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Survival of *Fusarium graminearum*, the causal agent of Fusarium head blight. A review

Johann Leplat · Hanna Friberg · Muhammad Abid · Christian Steinberg

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Abstract Wheat is one of the most cultivated crops worldwide. In 2010, 20 % of wheat and durum wheat were cultivated in Europe, 17 % in China and 9 % in Russia and in North America. 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 food-stuffs 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: (1) temperature, water, light and O₂ 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. (2) *F. graminearum* survival is enhanced by high quantities of available crop residues and by rich residues, while sexual reproduction structures occur on poor residues. (3) *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. In addition, the development of *F. graminearum* on crop residues can be limited by antagonistic fungi and soil animals growing at the expense of *F. graminearum*-infested residues. (4) Agricultural practices are key factors for the control of *F. graminearum* survival. A suitable crop rotation and an inversive tillage can limit the risk of Fusarium head blight development.

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Contents

1. Introduction	2
2. <i>Fusarium graminearum</i>	3
2.1 <i>Fusarium</i> diseases on wheat	3
2.2 Saprotrophic growth	4
2.3 Environmental factors controlling saprotrophic survival	5
3. Effect of crop residues as <i>F. graminearum</i> growth substrates in the soil	6
3.1 Effect of crop residues quantities	6
3.2 Effect of plant species	6
4. Competition and antagonism	7
4.1 Organisms succession during residue decomposition	7
4.2 Interactions with soil microorganisms	7
4.3 <i>Fusarium</i> species displacement on residues	8
4.4 Interactions with the soil fauna	8
5. Importance of agricultural practices for the disease development	9
5.1 Preceding crop	9
5.2 Soil tillage	9
5.3 Fertilization and pesticides	10
6. Conclusion	11

1 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 in plant–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* (Fig. 1), the anamorph stage of *Gibberella zeae* (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 (Fig. 2), 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

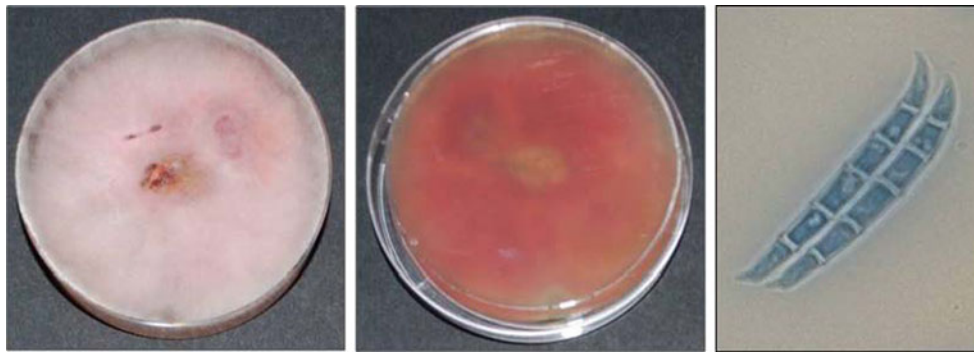


Fig. 1 Macroscopic and microscopic pictures of *Fusarium graminearum*, the causal agent of Fusarium head blight (photograph: courtesy of J. Leplat). Macroscopic pictures were taken after growth on potato dextrose agar. The undersurface shows the typical carmine red color of *F. graminearum* species. The microscopic picture shows macroconidia

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.

This review focuses on the saprotrophic phase of the life cycle of *F. graminearum*. Discussion includes several topics: (1) how environmental factors affect its saprotrophic survival; (2) in which ways crop residues provide a habitat for it and impact on its survival depending on their quantity and on plant species they come from; (3) whether crop residue colonization by it is a matter of competition and antagonism; and (4) what is the incidence of agricultural practices on its survival.



Fig. 2 Wheat ear infested by *Fusarium graminearum* (photograph: courtesy of J. Leplat). The ear shriveling suggests a low grains filling inferring yield losses. The orange spikelet is due to *F. graminearum* growth suggesting mycotoxins production

with the typical spindle shape which gives its name to the *Fusarium* genus. The cylindrical shape of the macroconidia, i.e., dorsal and ventral surfaces parallel, and the foot shape of the basal cell are typical of *F. graminearum* species

2 *Fusarium graminearum*

2.1 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 foot rot. In Europe and North America, these symptoms are mainly due to *Microdochium nivale* (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* overwinters 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. 3).

F. graminearum is one of the predominant species involved in Fusarium diseases. *F. graminearum* overwinters 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.

2.2 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). 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. 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

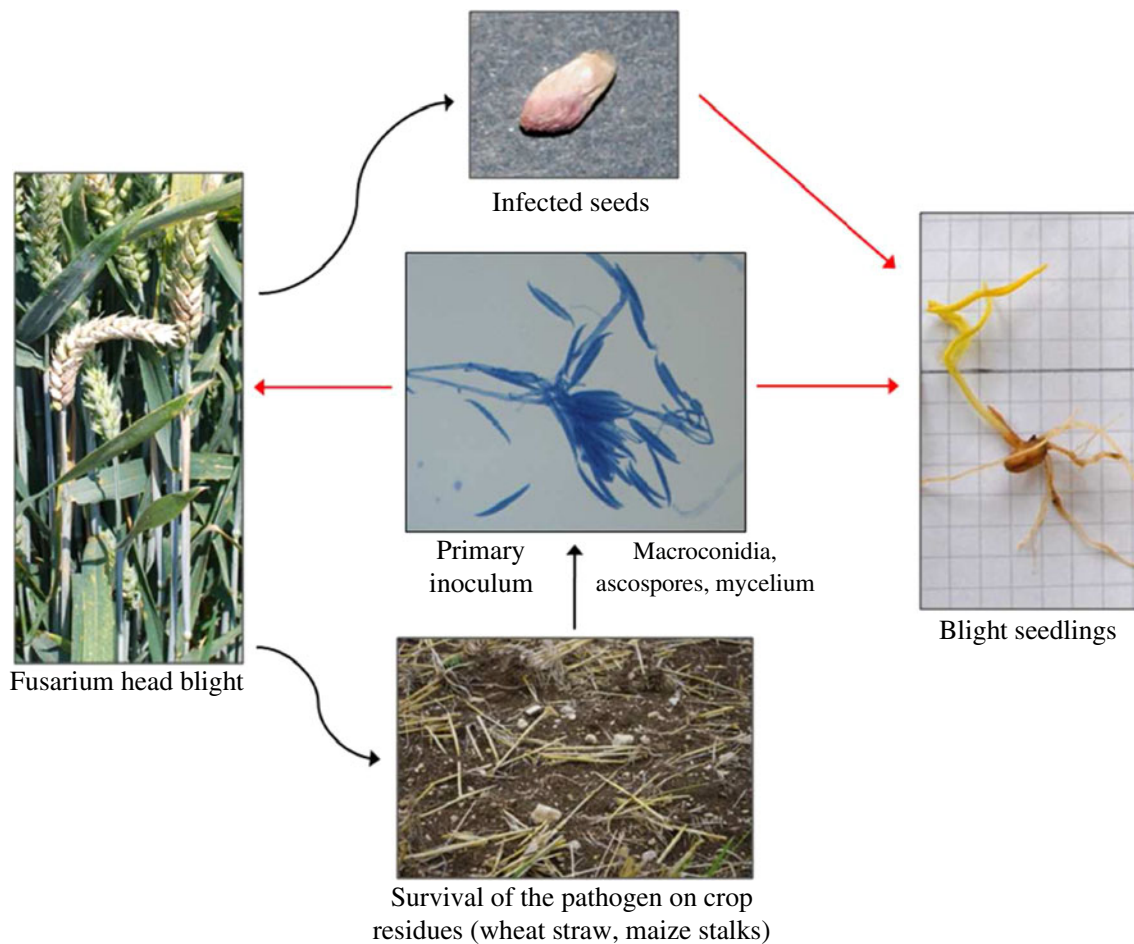


Fig. 3 Disease cycle of *Fusarium graminearum*. Black, sigmoid-like arrows indicate habitats provided by the crop and red arrows indicate infectious activity kept up by habitats (photograph: courtesy of J. Leplat). Crop residues allow the production of *F. graminearum* primary

inoculum. The primary inoculum can provoke seedling blight as well as Fusarium head blight by splash dispersal. *F. graminearum*-infested wheat ears can cause the production of infected seeds which lead to seedling blight

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* (Khonga and 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, i.e., hop cell wall, xylan, xylose or carboxymethylcellulose, 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.

2.3 Environmental factors controlling saprotrophic survival

Temperature, water activity and other physico-chemical factors can influence the different aspects of residues colonisation 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°C and 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).

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. The time 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 O₂ availabilities.

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

3.1 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 (Malhi et al. 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 non-inversion tillage. 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.

3.2 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 (i.e., *Digitaria sanguinalis* (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 spikelets 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 (Pereyra and 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 perithecia production 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 favourable to fungal development.

4 Competition and antagonism

4.1 Organisms' succession during residue decomposition

Organisms of different species and from different trophic groups are involved at different stages of the decomposition process (Frankland 1998; Thirup et al. 2001). The ability of a specific species to grow or survive on the material depends on its ability to use the nutrients available at a particular decomposition stage and on its ability to compete for them with other organisms that are colonising the material concomitantly. Among these groups, microarthropods, nematodes, protozoa, bacteria and fungi have important predator-prey interactions that may determine community assemblages during the early decomposition of crop residues depending on their nature (Ponge 2005). The fungal community seems to be the least affected by such interactions (Georgieva et al. 2005a), and the increase in fungal biomass that occurs later during succession is more correlated with the decomposition of different crop residues (Georgieva et al. 2005b). Therefore controlling the decomposition process could represent a way of controlling primary inoculum quantities of soil- and residue-borne plant pathogenic fungi such as *F. graminearum*. The succession of fungal populations and the decomposition process are also affected by external factors such as climatic conditions and agronomic practices, which may determine the competitive exclusion among the complex of *Fusarium* species (Doohan et al. 2003; Fernandez et al. 2008). Crop residues present in the soil or at the soil surface are degraded by a wide range of organisms that use the material for their growth. Larger soil organisms such as microarthropods and earthworms fragment the plant material, thereby making it more available for microbial degradation. In general, weak and aggressive pathogens dominate during the initial stages of degradation. Later, the material is more and more colonised by fungi that are specialised for saprotrophic growth (Frankland 1998; Kjöllér and Struwe 2002). Fresh residue-colonising microorganisms are copiotrophs, which can be considered as r-strategists using easily available carbon sources and maximising their intrinsic growth rate when resources are abundant (Pianka 1970). The microorganisms that colonise residues at later stages of decomposition are oligotrophs, which can be considered as K-strategists. Compared with r-strategists, K-strategists have a slower growth rate, a better ability to degrade recalcitrant organic substances and better survival rates when resources are limited (Bastian et al. 2009).

To sum up, the decomposition of the crop residues is a complex process involving the whole soil biota. *F. graminearum* survival can be controlled by driving the balance of this process.

4.2 Interactions with soil microorganisms

By applying the r- and K-strategy concept to the comparison of the different microorganisms involved in crop residues decomposition, we could consider *F. graminearum* as an r-strategist during its saprotrophic phase because it can grow rapidly when fresh matter is available. This can be linked to the enzymes it excretes in the presence of plant material. The many cellulases, hemicellulases and pectinases that *F. graminearum* produces are important early in the decomposition process (Phalip et al. 2005). The relative abundance of *F. graminearum* can be decreased rapidly by keeping the humidity of wheat residues at a high level, which favours the activity of other microbes and can hence hamper *F. graminearum* growth (Burgess and Griffin 1968). Indeed, *F. graminearum* seems to be a poor competitor over time, particularly compared with other *Fusarium* species. For instance, the amount of *F. graminearum* found on wheat residues rapidly decreases whereas those of *F. solani* (Mart.) Sacc., *F. oxysporum* Schlecht., *F. poae* and *F. sporotrichioides* increase. All these species are known to have better saprotrophic capacity in crop residues or in soil than *F. graminearum* (Pereyra and Dill-Macky 2008). Nevertheless, *F. graminearum* can survive on residues for more than 24 months (Pereyra et al. 2004). *Fusarium poae* and *F. sporotrichioides*, also involved in Fusarium head blight, are less aggressive than *F. graminearum* on plants, but they have a better saprotrophic capacity and can outcompete other organisms on residues (Fernandez et al. 2008). Few studies have been carried out about the interactions that occur among the different pathogens on residues in the field, but experiments in controlled conditions emphasise how specific these interactions are (Simpson et al. 2004; Velluti et al. 2000). *F. culmorum* growth and *M. nivale* var. *majus* growth were both limited when the strains were grown together in the same liquid medium, compared with their respective growth rates when they were inoculated alone (Simpson et al. 2004). On wheat seedlings, *F. culmorum* thoroughly inhibited *M. nivale* var. *nivale* and var. *majus* growth; however, when *M. nivale* var. *majus* was established before *F. culmorum*, it co-suppressed *F. culmorum* growth. Similarly, the presence of *F. graminearum* reduced *F. moniliforme* and *F. proliferatum* (T. Matsushima) Nirenberg growth on sterile maize grains, whereas its own growth was not affected by the other two species (Velluti et al. 2000).

Moreover, intraspecific diversity of phenotypic traits within *F. graminearum* species leads to interactions between *F. graminearum* populations for crop residues colonisation.

This can be revealed through different levels of aggressiveness or different chemotypes among any given set of *F. graminearum* strains interacting with host plants. This can also be revealed through the intrinsic competitive skills used by different *F. graminearum* populations to rapidly colonise and efficiently exploit crop residues such as maize stalks (Miedaner et al. 2004; Naef and Defago 2006).

The role of deoxynivalenol — and of mycotoxins in general — in the multitrophic interactions *F. graminearum* faces during its saprotrophic growth, is poorly understood. While the deleterious impact on animals, including humans, is rather well studied (Nielsen et al. 2011a, b; Pestka 2010; Sampietro et al. 2010), the impact it might have on soil organisms has less been considered (Abid et al. 2011). The different studies results are conflicting. In some cases, mycotoxins have been shown to have antimicrobial activities against *Trichoderma atroviride* P. Karst. (Lutz et al. 2003), and a possible regulatory role in bacterial–fungal interactions has been proposed (Duffy and Defago 1997), but in other case, the comparison of toxigenic and non-toxigenic *F. graminearum* strains showed that there was no evidence that deoxynivalenol played a role in the defence against *T. atroviride* (Naef et al. 2006). Moreover, the potential impact of mycotoxins on the microflora can be reduced by bacteria able to degrade these mycotoxins (Awad et al. 2010; Fuchs et al. 2002). Therefore the putative competitive advantage mycotoxins might confer to *F. graminearum* versus other antagonistic colonisers remains to be demonstrated.

F. graminearum seems to be a poor competitor over time for crop residues colonisation, even among *Fusarium* species. The enhancement of the residues decomposition processes by other organisms could be efficient to limit *F. graminearum* survival.

4.3 *Fusarium* species displacement on residues

It is possible to limit *F. graminearum* survival and growth on residues by adding microorganisms that can outcompete it. Already known biocontrol agents like *T. atroviride* and *T. harzianum* Rifai (Naef et al. 2006), or *Clonostachys rosea* (Link) Schroers, Samuels, Seifert and W. Gams (Gromadzka et al. 2009) are among the possible candidates. It is also possible to screen species isolated from residues (Luongo et al. 2005; Singh et al. 2009). The latter approach increases the likelihood that the microorganisms are adapted to the environment of the studied residues. Magan and Lynch (1986) tested ten fungal isolates for their capacity to colonise straw residues at different temperatures and at different water potentials. Among them, only *Penicillium* spp. and *F. culmorum* were able to grow at a low water potential, confirming the role played by water availability in competitive interactions. *T. harzianum*, *F. equiseti* and *F. nygamai* L.W.

Burgess & Trimboli, which were all isolated from wheat stubble, have been shown to reduce *F. pseudograminearum* growth on culture medium (Singh et al. 2009). The displacement of *F. pseudograminearum* by these fungal isolates on barley straw was tested at different temperatures (5–35°C) and at different water potentials (–0.3 to –5.0 MPa). *T. harzianum* was the most efficient antagonist but displaced *F. pseudograminearum* very poorly at low temperatures and low water potentials. *F. equiseti* and *F. nygamai* gave moderate displacement. *F. equiseti* was the most efficient at low temperatures and low water potentials, showing that field conditions need to be taken into account when looking for an efficient antagonistic agent. *C. rosea* isolates were found to suppress sporulation of *F. graminearum* and *F. culmorum* on wheat straw and to suppress sporulation of *F. graminearum*, *F. culmorum*, *F. proliferatum* and *F. verticillioides* (Sacc.) Nirenberg on maize stalks under controlled conditions. When tested under field conditions, however, their efficiency was limited (Luongo et al. 2005).

With regard to sexual reproduction, a *Microsphaeropsis* sp. isolate significantly reduced ascospore production by *F. graminearum* on wheat and maize residues under controlled conditions (Bujold et al. 2001). *Microsphaeropsis* sp. suppressed ascospore production when inoculated on wheat residues 2 weeks before the pathogen was inoculated, concomitantly, or 4 weeks later. Furthermore, it still suppressed ascospore production when inoculated on maize residues 6 weeks after the pathogen. However, *Microsphaeropsis* sp. significantly reduced the production of perithecia on crop residues under field conditions at only a few sampling dates. This highlights once again that although the antagonist can be found efficient under laboratory conditions, field application may not be so easy.

Along with their effect on pathogen growth and sporulation, competitors for residues can also decrease mycotoxin production. When *T. atroviride* and *F. graminearum* were inoculated together on autoclaved maize leaves, deoxynivalenol production by *F. graminearum* was 36 % lower per biomass unit of the pathogenic fungus than when *F. graminearum* was inoculated alone (Naef et al. 2006).

To sum up, the use of specific outcompeting microorganisms could be an efficient option to limit *F. graminearum* survival on crop residues. Several fungal species with an interesting effect under laboratory conditions were identified. However, the field efficiency of these fungal strains is still limited, highlighting the difficulties to transpose laboratory experiments to field application.

4.4 Interactions with the soil fauna

The soil animals influence pathogenic fungi and other soil microbes directly by feeding on them and by dispersing them. They also have an indirect influence: they alter the

physical environment by fragmenting organic matter, burrowing through the soil, mixing it and by depositing faeces (Brown 1995; Coleman and Crossley 1996; Swift et al. 1979). The soil fauna is often divided up into groups, which is useful for understanding how animals move within the soil and influence soil structure and other abiotic and biotic conditions (Coleman and Crossley 1996; Lavelle and Spain 2001; Swift et al. 1979). The smaller soil animals grazing on mycelia with selective feeding habits have an important influence on saprotrophically growing fungi. The larger soil animals, which are less selective in their feeding habits, are important consumers of plant residues and soil. Their main influence can probably be seen through their effects on the fragmentation of organic material and on soil mixing (Friberg et al. 2005).

Anecic earthworms, such as *Lumbricus terrestris* L. and *Aporrectodea longa* Ude, which take fresh litter from the soil surface and pull it down into the soil through their burrows, can reduce the quantities of fungal pathogens such as *Fusarium* spp. (Moody et al. 1996). The fact that infested wheat straw with high levels of deoxynivalenol was incorporated faster than straw with low levels of deoxynivalenol shows that deoxynivalenol is not repellent for *L. terrestris* and possibly attractive (Oldenburg et al. 2008). Earthworms also grew better on infested straw than on non-infested straw, either because the decomposition by *F. graminearum* made compounds in the straw more easily available or because the fungal biomass itself was a source of nutrients for them. Since, fungal biomass and deoxynivalenol degradation increased in the presence of earthworms, it is possible that earthworms take part in deoxynivalenol degradation, maybe through the activity of their associated gut microorganisms (Schrader et al. 2009).

It seems that soil animals able to feed on *F. graminearum*-infested crop residues could participate in *F. graminearum* survival control.

5 Importance of agricultural practices for the disease development

5.1 Preceding crop

The preceding crop is an important factor determining the risk for *Fusarium* diseases on wheat (Blandino et al. 2010; Klem et al. 2007; Muller et al. 2010). If the preceding crop is a good host of the pathogen, the disease risk increases due to the inoculum initially present on the crop. The severity of *Fusarium* head blight caused by *F. graminearum* on wheat and the amount of mycotoxins produced have been found higher after maize than after soya, and continuous wheat cropping implied a higher risk of crown rot development caused by *F. graminearum* than a wheat-pea or wheat-

fallow rotation (Dill-Macky and Jones 2000; Smiley et al. 1996; Teich and Hamilton 1985). Variations also exist among host plants: the disease is more severe after maize or durum wheat than after wheat or barley due to the quantities of residues produced and to their chemical composition. Schaafsma et al. (2005) found the number of viable propagules trapped at anthesis in wheat fields planted on maize or wheat stubble higher than the number of viable propagules in wheat fields following non-host crops, and the highest number of propagules was found after maize.

The composition of the fungal community causing *Fusarium* head blight changes depending on the preceding crop. In a survey performed in New Zealand on the community composition of *Fusarium* fungi isolated from harvested wheat grains in relation to the preceding crop, *F. graminearum* was recovered, along with *F. avenaceum*, *F. poae* and *F. culmorum* (Cromey et al. 2002). In each case, *F. graminearum* was the most common species. *F. graminearum* quantities were highest after maize, whereas *F. avenaceum* and *F. poae* quantities were highest after other crops. Where crown rot and *Fusarium* head blight were caused by *F. graminearum* and *F. culmorum*, the stem-bases were more frequently colonised by *F. culmorum* than by *F. graminearum*, but the situation was reversed on ears. And in this case, after maize, the stem-base disease was generally reduced whereas head blight increased (Bateman et al. 2007).

Most studies about the effects of different preceding crops on the development of *Fusarium* fungi were carried out on crops that are classically included in major rotation systems, such as wheat, maize or rape (Dill-Macky and Jones 2000; Klem et al. 2007; Muller et al. 2010). It could be worth assessing the role of specific, less frequently studied intermediate crops such as Indian mustard (*Brassica juncea* (L.) Czern & Coss), which has been shown to suppress *F. graminearum* growth (Kirkegaard et al. 1996; Sarwar et al. 1998).

Briefly, preceding crop is an important factor in the development of *Fusarium* head blight on wheat. Using a host of the disease as preceding crop carries a risk. Indeed, *F. graminearum* could settle on crop residues, in particular in case of maize which produces high quantities of residues. More care must be paid to the crop rotation scheme to limit the risk of *Fusarium* head blight development.

5.2 Soil tillage

Inversion tillage generally decreases the risk of *Fusarium* head blight compared with non-inversion tillage (Dill-Macky and Jones 2000; Fernandez et al. 2008; Steinkellner and Langer 2004). Several factors can explain why tillage can affect plant disease. Infection caused by splash dispersal

during rainfalls or overhead irrigation is increased in the presence of large amounts of infested crop residues at the soil surface (Bateman 2005; Osborne and Stein 2007; Sutton 1982). Bateman (2005) found that the presence of plant material infested by *F. culmorum* on the soil surface 3–4 weeks before anthesis was necessary to cause infection on ears. As for the preceding crop, tillage can have different effects on the different diseases caused by the same pathogens spectrum. In a study comparing disease on stem-bases and on ears, infection on stem-bases, mainly caused by *F. culmorum*, was decreased by non-inversion tillage, whereas infection on ears, mainly caused by *F. graminearum*, was increased (Bateman et al. 2007). However, a test using plating method to determine whether the quantity of *F. culmorum* in a soil sampled to a 10-cm depth was affected by soil tillage showed that the number of propagules per gram of soil was higher with non-inversion tillage than with inversion tillage (Bateman et al. 1998). As already mentioned, the fungus can survive in soil for a extend periods (more than 2 years) despite low O₂ availability and unfavourable abiotic conditions, but it cannot grow or produce ascospores (Champeil et al. 2004; Khonga and Sutton 1988).

Tillage has an effect on the decomposition rate of residues. Decomposition of buried residues is faster and more complete than decomposition of surface residues. Pereyra et al. (2004) found that for wheat residues that were buried for 24 months, only 2 % of dry matter remained, whereas 25 % remained when the residues were left at the soil surface. In a comparative study between barley straw and red clover foliage (*Trifolium pratense* L.), the limited contact between the soil matrix and the residues affected decomposition dynamics, particularly in the case of straw residues, which are rich in cellulose and hemicelluloses (Henriksen and Breland 2002). This slow decomposition may be due to insufficient colonisation and growth of holocellulose-degrading microorganisms. The influence of soil tillage on the composition of microbial communities was confirmed by the analysis of bacterial and fungal communities during the decomposition process. The genetic structure of communities on residues is specific to residue location within the soil (soil surface or incorporated in soil; Nicolardot et al. 2007). Comparison of buried and non-buried residues showed that the quantity of *F. graminearum* inoculum was twice as high on non-buried residues as on buried residues. Indeed, a slower decomposition at the soil surface allows a longer-lasting availability of nutrients that are essential for *F. graminearum* development (Pereyra et al. 2004). A positive effect of reduced tillage is that the soil fauna is better preserved and can play a more active role in the decomposition and mineralization of crop residues, thus limiting habitats for saprotrophically surviving plant pathogenic fungi.

Different tillage practices affect the presence of weeds. Weeds can be a source of inoculum: in particular, *F. graminearum* inoculum has been found on *Festuca*, *D. sanguinalis*, *Setaria* spp., *L. multiflorum* and *C. dactylon*. When *F. graminearum* was the most common isolated species, other fungi belonging to the complex such as *F. avenaceum*, *F. sambucinum* and *F. poae* were also found (Pereyra and Dill-Macky 2008). Over the years, the composition of fungi causing Fusarium head blight founds on weeds changes. In a study by Inch and Gilbert (2003b), *F. graminearum* was found on 11 out of 34 grass species investigated. *F. sporotrichioides*, *F. equiseti*, *F. avenaceum*, *F. culmorum* and *F. poae* were isolated too, but only *F. graminearum* and *F. sporotrichioides* were isolated in June. In July, *F. equiseti* and *F. culmorum* were isolated in addition to *F. graminearum* and *F. sporotrichioides*, while in August, all species were isolated. Although weed removal has been an important part in the control of different fungal plant diseases for many decades (Mantle et al. 1977; Miedaner et al. 2011), it is clear that the reduction soil tillage and sustainable pesticide use are clearly going to bring about with them a new focus on the role of weeds in Fusarium head blight mediation (Landschoot et al. 2011; Postic et al. 2012).

Shortly, soil tillage is an important factor in the development of Fusarium head blight on wheat. Inversion tillage reduces the risk of disease development in comparison to non-inversion tillage. Inversion tillage (1) hides the primary inoculum infecting wheat ears and prevents splash dispersal, (2) enhances the residues decomposition process and thus limits *F. graminearum* survival, and (3) allows controlling weed species which could be a source of *F. graminearum* inoculum.

5.3 Fertilization and pesticides

The fungi in the complex causing Fusarium head blight are able to use all forms of nitrogen; however, the effects of fertilizers are mainly indirect and mediated via increased plant vigour (Huber and Watson 1974). Different forms of nitrogen have different effects on the survival of pathogenic *Fusarium* spp. On one hand, in some cases, the number of propagules of *F. culmorum* in the soil and of *F. graminearum* on residues increases with inorganic nitrogen fertilization and with the application of calcium ammonium nitrate, respectively (Bateman and Coskun 1995; Lemmens et al. 2004; Yi et al. 2002). On the other hand, urea can hinder the reproduction of fungi, inhibit the formation of chlamydospores and also prevent ascospore maturation (Teich 1989).

The herbicides used can influence inoculum levels. As weeds can be inoculum source, applying herbicides could reduce the risks of disease break-outs; however, little information is available about the direct effect of herbicides on *F. graminearum*, or about the way its saprotrophic ability could

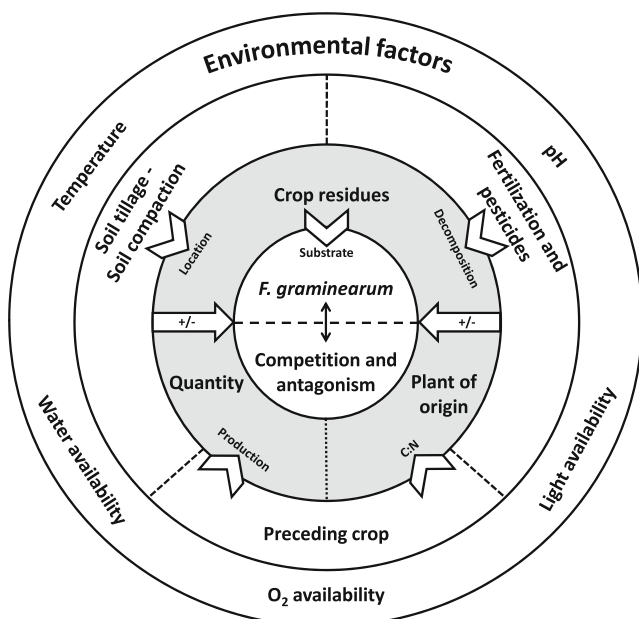


Fig. 4 Saprotrophic survival of *Fusarium graminearum*. Crop residues are the main habitat of *F. graminearum*. On the one hand, they provide spatial and trophic resources the fungus has to exploit in interaction with the rest of the microflora and the soil fauna. On the other hand, they buffer the impact of environmental factors, including agricultural practices

be affected by their presence. Some glyphosate-based herbicides can stimulate *F. avenaceum* and *F. graminearum* growth, under *in vitro* conditions as well as on crop residues in the field, which leads to an increase in wheat stem-base and ear infections (Fernandez et al. 2009; Hanson and Fernandez 2003). Weed control with glyphosate seems to provide a source of energy for *Fusarium* leading to a proliferation of populations. The numbers of other fungal species decrease when glyphosate is used, suggesting important changes in the structure of fungal communities that should in turn affect their functioning.

Data from European surveys have recently shown that organically produced cereal grains have an equal or a lower level of *Fusarium*-generated mycotoxins than conventionally produced cereals (Bernhofs et al. 2010; Birzele et al. 2002; Edwards 2009; Meister 2009). There are currently no clear explanations for that fact, but one factor may be differences in the microflora associated with the different cropping systems.

To summarise, little is known about the effect of fertilizers and pesticides on *F. graminearum* saprotrophic survival. Some glyphosate-based herbicides may stimulate *F. graminearum* survival by changing the structure of fungal communities and providing a source of energy.

6 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.

Figure 4 shows the proposed model exposing the role of the various factors that affect *F. graminearum* survival on crop residues. Depending on environmental factors, it is able to survive on crop residues, grow, and produce conidia and sexual structures which provide the primary inoculum causing disease on wheat heads. The development of *F. graminearum* is favoured by the presence of large amounts of residues and by nutrient rich residues, with a low C/N ratio. Since *F. graminearum* appears to be a poor competitor over time compared to other organisms that colonise crop residues, strategies based on competition for the growth substrate could be an efficient way to control the production of primary inoculum. Some fungal species have been found to suppress sporulation and ascospore production by *F. graminearum* under controlled conditions in that way, but their efficiency still remains to be confirmed under field conditions. In addition, strategies that favour residue decomposition, via the activity of the soil's microflora and fauna, may reduce *F. graminearum* survival.

Since *F. graminearum* overwinters on crop residues, agricultural practices including crop rotation and residue management play a large part in Fusarium head blight management. Primary inoculum production can be limited by using a non-host plant as a preceding crop. Inversion tillage buries the primary inoculum and thus prevents inoculum being splashed up to wheat heads. In addition, inversion tillage favours the decomposition of crop residues in comparison with non-inversion tillage. Finally, inversion tillage makes it possible to control the source of *F. graminearum* inoculum provided by weed species.

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