banik M, Beyene M, Wang X. 2016. Fusarium head blight of barley in Manitoba - 2015. Can Plant Dis Surv. 96:93–94. www.phytopath.ca/publication/cpds.

Banik M, Beyene M, Wang X. 2017. Fusarium head blight of barley in Manitoba - 2016. Can Plant Dis Surv. 97:100–101. www.phytopath.ca/publication/cpds.

Banik M, Beyene M, Wang X. 2018. Fusarium head blight of barley in Manitoba - 2017. Can Plant Dis Surv. 98:95–96. www.phytopath.ca/publication/cpds.

Beccari G, Caproni L, Tini F, Uhlig S, Covarelli L. 2016. Presence of Fusarium species and other toxigenic fungi in malting barley and multi-mycotoxin analysis by liquid chromatography-high-resolution mass spectrometry. J Agric Food Chem. 64(21):4390–4399.

Beccari G, Prodi A, Tini F, Bonciarelli U, Onofri A, Oueslati S, Limayma M, Covarelli L. 2017. Changes in the Fusarium head blight complex of malting barley in a three-year field experiment in Italy. Toxins. 9(4):120.

Beccari G, Senatore MT, Tini F, Sulyok M, Covarelli L. 2018. Fungal community, Fusarium head blight complex and secondary metabolites associated with malting barley grains harvested in Umbria, central Italy. Int J Food Microbiol. 273:33–42.

Beukes I, Rose L, van Coller G, Viljoen A. 2018. Disease development and mycotoxin production by the Fusarium graminearum species complex associated with South African maize and wheat. Eur J Plant Pathol. 150(4):893–910.

Beyene M, Banik M, Wang X. 2015. Fusarium head blight of barley in Manitoba – 2014. Can Plant Dis Surv. 95:74–75. www.phytopath.ca/publication/cpds.

Bianchini A, Horsley R, Jack MM, Kobielush B, Ryu D, Tittlemier S, Wilson WW, Abbas HK, Abel S, Harrison G, et al. 2015. DON occurrence in grains: A North American perspective. Cereal Food World. 60(1):32–56.

Bissonnette KM, Wharton P, Chen J, Marshall JM. 2018. Survey of Fusarium species associated with Fusarium head blight of spring wheat (Triticum aestivum) in Southeastern Idaho. Plant Health Prog. 19:125–127.

Boutigny A, Ward TJ, Ballois N, Iancu G, Ioos R. 2014. Diversity of the Fusarium graminearum species complex on French cereals. Eur J Plant Pathol. 138(1):133–148.

Boutigny A, Ward TJ, Van Coller GJ, Flett B, Lamprecht SC, O'Donnell K, Viljoen A. 2011. Analysis of the Fusarium graminearum species complex from wheat, barley and maize in South Africa provides evidence of species-specific differences in host preference. Fungal Genet Biol. 48(9):914–920.

Burlakoti RR, Neate SM, Adhikari TB, Gyawali S, Salas B, Steffenson BJ, Schwarz PB. 2011. Trichothecene profiling and population genetic analysis of Gibberella zeae from barley in North Dakota and Minnesota. Phytopathology. 101(6):687–695.

Burlakoti RR, Tamburic-Ilincic L, Limay-Rios V, Burlakoti P. 2017. Comparative population structure and trichothecene mycotoxin profiling of Fusarium graminearum from corn and wheat in Ontario, central Canada. Plant Pathol. 66(1):14–27.

Castañares E, Dinolfo MI, Del Ponte EM, Pan D, Stenglein SA. 2016. Species composition and genetic structure of Fusarium graminearum species complex populations affecting the main barley growing regions of South America. Plant Pathol. 65(6):930–939.

Cerón-Bustamante M, Ward TJ, Kelly A, Vaughan MM, McCormick SP, Cowger C, Leyva-Mir SG, Villaseñor-Mir HE, Ayala-Escobar V, Nava-Díaz C. 2018. Regional differences in the composition of Fusarium Head Blight pathogens and mycotoxins associated with wheat in Mexico. Int J Food Microbiol. 273:11–19.

Chandelier A, Nimal C, André F, Planchon V, Oger R. 2011. Fusarium species and DON contamination associated with head blight in winter wheat over a 7-year period (2003–2009) in Belgium. Eur J Plant Pathol. 130(3):403–414.

Chełkowski J, Gromadzka K, Ł S, Lenc L, Kostecki M, Berthiller F. 2012. Fusarium species, zearalenone and deoxynivalenol content in preharvest scabby wheat heads from Poland. World Mycotoxin J. 5 (2):133–141.

Covarelli L, Beccari G, Prodi A, Generotti S, Etruschi F, Juan C, Ferrer E, Mañes J. 2015. Fusarium species, chemotype characterisation and trichothecene contamination of durum and soft wheat in an area of central Italy. J Sci Food Agric. 95(3):540–551.

Dean R, Van Kan JA, Pretorius ZA, Hammond-Kosack KE, Di Pietro A, Spanu PD, Rudd JJ, Dickman M, Kahmann R, Ellis J, et al. 2012. The Top 10 fungal pathogens in molecular plant pathology. Mol Plant Pathol. 13(4):414–430.

Del Ponte EM, Spolti P, Ward TJ, Gomes LB, Nicolli CP, Kuhnem PR, Silva CN, Tessmann DJ. 2015. Regional and field-specific factors affect the composition of Fusarium head blight pathogens in subtropical no-till wheat agroecosystem of Brazil. Phytopathology. 105(2):246–254.

Del Ponte EM, Tessmann DJ, Spolti P, Kuhnem PR, Da Silva CN. 2013. Species identification, genetic diversity and phenotypic variation studies on the Fusarium graminearum complex populations from Brazil. In: Alconada Magliano TM, Chulze SN, editors. Fusarium head blight in Latin America. Dordrecht: Springer; p. 15–29.

Desjardins AE, Proctor RH. 2011. Genetic diversity and trichothecene chemotypes of the Fusarium graminearum clade isolated from maize in Nepal and identification of a putative new lineage. Fungal Biol. 115 (1):38–48.

Dong S, Raffaele S, Kamoun S. 2015. The two-speed genomes of filamentous pathogens: waltz with plants. Curr Opin Genet Dev. 35:57–65.

Duan C, Qin Z, Yang Z, Li W, Sun S, Zhu Z, Wang X. 2016. Identification of pathogenic Fusarium spp. causing maize ear rot and potential mycotoxin production in China. Toxins. 8(6):186.

Foroud NA, Eudes F. 2009. Trichothecenes in cereal grains. Int J Mol Sci. 10(1):147–173.

Foroud NA, McCormick SP, MacMillan T, Badea A, Kendra DF, Ellis BE, Eudes F. 2012. Greenhouse studies reveal increased aggressiveness of emergent Canadian Fusarium graminearum chemotypes in wheat. Plant Dis. 96(9):1271–1279.

Gai XT, Xuan YH, Gao ZG. 2017. Diversity and pathogenicity of Fusarium graminearum species complex from maize stalk and ear rot strains in northeast China. Plant Pathol. 66(8):1267–1275.

Gale LR, Harrison SA, Ward TJ, O'Donnell K, Milus EA, Gale SW, Kistler HC. 2011. Nivalenol-type populations of Fusarium graminearum and F. asiaticum are prevalent on wheat in southern Louisiana. Phytopathology. 101(1):124–134.

Gale LR, Ward TJ, Balmas V, Kistler HC. 2007. Population Subdivision of *Fusarium graminearum sensu stricto* in the Upper Midwestern United States. Phytopathology. 97(11):1434–1439.

Gomes LB, Ward TJ, Badiale-Furlong E, Del Ponte EM. 2015. Species composition, toxigenic potential and pathogenicity of *Fusarium graminearum* species complex isolates from southern Brazilian rice. Plant Pathol. 64(4):980–987.

Gorczyca A, Oleksy A, Gala-Czekaj D, Urbaniak M, Laskowska M, Waśkiewicz A, Stępień Ł. 2018. Fusarium head blight incidence and mycotoxin accumulation in three durum wheat cultivars in relation to sowing date and density. Sci Nat. 105(1):1–11.

Goswami RS, Kistler HC. 2004. Heading for disaster: *Fusarium graminearum* on cereal crops. Mol Plant Pathol. 5(6):515–525.

Gräfenhan T, Johnston PR, Vaughan MM, McCormick SP, Proctor RH, Busman M, Ward TJ, O'Donnell K. 2016. *Fusarium praegraminearum* sp. nov., a novel nivalenol mycotoxin-producing pathogen from New Zealand can induce head blight on wheat. Mycologia. 108(6):1229–1239.

Hietaniemi V, Rämö S, Yli-Mattila T, Jestoi M, Peltonen S, Kartio M, Sieviläinen E, Koivisto T, Parikka P. 2016. Updated survey of *Fusarium* species and toxins in Finnish cereal grains. Food Addit Contam Part A Chem Anal Control Expo Risk Assess. 33(5):831–848.

Infantino A, Santori A, Shah D. 2012. Community structure of the *Fusarium* complex on wheat seed in Italy. Eur J Plant Pathol. 132(4):499–510.

Isebaert S, Saeger SD, Devreese R, Verhoeven R, Maene P, Heremans B, Haesaert G. 2009. Mycotoxin-producing *Fusarium* species occurring in winter wheat in Belgium (Flanders) during 2002–2005. J Phytopathol. 157(2):108–116.

Jennings P, Coates ME, Walsh K, Turner JA, Nicholson P. 2004. Determination of deoxynivalenol- and nivalenol-producing chemotypes of *Fusarium graminearum* isolated from wheat crops in England and Wales. Plant Pathol. 53(5):643–652.

Karlsson I, Friberg H, Kolseth A, Steinberg C, Persson P. 2017. Agricultural factors affecting *Fusarium* communities in wheat kernels. Int J Food Microbiol. 252:53–60.

Keller M, Bergstrom G, Shields E. 2014. The aerobiology of *Fusarium graminearum*. Aerobiologia. 30(2):123–136.

Kelly A, Proctor RH, Belzile F, Chulze SN, Clear RM, Cowger C, Elmer W, Lee T, Obanor F, Waalwijk C, et al. 2016. The geographic distribution and complex evolutionary history of the NX-2 trichothecene chemotype from *Fusarium graminearum*. Fungal Genet Biol. 95:39–48.

Kelly AC, Clear RM, O'Donnell K, McCormick S, Turkington TK, Tekauz A, Gilbert J, Kistler HC, Busman M, Ward TJ. 2015. Diversity of Fusarium head blight populations and trichothecene toxin types reveals regional differences in pathogen composition and temporal dynamics. Fungal Genet Biol. 82:22–31.

Kelly AC, Ward TJ. 2018. Population genomics of *Fusarium graminearum* reveals signatures of divergent evolution within a major cereal pathogen. PLoS One. 13(3):e0194616.

Klix MB, Beyer M, Verreet J. 2008. Effects of cultivar, agronomic practices, geographic location, and meteorological conditions on the composition of selected *Fusarium* species on wheat heads. Can J Plant Pathol. 30(1):46–57.

Láday M, Á J, Mulè G, Moretti A, Á S, Logrieco A. 2004. Mitochondrial DNA diversity and lineage determination of European isolates of *Fusarium graminearum* (*Gibberella zeae*). Eur J Plant Pathol. 110:545–550.

Laurent B, Moinard M, Spataro C, Ponts N, Barreau C, Foulongne-Oriol M. 2017. Landscape of genomic diversity and host adaptation in *Fusarium graminearum*. BMC Genomics. 18:203.

Laurent B, Palaiokostas C, Spataro C, Moinard M, Zehraoui E, Houston RD, Foulongne-Oriol M. 2018. High-resolution mapping of the recombination landscape of the phytopathogen *Fusarium graminearum* suggests two-speed genome evolution. Mol Plant Pathol. 19(2):341–354.

Lee J, Chang I, Kim H, Yun S, Leslie JF, Lee Y. 2009. Genetic diversity and fitness of *Fusarium graminearum* populations from rice in Korea. Appl Environ Microbiol. 75(10):3289–3295.

Lee J, Kim H, Jeon J, Kim H, Zeller KA, Carter LLA, Leslie JF, Lee Y. 2012. Population structure of and mycotoxin production by *Fusarium graminearum* from maize in South Korea. Appl Environ Microbiol. 78(7):2161–2167.

Lee S, Lee J, Nam Y, Lee S, Ryu J, Lee T. 2010. Population structure of *Fusarium graminearum* from maize and rice in 2009 in Korea. Plant Pathol J. 26(4):321–327.

Liang J, L L, Ma Z, Ward TJ, Kistler HC. 2015. Population Subdivision of *Fusarium graminearum* from barley and wheat in the Upper Midwestern United States at the turn of the century. Phytopathology. 105(11):1466–1474.

Liang JM, Xayamongkhon H, Broz K, Dong Y, McCormick SP, Abramova S, Ward TJ, Ma ZH, Kistler HC. 2014. Temporal dynamics and population genetic structure of *Fusarium graminearum* in the upper Midwestern United States. Fungal Genet Biol. 73:83–92.

Lofgren L, Riddle J, Dong Y, Kuhnem P, Cummings J, Del Ponte E, Bergstrom G, Kistler HC. 2018. A high proportion of NX-2 genotype strains are found among *Fusarium graminearum* isolates from northeastern New York State. Eur J Plant Pathol. 150(3):791–796.

Madgwick J, West J, White R, Semenov M, Townsend J, Turner J, Fitt B. 2011. Impacts of climate change on wheat anthesis and Fusarium ear blight in the UK. Eur J Plant Pathol. 130(1):117–131.

Malihipour A, Gilbert J, Piercey-Normore M, Cloutier S. 2012. Molecular phylogenetic analysis, trichothecene chemotype patterns, and variation in aggressiveness of *Fusarium* isolates causing head blight in wheat. Plant Dis. 96(7):1016–1025.

McMullen M, Bergstrom G, De Wolf E, Dill-Macky R, Hershman D, Shaner G, Van Sanford D. 2012. A unified effort to fight an enemy of wheat and barley: Fusarium Head Blight. Plant Dis. 96(12):1712–1728.

McMullen M, Jones R, Gallenberg D. 1997. Scab of wheat and barley: A re-emerging disease of devastating impact. Plant Dis. 81(12):1340–1348.

Minervini F, Fornelli F, Flynn KM. 2004. Toxicity and apoptosis induced by the mycotoxins nivalenol, deoxynivalenol and fumonisin B1 in a human erythroleukemia cell line. Toxicol In Vitro. 18(1):21–28.

Monds RD, Cromey MG, Lauren DR, Di Menna M, Marshall J. 2005. *Fusarium graminearum, F. cortaderiae* and *F. pseudograminearum* in New Zealand: molecular phylogenetic analysis, mycotoxin chemotypes and co-existence of species. Mycol Res. 109(Pt4):410–420.

Nganje WE, Bangsund DA, Leistritz FL, Wilson WW, Tiapo NM. 2004. Regional economic impacts of Fusarium head blight in wheat and barley. Appl Econ Perspect Policy. 26(3):332–347.

Nielsen LK, Jensen JD, Nielsen GC, Jensen JE, Spliid NH, Thomsen IK, Justesen AF, Collinge DB, Jørgensen LN. 2011. Fusarium head blight of cereals in Denmark: species complex and related mycotoxins. Phytopathology. 101(8):960–969.

Nogueira MS, Decundo J, Martinez M, Dieguez SN, Moreyra F, Moreno MV, Stenglein SA. 2018. Natural contamination with mycotoxins produced by *Fusarium graminearum* and *Fusarium poae* in malting Barley in Argentina. Toxins. 10(2):78.

O'Donnell K, Kistler HC, Tacke BK, Casper HH. 2000. Gene genealogies reveal global phylogeographic structure and reproductive isolation among lineages of *Fusarium graminearum*, the fungus causing wheat scab. PNAS. 97(14):7905–7910.

O'Donnell K, McCormick SP, Busman M, Proctor RH, Ward TJ, Doehring G, Geiser DM, Alberts JF, Rheeder JP. 2018. Marasas et al. 1984 "Toxigenic *Fusarium* Species: identity and Mycotoxicology" revisited. Mycologia. 110(6):1058–1080.

O'Donnell K, Rooney AP, Proctor RH, Brown DW, McCormick SP, Ward TJ, Frandsen RJN, Lysøe E, Rehner SA, Aoki T, et al. 2013.

Phylogenetic analyses of *RPB1* and *RPB2* support a middle Cretaceous origin for a clade comprising all agriculturally and medically important fusaria. Fungal Genet Biol. 52:20–31.

O'Donnell K, Ward TJ, Geiser DM, Corby Kistler H, Aoki T. 2004. Genealogical concordance between the mating type locus and seven other nuclear genes supports formal recognition of nine phylogenetically distinct species within the *Fusarium graminearum* clade. Fungal Genet Biol. 41(6):600–623.

O'Donnell K, Ward TJ, Robert VARG, Crous PW, Geiser DM, Kang S. 2015. DNA sequence-based identification of *Fusarium*: current status and future directions. Phytoparasitica. 43(5):583–595.

Pancaldi D, Tonti S, Prodi A, Salomoni D, Dal Prà M, Nipoti P, Alberti I, Pisi A. 2010. Survey of the main causal agents of Fusarium head blight of durum wheat around Bologna, northern Italy. Phytopathol Mediterr. 49(2):258–266.

Parikka P, Hakala K, Tiilikkala K. 2012. Expected shifts in *Fusarium* species' composition on cereal grain in Northern Europe due to climatic change. Food Addit Contam Part A. 29(10):1543–1555.

Parry DW, Jenkinson P, McLeod L. 1995. Fusarium ear blight (scab) in small grain cereals—a review. Plant Pathol. 44(2):207–238.

Pasquali M, Giraud F, Brochot C, Cocco E, Hoffmann L, Bohn T. 2010. Genetic *Fusarium* chemotyping as a useful tool for predicting nivalenol contamination in winter wheat. Int J Food Microbiol. 137(2–3):246–253.

Pasquali M, Giraud F, Brochot C, Hoffmann L, Bohn T. 2009. First report of the nivalenol chemotype of *Fusarium graminearum* causing head blight of wheat in the Grand Duchy of Luxembourg. Plant Dis. 93 (11):1217.

Pereira CB, Ward TJ, Tessmann DJ, Ponte EMD, Laraba I, Vaughan MM, McCormick SP, Busman M, Kelly A, Proctor RH, et al. 2018. *Fusarium subtropicale*, sp. nov., a novel nivalenol mycotoxin–producing species isolated from barley (*Hordeum vulgare*) in Brazil and sister to *F. praegraminearum*. Mycologia. 110(5):860–871.

Pestka JJ, Smolinski AT. 2005. Deoxynivalenol: toxicology and potential effects on humans. J Toxicol Environ Health B. 8(1):39–69.

Puri KD, Zhong S. 2010. The 3ADON population of *Fusarium graminearum* found in North Dakota is more aggressive and produces a higher level of DON than the prevalent 15ADON population in spring wheat. Phytopathology. 100(10):1007–1014.

Qiu J, Dong F, Yu M, Xu J, Shi J. 2016. Effect of preceding crop on *Fusarium* species and mycotoxin contamination of wheat grains. J Sci Food Agric. 96(13):4536–4541.

Sampietro DA, Díaz CG, Gonzalez V, Vattuone MA, Ploper LD, Catalan CAN, Ward TJ. 2011. Species diversity and toxigenic potential of *Fusarium graminearum* complex isolates from maize fields in northwest Argentina. Int J Food Microbiol. 145(1):359–364.

Schmale DG, Ross SD, Fetters TL, Tallapragada P, Wood-Jones AK, Dingus B. 2012. Isolates of *Fusarium graminearum* collected 40–320 meters above ground level cause Fusarium head blight in wheat and produce trichothecene mycotoxins. Aerobiologia. 28(1):1–11.

Schmale DG, Wood-Jones AK, Cowger C, Bergstrom GC, Arellano C. 2011. Trichothecene genotypes of *Gibberella zeae* from winter wheat fields in the eastern USA. Plant Pathol. 60(5):909–917.

Shah D, Pucci N, Infantino A. 2005. Regional and varietal differences in the risk of wheat seed infection by fungal species associated with Fusarium head blight in Italy. Eur J Plant Pathol. 112(1):13–21.

Shin S, Son J, Park J, Kim K, Yoon Y, Cheong Y, Kim K, Hyun J, Park CS, Dill-Macky R, et al. 2018. Comparative pathogenicity of *Fusarium graminearum* isolates from wheat kernels in Korea. Plant Pathol J. 34(5):347–355.

Somma S, Petruzzella AL, Logrieco AF, Meca G, Cacciola OS, Moretti A. 2014. Phylogenetic analyses of *Fusarium graminearum* strains from cereals in Italy, and characterisation of their molecular and chemical chemotypes. Crop Pasture Sci. 65(1):52–60.

Spolti P, Del Ponte EM, Cummings JA, Dong Y, Bergstrom GC. 2014. Fitness attributes of *Fusarium graminearum* isolates from wheat in New York possessing a 3-ADON or 15-ADON trichothecene genotype. Phytopathology. 104(5):513–519.

Starkey DE, Ward TJ, Aoki T, Gale LR, Kistler HC, Geiser DM, Suga H, Tóth B, Varga J, O'Donnell K. 2007. Global molecular surveillance reveals novel Fusarium head blight species and trichothecene toxin diversity. Fungal Genet Biol. 44(11):1191–1204.

Stępień Ł, Chełkowski J. 2010. Fusarium head blight of wheat: pathogenic species and their mycotoxins. World Mycotoxin J. 3(2):107–119.

Stępień Ł, Popiel D, Koczyk G, Chełkowski J. 2008. Wheat-infecting *Fusarium* species in Poland–their chemotypes and frequencies revealed by PCR assay. J Appl Genet. 49(4):433–441.

Sumíková T, Chrpová J, Džuman Z, Salava J, Štěrbová L, Palicová J, Slavíková P, Stránská-Zachariášová M, Hajšlová J. 2017. Mycotoxins content and its association with changing patterns of *Fusarium* pathogens in wheat in the Czech Republic. World Mycotoxin J. 10(2):143–151.

Tamburic-Ilincic L, Wragg A, Schaafsma A. 2015. Mycotoxin accumulation and *Fusarium graminearum* chemotype diversity in winter wheat grown in southwestern Ontario. Can J Plant Sci. 95(5):931–938.

Tangni EK, Motte J, Callebaut A, Pussemier L. 2010. Cross-Reactivity of antibodies in some commercial deoxynivalenol test kits against some fusariotoxins. J Agric Food Chem. 58(24):12625–12633.

Tekauz A, Stulzer M, Beyene M, Gompf J, Moncomble C. 2013. Fusarium head blight of barley in Manitoba – 2012. Can Plant Dis Surv. 93:91–92.

Tóth B, Á M, Horváth Z, Bartók T, Varga M, Varga J. 2005. Genetic variability of central European isolates of the *Fusarium graminearum* species complex. Eur J Plant Pathol. 113(1):35–45.

Trail F. 2009. For blighted waves of grain: *Fusarium graminearum* in the postgenomics Era. Plant Physiol. 149(1):103–110.

Umpiérrez-Failache M, Garmendia G, Pereyra S, Rodríguez-Haralambides A, Ward TJ, Vero S. 2013. Regional differences in species composition and toxigenic potential among Fusarium head blight isolates from Uruguay indicate a risk of nivalenol contamination in new wheat production areas. Int J Food Microbiol. 166 (1):135–140.

van der Fels-Klerx HJ, de Rijk TC, Booij CJH, Goedhart PW, Boers EAM, Zhao C, Waalwijk C, Mol HGJ, van der Lee TAJ. 2012. Occurrence of Fusarium head blight species and *Fusarium* mycotoxins in winter wheat in the Netherlands in 2009. Food Addit Contam Part A. 29(11):1716–1726.

van der Lee T, Zhang H, van Diepeningen A, Waalwijk C. 2015. Biogeography of *Fusarium graminearum* species complex and chemotypes: a review. Food Addit Contam Part A. 32(4):453–460.

Vanheule A, De Boevre M, Moretti A, Scauflaire J, Munaut F, De Saeger S, Bekaert B, Haesaert G, Waalwijk C, Van Der Lee T, et al. 2017. Genetic divergence and chemotype diversity in the Fusarium head blight pathogen *Fusarium poae*. Toxins. 9(9):255.

Varga E, Wiesenberger G, Hametner C, Ward TJ, Dong Y, Schöfbeck D, McCormick S, Broz K, Stückler R, Schuhmacher R, et al. 2015. New tricks of an old enemy: isolates of *Fusarium graminearum* produce a type A trichothecene mycotoxin. Environ Microbiol. 17(8):2588–2600.

Vaughan M, Backhouse D, Del Ponte EM. 2016. Climate change impacts on the ecology of *Fusarium graminearum* species complex and susceptibility of wheat to Fusarium head blight: a review. World Mycotoxin J. 9(5):685–700.

Vujanovic V, Goh YK, Daida P. 2012. Heat- and cold-shock responses in *Fusarium graminearum* 3 acetyl- and 15 acetyl-deoxynivalenol chemotypes. J Microbiol. 50(1):97–102.

Waalwijk C, Kastelein P, Vries I, Kerényi Z, Tvd L, Hesselink T, Köhl J, Kema G. 2003. Major changes in *Fusarium* spp. in wheat in the Netherlands. Eur J Plant Pathol. 109(7):743–754.

Ward TJ, Bielawski JP, Kistler HC, Sullivan E, O'Donnell K. 2002. Ancestral polymorphism and adaptive evolution in the trichothecene mycotoxin gene cluster of phytopathogenic *Fusarium*. PNAS. 99 (14):9278–9283.

Ward TJ, Clear RM, Rooney AP, O'Donnell K, Gaba D, Patrick S, Starkey DE, Gilbert J, Geiser DM, Nowicki TW. 2008. An adaptive evolutionary shift in Fusarium head blight pathogen populations is driving the rapid spread of more toxigenic *Fusarium graminearum* in North America. Fungal Genet Biol. 45(4):473–484.

Wegulo SN, Valverde-Bogantes E, Bolanos-Carriel C, Hallen-Adams H, Bianchini A, McMaster N, Schmale DG. 2018. First report of *Fusarium boothii* causing head blight of wheat in the United States. Plant Dis. 102(12):2646.

West JS, Holdgate S, Townsend JA, Edwards SG, Jennings P, Fitt BDL. 2012. Impacts of changing climate and agronomic factors on Fusarium ear blight of wheat in the UK. Fungal Ecol. 5(1):53–61.

Xu X, Parry D, Nicholson P, Thomsett M, Simpson D, Edwards S, Cooke B, Doohan F, Brennan J, Moretti A, et al. 2005. Predominance and association of pathogenic fungi causing Fusarium ear blight in wheat in four European countries. Eur J Plant Pathol. 112(2):143–154.

Xu XM, Nicholson P, Thomsett MA, Simpson D, Cooke BM, Doohan FM, Brennan J, Monaghan S, Moretti A, Mule G, et al. 2008. Relationship between the fungal complex causing *Fusarium* head blight of wheat and environmental conditions. Phytopathology. 98(1):69–78.

Xue AG, Armstrong KC, Voldeng HD, Fedak G, Babcock C. 2004. Comparative aggressiveness of isolates of *Fusarium* spp. causing head blight on wheat in Canada. Can J Plant Pathol. 26(1):81–88.

Yang L, van der Lee T, Yang X, Yu D, Waalwijk C. 2008. *Fusarium* populations on Chinese barley show a dramatic gradient in mycotoxin profiles. Phytopathology. 98(6):719–727.

Yang M, Zhang H, Kong X, van der Lee T, Waalwijk C, van Diepeningen A, Xu J, Xu J, Chen W, Feng J. 2018. Host and cropping system shape the *Fusarium* population: 3ADON-producers are ubiquitous in wheat whereas NIV-producers are more prevalent in rice. Toxins. 10(3):115.

Yli-Mattila T, Gagkaeva T, Ward TJ, Aoki T, Kistler HC, O'Donnell K. 2009. A novel Asian clade within the *Fusarium graminearum* species complex includes a newly discovered cereal head blight pathogen from the Russian Far East. Mycologia. 101 (6):841–852.

Zeller KA, Bowden RL, Leslie JF. 2004. Population differentiation and recombination in wheat scab populations of *Gibberella zeae* from the United States. Mol Ecol. 13(3):563–571.

Zhang H, Brankovics B, Xu J, Xu JS, Guo C, Guo JG, Jin SJ, Chen WQ, Feng J, van Diepeningen AD, et al. 2016. Crops are a main driver for species diversity and the toxigenic potential of *Fusarium* isolates in maize ears in China. World Mycotoxin J. 9 (5):701–715.

Zhang H, van der Lee T, Waalwijk C, Chen W, Xu J, Xu J, Zhang Y, Feng J. 2012. Population analysis of the *Fusarium graminearum* species complex from wheat in China show a shift to more aggressive isolates. PLoS One. 7(2):e31722.

Zhang H, Zhang Z, van der Lee T, Chen WQ, Xu J, Xu JS, Yang L, Yu D, Waalwijk C, Feng J. 2010. Population genetic analyses of *Fusarium asiaticum* populations from barley suggest a recent shift favoring 3ADON producers in southern China. Phytopathology. 100 (4):328–336.

Zhang X, Halder J, White RP, Hughes DJ, Ye Z, Wang C, Xu R, Gan B, Fitt B. 2014. Climate change increases risk of fusarium ear blight on wheat in central China. Ann Appl Biol. 164(3):384–395.