

Fusarium graminearum Species Complex: A Bibliographic Analysis and Web-Accessible Database for Global Mapping of Species and Trichothecene Toxin Chemotypes

Emerson M. Del Ponte,^{1,†} Gláucia M. Moreira,¹ Todd J. Ward,² Kerry O'Donnell,² Camila P. Nicolli,¹ Franklin J. Machado,¹ Máira R. Duffeck,¹ Kaique S. Alves,¹ Dauri J. Tessmann,³ Cees Waalwijk,⁴ Theo van der Lee,⁴ Hao Zhang,⁵ Sofia N. Chulze,⁶ Sebastian A. Stenglein,⁷ Dinorah Pan,⁸ Silvana Vero,⁸ Lisa J. Vaillancourt,⁹ David G. Schmale III,¹⁰ Paul D. Esker,¹¹ Antonio Moretti,¹² Antonio F. Logrieco,¹² H. Corby Kistler,¹³ Gary C. Bergstrom,¹⁴ Altus Viljoen,¹⁵ Lindy J. Rose,¹⁵ Gert J. van Coller,¹⁶ and Theresa Lee¹⁷

¹ Departamento de Fitopatologia, Universidade Federal de Viçosa, Viçosa, MG, 36570-900 Brazil

² Agricultural Research Service, National Center for Agricultural Utilization Research, U.S. Department of Agriculture, Peoria 61604, U.S.A.

³ Departamento de Agronomia, Universidade Estadual de Maringá, Maringá, PR, 87020-900 Brazil

⁴ Biointeractions & Plant Health, Wageningen Plant Research, Wageningen, 6708PB, The Netherlands

⁵ State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing, 100193, China

⁶ Universidad Nacional de Río Cuarto, Río Cuarto, 5800 Argentina

⁷ Laboratorio de Biología Funcional y Biotecnología, Facultad de Agronomía, Universidad Nacional del Centro, Buenos Aires, 7300, Argentina

⁸ Universidad de la República, Facultad de Ciencias-Facultad de Ingeniería, Montevideo, 11800, Uruguay

⁹ Department of Plant Pathology, University of Kentucky, Lexington, 40546-0312, U.S.A.

¹⁰ School of Plant and Environmental Sciences, Virginia Tech, Blacksburg, 24061-0390, U.S.A.

¹¹ Department of Plant Pathology and Environmental Microbiology, Pennsylvania State University, University Park, 16802, U.S.A.

¹² National Research Council of Research, Institute of Sciences of Food Production, 70126 Bari, Italy

¹³ Agricultural Research Service, Cereal Disease Laboratory, U.S. Department of Agriculture, St. Paul 55108, U.S.A.

¹⁴ School of Integrative Plant Science, Plant Pathology and Plant-Microbe Biology Section, Cornell University, Ithaca 14853-5904, U.S.A.

¹⁵ Department of Plant Pathology, Stellenbosch University, Stellenbosch, 7602, South Africa

¹⁶ Plant Science, Western Cape Department of Agriculture, Elsenburg, 7607, South Africa

¹⁷ Microbial Safety Team, National Institute of Agricultural Sciences, Wanju, 55365, Republic of Korea

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†Corresponding author: E. M. Del Ponte; delponte@ufv.br

E. M. Del Ponte and G. M. Moreira contributed equally to the work.

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ABSTRACT

Fusarium graminearum is ranked among the five most destructive fungal pathogens that affect agroecosystems. It causes floral diseases in small grain cereals including wheat, barley, and oats, as well as maize and rice. We conducted a systematic review of peer-reviewed studies reporting species within the *F. graminearum* species complex (FGSC) and created two main data tables. The first contained summarized data from the articles including bibliographic, geographic, methodological (ID methods), host of origin and species, while the second data table contains information about the described strains such as publication, isolate code(s), host/substrate, year of isolation, geographical coordinates, species and trichothecene genotype. Analyses of the bibliographic data obtained from 123 publications from 2000 to 2021 by 498 unique authors and published in 40 journals are summarized. We describe the frequency of species and chemotypes for 16,274 strains for which geographical information was available, either provided as raw data or extracted from the publications, and sampled across six continents and 32 countries. The database and interactive interface are publicly available, allowing for searches, summarization, and mapping of strains according to several criteria including article, country, host, species and trichothecene genotype. The database will be updated as new articles are published and should be useful for guiding future surveys and exploring factors associated with species distribution such as climate and land use. Authors are encouraged to submit data at the strain level to the database, which is accessible at <https://fgsc.netlify.app>.

Keywords: fungal pathogens

Members of the *Fusarium graminearum* species complex (FGSC) include some of the top fungal plant pathogens of global importance given the serious diseases they cause in most major cereal crops, including wheat, maize, rice, and barley (Dean et al. 2012; van der Lee et al. 2015). Crop yields are often severely reduced due to infection of roots, stalks, or ears/heads (Duffeck et al. 2020; McMullen et al. 1997; Munkvold 2003; Vaughan et al. 2016). Kernel infections are of particular concern, since members of the FGSC can synthesize a wide range of mycotoxins during plant infection and colonization (D’Mello et al. 1999). The most important mycotoxins are the trichothecenes, including deoxynivalenol, nivalenol, and their acetylated derivatives, which can be produced at high levels in cereal grains, and are highly toxic to humans and other animals. Ingestion of grain or grain products contaminated by these toxins can cause diarrhea, nausea, and vomiting (Chen et al. 2019; Pestka 2010).

In wheat and barley, members of the FGSC cause Fusarium head blight (FHB), which re-emerged as a major concern throughout the world in the early 1990s (Goswami and Kistler 2004; McMullen et al. 1997, 2012). Numerous surveys of disease incidence and severity, pathogen population diversity, and mycotoxin contamination have been conducted during the past three decades in the main cereal-growing regions of the world where FHB epidemics have occurred (Cowger et al. 2020; Pereira et al. 2021; van der Lee et al. 2015; Vogelgsang et al. 2019).

Multilocus sequencing of a global collection of strains that were morphologically defined as a single panmictic species, previously known as “*Fusarium graminearum*,” revealed significant phylogeographic structure and reproductive isolation of seven lineages (i.e., phylopecies; O’Donnell et al. 2000). Employing the concept of genealogical concordance phylogenetic species recognition (GCPSR) (Taylor et al. 2000), a later study based on portions of 11 genes, identified nine distinct phylogenetic species within the morphospecies *F. graminearum sensu lato*, and the eight newly discovered species were formally described (O’Donnell et al. 2004). Subsequently, six additional species were discovered and described; however, a singleton phylospecies from soil in Umyaka, South Africa, represented by NRRL 34461 *Fusarium* sp., remains unnamed. Morphological differences among species within the FGSC are either nonexistent or too subtle to be used to accurately identify these species (O’Donnell et al. 2008; Sarver et al. 2011; Starkey et al. 2007; Yli-Mattila et al. 2009). These and other studies have also investigated the toxigenic profile (chemotype) of isolates using genetic markers and chemical analyses. Within the FGSC, differences in trichothecene chemotype are encoded by interacting balanced polymorphisms at both ends of the TRI biosynthetic gene cluster (Alexander et al. 2011; Kimura et al. 2003; Lee et al. 2002; Ward et al. 2002) and by differences in the unlinked *TriI* gene (Varga et al. 2015). This genetic variation has

been exploited for the development of PCR primers (Lee et al. 2001; Liang et al. 2014; Nielsen et al. 2012; Pasquali and Migheli 2014; Ward et al. 2002) or Luminex probes (Garmendia et al. 2018; Sarver et al. 2011; Ward et al. 2008) for genotyping to predict the type of trichothecene produced by individual isolates.

Recently, two reviews were published focusing on the systematics, occurrence, and distribution of species and chemotypes of the FGSC (Aoki et al. 2012; van der Lee et al. 2015). Two quantitative reviews on the distribution of FGSC have also been published, but these are limited in the geographic coverage and species included. The first summarizes occurrence and spatial distribution within the FGSC and *Fusarium culmorum*, with an associated database of chemotype diversity, but is restricted to strains isolated from cereals in several countries in Europe (Pasquali et al. 2016). In the second review, the focus was on how climate might affect the occurrence and distribution of three members of the FGSC members, *F. graminearum sensu stricto* (hereafter *F. graminearum*), *Fusarium asiaticum*, and *Fusarium boothii* (Backhouse 2014).

In this study, we conducted a systematic analysis of the peer-reviewed literature to summarize and map the global distribution of FGSC species and associated trichothecene chemotypes. The specific objectives were to (i) screen the literature since 2000 and organize a database of peer-reviewed studies within which members of the FGSC were identified; (ii) conduct a bibliographic and authorship network analysis; (iii) collect strain ID data and metadata at both the strain and study (summary of frequency) level; (iv) summarize trends in the identification methods and distribution of species and chemotypes by geography, host, and year; and (v) build an online dashboard for searching and visualizing publication and strain data from the database. The database and interactive interface are publicly available (<https://fgsc.netlify.app>) allowing for searches, summarization, and mapping of strains according to several criteria including article, country, host, species, and trichothecene genotype. The database will be updated as new articles are published with the expectation that it will be useful for guiding future surveys and exploring factors associated with species distribution such as climate and land use. Authors are encouraged to submit data at the strain level to the database.

MATERIALS AND METHODS

Literature search and data gathering for the databases. Since 2017, we have been conducting bibliographic searches across three major databases (Google Scholar, Scopus, and Web of Science) using the following keywords: “FGSC” and “*Fusarium graminearum* species complex.” To facilitate the task, a “Google Alert” was employed

using these keywords, so that automatic messages were sent each time a study containing either of these keywords was published.

Titles and abstracts of the search results were examined, and when these suggested that the strains had been identified to the species level by sequence-based molecular methods, the main text was further scrutinized. Several associated metadata were collected from each selected publication, and each was added to one or two separate databases (maintained as online Google spreadsheets): 1) a spreadsheet named “FGSC publication database,” which contained all metadata of bibliographic information as well as the number and identity of FGSC strains and hosts; and 2) a spreadsheet named “FGSC isolate database,” which included year, geographic location (municipality, state/province, country), latitude, longitude, and host sampled, and the species and trichothecene chemotype (toxin production using chemical methods) or genotype (toxigenic potential using molecular assays targeting *TRI* genes) together with the respective method utilized. The overall workflow for gathering of data for the two databases is presented in Fig. 1.

Data description and summary. Metadata were described with summary statistics, tables, graphs, and maps to display absolute numbers and relative frequencies for several categorical and numerical variables (see metadata of the two databases in Fig. 1). A multiple correspondence analysis (MCA) was performed, given that the nature of multiple variables describing the isolates was nominal, to detect and represent underlying structure in the strain database (Hjellbrekke 2018).

Scholarly and country network analysis of article database. A scholarly collaborative network analysis was used to detect connections among authors and identify research communities (Kolaczyk and Csárdi 2020). Authors on the same publication (coauthors) were grouped together and linked to other publications

whenever authorship was shared. Each author is considered a “node” in the network, and the connections between them are the “edges” (or links). Several statistics were used in this analysis including community detection (group of authors), network transitivity (the odds of two scholars sharing a common collaborator), node degree (number of connections for a single author), and betweenness (individuals who influence the flow around a system) (Kolaczyk and Csárdi 2020). The same analysis was conducted using countries as nodes. The Walktrap method, in which short random walks tend to stay in the same community, was used to detect communities in the network graphs, which were represented by different colors. The network analysis was performed in R using the *igraph* package (Csárdi and Nepusz 2006).

RESULTS

Peer-reviewed article database. Bibliographic analysis. Scrutiny of the literature yielded 123 peer-reviewed publications that reported phylogenetic species within the FGSC (Supplementary Table S1). The earliest publications included the foundational phylogeographic study by O’Donnell et al. (2000) identifying seven distinct species within the FGSC, identification of an eighth phylogenetic species within this complex and demonstration that trichothecene chemotype diversity had been maintained by selection throughout the evolution of the FGSC and related species (Ward et al. 2002), and the first formal description of seven unnamed members of the FGSC and assignment of species names with *F. graminearum* retained for the most common species within Europe and North America, the continents where *F. graminearum* and *Gibberella zeae*, respectively, were formally described (O’Donnell

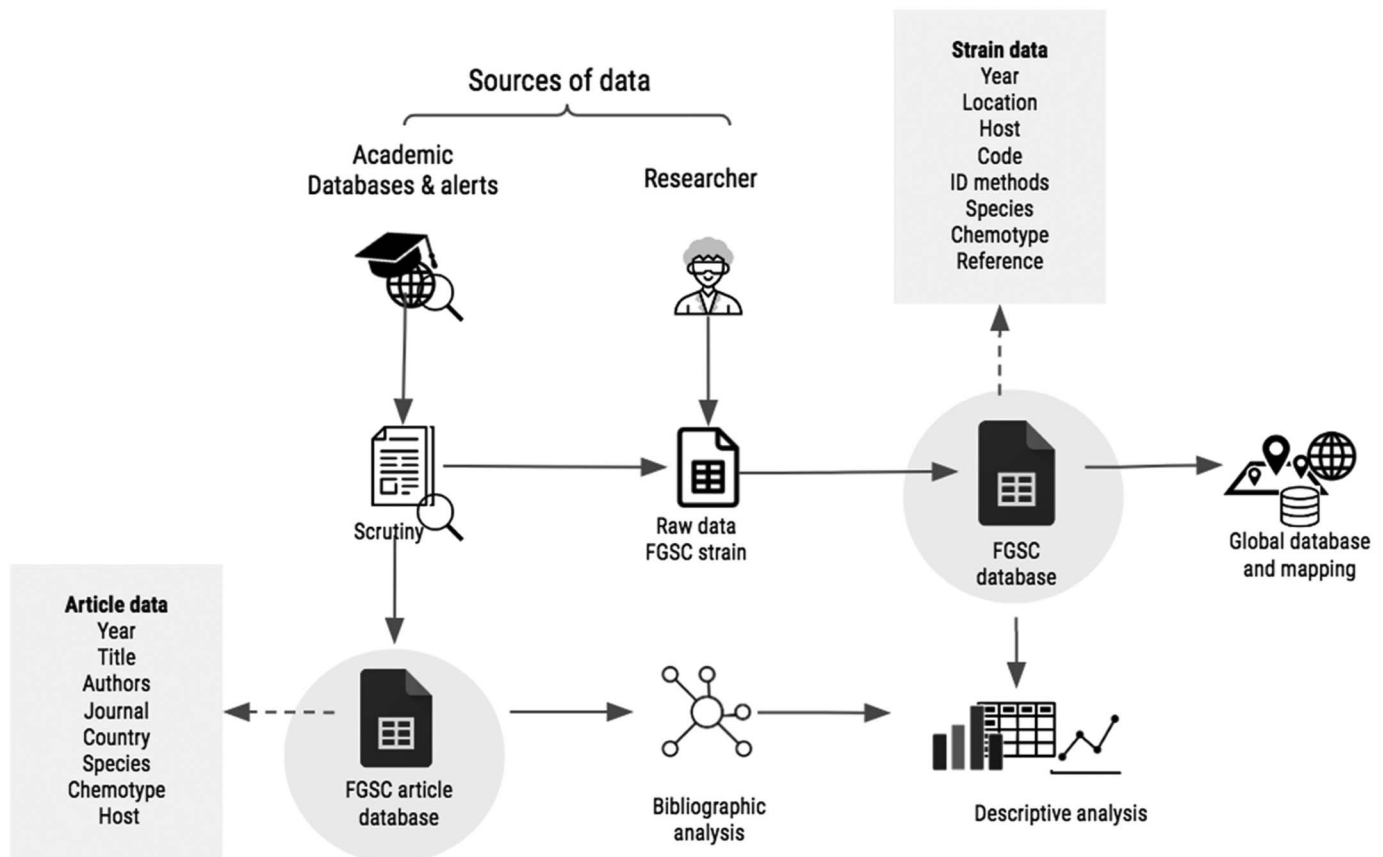


FIGURE 1

General workflow for compiling data on bibliographic references and strains of *Fusarium graminearum* species complex for further analysis and development of a global database for mapping, which is accessible at <https://fgsc.netlify.app>.

publication ranged from three to nine, with a median of eight authors. Twelve researchers authored at least six articles, while four researchers authored at least 10 articles (data not shown).

The authorship network positioned the most prolific (degree of 190) and influential (betweenness = 0.31) researcher in the central position (largest node) (Ward, TJ; Fig. 5). Six additional highly influential researchers had betweenness values of at least 0.035. The authorship network highlighted 14 authors (largest nodes) who collaborated with at least 38 individuals (degree), and who are centrally located and highly connected to other larger communities, identified by color. The probability that two authors with a common coauthor were themselves coauthors (transitivity) was 0.473. The subgraphs depict communities that are mostly grouped by country, as expected. The largest of these included the U.S. community (Ward, O'Donnell, Kistler, Gale); Dutch (Waalwijk, van der Lee) and Chinese researchers (Zhang, Feng); South Korea (Lee, Choi); China (Chen); Brazil (Del Ponte); and Argentina (Chulze). Twenty-three of 123 single studies formed isolated, small clusters (see the outer edge of the network) representing authors who did not publish with authors from the other studies.

FGSC species and chemotypes by publication. A total of 26,644 isolates identified to species level were reported by the 123 peer-reviewed studies. The number of strains per study ranged from one (Dong et al. 2020) to 4,062 from a continent-wide survey (Kelly et al. 2015). The mean number of strains per study was 218.4, but half of the studies included at least 62 strains (median).

The dominant species was *F. graminearum*, reported in 106 studies. Five other species appeared in at least eight studies: *F. asiaticum* (47 studies), *Fusarium meridionale* (36), *F. boothii* (20), *Fusarium cortaderiae* (18) and *Fusarium austroamericanum* (9). Ten additional species were each reported in at least one study.

Trichothecene chemotype diversity varied across the FGSC, with chemotype polymorphism observed in some species while others appear to be fixed for a specific trichothecene type. For example, *F. graminearum* and *F. asiaticum* were segregating for all three type B trichothecene chemotypes. The most prevalent was DON/15-ADON ($n = 84$ studies), followed by DON/3-ADON ($n = 41$) and NIV ($n = 23$). Two studies reported the presence of a DON/NIV chemotype in *F. graminearum*. In *F. asiaticum*, the NIV type was reported in 35/47 studies, followed by DON/3-ADON ($n = 21$ studies), and DON/15-ADON ($n = 10$ studies). Five of the six FGSC are segregating for NIV and 3-ADON. *F. meridionale* was the only species segregating for NIV and 15-ADON, but the 15-ADON type was found in just one isolate (Del Ponte et al. 2015). However, the

NIV chemotype was reported in 28 of the 35 *F. meridionale* studies. Despite being reported in 20 studies, *F. boothii* appears to be fixed for the 15-ADON chemotype. More recently, the type A trichothecene NX-3 and its 3-acetyl derivative, NX-2 were reported ($n = 4$ studies) in *F. graminearum* from North America.

Cereal hosts by publication. A total of 45 hosts were included in the 123 studies. The top six hosts sampled were wheat ($n = 71$ studies), maize ($n = 33$), barley ($n = 29$), rice ($n = 12$), soybean ($n = 8$), and oats ($n = 6$). Other hosts were included in fewer than three publications each, with 30 represented by a single report.

Summary of the FGSC strain database. Strains by country. Strains associated with geographical information ($n = 16,274$), either provided as raw data or extracted from the publications, were sampled across six continents and 32 countries (Fig. 6). The majority (>10,000 strains) were obtained from cereal crops grown in the Americas (Canada, Brazil, and the United States) and in China. In Europe, the most sampled countries (>100 strains) were France, The Netherlands, and Norway. In Asia, aside from China, the most sampled countries (>100 strains) were Japan and South Korea. The only study from Africa that included >100 strains was from South Africa (560 strains) (Boutigny et al. 2011).

Methodology for species and chemotype identification. Morphological characters have proven to be inadequate for the identification of individual species within the FGSC (Aoki et al. 2012). As such, species identifications are performed using a variety of DNA-based methods. Analyses of DNA sequences from individual genes represents the gold standard for identifying individual isolates to species level within the FGSC. Unfortunately, many of the sequences available in the GenBank database are associated with inaccurate species information and may be misleading (O'Donnell et al. 2015). To address this, the *FUSARIUM-ID* (<http://isolate.fusariumdb.org/blast.php>) and *Fusarium MLST* (<https://fusarium.mycobank.org>) databases of curated DNA sequence data, primarily from translation elongation factor 1- α (*TEF1*) and the DNA-directed RNA polymerase II largest (*RPB1*) and second largest subunit (*RPB2*), were developed to facilitate identification of the FGSC and other fusaria via BLASTn queries. A primer for conducting and interpreting the results of such analyses was provided by O'Donnell et al. (2015). However, targeted sequencing of individual genes and associated analyses can be relatively laborious and has been used to identify 11% ($n = 1,807$) of the FGSC isolates included in the studies analyzed here.

Some studies employed multiple methods to identify species within the FGSC, but most of the strains were identified using a multilocus

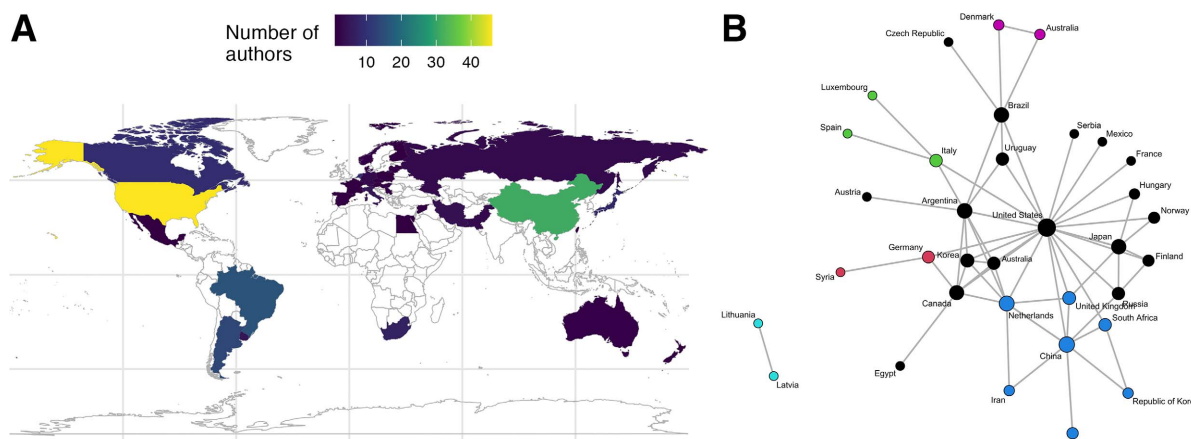


FIGURE 4

A, Global map depicting the number of authors per country of origin. **B**, Network graph depicting countries as nodes and subgraphs (represented by different colors of the nodes) as communities of countries. These were defined using a Walktrap method (in which short random walks tend to stay in the same community). The data represents 121 peer-reviewed studies reporting species and chemotypes of the *Fusarium graminearum* species complex sampled across several hosts and published between 2000 and 2021.

genotyping assay (MLGT) employing a Luminex flow cytometer ($n = 12,317$ strains; 75.6%). This extensively validated and high-throughput method relies on probes targeting nucleotide variation within multiple genes to simultaneously determine the species identity and trichothecene chemotype of isolates (Ward et al. 2008). The MLGT method has also enabled the discovery of novel FGSC and *F. graminearum* Clade species (sensu Laraba et al. 2021) and interspecific hybrids (Boutigny et al. 2011, 2014; Pereira et al. 2018; Sarver et al. 2011). A smaller number of studies have employed fragment analysis of polymorphic markers (RFLP, AFLP or ISSR; $n = 1,686$;

10.3%), and polymerase chain reaction (PCR) with species-specific primers (e.g., Fg16; $n = 1,427$; 8.7%).

Genotype analysis was the most common method for assessing the trichothecene type of individual strains. The MLGT method was most frequently used ($n = 11,032$ strains; 67.8%), followed by chemotype-specific PCR primers targeting at least one of the TRI genes ($n = 4,103$ strains; 10.3%). The recent discovery of a relatively small number of *F. graminearum* isolates producing NX-2 and related type A trichothecenes represents variation that was not accounted for in the original design of many genotype-based

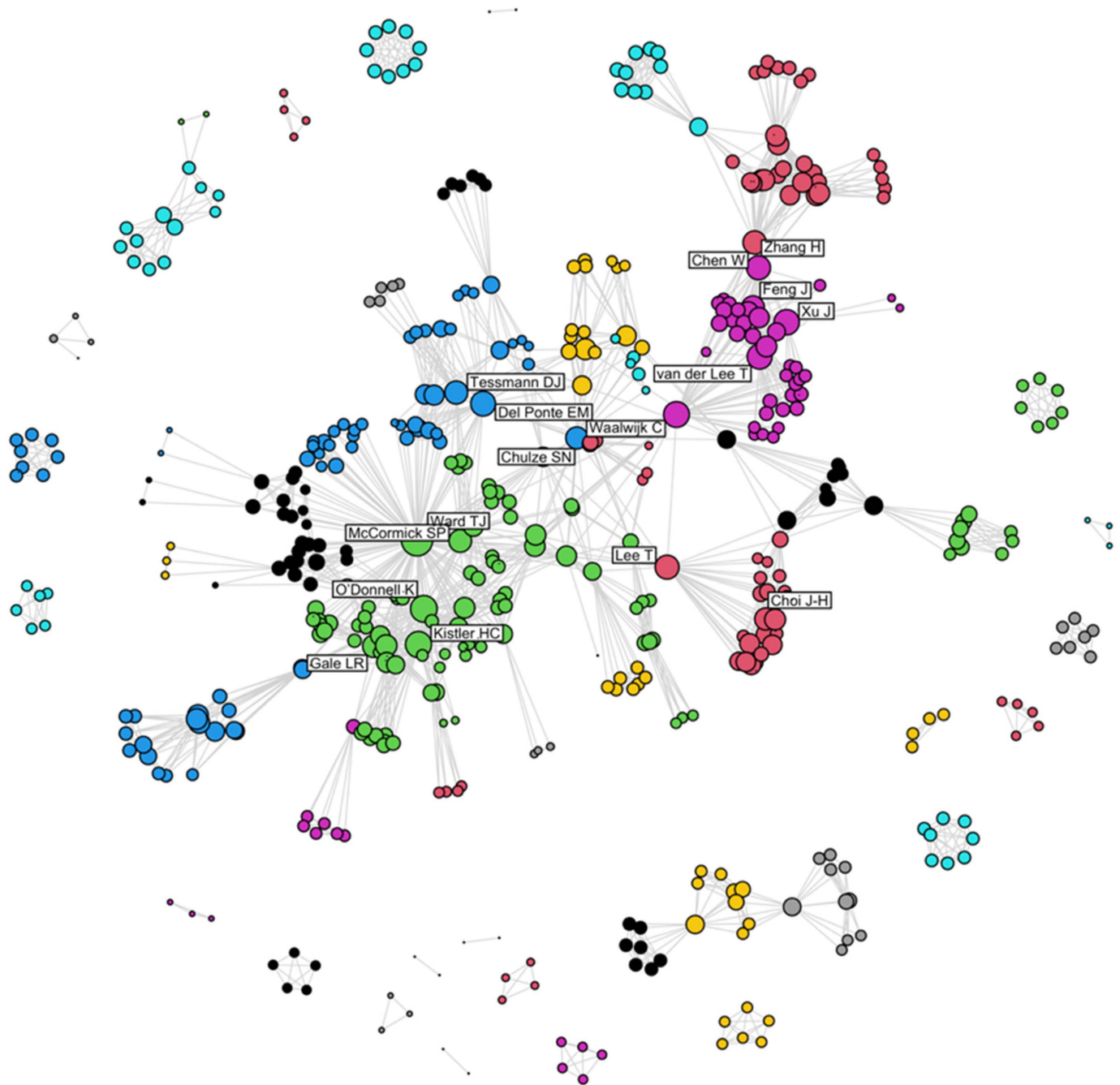


FIGURE 5

Network graph depicting authors as nodes and subgraphs (represented by different colors of the nodes) as communities of authors. These were defined using a Walktrap method in which short random walks tend to stay in the same community. The communities are highly connected due to shared authorship of 123 studies reporting species and chemotypes of *Fusarium graminearum* species complex (FGSC) isolates sampled across several hosts published between 2000 and 2021. Larger nodes are labeled with the names of authors with more than 37 connections (coauthors).

methods. A PCR-RFLP approach targeting *TRII* was developed to distinguish NX-2 from the 3-ADON chemotype (Liang et al. 2014), and the MLGT assay was subsequently upgraded to differentiate these chemotypes as well (Garmendia et al. 2018).

Chemical analyses can be used to document the actual production of trichothecene metabolites or the relative amounts of different trichothecenes that may be produced by an isolate under specific conditions. However, their application has been limited by cost and availability. Analytical chemistry was used to determine trichothecene toxin production in 1,286 strains (~8% of the strains). The most common method was chromatography (e.g., high-performance liquid chromatography, gas chromatography-mass spectrometry, liquid chromatography-mass spectrometry), which was used to chemotype 1,099 strains (85%).

Strains by host. The most sampled hosts, with at least 801 strains recovered from each, were four commercially grown cereal crops: wheat ($n = 12,233$ strains, 75.1%), maize ($n = 1,706$, 10.5%), barley ($n = 980$, 6%), and rice ($n = 801$ strains, 4.9%). Fewer than 90 strains were obtained from oats ($n = 89$, 0.54%), and soybean ($n = 77$, 0.47%). Fewer than 26 strains (0.15%) were recovered from the other hosts (cereal and noncereals). The host of origin was not reported for 201 strains.

Strains by FGSC species. Within the whole collection of characterized strains ($n = 16,274$), *F. graminearum* was dominant, with 11,760 strains (72.2%), followed by *F. asiaticum* ($n = 3,052$, 18.7%), *F. meridionale* ($n = 816$; 5%), *F. boothii* ($n = 279$; 1.7%), *F. cortaderiae* ($n = 201$; 1.3%) and *F. austroamericanum* ($n = 50$, 0.3%). The following species were represented by 10 to 50 strains each: *Fusarium nepalense* ($n = 41$), *Fusarium aethiopicum* ($n = 22$), *Fusarium vorosii* ($n = 16$), *Fusarium ussuriense* ($n = 12$), and *Fusarium acaciae-mearnsii* ($n = 10$). Finally, species with less than 10 strains were *Fusarium brasiliense* ($n = 5$ strains), *F. boothii* × *F. graminearum* hybrid ($n = 3$), *Fusarium gerlachii* ($n = 3$), *Fusarium louisianense* ($n = 2$), and *Fusarium mesoamericanum* ($n = 2$).

Strains by chemotypes. Among the three most frequent chemotypes, DON/15-ADON was dominant ($n = 9,067$ strains) followed by DON/3-ADON ($n = 3,475$) and NIV ($n = 2,437$). Other less frequently chemotypes, as reported, were: DON ($n = 39$), NX2 ($n = 36$), DON/NIV ($n = 18$), NX2/3ADON ($n = 5$), and 4,15-diANIV ($n = 2$).

Strains by host × species × chemotypes. The MCA was conducted to depict associations among the four most sampled hosts, six most represented species, and three most frequent chemotypes, totaling 14,393 strains. The MCA map confirmed the close associations between these levels and factors. The first and second dimensions retained a modest proportion of 37.1% (16.7% + 20.4%) of the total inertia (variation) contained in the data. This was similar to the result when each factor was analyzed separately, but the MCA more clearly connected the host with the species, and the species with the chemotypes. For example, *F. graminearum*, a species composed primarily of the DON/15-ADON chemotype, clustered more with wheat and barley than with the other crops. *F. asiaticum*, which was more commonly NIV or 3-ADON, was more closely related to rice. *F. meridionale* (NIV chemotype) and *F. boothii* (15-ADON chemotype) were more closely associated with maize. *F. austroamericanum*, found mainly in wheat and barley, was represented primarily by the 3-ADON chemotype.

Global mapping of species and trichothecene toxin chemotypes.

The global species composition appeared to be structured by region and host of origin. For example, *F. meridionale* was most prevalent in the lower latitudes of South America (associated with maize) and also in central-south region of China (Fig. 7A). *F. graminearum* was the most frequent species globally and was recovered across a wide range of latitudes. *F. boothii* was found primarily in South Africa, México, Argentina, and north Asia, with scattered incidence across other continents. *F. asiaticum* was most prevalent in Asia but has also been reported on rice and wheat in South America and wheat in a major rice-growing region of North America (Fig. 8).

DISCUSSION

We conducted a systematic analysis of peer-reviewed studies reporting on species within the FGSC. After a comprehensive and quantitative analysis of the literature, we have summarized the past 20 years of research on FGSC strains isolated from cereal and non-cereal hosts worldwide. Our study updates and complements a recent review of the global composition and spatial distribution of FGSC (van der Lee et al. 2015). Collectively, the studies included

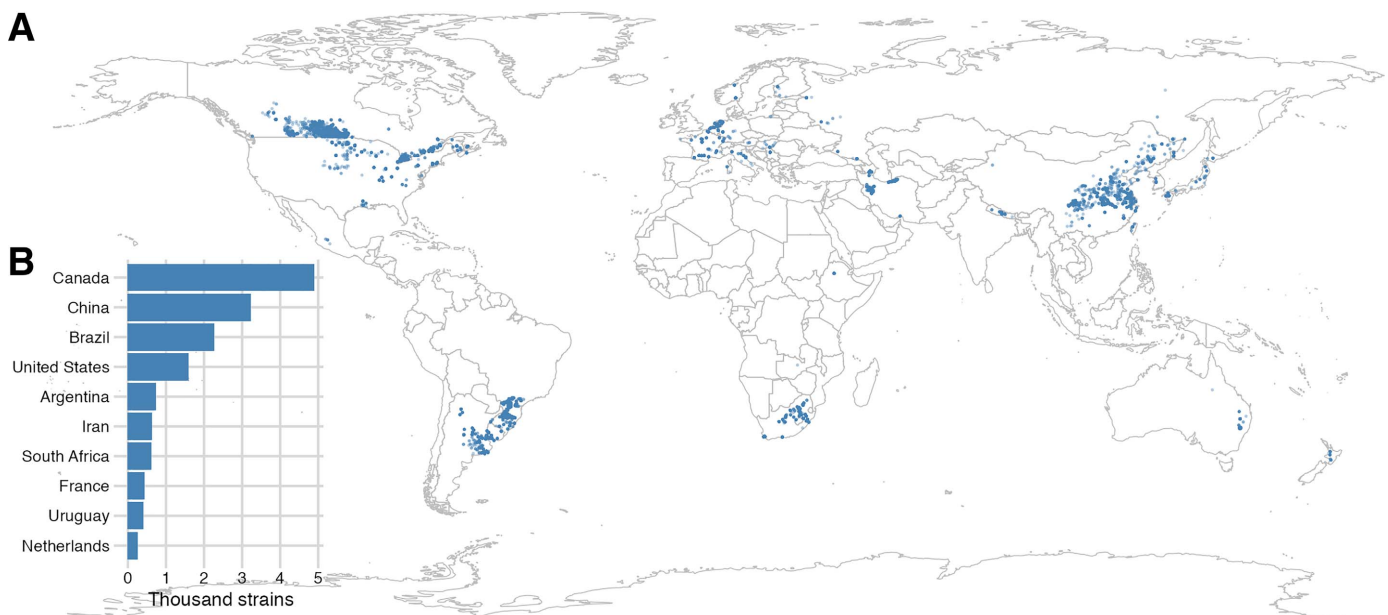


FIGURE 6

A, Global distribution of 16,274 *Fusarium graminearum* complex strains identified to species using molecular methods. These were reported in 123 peer-reviewed studies published in 30 journals from 2000 to 2021. **B**, The map represents the number of strains in the top 10 most sampled countries.

here provide a broad geographic assessment of FGSC species and chemotype diversity from different crops/substrates. The extent to which FGSC diversity was incorporated into the design and validation of different typing methods should be considered when interpreting the results of individual studies.

FGSC research during the past two decades can be divided into two phases. The first phase was characterized by the discovery that the morphospecies *F. graminearum* comprises at least 16 phylogenetic species, and development of tools to facilitate identification of these species and their trichothecene genotypes. It should be noted that four species basal to the FGSC, in what is now recognized as the Graminearum Clade (Laraba et al. 2021), were discovered and described during roughly the same period. These included *Fusarium pseudograminearum*, which was previously discovered and/or described as the group 1 population of *F. graminearum* (Aoki and O'Donnell 1999), *Fusarium dactylidis* from orchard grass in Oregon and New Zealand (Aoki et al. 2015), *Fusarium praegraminearum* from maize field litter in New Zealand (Gräfenhan et al. 2016), and *Fusarium subtropicale* from barley in Brazil (Pereira et al. 2018). During the second phase, these advancements were widely adopted, including use of binomials for the phylopecies and genotyping tools for large-scale surveys, leading to a rapid rise in the number of studies published each year. Some of this increase was related to wider availability of cost-effective methods for species identification and chemotyping. More intensive within-continent and cross-continent scientific cooperation, led by research groups from North America and Europe that appear as major nodes in our network analysis, also played an important role. Strengthened global collaborations have facilitated the extension and expansion of surveys to crops other than wheat and barley, including maize and rice. There has also been an expansion in regional surveys in previously underrepresented areas, and these efforts have dramatically increased the number of peer-review studies assessing FGSC species and chemotype diversity over the past 10 years.

Overall, the research included in the present study was published in more than 40 journals with a broad range of impact factors and target audiences. This was likely driven by an interest in delivering information at more regional or local levels, and by close connections with a range of fields including mycotoxicology, plant

pathology, mycology, and food microbiology. Expanded collaboration among groups worldwide, particularly during the last decade, has increased the number of studies published in international journals with a more global audience, mainly in the field of plant pathology. One-third of the papers appeared in four journals published by international plant pathology professional societies.

The present review highlights two interesting points regarding FGSC species diversity. First, no novel member of the FGSC has been discovered since the study by Sarver et al. (2011), despite the several thousands of strains that were molecularly identified. Second, 11 of the 16 species comprise only 1.3% of all strains in the database. The available data suggests that the 11 less commonly collected species may be restricted in their geographic distribution and/or host, and further documentation of their distribution should be made based on pathogen surveys rather than speculation.

It is apparent that host is an important driver of the regional composition of FGSC species. Sampling to date has been conducted primarily in commercial cereal fields where a few species are globally dominant. The most common FGSC species in the surveys, *F. graminearum*, was distributed worldwide on wheat and other cereals. However, *F. asiaticum* appears to be better adapted to rice agroecosystems and is the most common member of the FGSC on rice in Asia (Lee et al. 2010), but also in other crops in some parts of Asia including barley (Yang et al. 2008) and wheat (Zhang et al. 2012), depending on the crop rotation. More recently, *F. asiaticum* was found to be the dominant species on rice in South America (Gomes et al. 2015) and has also been observed on wheat in rice production regions of the United States (Gale et al. 2011) and Uruguay (Umpiérrez-Failache et al. 2013). Similarly, *F. meridionale* was more prevalent than *F. graminearum* on maize and rice in South America, and *F. boothii* was dominant on South African maize (Boutigny et al. 2011). The reasons for the observed variation in species dominance are not entirely clear, but recent studies have suggested that differences in aggressiveness among the species may play a role (Machado et al. 2021).

Higher FGSC species diversity was found in wheat crops grown at lower latitudes, near to or within subtropical environments (Pereira et al. 2021; Umpiérrez-Failache et al. 2013). This suggests that there is also an effect of climate in shaping species distributions, as posited previously by a modeling study (Backhouse 2014). For

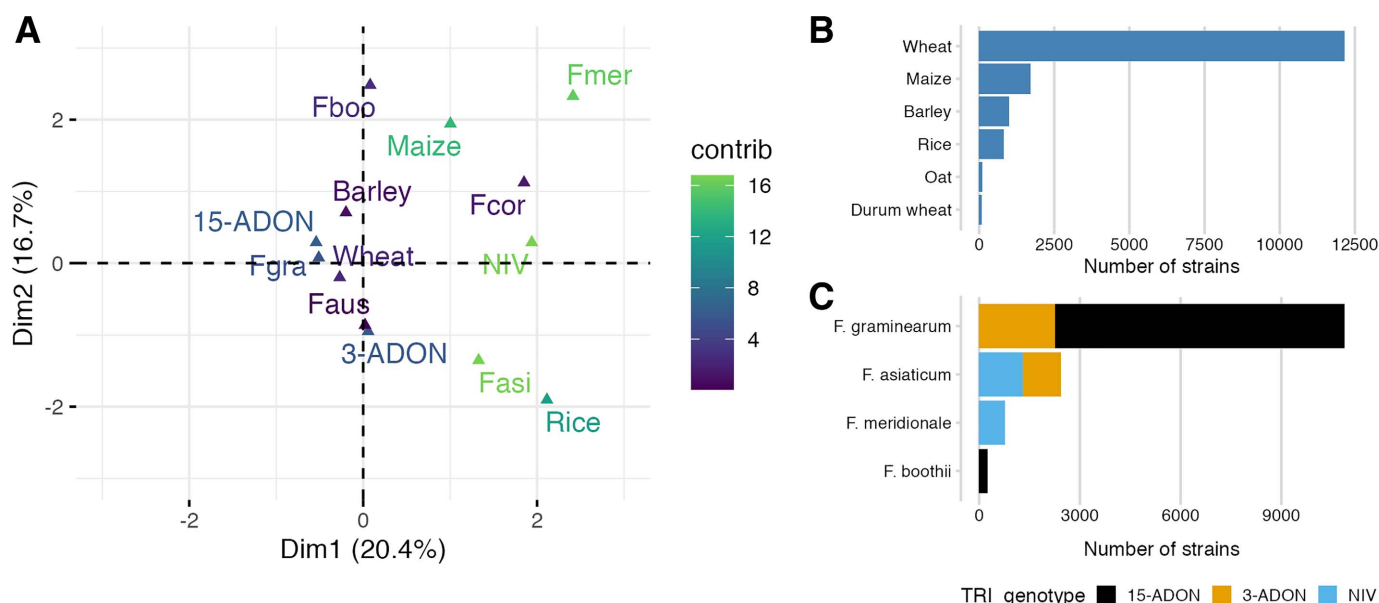


FIGURE 7

A, Multiple correspondence analysis plot depicting association among variables representing cereal hosts, *Fusarium graminearum* species complex species, and trichothecene chemotypes (sample size = 14,393 strains). The number of **B**, strains per host and **C**, species are shown.

example, although members of the FGSC can be found in the tropics, a drier environment during the season limits disease occurrence, which, in turn, decreases inoculum availability. However, this can be easily confounded with the effect of different host species, which is also dependent on climate. It appears that a small group of minor species including *F. meridionale*, *F. boothii*, and *F. cortaderiae* are more frequent in subtropical conditions where there is an abundance of other grasses year-round. A study in Brazil that surveyed a relatively small collection of FGSC in annual ryegrass showed an increased frequency of these minor species in comparison with their composition on major crops like wheat (Machado et al. 2015). A recent study in the United States reported FGSC as endophytes in several wild grasses, but the phylogenetic species were not identified (Lofgren et al. 2018).

Among the three main chemotypes from global surveys, 15-ADON represented more than half of the strains, while 3-ADON and NIV were less frequent and restricted in distribution (Fig. 9). The 3-ADON chemotype prevailed at higher latitudes, while NIV was more frequent at lower ones, as suggested by our global map. Whether these species have different requirements of temperature is not entirely clear, as it is

difficult to disentangle a triple interaction effect that includes climate, host, and fungal species that shape chemotype composition. Additional global surveys are needed to address whether some of the rarely collected species are fixed for a specific chemotype. Relative chemotype frequencies in *F. graminearum* and *F. asiaticum*, which are segregating for all three trichothecene toxin chemotypes globally, appear to be shaped by region-specific factors. However, changes in chemotype frequency can change rapidly as evidenced by the introduction and spread of a nonnative 3-ADON population in North America (Ward et al. 2008).

As further steps in research, we suggest that results of the pathogen and trichothecene toxin surveys need to be translational with the goal of providing plant disease specialists with critical information needed to employ effective plant disease strategies and inform plant breeder's efforts focused on developing cultivars with broad-based resistance to the spectrum of FGSC species present in a specific area. Knowledge that some FGSC species are more competitive, on a particular cereal than others, should be used by genome biologists to identify host-specific virulence factors, and QTLs in the host to breed more resistant cultivars.

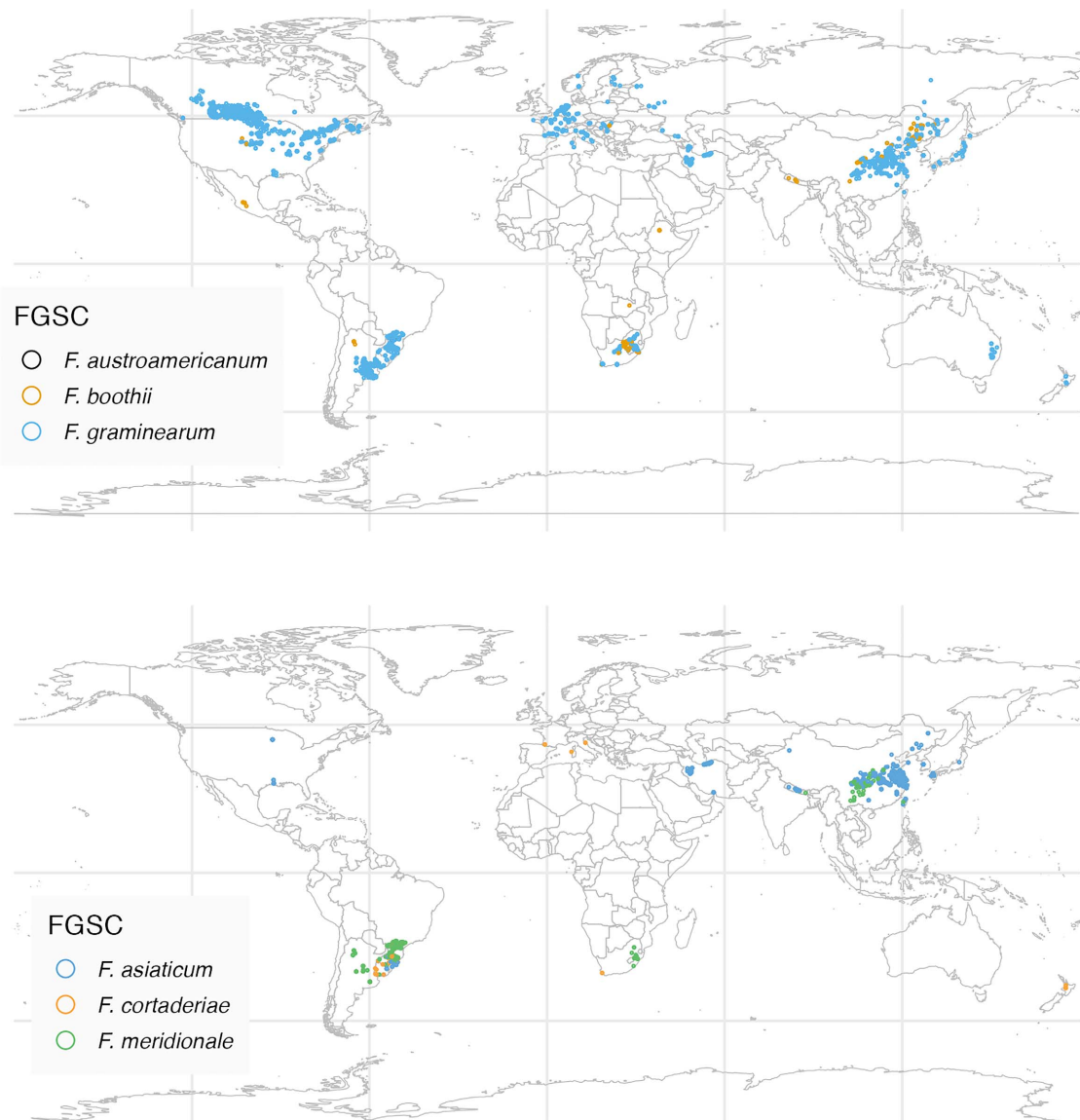
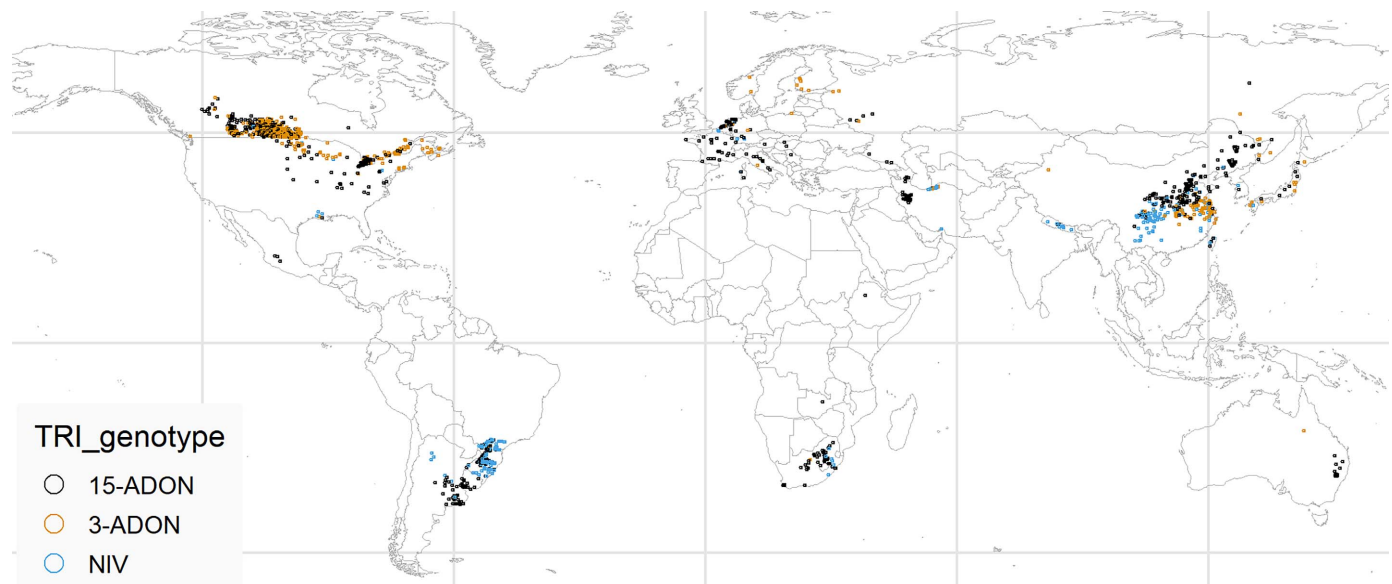


FIGURE 8

Global distribution of the six most prevalent species of the *Fusarium graminearum* species complex. The geolocations of 16,158 of 16,274 strains of these six species were obtained from authors or extracted from studies published in 121 scientific journals between 2000 and 2021.

**FIGURE 9**

Global distribution of the three most prevalent tricothecene chemotypes (15-ADON, 15-acetyl deoxynivalenol; 3-ADON, 3-acetyl deoxynivalenol; and NIV, nivalenol) identified for 14,979 strains of 15,274 with geolocation data. The chemotype data were obtained from authors or extracted from studies of *Fusarium graminearum* complex species isolated from a range of hosts reported in studies published between 2000 and 2021.

An important outcome of the present research is a website (<https://fgsc.netlify.app>) that facilitates searching, visualization, and downloading of data and reports in both tabular and graphic format. The system is composed of three main views (grid, map, and chart), all of which allow for interactive navigation, searching, and selection of data for display. For example, data filtered or searched for in the grid view can be downloaded in csv or xlsx format, and screenshots can be taken from the maps and plots. All website content (data and summaries) can be downloaded and used freely according to a Creative Commons Attribution 4.0 International (CC BY 4.0). The database will be updated as more papers are published, and we encourage all members of the research community to deposit raw data from their prior and future work on the topic following instructions on the website, which is an online spreadsheet of the web-based Google Docs Editor Suite.

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Mention of trade names or commercial products in this article is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture (USDA). USDA is an equal opportunity provider and employer. All data and R scripts generated for the analysis of the data and production of the figures are publicly available at <https://github.com/emdelponete/paper-FGSC-database>.

LITERATURE CITED

- Alexander, N. J., McCormick, S. P., Waalwijk, C., van der Lee, T., and Proctor, R. H. 2011. The genetic basis for 3-ADON and 15-ADON tricothecene chemotypes in *Fusarium*. *Fungal Genet. Biol.* 48:485-495.
- Aoki, T., and O'Donnell, K. 1999. Morphological and molecular characterization of *Fusarium pseudograminearum* sp. nov., formerly recognized as the Group 1 population of *F. graminearum*. *Mycologia* 91:597-609.
- Aoki, T., Vaughan, M. M., McCormick, S. P., Busman, M., Ward, T. J., Kelly, A., and O'Donnell, K. 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* 107:409-418.
- Aoki, T., Ward, T. J., Kistler, H. C., and O'Donnell, K. 2012. Systematics, phylogeny and tricothecene mycotoxin potential of *Fusarium* head blight cereal pathogens. *JSM Mycotoxins* 62:91-102.
- Backhouse, D. 2014. Global distribution of *Fusarium graminearum*, *F. asiaticum* and *F. boothii* from wheat in relation to climate. *Eur. J. Plant Pathol.* 139:161-173.
- Boutigny, A.-L., Ward, T. J., Ballois, N., Iancu, G., and Ioos, R. 2014. Diversity of the *Fusarium graminearum* species complex on French cereals. *Eur. J. Plant Pathol.* 138:133-148.
- Boutigny, A.-L., Ward, T. J., Van Collier, G. J., Flett, B., Lamprecht, S. C., O'Donnell, K., and 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.* 48:914-920.
- Chen, Y., Kistler, H. C., and Ma, Z. 2019. *Fusarium graminearum* tricothecene mycotoxins: Biosynthesis, regulation, and management. *Annu. Rev. Phytopathol.* 57:15-39.
- Cowger, C., Smith, J., Boos, D., Bradley, C. A., Ransom, J., and Bergstrom, G. C. 2020. Managing a destructive, episodic crop disease: A national survey of wheat and barley growers' experience with *Fusarium* head blight. *Plant Dis.* 104:634-648.
- Csárdi, G., and Nepusz, T. 2006. The igraph software package for complex network research. *InterJournal Complex Systems* 1695:1-9.
- D'Mello, J. P. F., Placinta, C. M., and Macdonald, A. M. C. 1999. *Fusarium* mycotoxins: A review of global implications for animal health, welfare and productivity. *Anim. Feed Sci. Technol.* 80:183-205.
- Dean, R., Kan, J. A. L. V., Pretorius, Z. A., Hammond-Kosack, K. E., Pietro, A. D., Spanu, P. D., Rudd, J. J., Dickman, M., Kahmann, R., Ellis, J., and Foster, G. D. 2012. The top 10 fungal pathogens in molecular plant pathology. *Mol. Plant Pathol.* 13:414-430.
- Del Ponte, E. M., Spolti, P., Ward, T. J., Gomes, L. B., Nicolli, C. P., Kuhnem, P. R., Silva, C. N., and Tessmann, D. J. 2015. Regional and field-specific factors affect the composition of *Fusarium* head blight pathogens in subtropical no-till wheat agroecosystem of Brazil. *Phytopathology* 105:246-254.
- Dong, F., Xu, J. H., Shi, J. R., Mokoena, M. P., Olaniran, A. O., Chen, X. Y., and Lee, Y. W. 2020. First report of *Fusarium* head blight caused by *Fusarium meridionale* in rice in China. *Plant Dis.* 104:2726.
- Duffeck, M. R., Alves, K. S., Machado, F. J., Esker, P. D., and Del Ponte, E. M. 2020. Modeling yield losses and fungicide profitability for managing *Fusarium* head blight in Brazilian spring wheat. *Phytopathology* 110:370-378.
- Gale, L. R., Harrison, S. A., Ward, T. J., O'Donnell, K., Milus, E. A., Gale, S. W., and Kistler, H. C. 2011. Nivalenol-type populations of *Fusarium graminearum* and *F. asiaticum* are prevalent on wheat in southern Louisiana. *Phytopathology* 101:124-134.
- Garmendia, G., Pattarino, L., Negrin, C., Martínez-Silveria, A., Pereyra, S., Ward, T. J., and Vero, S. 2018. Species composition, toxigenic potential and aggressiveness of *Fusarium* isolates causing Head Blight of barley in Uruguay. *Food Microbiol.* 76:426-433.

- Gomes, L. B., Ward, T. J., Badiale-Furlong, E., and Del Ponte, E. M. 2015. Species composition, toxigenic potential and pathogenicity of *Fusarium graminearum* species complex isolates from southern Brazilian rice. *Plant Pathol.* 64:980-987.
- Goswami, R. S., and Kistler, H. C. 2004. Heading for disaster: *Fusarium graminearum* on cereal crops. *Mol. Plant Pathol.* 5:515-525.
- Gräfenhan, T., Johnston, P. R., Vaughan, M. M., McCormick, S. P., Proctor, R. H., Busman, M., Ward, T. J., and O'Donnell, K. 2016. *Fusarium praegraminearum* sp. nov., a novel nivalenol mycotoxin-producing pathogen from New Zealand can induce head blight on wheat. *Mycologia* 108:1229-1239.
- Hjellbrekke, J. 2018. Multiple Correspondence Analysis for the Social Sciences. Routledge.
- Kelly, A. C., Clear, R. M., O'Donnell, K., McCormick, S., Turkington, T. K., Tekauz, A., Gilbert, J., Kistler, H. C., Busman, M., and Ward, T. J. 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.
- Kimura, M., Tokai, T., O'Donnell, K., Ward, T. J., Fujimura, M., Hamamoto, H., Shibata, T., and Yamaguchi, I. 2003. The trichothecene biosynthesis gene cluster of *Fusarium graminearum* F15 contains a limited number of essential pathway genes and expressed non-essential genes. *FEBS Lett.* 539:105-110.
- Kolaczyk, E. D., and Csárdi, G. 2020. Statistical Analysis of Network Data with R. Springer-Verlag, New York.
- Laraba, I., McCormick, S. P., Vaughan, M. M., Geiser, D. M., and O'Donnell, K. 2021. Phylogenetic diversity, trichothecene potential, and pathogenicity within *Fusarium sambucinum* species complex. *PLoS One* 16:e0245037. Erratum in: *PLoS One* 16:e0250812.
- Lee, S.-H., Lee, J.-K., Nam, Y.-J., Lee, S.-H., Ryu, J.-G., and Lee, T. 2010. Population structure of *Fusarium graminearum* from maize and rice in 2009 in Korea. *Plant Pathol. J.* 26:321-327.
- Lee, T., Han, Y. K., Kim, K. H., Yun, S. H., and Lee, Y. W. 2002. *Tri13* and *Tri7* determine deoxynivalenol- and nivalenol-producing chemotypes of *Gibberella zeae*. *Appl. Environ. Microbiol.* 68:2148-2154.
- Lee, T., Oh, D.-W., Kim, H.-S., Lee, J., Kim, Y.-H., Yun, S.-H., and Lee, Y.-W. 2001. Identification of deoxynivalenol- and nivalenol-producing chemotypes of *Gibberella zeae* by using PCR. *Appl. Environ. Microbiol.* 67:2966-2972.
- Liang, J. M., Xayamongkhon, H., Broz, K., Dong, Y., McCormick, S. P., Abramova, S., Ward, T. J., Ma, Z. H., and Kistler, H. C. 2014. Temporal dynamics and population genetic structure of *Fusarium graminearum* in the upper Midwestern United States. *Fungal Genet. Biol.* 73:83-92.
- Lofgren, L. A., LeBlanc, N. R., Certano, A. K., Nachtigall, J., LaBine, K. M., Riddle, J., Broz, K., Dong, Y., Bethan, B., Kafer, C. W., and Kistler, H. C. 2018. *Fusarium graminearum*: Pathogen or endophyte of North American grasses? *New Phytol.* 217:1203-1212.
- Machado, F. J., Kuhnem, P., Casa, R. T., McMaster, N., Schmale, D., Vaillancourt, L. J., and Del Ponte, E. 2021. The dominance of *Fusarium meridionale* over *F. graminearum* causing *Gibberella* ear rot in Brazil may be due to increased aggressiveness and competitiveness. *Phytopathology* 111:1774-1781.
- Machado, F. J., Möller, P. A., Nicolli, C. P., Del Ponte, E. M., and Ward, T. J. 2015. First report of *Fusarium graminearum*, *F. asiaticum*, and *F. cortaderiae* as head blight pathogens of annual ryegrass in Brazil. *Plant Dis.* 99:1859.
- McMullen, M., Bergstrom, G., De Wolf, E., Dill-Macky, R., Hershman, D., Shaner, G., and Van Sanford, D. 2012. A unified effort to fight an enemy of wheat and barley: *Fusarium* Head Blight. *Plant Dis.* 96:1712-1728.
- McMullen, M., Jones, R., and Gallenberg, D. 1997. Scab of wheat and barley: A re-emerging disease of devastating impact. *Plant Dis.* 81:1340-1348.
- Munkvold, G. P. 2003. Epidemiology of *Fusarium* diseases and their mycotoxins in maize ears. Pages 705-713 in: *Epidemiology of Mycotoxin Producing Fungi*. X. Xu, J. A. Bailey, and B. M. Cooke, eds. Springer, Dordrecht, The Netherlands.
- Nielsen, L. K., Jensen, J. D., Rodríguez, A., Jørgensen, L. N., and Justesen, A. F. 2012. *TRI12* based quantitative real-time PCR assays reveal the distribution of trichothecene genotypes of *F. graminearum* and *F. culmorum* isolates in Danish small grain cereals. *Int. J. Food Microbiol.* 157:384-392.
- O'Donnell, K., Kistler, H. C., Tacke, B. K., and Casper, H. H. 2000. Gene genealogies reveal global phylogeographic structure and reproductive isolation among lineages of *Fusarium graminearum*, the fungus causing wheat scab. *Proc. Natl. Acad. Sci. USA* 97:7905-7910.
- O'Donnell, K., Ward, T. J., Aberra, D., Kistler, H. C., Aoki, T., Orwig, N., Kimura, M., Bjørnstad, Å., and Klemsdal, S. S. 2008. Multilocus genotyping and molecular phylogenetics resolve a novel head blight pathogen within the *Fusarium graminearum* species complex from Ethiopia. *Fungal Genet. Biol.* 45:1514-1522.
- O'Donnell, K., Ward, T. J., Geiser, D. M., Kistler, H. C., and 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.* 41:600-623.
- O'Donnell, K., Ward, T. J., Robert, V. A. R. G., Crous, P. W., Geiser, D. M., and Kang, S. 2015. DNA sequence-based identification of *Fusarium*: Current status and future directions. *Phytoparasitica* 43:583-595.
- Pasquali, M., Beyer, M., Logrieco, A., Audenaert, K., Balmas, V., Basler, R., Boutigny, A.-L., Chrpová, J., Czembor, E., Gagkaeva, T., González-Jaén, M. T., Hofgaard, I. S., Köycü, N. D., Hoffmann, L., Lević, J., Marin, P., Miedaner, T., Migheli, Q., Moretti, A., Müller, M. E. H., Munaut, F., Parikka, P., Pallez-Barthel, M., Piec, J., Scaufflaire, J., Scherm, B., Stanković, S., Thrane, U., Uhlig, S., Vanheule, A., Yli-Mattila, T., and Vogelgsang, S. 2016. A European database of *Fusarium graminearum* and *F. culmorum* trichothecene genotypes. *Front. Microbiol.* 7:406.
- Pasquali, M., and Migheli, Q. 2014. Genetic approaches to chemotype determination in type B-trichothecene producing *Fusaria*. *Int. J. Food Microbiol.* 189:164-182.
- Pereira, C. B., Ward, T. J., Ponte, E. M. D., Moreira, G. M., Busman, M., McCormick, S. P., Feksa, H. R., Almeida, J. L. D., and Tessmann, D. J. 2021. Five-year survey uncovers extensive diversity and temporal fluctuations among *Fusarium* head blight pathogens of wheat and barley in Brazil. *Plant Pathol.* 70:426-435.
- Pereira, C. B., Ward, T. J., Tessmann, D. J., Del Ponte, E. M., Laraba, I., Vaughan, M. M., McCormick, S. P., Busman, M., Kelly, A., Proctor, R. H., and O'Donnell, K. 2018. *Fusarium subtropicale* sp. nov., a novel nivalenol mycotoxin-producing species isolated from barley (*Hordeum vulgare*) in Brazil and sister to *F. praegraminearum*. *Mycologia* 110:860-871.
- Pestka, J. J. 2010. Deoxynivalenol: Mechanisms of action, human exposure, and toxicological relevance. *Arch. Toxicol.* 84:663-679.
- Sarver, B. A. J., Ward, T. J., Gale, L. R., Broz, K., Kistler, H. C., Aoki, T., Nicholson, P., Carter, J., and O'Donnell, K. 2011. Novel *Fusarium* head blight pathogens from Nepal and Louisiana revealed by multilocus genealogical concordance. *Fungal Genet. Biol.* 48:1096-1107.
- Starkey, D. E., Ward, T. J., Aoki, T., Gale, L. R., Kistler, H. C., Geiser, D. M., Suga, H., Tóth, B., Varga, J., and O'Donnell, K. 2007. Global molecular surveillance reveals novel *Fusarium* head blight species and trichothecene toxin diversity. *Fungal Genet. Biol.* 44:1191-1204.
- Taylor, J. W., Jacobson, D. J., Kroken, S., Kasuga, T., Geiser, D. M., Hibbett, D. S., and Fisher, M. C. 2000. Phylogenetic species recognition and species concepts in fungi. *Fungal Genet. Biol.* 31:21-32.
- Umpiérrez-Failache, M., Garmendia, G., Pereyra, S., Rodríguez-Haralambides, A., Ward, T. J., and 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.* 166:135-140.
- van der Lee, T., Zhang, H., van Diepeningen, A., and Waalwijk, C. 2015. Biogeography of *Fusarium graminearum* species complex and chemotypes: A review. *Food Addit. Contam. Part A Chem. Anal. Control Expo. Risk Assess.* 32:453-460.
- Varga, E., Wiesenberger, G., Hametner, C., Ward, T. J., Dong, Y., Schöfbeck, D., McCormick, S., Broz, K., Stückler, R., Schuhmacher, R., Krska, R., Kistler, H. C., Berthiller, F., and Adam, G. 2015. New tricks of an old enemy: Isolates of *Fusarium graminearum* produce a type A trichothecene mycotoxin. *Environ. Microbiol.* 17:2588-2600.
- Vaughan, M., Backhouse, D., and Ponte, E. M. D. 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.* 9:685-700.
- Vogelgsang, S., Beyer, M., Pasquali, M., Jenny, E., Musa, T., Bucheli, T. D., Wettstein, F. E., and Forrer, H.-R. 2019. An eight-year survey of wheat shows distinctive effects of cropping factors on different *Fusarium* species and associated mycotoxins. *Eur. J. Agron.* 105:62-77.
- Ward, T. J., Bielawski, J. P., Kistler, H. C., Sullivan, E., and O'Donnell, K. 2002. Ancestral polymorphism and adaptive evolution in the trichothecene mycotoxin gene cluster of phytopathogenic *Fusarium*. *Proc. Natl. Acad. Sci. USA* 99:9278-9283.
- Ward, T. J., Clear, R. M., Rooney, A. P., O'Donnell, K., Gaba, D., Patrick, S., Starkey, D. E., Gilbert, J., Geiser, D. M., and Nowicki, T. W. 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.* 45:473-484.
- Yang, L., van der Lee, T., Yang, X., Yu, D., and Waalwijk, C. 2008. *Fusarium* populations on Chinese barley show a dramatic gradient in mycotoxin profiles. *Phytopathology* 98:719-727.
- Yli-Mattila, T., Gagkaeva, T., Ward, T. J., Aoki, T., Kistler, H. C., and 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* 101:841-852.
- Zhang, H., van der Lee, T., Waalwijk, C., Chen, W., Xu, J., Xu, J., Zhang, Y., and 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:e31722.