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Permanence of *Fusarium graminearum*, the cause agent of *Fusarium* head blight (FHB)

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ABSTRACT: The rapid global re-emergence of *Fusarium* head blight disease of wheat and barley in the last decade along with contamination of grains with mycotoxins attributable to the disease have spurred basic research on the fungal causal agent. Wheat yield can be highly decreased by several factors. In particular *Fusarium graminearum* Schwabe is a worldwide fungal pest impacting wheat production. *F. graminearum* is the causal agent of Fusarium head blight, root and stem-base rot of cereals. Losses caused by *Fusarium* head blight in Northern and Central America from 1998 to 2002 reached $2.7 billion. Moreover, *F. graminearum* produces mycotoxins which affect human and animal health. The threshold of these mycotoxins in foodstuffs is regulated in Europe since 2007. *F. graminearum* survives for several years saprotrophically in the soil, on dead organic matter, particularly on crop residues. *F. graminearum* adapts to a wide range of environmental variations, and produces extracellular enzymes allowing feeding on different crop residues. However, *F. graminearum* competes with other decomposers such as other *Fusarium* spp. belonging to the same complex of species. Actually, it is not known whether *F. graminearum* mycotoxins give *F. graminearum* a competitive advantage during the saprotrophic period. Anthropogenic factors including preceding crops, tillage system and weed management can alter the development of the soil biota, which in turn can change the saprotrophic development of *F. graminearum* and disease risk.We review the ecological requirements of *F. graminearum* saprotrophic persistence. The major conclusions are: (A) temperature, water, light and O_2 are key conditions for *F. graminearum* growth and the development of its sexual reproduction structures on crop residues, although the fungus can resist for a long time under extreme conditions. (B) *F. graminearum* survival is enhanced by high quantities of available crop residues and by rich residues, while sexual reproduction structures occur on poor residues. (C) *F. graminearum* is a poor competitor over time for residues decomposition. *F. graminearum* survival can be controlled by the enhancement of the decomposition processes by other organisms.

Keywords: Crop residues, Ecological requirements, *Fusarium graminearum*, *Fusarium* head blight, Wheat diseases

INTRODUCTION

Wheat (*Triticum aestivum* L. ssp. aestivum) is the second most cultivated crop in the world after maize (*Zea mays* L.). In 2010, 653 million tons of wheat and durum wheat were produced in the world, of which 140.7 million tons were produced in Europe (FAO 2011). Moreover, the wheat is one of the most traded crops worldwide, with 125.9 million tons traded in 2010 (AGPB 2012). The cultural practices trends due to economical and environmental reasons, i.e., reduction of soil tillage and pesticides use, raise the issue of re-emerging wheat diseases, such as fungal diseases (McMullen *et al.* 1997; Millennium Ecosystem Assessment 2005). Studies of plant pathogenic fungi generally focus on infection processes, disease development and other concerns inplant-microorganism interactions.

But the saprotrophic period of these pathogens' life cycle is not well known. Most soil fungi are decomposers or saprotrophs that feed on decaying organic material. In fact, they play a key role in the decomposition of organic polymers that takes place in the soil. Fungi are considered primary decomposers in forests, where litter contains high concentrations of complex polymers. Fungi have a unique role in the degradation of plant-derived woody substrates containing lignocellulose, *i.e*., cellulose complexed with lignin (Finlay 2007; Sinsabaugh 2005). They also play an important role in arable soils by breaking down and recycling plant residues, primarily cellulose and hemicellulose (Stromberg 2005). Among them, some plant pathogenic fungi take place and their role should be considered. Indeed, plant pathogenic fungi are categorised as either biotrophs or necrotrophs, and as either obligate pathogens or facultative saprotrophs.

For example, the disease cycle of the deleterious fungus *Fusarium graminearum*, the anamorph stage of Gibberellazeae (Schwein.) Petch is well studied (Trail 2009). In a previous review, Goswami and Kistler (2004) provided an update on the pathogenesis, genetics, evolution and genomics of *F. graminearum* but the ecological requirements of its saprotrophic stage are less well understood. *Fusarium* head blight, root rot and foot rot (crown rot) are diseases that cause significant yield loss in several crops worldwide such as wheat, maize, oat (*Avena sativa* L.), barley (*Hordeum vulgare* L.) and rice (*Oryza sativa* L.) (Parry *et al.* 1995; Pereyra and Dill-Macky 2008; Trail *et al.* 2003). Yield losses caused by *Fusarium* head blight in Northern and Central America from 1998 to 2002 were evaluated to reach $2.7 billion (Nganje *et al.* 2002). Several species are involved in the fungal complex that causes these diseases. Many of them also produce mycotoxins, such as deoxynivalenol (commonly known as DON) and its acetylated forms 3-acetyl-4-deoxynivalenol (3-ADON) and 15- acetyl-4-deoxynivalenol (15-ADON), nivalenol (NIV) and zearalenone (ZEA) (Desjardins and Proctor 2007). These mycotoxins are of major concern because of their effect on human and animal health and because they persist during storage and are heat-resistant (JEFCA 2001). The threshold of these mycotoxins in foodstuffs is regulated in Europe since 2007 (CE N°1881/2006). Among the species involved in the complex causing Fusarium disease on wheat, *F. graminearum* predominates in many parts of the world (Bottalico 1998; Bottalico and Perrone 2002; Parry *et al.* 1995). Like other *Fusarium* species in the complex, *F. graminearum* survives saprotrophically on crop residues in the absence of its hosts (Sutton 1982). *Fusarium* head blight severity and deoxynivalenol contamination significantly increase with the density of residues left from the preceding crop (Blandino *et al.* 2010). Moreover, surface residues provide a substrate for active growth of *F. graminearum* for a longer period of time than buried residues (Pereyra *et al.* 2004). Burying *F. graminearum* -infested crop residues deeper in the soil can efficiently reduce *F. graminearum* populations; however, the pathogen may survive for several years. During the decomposition process, the chemical composition and the availability of the plant material changes as some resources are used up while others are made available for saprotrophic growth. To survive over time, *F. graminearum* has to be able to use available resources and to compete with the different organisms that are invading the material, each of them being specific for each of the decomposition stages. To develop control strategies of *F. graminearum* primary inoculum, a better understanding of the complex interactions that determine its ability to grow and compete for crop residues is needed.

Fusarium graminearum

***Fusarium* diseases on wheat.** On wheat, Fusarium fungi cause several distinct diseases (Colbach *et al.* 1996; Kohl *et al*. 2007). First, seedling diseases, which cause damping-off, seedling blight, and footrot. In Europe and North America, these symptoms are mainly due to Microdochiumnivale (Fr.) Samuels & I.C. Hallet, but *F. culmorum* (Wm.G. Sm.) Sacc., *F. graminearum* and *F. pseudograminearum* O'Donnell & T. Aoki are also frequently associated depending on the geographical conditions and climatic conditions (Bateman 1993; Smiley *et al.* 2005). Second, *Fusarium* head blight, which is the mature plant disease caused by a complex of species. The *Fusarium* species predominantly found in Europe are *F. graminearum*, *F. avenaceum* (Fr.) Sacc. And *F. Culmorum* (Bottalico 1998; Bottalico and Perrone 2002; Nielsen *et al.* 2011a, b). A survey conducted in France between 2000 and 2002 showed that, in addition to *F. graminearum*, *F. avenaceum* and *F. poae* (Peck) Wollenw. were also found regularly, whereas *M. nivale* and *F. culmorum* were less frequent than previously recorded. Other species, such as *F. tricinctum* (Corda) Sacc., *F. sambucinum* Fuckel, *F. equiseti* (Corda) Sacc., *F. acuminatum* Ellis & Everh. And *F. sporotrichioides* Sherb., were found in lower quantities (Ioos *et al.* 2004). The composition, the development and the structure of the *Fusarium* community depend on a combination of factors, among which climate plays a major role (Muller *et al.* 2010). *F. graminearum*, together with several other encountered species, can produce toxigenic compounds (Bottalico 1998). Like the other *Fusarium* species associated with *Fusarium* head blight, *F. graminearum* over winters in soil and on infested crop residues (Fernandez *et al.* 2008; Pereyra and Dill-Macky 2008; Sutton 1982). The mycelium on crop residues allows the production of both macroconidia (asexual spores) and ascospores (sexual spores produced in perithecia), which constitute the primary inoculum that causes primary infection of wheat heads (Parry *et al.* 1995; Shaner 2003; Yuen and Schoneweis 2007; Fig. 2). *F. graminearum* is one of the predominant species involved in *Fusarium* diseases. *F. graminearum* over winters on crop residues which provide the primary inoculum for *Fusarium* head blight development. Therefore, a better knowledge of *F. graminearum* survival on crop residues is important to control this disease development.

Saprotrophic growth. Cell-wall degrading enzymes produced by plant pathogenic fungi are considered important during the pathogenic part of the life cycle and may also be relevant during the saprotrophic part (Belien *et al.* 2006; Van den Brink and de Vries 2011).

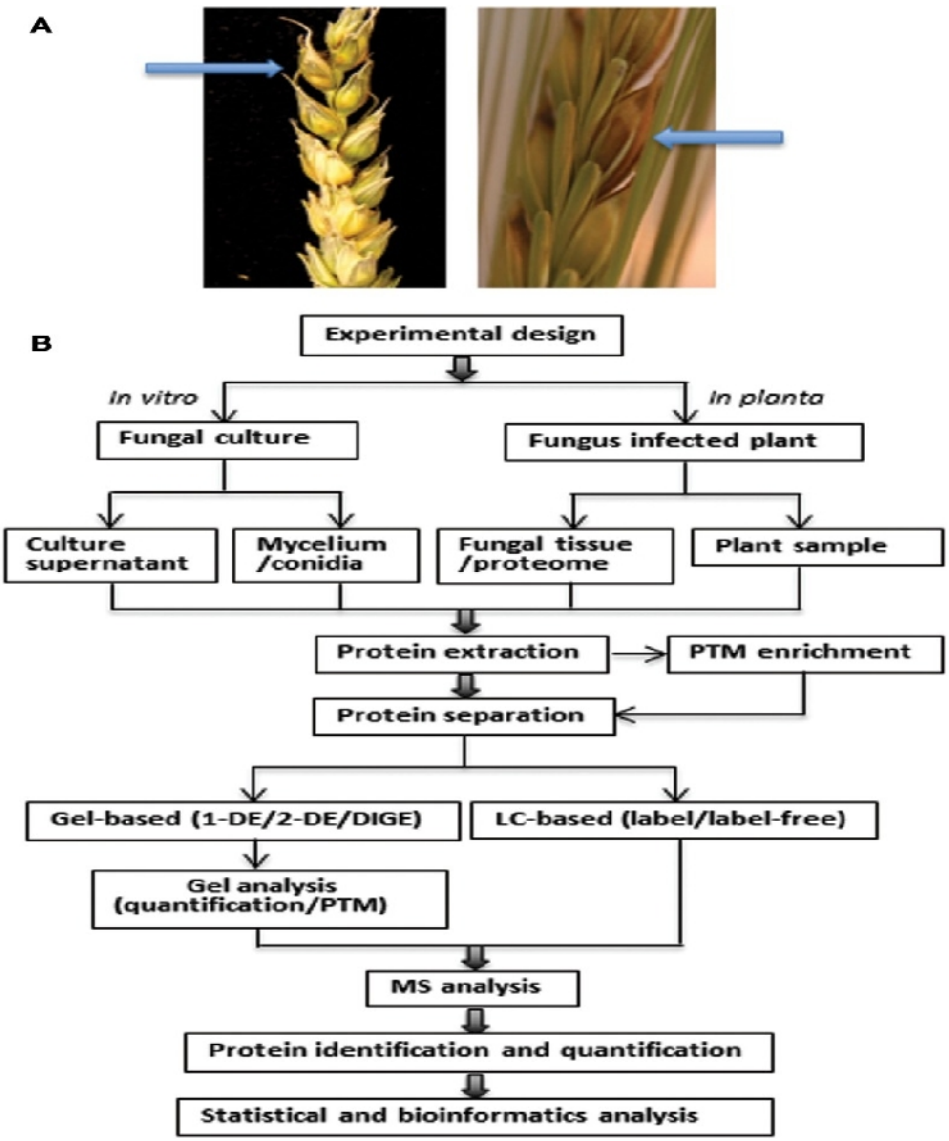

Fig. 1. Symptoms (indicated by arrows) of *Fusarium* head blight in the spikelets of wheat (left) and barley (right). (A) Symptoms (indicated by arrows) of *Fusarium* head blight in the spikelets of wheat (left) and barley (right). Bleaching and dark necrotic lesions can be observed in the infected wheat spikelets. Infected barley spikelets show a browning or water-soaked appearance. The spikelets were point-inoculated with *F. graminearum* at anthesis and photographed at 6 dai by Jens Due Jensen and David B. Collinge, University of Copenhagen. (B) Schematic overview of proteomics workflow in phytopathogenic fungi. The major steps include experiment design, sampling, protein extraction, PTM enrichment, protein separation, MS analysis, protein identification, and quantification, followed by bioinformatics analysis of the data.

In the case of *F. graminearum*, scanning electron micrographs and immuno-labelling showed that the fungus penetrates and invades its hosts by secreting cell wall degrading enzymes (Kikot *et al.* 2009). The plant cell-wall components cellulose, xylan, and pectin are damaged when they are in direct contact with the pathogen growing inter and intracellularly in the tissues of wheat spikelets (Wanjiru *et al.* 2002). Kikot *et al.* (2010) examined *F. graminearum* isolates for their production of different extracellular enzymes with activities of potential biotechnological interest: pectinases (polygalacturonase and polymethylgalacturonase), cellulase (carboxymethylcellulase) and hemicellulase (xylanase). Although enzymatic activities varied among the different isolates, polygalacturonase activity was evidenced early (after 2 days' incubation in the presence of oat bran) and was the highest for all isolates.

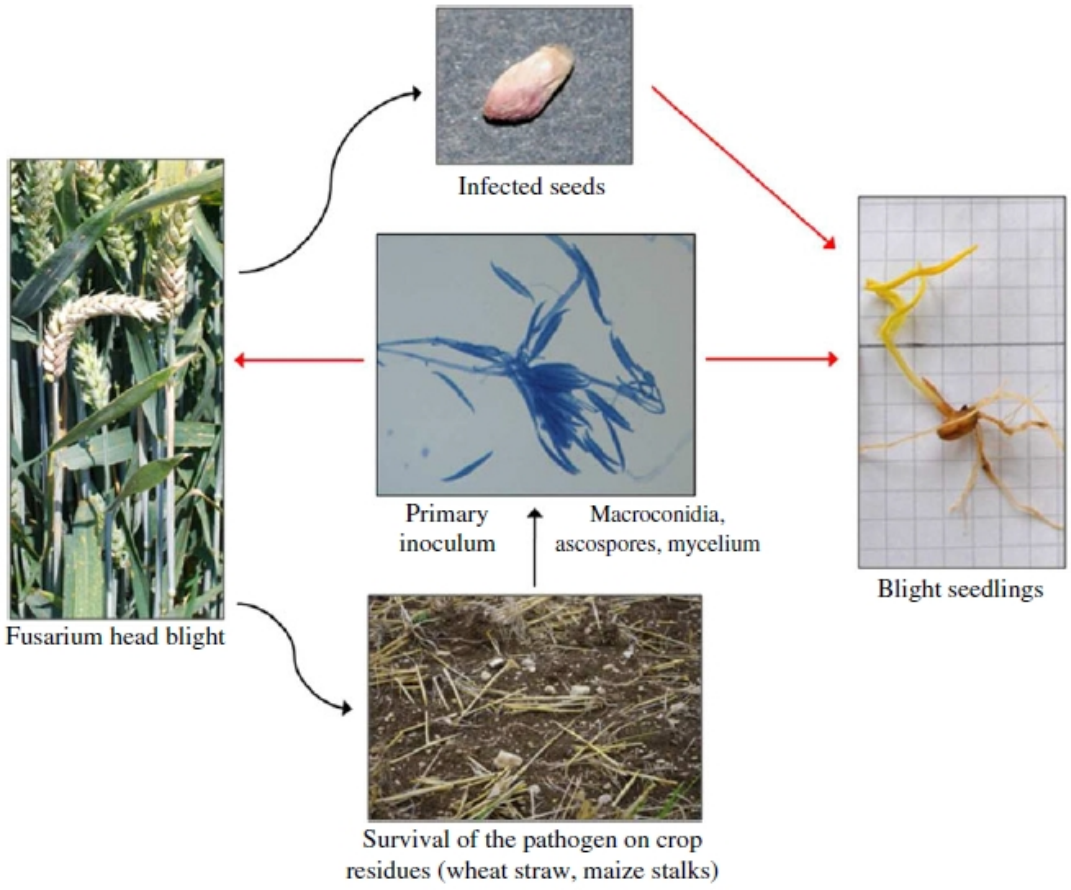

Fig. 2 Disease cycle of *Fusarium graminearum*. Black, sigmoid-like arrows indicate habitats provided by the crop and red arrows indicate infectious activity kept up by habitats (photograph: courtesy of J. Leplat). Crop residues allow the production of *F. graminearum* primary inoculum. The primary inoculum can provoke seedling blight as well as *Fusarium* head blight by splash dispersal. *F. graminearum*-infestedmwheat ears can cause the production of infected seeds which lead to seedling blight.

Only some of the isolates showed a high level of polymethylgalacturonase activity; carboxymethylcellulase and endoxylanase activities were particularly high at late stages, i.e., after 4 and 7 days' incubation, respectively, and their maximum values were lower than pectinase values (Kikot *et al.* 2010). The production of these enzymes requires inducers that are likely to be present in the substrate and regulated by various mitogen-activated proteins (MAP) kinases, some of which have already been identified (Jenczmionka and Schafer 2005). Besides being factors involved during infection, these polysaccharide-degrading enzymes are also important for the colonisation of crop residues. The chemical composition of crop biomass differs from one plant species to another and from one plant part to another. This may influence the decomposition of the crop residues by microbial colonisers, and thereby the saprotrophic survival of pathogens such as *F. graminearum* (Khongaand Sutton 1988; Nicolardot *et al.* 2007). There are also consequences on soil organic C inputs, which have been discussed elsewhere (Johnson *et al.* 2007). A comparative screening of *F. graminearum* exoproteome on culture media containing glucose or hop (*Humulus lupulus* L.) showed that the number of enzymes secreted by the fungus was higher in the presence of plant material (Phalip *et al.* 2005). Eighty four proteins were identified on medium containing hops, whereas only 23 were identified on medium containing glucose. Among them, 11 degraded cellulose, 19 degraded pectin and 25 degraded hemicellulose. Two amylases and two chitinases were also identified. Obviously, *F. graminearum* has the enzymatic ability to degrade compounds of the primary cell wall.

Moreover, 30 xylanase-related genes were transcribed in the presence of different carbon sources, hop cell wall, xylan, xylose or carboxymethyl cellulose, with different expression patterns for a specific enzyme, which suggests that *F. graminearum* can also adapt to a range of variations in its environment (Hatsch *et al.* 2006). Briefly, *F. graminearum* can overwinter on crop residues thanks to its enzymatic ability to degrade and use these residues as nutrients.

Environmental factors controlling saprotrophic survival. Temperature, water activity and other physico-chemical factors can influence the different aspects of residues colonization by *F. graminearum*. Its growth and the germination of conidia and ascospores are favoured by warm, humid conditions. Ramirez *et al.* (2006) found that the mycelial growth of two strains of *F. graminearum* reached an optimum at 25°C at water activities ranging between 0.950 and 0.995, and that no growth was observed below 5°C. Both strains were able to grow in drier conditions, at a minimum water activity of 0.900.

By contrast, when the water activity was maintained at high levels, overall microbial activity was stimulated, resulting in a rapid decrease in the quantity of *F. graminearum* on wheat and maize residues buried in the soil (Burgess and Griffin 1968). Soil characteristics such as soil compaction affect water availability. *M. nivale* caused more foot rot in a non-compacted soil than in a compacted soil, probably due to reduced water availability leading to poor fungal development and mobility (Colbach *et al.* 1996; Toyota *et al.* 1996).

Inch and Gilbert (2003a) studied the maturation of *F. graminearum* sexual structures on damaged kernels of wheat at three different temperatures. Even if the fungus survives at -10°C, perithecia are only formed between 2°C and 20°Cand ascospores only appear at 20°C. The optimal temperature range for the maturation of perithecia is between 15.0°C and 28.5°C, whereas the optimum for the production of ascospores is between 25°C and 28°C at high water activity (Dufault *et al.* 2006; Sutton 1982; Tschanz *et al.* 1976).

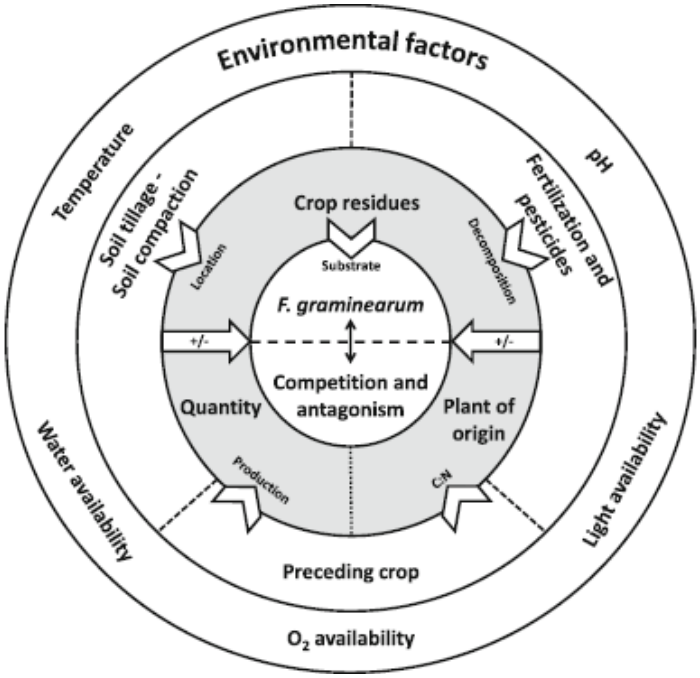

Fig. 3. Saprotrophic survival of *Fusarium graminearum*. Crop residues are the main habitat of *F. graminearum*. On the one hand, they provide spatial and trophic resources the fungus has to exploit in interaction with the rest of the microflora and the soil fauna. On the other hand, they buffer the impact of environmental factors, including agricultural practices.

The optimal temperature for the production of compounds such as mycotoxins is different. For two strains of *F. graminearum*, mycotoxin production was highest at a temperature of 30°C at a water activity of 0.995 (Ramirez *et al.* 2006). Deoxynivalenol was only produced at water activities between 0.950 and 0.995 even though growth was possible between 0.900 and 0.995, which indicates that mycotoxin production requires more specific conditions than growth. Although *F. graminearum* can survive on residues buried 20 to 25 cm deep for more than 4 years, it can only develop on plant debris in the upper centimetres of the soil (Champeil *et al.* 2004). In addition to favourable temperature and water availability, its development depends on soil aeration (Cassini 1970).

Furthermore, some stages of its life cycle require light. For example, perithecia initiation and ascospore production are light-dependent (Gilbert and Tekauz 2000; Sutton 1982; Tschanz *et al.* 1976). A *F. graminearum* survival test on damaged kernels left on the soil surface or buried in the first layer of the soil at 5- and 10-cm depths for 24 months showed that perithecia were produced at all depths but ascospores were only formed at the soil surface (Inch and Gilbert 2003a). Soil characteristics such as pH could also have an effect on F. *graminearum* survival. A negative correlation between soil pH values ranging between 4.4 and 6.4, and the amount of crown rot on wheat has been found, but it was not clear whether this is because *F. graminearum* has a better saprotrophic capacity in acidic soils or because it is more aggressive under these conditions (Smiley *et al.* 1996). Although mycelial growth and conidial germination were limited under acidic and alkaline conditions, *F. graminearum* could grow on media whose pH values range between 4 and 10 (Thompson *et al.* 1993). Macroconidia germination on solid media reached almost 100 % after 18 h at pH values ranging between 3 and 7 (Beyer *et al.* 2004). The time needed for freshly discharged ascospores to germinate and the rate of ascospore germination were both affected by the pH. Thetime required for 50 % of the viable ascospores to germinate was shortest at pH 3.5, and ascospore germination was highest at pH 3.7. Changing the pH from 3.7 to 2.5 and from 3.7 to 6.5 decreased the germination of ascospores by 66 % and 56 %, respectively (Beyer and Verreet 2005). This might explain the better saprotrophic capacity of the fungus in soil at pH 4.4 than in soil at pH 6.4. Although *F. graminearum* can survive when exposed to unfavourable environmental conditions, its growth and the development of its sexual reproduction structures require sufficient temperature, water, light and O_2 availabilities. 3 Effect of crop residues as *F. graminearum* growth substrates in the soil.

Table 1: Original proteomics papers published on *F. graminearum* and its interactions with wheat and barley.

Growth conditions	Sampling times	Sample materials	Proteomics techniques	Remarks	Reference
In the growth media containing either glucose or hop cell walls	6 d, 9 d	Culture supernatants	1-DE, 2-DE, LC-MS/MS	Analysis of the fungal *in vitro* secretomes	Phalip *et al.* (2005)
In the synthetic media containing polysaccharide supplements	7 d	Culture supernatants	1-DE, LC-MS/MS	High-throughput analysis of the fungal *in vitro* secretomes	Paper *et al.* (2007)
In the wheat grains	Maturity	Fungal secretome	1-DE, LC-MS/MS	Analysis of the fungal *in planta* secretomes	Paper *et al.* (2007)
In the growth medium promoting trichothecene biosynthesis after 2-day growth in the rich medium	0, 4 d, 9 d, 12 d	Fungal tissues	iTRAQ, LC-MS/MS 2-DE, MS/MS	*In vitro* time course study of the changes in fungal intercellular proteomes due to the induction of trichothecene production	Taylor *et al.* (2008)
In the growth media containing only barley or wheat flour	7 d	Culture supernatants	2-DE, MALDI-MS/MS	Study of the fungal *in vitro* secretomes under growth conditions which mimic *in planta* nutritional situation	Yang *et al.* (2012)
In the growth medium with limited nitrogen after 2-day growth in the rich medium	0, 6 h, 12 h	Fungal tissues	2-DE, MALDI-MS, 1-DE, IMAC, TiO_2, LC-MS, SAX, IMAC, LC-MS/MS	Analysis of the fungal phosphoproteomes under the *in vitro* growth condition that activates trichothecene pathway	Rampitsch *et al.* (2010)
In the growth medium with unlimited nutrients	1 d	Fungal tissues	SCX, IMAC, LC-MS/MS	Analysis of the fungal *in vitro* phosphoproteomes	Rampitsch *et al.* (2012)
Virus-free and -infected strains grown in the complete medium	5 d	Fungal tissues	2-DE, LC-MS/MS	Study of the fungal proteomes in response to viral infection	Kwon *et al.* (2009)

Growth conditions	Sampling times	Sample materials	Proteomics techniques	Remarks	Reference
In the resistant wheat spikes	6 h, 12 h, 24 h	Wheat spikes	2-DE, MALDI MS	Study of the differential expressed wheat proteins in response to fungal infection	Wang *et al.* (2005)
In the susceptible and resistant wheat spikes	5 d	Wheat spikelets	2-DE, LC-MS/MS	Study of the differential expressed wheat proteins in response to fungal infection	Zhou *et al.* (2005)
In the susceptible wheat spikes	1 d, 2 d, 3 d	Wheat spikelets	2-DE, LC-MS/MS	Identification of wheat proteins regulated by the fungus and fungal expressed proteins *in planta*	Zhou *et al.* (2006)
In the susceptible wheat ears	5 d, 15 d, 25 d	Wheat ears	DIGE, MALDI MS/MS	Investigation of the changes in xylanase inhibitors (iso) forms of wheat due to fungal *Tir5* mutant infection	Dornez *et al.* (2010)
In the susceptible and resistant wheat spikes	12 h	Wheat spikes	2-DE, MALDI MS	Study of the differential expressed wheat proteins and genes in response to fungal infection	Ding *et al.* (2011)
In the moderate resistant wheat spikes	48 h	Wheat spikes	2-DE, MALDI MS	Study of the differential expressed wheat proteins in response to fungal infection	Shin *et al.* (2011)
In wheat carrying either resistant or susceptible alleles at the *Fhb 1* locus	72 h	Wheat spikelets	LC-MS/MS, spectral counting	Identification of mechanisms of resistance governed by the FHB resistance locus *Fhb 1*	Gunnaiah *et al.* (2012)
In emmer heads and co-colonization with *Fusariumculmorum*	Maturity	Emmer grains	2-DE, LC-MS/MS	Study of the differential expressed emmer seed proteins in response to fungal infection	Eggert *et al.* (2011)
In the spikes of six barley genotypes of varying resistance	3 d	Barley spikelets	2-DE, LC-MS/MS	Study of the differential expressed barley proteins in response to fungal infection	Geddes *et al.* (2008)
In the susceptible barley spikes grown under different N fertilizers	Maturity	Barley seeds	2-DE, MALDI MS/MS	Investigation of effect of nitrogen fertilizer mounts on the severity of FHB and identification of fungal proteins *in planta*	Yang *et al.* (2010a)
In the susceptible barley spikes	2 d	Barley spikelets	2-DE, MALDI MS/MS	Definition of infection levels correlated to fungal induced plant proteome degradation and identification of the differential expressed barley proteins in response to fungal infection	Yang *et al.* (2010b)
In the susceptible barley seeds	3 d	Germinating barley seeds	2-DE, MALDI MS/MS	Study of the differential expressed barley seed proteins in response to fungal infection during germination	Yang *et al.* (2011)

Growth conditions	Sampling times	Sample materials	Proteomics techniques	Remarks	Reference
In the spikes of eleven barley genotypes of varying resistance	Maturity	Barley seeds	2-DE, LC-MS/MS	Study of the differential expressed barley seed proteins in response to fungal infection	Zantinge *et al.* (2010)
In the naked barley heads and co-colonization with *Fusarium culmorum*	Maturity	Naked barley grains	2-DE, MALDI MS, LC-MS/MS	Identification of the differentially expressed seed proteins in response to fungal infection and to growing location of the plant	Eggert and Pawelzik (2011)

Effect of crop residues as F. graminearum growth substrates in the soil

Effect of crop residues quantities. There is a general relationship between the yield of a given crop and the amount of residues left on the ground after harvesting. In most cases, the residues/yield ratio is between 1 and 2 (Kumar *et al.* 2003; Scarlat *et al*. 2011). The amount of residue may vary from 2 to 9 tons ha^{-1}, depending on the type of crop: in rape (*Brassica napus* L.), barley and wheat leaves, values were 2.0, 2.5 and 3.5 tons residues ha^{-1}, respectively, whereas in alfalfa (*Medicago sativa* L.) and maize leaves they were 8.5 and 9.0 tons residues ha^{-1}, respectively (Morel 1996; Vilain 1989). Part of the residues is exported for further transformation (e.g., animal bedding, animal feed and biofuel production; Berndes *et al.* 2003); however, a large part of them is left in and on the soil (Malhiet *al. et* ., 2011). The residues are either ploughed down (inversion tillage) or left at the surface when conservation tillage is being practiced, as in zero-tillage or other types of noninversiontillage. Non-inversion tillage may increase wheat grain infection by *F. graminearum* as compared to inversion tillage whereby residues are buried in the soil. The effects vary to a great extent with climatic conditions and preceding crop type (Blandino *et al.* 2010; Fernandez et al. 2008). In conservation tillage, more than 30 % of the soil surface is covered by crop residues (Bockus and Shroyer 1998). Steinkellner and Langer (2004) found up to 9.103 colony-forming units of *F. graminearum* and of *F. culmorum* g^{-1} of soil when non-inversion tillage was used, whereas ten times as few colony-forming units were found after 20-cm deep inversion tillage. *F. graminearum* and *F. culmorum* survival is favoured by high quantities of available residues (Bateman *et al.* 1998). For example, maize production results in large amounts of residues which promote the production of inoculum (Champeil *et al.* 2004). Comparing four different densities of maize residues left on the soil surface showed that disease severity and deoxynivalenol occurrence in wheat grains both increased with residue quantity (Blandino *et al.* 2010; Maiorano *et al.* 2008). To sum up, *F. graminearum* survival is enhanced by important quantities of available crop residues, which depends on the production capacity of the preceding crop and on the crop residues management.

Effect of plant species. Not only can climatic conditions and residue quantities influence *F. graminearum* development, but the nature of crop residues can also affect its biology. For example, wheat and durum wheat produce similar amounts of residues, but wheat infection is more severe after durum wheat than after wheat (Champeil *et al.* 2004). The production of reproductive structures also varies with the plant species. Pereyra and Dill-Macky (2008) found the induction of a higher ascospore production on wheat and barley than on maize or on some selected weed species (*Digitarias anguinalis* (L.) Scop., *Setaria* spp., *Lolium multiflorum* Lam. and *Cynodon dactylon* (L.) Pers.), while no ascospore production was found on sunflower (*Helianthus annuus* L.) residues. Similarly, inoculum production varies over time, and depends on the plant part. *F. graminearum* survival on maize stems and ears on the one hand and on wheat stems, spikelets and grains on the other hand, was compared over 3 years. The length of macroconidia and perithecia production varied according to the type of residue. For example, perithecia were produced on all types of residues during the first year, while only wheat spiklets and grains allowed the perithecia production during the third year. (Khonga and Sutton 1988).

Similarly, the amount of *Fusarium* was found to decrease faster on wheat internodes than on stem bases, and faster on nodes than on internodes (Kohl *et al.* 2007; Pereyra *et al.* 2004). Finally, *F. graminearum* ascospore production was higher on kernels than on nodes and floral bracts (Pereyraand Dill-Macky 2005). These observations can be partly explained by the chemical composition of the residues and particularly by their C/N ratio: the C/N ratio varies over time depending on the decomposition stage of the residues, and influences growth and the production of macroconidia and sexual structures. For example, the C/N value of wheat straw is high (134), whereas the C/N value of wheat leaves is ten times as low (13.4; Nicolardot *et al.* 2001). Macroconidia are produced on residues that are in the early stage of decomposition whereas peritheciaproduction occurs later, when decomposition is much more advanced and growth conditions are less favourable.

Rich residues with a low C/N ratio (such as maize stems, maize kernels, wheat spikelets and lowly infested wheat grains) provide a favourable habitat, allowing longer saprotrophic development before perithecia production, as compared to poor residues with a high C/N ratio, such as wheat stems and severely infested wheat grains (Khonga and Sutton 1988). Briefly, *F. graminearum* survival depends on the C/N ratio of the residues, and consequently on the plant species, on the plant part and on the degradation rate of the residues. *F. graminearum* survival is enhanced by rich residues, with a low C/N ratio. *F. graminearum* sexual reproductive structures appear on residues with high C/N, when growth conditions are less favourableto fungal development.

CONCLUSION

An important part of the life cycle of *F. graminearum*, the main causal agent of *Fusarium* head blight, takes place outside the plant. The fungus produces an array of enzymes which allow it to use crop residues as a trophic and spatial resource for its saprotrophic development.

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