Title: How can a knowledge of microbiota-pathogen interactions in cereal cropping systems help us to manage residue-borne fungal diseases?

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Abstract
The epidemiological contribution of crop residues as a source of inoculum for fungal diseases on plants, especially in cereal cropping systems, is well established. However, microbial ecologists have long reported positive effects of crop residues on the stability and productivity of several agrosystems. For this reason, no-till practices have become increasingly widespread, leading to the expression of trade-offs, or even incompatibilities, between different agro-ecological challenges. In this context, we propose a literature-based reflection on how to bridge the gap between "crop debris management" and "enhancing the action of microbes as direct or indirect biological control agents". Most studies focusing on the microbiota have suggested that microbial communities should be taken into account in plant disease management, but we still know much less about their ecological interaction with pathogens in the crop residue compartment than in the phyllosphere or rhizosphere. In this review, we provide an overview of what is currently known about the impact of residues on plant disease epidemics and describe how microbial interactions on these residues could be exploited to develop innovative crop protection strategies. Starting from the classical view of residues as a source of inoculum, we considered possibilities for the quantitative management of residues in crop protection. We describe residues as a transient half-plant/half-soil
compartment constituting a key fully fledged microbial ecosystem. We focus on microbial communities, the changes in these communities over time and the factors influencing them. Finally, we discuss how these communities present on residues and their interactions with pathogens could be used: from the identification of beneficial groups of microorganisms naturally present to their preservation, rather than the introduction of exogenous biocontrol agents as a “treatment”.

**Keywords**

Agroecology, crop residues, fungal plant pathogen, microbiota, microbial communities, plant disease epidemiology, primary inoculum
Crop residues (i.e. the parts of the crop plant not harvested), historically considered as waste, are now seen as a source of essential environmental services necessary for the perpetuation of productive agrosystems (Smil, 1999). No-tillage practices or conservation tillage (i.e. minimal soil disturbance) systems allow the formation of soil organic carbon, improve soil structure, prevent erosion, filter and retain water, and reduce evaporation (Derpsch et al., 2010; Govaerts et al., 2007). However, these practices, which are becoming increasingly common worldwide (Awada et al., 2014; de Freitas and Landers, 2014; Kertész and Madarász, 2014), increase the risk of "residue-borne" or "stubble-borne" disease epidemics, due to the presence of crop residues, which can act as a source of primary inoculum, on the soil surface (Bailey, 1996; Bailey and Lazarovits, 2003; Bockus and Shroyer, 1998). Indeed, several leaf-, stem-, and head-infecting microorganisms are known to survive on crop residues between cropping seasons (Bockus and Shroyer, 1998; Cook et al., 1978). Residue conservation tends to increase the risk of epidemics for many foliar diseases on cereals (Bailey, 1996; Bailey and Lazarovits, 2003; Bockus and Shroyer, 1998), particularly those initiated by ascospores produced by fruiting bodies resulting from sexual reproduction (perithecia). Wheat pathogens, such as *Pyrenophora tritici repentis* (Adee and Pfender, 1989), *Ocimumacula yallundae* (Vero and Murray, 2016), and *Zymoseptoria tritici* (Suffert and Sache, 2011), have been shown to be more likely to infect the subsequent crop if wheat residues are present in the field.

Not only has there be a change in agricultural techniques, but epidemiological considerations have expanded to include new concepts, such as the “pathobiome”, defined as the pathogen and the cohort of microorganisms associated with it and likely to influence its persistence, transmission and evolution (Vayssier-Taussat et al., 2014). This concept encompasses the “microbiota” (defined as the microorganisms present in the environment, whereas the “microbiome” is defined as the genes of the microorganisms present in the environment;
Marchesi and Ravel, 2015) as a distinct additional node, influenced by the three components of the classic epidemiological triangle (Figure 1; Foxman and Rosenthal, 2013; Hanson and Weinstock, 2016). A particular feature of this concept is the redefinition of the “pathogen” responsible for disease as one of or many species interacting with other microorganisms present in the same ecological niche, which can affect each other positively or negatively. Disease expression seems to be the result of an imbalance between a potentially pathogenic species and the rest of the microbial community on host tissues, rather than simply a consequence of the presence of this pathogen species (Vayssier-Taussat et al., 2014). The situation is often rendered more complex by the presence of several microorganisms reported to act as crop pathogens or endophytes, which can develop without symptom development, or as saprophytes in the soil and plant residues. Theoretically, some of these other microorganisms could be favored by management practices to reduce pathogen propagation and infection of the plant. The key questions are: which microorganisms? And how could they be favored?

Despite the key role of residues in agrosystems, in terms of both soil conservation and disease risk, the communities present in this compartment have been little studied, while a large numbers of studies focused on plant microbiota, the detritusphere and bulk soil. Most studies have focused on the impact of residues on soil communities, rather than on the residue itself. In addition, the few studies focusing on crop residues conducted to date were performed in microcosms, with sterilized residues (Bastian et al., 2009; Cookson et al., 1998; Nicolardot et al., 2007), greatly decreasing the complexity of this compartment, which is very rich in natural conditions, as it originates from the plant and is in close contact with soil.

This review, which is designed to be thought-provoking, gathers together knowledge about the impact of residues in plant disease epidemics and describes how interactions between the
microorganisms present on these residues could be exploited to develop innovative crop protection strategies. To this end, we started from the classical view of residues as a source of inoculum, highlighting the limits of their quantitative management. We then move away from this view, by defining the residues as a “compartment” that has strong spatial and temporal relationships with other compartments of the agrosystem, firstly developing a normative static perception, and then focusing on more dynamic processes and interactions. We pass from the notions of substrate to pathobiome by focusing on the microbial communities present on residues, changes in these communities over time and the factors likely to influence these communities. Finally, we reflect on the possible uses of the communities present on the residues and possible interactions with pathogens, considering the possibility of identifying potential biocontrol agents (BCA) through such integrative approaches.

1. Residue management in agrosystems: a brief history

Tillage, defined as the mechanical manipulation of soil and plant residues for seedbed preparation (Reicosky and Allmaras, 2003), has been associated with agriculture for several millennia. The "wooden plow" was developed in Mesopotamia at about 4000 to 6000 BC, and the "Roman plow" was developed at about 1 AD (Lal et al., 2007). The emergence of "modern", "deep plow" tillage dates back to about 1000 AD, when a moldboard was added, making it possible to turn the soil over and, therefore, to bury residues (Lal et al., 2007). Deep tillage systems has several benefits, including greater yields and root length densities for some species (Varsa et al., 1997), but it also has negative effects on the soil. The retention of residues at the soil surface has repeatedly been show to have beneficial effects on soil preservation. The presence of residues prevents water erosion, by reducing the direct impact of raindrops (Chambers et al., 2000; Hobbs, 2007), reducing runoff velocity and giving water longer to infiltrate (Pimentel et al., 1995). It also prevents wind erosion by protecting the soil,
and enhancing the soil’s physical, chemical, and biological properties, resulting in long-term sustainable productivity (Kassam et al., 2015; Verhulst et al., 2010). Conservation agriculture has another positive impact, in that it decreases the emissions from farming activities through the reduction of tillage operations (Govaerts et al., 2007). Due to the negative consequences of tillage in terms of erosion (Borrelli et al., 2017), conservation agriculture and no-tillage practices, and the use of permanent soil cover and rotations (Hobbs, 2007) have steadily increased (from 2.8 million ha in 1973/1974, to 110.8 million ha in 2007/2008; Derpsch et al., 2010).

2. Impact of crop residues on the development of fungal disease epidemics in cereal cropping systems

Despite the benefits of conservation agriculture, the retention of residues at the soil surface can also have a negative effect: the promotion of so-called “stubble-borne” diseases. These diseases, many of which are foliar, are caused by pathogens that can overwinter on residues (in different forms: mycelium, spores, sclerotia), or even carry out part of their life cycles on residues (Dyer et al., 1996; Vero and Murray, 2016), including the production of primary inoculum (Leplat et al., 2013; Shaw and Royle, 1989; Suffert and Sache, 2011; Vero and Murray, 2016). Unburied crop residues, lying on the soil surface and between crop plants in low-tillage systems, can be seen as a “brown bridge” of dead plant material that can harbor multiple pathogenic, saprobic or endophytic species (Thompson et al., 2015). This notion is comparable to the classical notion of a “green bridge” of crop volunteers or alternative weed hosts allowing biotrophic species, such as wheat leaf rust (Puccinia triticina), to survive locally between cropping seasons (Soubeyrand et al., 2017).
2.1. Residues are the main, recurrent source of inoculum for several pathogens (“brown bridge”)

The survival of pathogens on residues seems to be inversely correlated with the degree of residue degradation (Gosende et al., 2003; Hershman and Perkins, 1995; Leplat et al., 2013; Marcroft et al., 2003; Pereyra et al., 2004). The rapid degradation of residues (Leplat et al., 2013; Pereyra and Dill-Macky, 2008; Pereyra et al., 2004; Summerell and Burgess, 1989), or their burial (Bockus and Claassen, 1992; Carignano et al., 2008; Dill-Macky and Jones, 2000; Guo et al., 2005; Jørgensen and Olsen, 2007), may therefore prevent ascospore release. Residue management is a particularly important issue as residues can have a major impact as a recurrent source of inoculum over long periods, often exceeding the interepidemic phase. For instance, ascospores of *Fusarium* species, a pathogen of wheat, may be released for up to 23 months (Pereyra et al., 2004). However, it is difficult to generalize the quantitative impact of residues as an effective source of inoculum (e.g. Morais et al., 2016), because the nature of the survival structures depends on the biology of the pathogen.

2.2. Equivocal relationship between the amount of residues and disease severity

Most disease management strategies target the epidemic phase of the disease, although interepidemic phases are also crucial for pathogen survival. Decreasing the presence of pathogens during this phase (i.e. reducing primary inoculum levels) could, theoretically, limit disease development in the next crop, and even over the next few years. Indeed, for some diseases, a correlation has been established between the amount of primary inoculum at the end of the growing season, and disease severity during the next season. Such a correlation has been demonstrated for *Leptosphaeria maculans* (Lô-Pelzer et al., 2009), *Pyrenophora tritici*
repentis (Adee and Pfender, 1989; Bockus and Claassen, 1992), *Paragonospora nodorum* (Mehra et al., 2015), and *Zymoseptoria tritici* (Suffert et al., 2018).

A number of studies have demonstrated the value of managing the primary inoculum to limit disease severity during the year (Adee and Pfender, 1989; Filho et al., 2016), but the inoculum generated on residues is not always the most important driver of epidemics when several cycles of the disease and environmental factors are considered. This is the case, for example, for polycyclic diseases, in which the secondary inoculum produced during the asexual phase of the pathogen’s life cycle plays a crucial role. The amount of primary inoculum is not always a limiting factor for plant infection (Alabouvette et al., 2006). Consequently, disease control by quantitative residue management alone would not be complete. The burial of residues at a field scale cannot therefore eliminate certain diseases.

3. **Crop residues, a key, shifting platform hosting microbial communities interacting with other compartments**

3.1. **The place of the residues “compartment”, between plant and soil: definitions and concepts**

Crop residues are the part of the crop plant that is not harvested (decaying plant material). Buried and non-buried plant residues can be distinguished (Figure 2) according to their location: above- and below-ground, respectively. This distinction makes perfect sense in terms of the epidemiology of plant diseases, as buried residues have not a positive impact on soil properties but, as they are no longer in the open air, they are no longer a source of inoculum for airborne diseases. It is tempting to adopt the term “residuesphere” to identify the microhabitat consisting of all crop residues, whether buried or non-buried. However, this term
has occasionally been used as a synonym of “detritusphere” (Magid et al., 2006; Sengeløv et al., 2000), which is defined as the soil adjacent to plant residues (Marschner et al., 2011; Pascault et al., 2010a; Poll et al., 2008). The detritusphere is considered to be the part of the soil immediately affected by residue decomposition, and is generally assumed to include the first 6 mm (Bastian et al., 2009; Nicolardot et al., 2007) or 10 mm (Magid et al., 2006) of soil surrounding the residues at all times in stratified experiments. This top layer of the soil is very thin but has high levels of microbial activity (Kuzyakov and Blagodatskaya, 2015). The term “detritusphere” has been defined ambiguously by some authors as the layer of soil including the litter and the adjacent soil influenced by the litter (Gaillard et al., 1999; Ingwersen et al., 2008). An experimental comparison of the various soil zones (residues, detritusphere, and bulk soil) indicated that the bacterial and fungal communities are specific to a residue type in the detritusphere and to the location of residues (Nicolardot et al., 2007). Residue degradation has been shown to induce a particular genetic structure of the microbial community with a gradient from residue to bulk soil. Based on these findings, it was concluded that the residues, detritusphere and bulk soil corresponded to different trophic and functional niches for microorganisms.

Residues should be considered as a distinct microbial substrate (Bastian et al., 2009), characterized by the plant from which they originate, and by their “degradation” stage, implying chemical and physical changes dependent on their position relative to the ground surface. For this reason, as recently highlighted by Kerdraon et al. (Kerdraon et al., 2019) in a study focusing on wheat-oilseed rape cropping systems, residues are not merely a specific “static” compartment and should be viewed as both a fully-fledged matrix and a transient compartment (Figure 3). They originate from the plant (temporal link; see part 3.2), are in close contact with the soil (spatial link; see part 3.3) and decay over the following cropping season, at rates dependent on plant species, cropping practices (Hadas et al., 2004), and year (climate effect).
3.2. The microbial community of residues is inherited from the plant

The plant compartment hosting the “phytobiome” (communities present in and on plants, including the phyllosphere, rhizosphere and endophytic compartments; Figure 2) makes a crucial contribution to the crop residues. Microorganisms are adapted to particular ecological niches and physiological conditions (Grudzinska-Sterno et al., 2016; Larran et al., 2007; Vorholt, 2012) and are driven by numerous biotic and abiotic factors (e.g. temperature, humidity, light; Carvalho and Castillo, 2018), including the plant itself, whether considered at species or genotype level (Bodenhausen et al., 2014; Wagner et al., 2016). The effect of the plant is therefore mainly due to two aspects: (i) it is already colonized by microorganisms that can remain on the residues (e.g. hemibiotrophic pathogens) and (ii) it has different biochemical compositions, which can affect the rate of degradation and the changes in the chemical and physical properties of the residues. These two aspects are closely linked, because the microorganisms present on plants are partly dependent on the biochemistry of the plant (species, genotype), and because these microorganisms can have a reciprocal impact on the plant properties, even before any degradation has occurred (changes in C/N ratio, production of defense compounds by plants in response to colonization by microorganisms, etc.). This aspect must be taken into account when trying to understand how new microorganisms colonize residues and how their microbiota changes over time in the agrosystem.

3.2.1. Pathogenic and non-pathogenic microorganisms present on plants can remain on the residues and influence the subsequent dynamics of colonization by other microorganisms
The structure of bacterial and fungal communities depends on plant species (Nicolardot et al., 2007). Moreover, plant genotype also determines the structure of communities, particularly in cases of resistance to certain pathogens, but also for endophytes on wheat (Sapkota et al., 2015). Comby et al. (2017) showed that the temporal variation of wheat microbial communities in natural conditions was driven by a succession of plant pathogens. The communities present on plants also depend on the organ considered. This is particularly true for aerial organs and roots, because of the differences between habitats in terms of nutrients and exposure (Comby et al., 2016). However, several species, such as *Cladosporium* sp. and *Michrodochium nivale*, can colonize all parts of the plant (Gdanetz and Trail, 2017; Grudzinska-Sterno et al., 2016). Moreover, the age of each organ has been shown to determine the communities present (Wagner et al., 2016). In some cases, the proportion of pathogenic fungi increases with plant development (Grudzinska-Sterno et al., 2016). Crop rotation does not appear to affect the communities associated with leaves, but does seem to affect root-associated communities, as demonstrated in a wheat-pea rotation (Granzow et al., 2017). In summary, the microbial communities present on the residues at the beginning of their degradation depend on the plant (species, genotype, organ) and on a pool of other organisms that differ according to the events in the plant's life and the environment in which it was grown (biotic and abiotic stresses).

3.2.2. The physicochemical composition of the plant also drives the colonization of residues by specific microorganisms

The biochemical composition of crop residues, which depends on the plant species from which they are derived, is one of the factors determining the structure and diversity of bacterial communities (Baumann et al., 2009; Pascault et al., 2010b). Even after the residues come into contact with the soil, the influence of the plant on residue colonization is evident.
Residue decomposition has been shown to depend on the complex chemical composition of the residues, taking into account the C/N ratio, and the nitrogen and lignin contents of the plant (Kriaučiuniene et al., 2012). The colonizing microbial communities differ between plant species, on identical soils. This has been established, for example, by a comparison between soybean, corn and wheat (Broder and Wagner, 1988), and by a comparison between wheat, rapeseed, and alfalfa, for which "easily degradable" residues underwent faster changes than "recalcitrant" residues, due to differences in the communities present, which consisted mostly of copiotrophic genera (developing preferentially in an environment rich in organic substrates) and oligotrophic genera (developing in an environment poor in organic substrates; Kerdraon et al., 2019; Pascault et al., 2010a). According to Boer (Boer et al., 2005), fungi are the main decomposers of recalcitrant compounds, whereas bacteria break down simple substrates.

3.3. Impact of the soil on changes in the microbial communities of residues during their degradation

Biochemical transformations of wheat residues induce changes in the structure of microbial communities, and these microbial communities have a reciprocal effect, inducing biochemical transformations in the wheat residues hosting them. Bastian (Bastian et al., 2009) described a change in the bacterial and fungal communities present on wheat residues between early stages of decomposition (14 and 56 days after the incorporation of residues into the soil) and later stages (56 to 168 days), which was interpreted as a change in the balance between copiotrophic and oligotrophic organisms. Residue communities are also influenced by cultivation techniques: residues are degraded differently in aerobic and anaerobic conditions (Cookson et al., 1998). This also results in different mobilized communities, including different bacterial and fungal cellulolytic species (Boer et al., 2005), as degradation processes
are not the same (Nicolardot et al., 2007). The functional composition of the microbial communities (cellulolytic vs. lignolytic) depends on the physicochemical properties of the soil, such as pH.

Investigations of the impact of the soil compartment on changes in residue microbial communities during their degradation are subject to two difficulties. First, it is difficult to separate the "plant inheritance" effects (see part 3.2) from the "soil" effect when considering degradation processes, except for species for which the origin can be determined with certainty because of specificities of their life cycle (phyllosphere for certain strictly biotrophic fungi, such as rust or mildew, or bulk soil for strictly telluric bacteria or arbuscular mycorrhizal fungi). This difficult issue has rarely been investigated. The second difficulty is that there are still significant gaps in our knowledge of the functional ecology and diversity of the soil microbial communities responsible for organic matter degradation from non-buried residues. Recent studies were performed under controlled laboratory conditions to characterize the impact of crop residues inputs on the diversity of soil microbial communities (e.g. Bastian et al., 2009; Nicolardot et al., 2007), but the converse is not true. These studies showed that the addition of crop residues to soil led to considerable heterogeneity in soil microbial community diversity, and identified three different zones in the soil: (i) the residues themselves, (ii) the detritusphere (the soil zone in close contact with the residues, see section 3.1), and (iii) the bulk soil. They reported the strongest microbial diversity dynamics on the residues, suggesting that the distinction between these compartments is not only “static” (Figure 2) but also “dynamic” (Figure 3).

Evidence for a major impact of soil compartment on the dynamics of microbial communities can only be indirect (comparison of communities) or partial (characterization of ecological functions). For instance, the importance of soil microorganisms in the mineralization of plant
residues is well established, but the microbial colonization of residues left on the surface (for example in autumn, 3-4 months after harvest, when ascospore production peaks on residues of wheat infected with Z. tritici) is not documented.

Henriksen and Breland (Henriksen and Breland, 2002) showed that the degree of contact between crop residues and the soil matrix, which is determined by the method of residue incorporation, affects decomposition dynamics under both natural and experimental conditions. They showed that poor residue-soil contact reduces the decomposition of structural plant constituents by delaying colonization with microorganisms degrading cellulose and hemicellulose. Some studies have also focused on the location of residues (incorporated vs. left on the soil surface), to analyze the effect of different types of residue management on soil microbial communities during degradation, but very few have looked at the interactions between pathogens present on residues and the microbiota driving residue degradation. However, the richness of the residue compartment, at the interface between the plant and soil communities, suggests potentially interesting prospects for biocontrol.

4. Characterization of the microbial communities in crop residues, which can be seen as a transient but fully fledged half-plant/half-soil compartment, for the sustainable management of residue-borne diseases: towards the identification of potential biological control agents to limit the impact of inoculum sources

This review shows that crop residues, a transient half-plant/half-soil compartment, constitute a key fully fledged microbial ecosystem. The residue microbiota should be taken into account in the management of residue-borne diseases. It may be possible to identify groups of beneficial microorganisms naturally present on residues, which could then be preserved, or
even selected, characterized and used as biological control agents against the pathogens that complete their life cycle on residues.

Certain residue-borne fungal diseases can be managed by decreasing the amount of residues (Bailey and Lazarovits, 2003; Bockus, 1998; Bockus and Claassen, 1992; Guo et al., 2005). For other plant diseases, the management of residues at the field scale may be less effective for decreasing final disease severity and yield losses over time in a sustained manner. Such a decrease could only be achieved by limiting the primary inoculum over a larger scale, considering the sources of local inoculum in a given plot to be sources of inoculum for more distant plots too. The best way to improve crop protection through a purely quantitative management of inoculum sources by cropping practices, therefore involves complex spatiotemporal management, based on more detailed knowledge of the rate at which concentrations of viable ascospores decline with distance from a source, for *Z. tritici*, for example. This review suggests that another, complementary approach could be considered.

Would it be possible for the same amount of residue to reduce the presence and activity of a pathogen in the microbial community of the residues, through interactions with other species: competition for resources, antagonism, or parasitism? If this is, indeed, possible, it would not be performed by classical biocontrol (introduction of an exogenous microorganism, which does not always give satisfactory results in field conditions), but would be through the exploitation of functional, agro-ecological relationships to identify the microorganisms that constitute the “beneficial fraction” of the community and then to promote them. The factors favoring microorganisms must first be identified, and this is an issue of growing importance for both academic and operational research working towards the development of biological control solutions. An accurate descriptive approach and the characterization of interactions within the residue microbiota are required. Next-generation sequencing is a promising
technology for this approach. It provides access to the diversity of “non-culturable” microbes, facilitating the discovery of new species (Lagier et al., 2016) and more detailed community description. Some of the techniques available could be used to characterize the diversity of the microbial communities associated with the pathogen throughout its life cycle, during both epidemic and interepidemic period, even if these periods are cryptic. Non-culturable microorganisms clearly cannot be used for biocontrol methods involving the introduction of exogeneous species, but we need to know more about their activity in natural conditions. It would then be possible to test, in vitro or in planta, the culturable species isolated from residues and identified as potential biocontrol agents, based on integrative strategies focusing on plants during their development (e.g. Gdanetz and Trail, 2017). Moreover, even if such species have an impact on the plant, it is important to be aware that the epidemic phase is probably not the only phase to study. The objective is not to find a species that can replace a fungicide applied during crop growth, but to understand how species, from single taxa to more complex microbial assemblage, can affect primary inoculum levels during the interepidemic period.

There are currently no examples or studies supporting the strategy described above that have led to efficient and practical solutions applied in cereal cropping systems at a large scale. However, some promising results have been obtained. For instance, some microorganisms commonly present in the phyllosphere (P. lilacinus, F. moniliforme var. anthophilum, E. nigrum, Bacillus sp., Cryptococcus sp. and Nigrospora sphaerica) have been shown to affect the germination of Z. tritici spores (Perello et al., 2002), and some members of the microbial community may have an impact on resistance to certain diseases (Ritpitakphong et al., 2016). A number of effects can be targeted on residues, including increasing the rate of residue degradation, shortening the survival of certain organisms and promoting interactions affecting the saprophytic development of pathogens, and the limitation of primary inoculum
production. Some studies have reported beneficial effects of cropping practices, such as decreases in *F. graminearum* survival due to an increase in the population of microbial soil antagonists induced by the addition of green manure to the soil (Perez et al., 2008). A recent study combining metabarcoding and co-occurrence network analysis allowed to profile microbial communities presents in maize residues and their potential interactions with the different pathogenic *Fusarium* species (Cobo-Díaz et al., 2019). The author suggested that these communities present an important amount of taxa that may be of interest as part of biocontrol strategies against Fusarium Head Blight. Given the high diversity of microorganisms on residues, various modes of action could be used to increase biocontrol efficiency (antibiosis, competition, antagonism; Alabouvette et al., 2006; Guetsky et al., 2001). Studies of this kind have been performed on chickpea residues infected with *Didymella rabiei*, for example (Dugan et al., 2005). Diverse modes of action were described for various organisms present on the residues. For example, *A. pullulans* can grow faster than *D. rabiei*, thereby limiting its propagation by competition, and *Clonostachys rosea*, which has mycoparasitic capacity, can decrease or even totally abolish the sexual and asexual reproduction of *D. rabiei*. *Microsphaeropsis*, which is also known to have mycoparasitic capacity (Benyagoub et al., 1998), has been shown to affect the production of *Fusarium graminearum* ascospores on wheat and maize residues (Bujold et al., 2001). Bastian et al. (2009) highlighted the colonization of tailings (sterile tailings deposited on the soil) by bacteria such as *Pseudomonas fluorescens*, *Pseudomonas aurantiaca* and *Pseudomonas putida* and fungi such as *Chaetomium globosum*. All these species have been described as potential biocontrol agents (Clarkson and Lucas, 1993, Cordero et al., 2014; Flaishman et al., 1996; Kildea et al., 2008; Larran et al., 2016; Perello et al., 2002; Pfender et al., 1993; Ramarathnam and Dilantha Fernando, 2006).

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References

Adee, E.A., and Pfender, W.F. (1989). The effect of primary inoculum level of Pyrenophora tritici-repentis on tan spot epidemic development in wheat. Phytopathology 79, 873–877.

Alabouvette, C., Olivain, C., and Steinberg, C. (2006). Biological Control of Plant Diseases: The European Situation. Eur. J. Plant Pathol. 114, 329–341.

Awada, L., Lindwall, C.W., and Sonntag, B. (2014). The development and adoption of conservation tillage systems on the Canadian Prairies. Int. Soil Water Conserv. Res. 2, 47–65.

Bailey, K.L. (1996). Diseases under conservation tillage systems. Can. J. Plant Sci. 76, 635–639.

Bailey, K., and Lazarovits, G. (2003). Suppressing soil-borne diseases with residue management and organic amendments. Soil Tillage Res. 72, 169–180.

Bastian, F., Bouziri, L., Nicolardot, B., and Ranjard, L. (2009). Impact of wheat straw decomposition on successional patterns of soil microbial community structure. Soil Biol. Biochem. 41, 262–275.

Baumann, K., Marschner, P., Smernik, R.J., and Baldock, J.A. (2009). Residue chemistry and microbial community structure during decomposition of eucalypt, wheat and vetch residues. Soil Biol. Biochem. 41, 1966–1975.

Benyagoub, M., Benhamou, N., and Carisse, O. (1998). Cytochemical Investigation of the Antagonistic Interaction Between a Microsphaeropsis sp. (Isolate P130A) and Venturia inaequalis. Phytopathology 88, 605–613.

Bockus, W.W. (1998). Control strategies for stubble-borne pathogens of wheat. Can. J. Plant Pathol. 20, 371–375.

Bockus, W., and Claassen, M.M. (1992). Effects of crop rotation and residue management practices on severity of tan spot of winter wheat. Plant Dis. 76, 633–636.

Bockus, W.W., and Shroyer, J.P. (1998). The impact of reduced tillage on soilborne plant pathogens. Annu. Rev. Phytopathol. 36, 485–500.

Bodenhausen, N., Bortfeld-Miller, M., Ackermann, M., and Vorholt, J.A. (2014). A synthetic community approach reveals plant genotypes affecting the phyllosphere microbiota. PLoS Genet. 10, e1004283.
Boer, W. de, Folman, L.B., Summerbell, R.C., and Boddy, L. (2005). Living in a fungal world: impact of fungi on soil bacterial niche development. FEMS Microbiol. Rev. 29, 795–811.

Borrelli, P., Robinson, D.A., Fleischer, L.R., Lugato, E., Ballabio, C., Alewell, C., Meusburger, K., Modugno, S., Schütt, B., Ferro, V., et al. (2017). An assessment of the global impact of 21st century land use change on soil erosion. Nat. Commun. 8, 2013.

Broder, M.W., and Wagner, G.H. (1988). Microbial colonization and decomposition of corn, wheat, and soybean residue. Soil Sci. Soc. Am. J. 52, 112–117.

Bujold, I., Paulitz, T.C., and Carisse, O. (2001). Effect of Microsphaeropsis sp. on the Production of Perithecia and Ascospores of Gibberella zeae. Plant Dis. 85, 977–984.

Carignano, M., Staggenborg, S.A., and Shroyer, J.P. (2008). Management practices to minimize tan spot in a continuous wheat rotation. Agron. J. 100, 145–153.

Carvalho, S.D., and Castillo, J.A. (2018). Influence of Light on Plant–Phyllosphere Interaction. Front. Plant Sci. 9.

Chambers, B.J., Garwood, T.W.D., and Unwin, R.J. (2000). Controlling Soil Water Erosion and Phosphorus Losses from Arable Land in England and Wales. J. Environ. Qual. 29, 145–150.

Clarkson, J., and Lucas, J. (1993). Screening for potential antagonists of Pseudocercosporella herpotrichoides, the causal agent of eyespot disease of cereals: 1. Bacteria. Plant Pathol. 42, 543–551.

Cobo-Díaz, J.F., Baroncelli, R., Le Floc’h, G., and Picot, A. (2019). Combined metabarcoding and co-occurrence network analysis to profile the bacterial, fungal and Fusarium communities and their interactions in maize stalks. Front. Microbiol. 10.

Comby, M., Lacoste, S., Baillieu, F., Profizi, C., and Dupont, J. (2016). Spatial and temporal variation of cultivable communities of co-occurring endophytes and pathogens in wheat. Front. Microbiol. 7, 403.

Comby, M., Gacoin, M., Robineau, M., Rabenelina, F., Ptas, S., Dupont, J., Profizi, C., and Baillieu, F. (2017). Screening of wheat endophytes as biological control agents against Fusarium head blight using two different in vitro tests. Microbiol. Res. 202, 11–20.

Cook, R.J., Boosalis, M.G., and Doupnik, B. (1978). Influence of crop residues on plant diseases. Crop Residue Manag. Syst. 147–163.

Cookson, W.R., Beare, M.H., and Wilson, P.E. (1998). Effects of prior crop residue management on microbial properties and crop residue decomposition. Appl. Soil Ecol. 7, 179–188.

Cordero, P., Príncipe, A., Jofré, E., Mori, G., and Fischer, S. (2014). Inhibition of the phytopathogenic fungus Fusarium proliferatum by volatile compounds produced by Pseudomonas. Arch. Microbiol. 196, 803–809.

Derpsch, R., Friedrich, T., Kassam, A., and Hongwen, L. (2010). Current status of adoption of no-till farming in the world and some of its main benefits. Biol Eng 3, 25.
Dill-Macky, R., and Jones, R.K. (2000). The effect of previous crop residues and tillage on Fusarium head blight of wheat. Plant Dis. 84, 71–76.

Dugan, F.M., Lupien, S.L., Hernandez-Bello, M., Peever, T.L., and Chen, W. (2005). Fungi resident in chickpea debris and their suppression of growth and reproduction of Didymella rabiei under laboratory conditions. J. Phytopathol. 153, 431–439.

Dyer, P.S., Nicholson, P., Lucas, J.A., and Peberdy, J.F. (1996). Tapesia acuformis as a causal agent of eyespot disease of cereals and evidence for a heterothallic mating system using molecular markers. Mycol. Res. 100, 1219–1226.

Filho, A.B., Inoue-Nagata, A.K., Bassanezi, R.B., Belasque, J., Amorim, L., Macedo, M.A., Barbosa, J.C., Willocquet, L., and Savary, S. (2016). The importance of primary inoculum and area-wide disease management to crop health and food security. Food Secur. 8, 221–238.

Flaishman, M.A., Eyal, Z., Zilberstein, A., Voisard, C., and Haas, D. (1996). Suppression of Septoria tritici blotch and leaf rust of wheat by recombinant cyanide-producing strains of Pseudomonas putida. MPMI-Mol. Plant Microbe Interact. 9, 642–645.

Foxman, B., and Rosenthal, M. (2013). Implications of the Human Microbiome Project for Epidemiology. Am. J. Epidemiol. 177, 197–201.

de Freitas, P.L., and Landers, J.N. (2014). The transformation of agriculture in Brazil through development and adoption of zero tillage conservation agriculture. Int. Soil Water Conserv. Res. 2, 35–46.

Gaillard, V., Chenu, C., Recous, S., and Richard, G. (1999). Carbon, nitrogen and microbial gradients induced by plant residues decomposing in soil. Eur. J. Soil Sci. 50, 567–578.

Gdanetz, K., and Trail, F. (2017). The Wheat Microbiome Under Four Management Strategies, and Potential for Endophytes in Disease Protection. Phytobiomes 1, 158–168.

Gosende, S., Penaud, A., Aubertot, J.N., Schneider, O., and Pinochet, X. (2003). Evolution of soil surface oilseed rape stubbles and their ability to produce spores of Leptosphaeria maculans: preliminary results. Proc 11th Int Rapeseed Congr Cph. Den. 1166–1168.

Govaerts, B., Mezzalama, M., Unno, Y., Sayre, K.D., Luna-Guido, M., Vanherck, K., Dendooven, L., and Deckers, J. (2007). Influence of tillage, residue management, and crop rotation on soil microbial biomass and catabolic diversity. Appl. Soil Ecol. 37, 18–30.

Granzow, S., Kaiser, K., Wemheuer, B., Pfeiffer, B., Daniel, R., Vidal, S., and Wemheuer, F. (2017). The Effects of Cropping Regimes on Fungal and Bacterial Communities of Wheat and Faba Bean in a Greenhouse Pot Experiment Differ between Plant Species and Compartment. Front. Microbiol. 8.

Grudzinska-Sterno, M., Yuen, J., Stenlid, J., and Djurle, A. (2016). Fungal communities in organically grown winter wheat affected by plant organ and development stage. Eur. J. Plant Pathol.

Guetsky, R., Shtienberg, D., Elad, Y., and Dinoor, A. (2001). Combining biocontrol agents to reduce the variability of biological control. Phytopathology 91, 621–627.
Guo, X.W., Fernando, W.G.D., and Entz, M. (2005). Effects of crop rotation and tillage on blackleg disease of canola. Can. J. Plant Pathol. 27, 53–57.

Hadas, A., Kautsky, L., Goek, M., and Erman Kara, E. (2004). Rates of decomposition of plant residues and available nitrogen in soil, related to residue composition through simulation of carbon and nitrogen turnover. Soil Biol. Biochem. 36, 255–266.

Hanson, B.M., and Weinstock, G.M. (2016). The importance of the microbiome in epidemiologic research. Ann. Epidemiol. 26, 301–305.

Henriksen, T., and Breland, T. (2002). Carbon mineralization, fungal and bacterial growth, and enzyme activities as affected by contact between crop residues and soil. Biol. Fertil. Soils 35, 41–48.

Hershman, D.E., and Perkins, D.M. (1995). Etiology of Canola Blackleg in Kentucky and Seasonal Discharge Patterns of Leptosphaeria maculans Ascospores from Infested Canola Stubble. Plant Dis. 79, 1225.

Hobbs, P.R. (2007). Conservation agriculture: what is it and why is it important for future sustainable food production? J. Agric. Sci. 145, 127.

Ingwersen, J., Poll, C., Streck, T., and Kandeler, E. (2008). Micro-scale modelling of carbon turnover driven by microbial succession at a biogeochemical interface. Soil Biol. Biochem. 40, 864–878.

Jørgensen, L.N., and Olsen, L.V. (2007). Control of tan spot (Drechslera tritici-repentis) using cultivar resistance, tillage methods and fungicides. Crop Prot. 26, 1606–1616.

Kassam, A., Friedrich, T., Derpsch, R., and Kienzle, J. (2015). Overview of the worldwide spread of conservation agriculture. Field Actions Sci. Rep. J. Field Actions 8.

Kerdranon, L., Balesdent, M.-H., Barret, M., Laval, V., and Suffert, F. (2019). Crop residues in wheat-oilseed rape rotation system: a pivotal, shifting platform for microbial meetings. Accepted in Microb. Ecol. (BioRxiv 456178.)

Kertész, Á., and Madarász, B. (2014). Conservation agriculture in Europe. Int. Soil Water Conserv. Res. 2, 91–96.

Kildea, S., Ransbotyn, V., Khan, M.R., Fagan, B., Leonard, G., Mullins, E., and Doohan, F.M. (2008). Bacillus megaterium shows potential for the biocontrol of septoria tritici blotch of wheat. Biol. Control 47, 37–45.

Kriauciuniene, Z., Velička, R., and Raudonius, S. (2012). The influence of crop residues type on their decomposition rate in the soil: A litterbag study. Zemdirbyste 99, 227–236.

Kuzyakov, Y., and Blagodatskaya, E. (2015). Microbial hotspots and hot moments in soil: Concept & review. Soil Biol. Biochem. 83, 184–199.

Lagier, J.-C., Khelaifia, S., Alou, M.T., Ndongo, S., Dione, N., Hugon, P., Caputo, A., Cadoret, F., Traore, S.I., Seck, E.H., et al. (2016). Culture of previously uncultured members of the human gut microbiota by culturomics. Nat. Microbiol. 1, 16203.
Lal, R., Reicosky, D.C., and Hanson, J.D. (2007). Evolution of the plow over 10,000 years and the rationale for no-till farming. Soil Tillage Res. 93, 1–12.

Larran, S., Perelló, A., Simón, M.R., and Moreno, V. (2007). The endophytic fungi from wheat (Triticum aestivum L.). World J. Microbiol. Biotechnol. 23, 565–572.

Larran, S., Simón, M.R., Moreno, M.V., Siurana, M.S., and Perelló, A. (2016). Endophytes from wheat as biocontrol agents against tan spot disease. Biol. Control 92, 17–23.

Leplat, J., Friberg, H., Abid, M., and Steinberg, C. (2013). Survival of Fusarium graminearum, the causal agent of Fusarium head blight. A review. Agron. Sustain. Dev. 33, 97–111.

Lô-Pelzer, E., Aubertot, J.N., David, O., Jeuffroy, M.H., and Bousset, L. (2009). Relationship between severity of blackleg (Leptosphaeria maculans/L. biglobosa species complex) and subsequent primary inoculum production on oilseed rape stubble. Plant Pathol. 58, 61–70.

Magid, J., de Neergaard, A., and Brandt, M. (2006). Heterogeneous distribution may substantially decrease initial decomposition, long-term microbial growth and N-immobilization from high C-to-N ratio resources. Eur. J. Soil Sci. 57, 517–529.

Marchesi, J.R., and Ravel, J. (2015). The vocabulary of microbiome research: a proposal.

Marcroft, S.J., Sprague, S.J., Pymer, S.J., Salisbury, P.A., and Howlett, B.J. (2003). Factors affecting production of inoculum of the blackleg fungus (Leptosphaeria maculans) in southeastern Australia. Aust. J. Exp. Agric. 43.

Marschner, P., Umar, S., and Baumann, K. (2011). The microbial community composition changes rapidly in the early stages of decomposition of wheat residue. Soil Biol. Biochem. 43, 445–451.

Mehra, L.K., Cowger, C., Weisz, R., and Ojiambo, P.S. (2015). Quantifying the Effects of Wheat Residue on Severity of Stagonospora nodorum Blotch and Yield in Winter Wheat. Phytopathology 105, 1417–1426.

Morais, D., Gélisse, S., Laval, V., Sache, I., and Suffert, F. (2016). Inferring the origin of primary inoculum of Zymoseptoria tritici from differential adaptation of resident and immigrant populations to wheat cultivars. Eur. J. Plant Pathol. 145, 393–404.

Nicolardot, B., Bouziri, L., Bastian, F., and Ranjard, L. (2007). A microcosm experiment to evaluate the influence of location and quality of plant residues on residue decomposition and genetic structure of soil microbial communities. Soil Biol. Biochem. 39, 1631–1644.

Pascault, N., Nicolardot, B., Bastian, F., Thiébeau, P., Ranjard, L., and Maron, P.-A. (2010a). In Situ Dynamics and Spatial Heterogeneity of Soil Bacterial Communities Under Different Crop Residue Management. Microb. Ecol. 60, 291–303.

Pascault, N., Cécillon, L., Mathieu, O., Hénault, C., Sarr, A., Lévêque, J., Farcy, P., Ranjard, L., and Maron, P.-A. (2010b). In Situ Dynamics of Microbial Communities during Decomposition of Wheat, Rape, and Alfalfa Residues. Microb. Ecol. 60, 816–828.
Perello, A., Simon, M.R., and Arambarri, A.M. (2002). Interactions between foliar pathogens and the saprophytic microflora of the wheat (Triticum aestivum L.) phylloplane. J. Phytopathol. 150, 232–243.

Pereyra, S.A., and Dill-Macky, R. (2008). Colonization of the Residues of Diverse Plant Species by Gibberella zeae and Their Contribution to Fusarium Head Blight Inoculum. Plant Dis. 92, 800–807.

Pereyra, S.A., Dill-Macky, R., and Sims, A.L. (2004). Survival and inoculum production of Gibberella zeae in wheat residue. Plant Dis. 88, 724–730.

Perez, C., Dill-Macky, R., and Kinkel, L.L. (2008). Management of soil microbial communities to enhance populations of Fusarium graminearum-antagonists in soil. Plant Soil 302, 53–69.

Pfender, W.F., Zhang, W., and Nus, A. (1993). Biological control to reduce inoculum of the tan spot pathogen Pyrenophora tritici-repentis in surface-borne residues of wheat fields. Phytopathology 83, 371–375.

Pimentel, D., Harvey, C., Resosudarmo, P., Sinclair, K., Kurz, D., McNair, M., Crist, S., Shpritz, L., Fitton, L., Saffouri, R., et al. (1995). Environmental and Economic Costs of Soil Erosion and Conservation Benefits. Science 267, 1117.

Poll, C., Marhan, S., Ingwersen, J., and Kandeler, E. (2008). Dynamics of litter carbon turnover and microbial abundance in a rye detritusphere. Soil Biol. Biochem. 40, 1306–1321.

Ramarathnam, R., and Dilantha Fernando, W. (2006). Preliminary phenotypic and molecular screening for potential bacterial biocontrol agents of Leptosphaeria maculans, the blackleg pathogen of canola. Biocontrol Sci. Technol. 16, 567–582.

Reicosky, D.C., and Allmaras, R.R. (2003). Advances in Tillage Research in North American Cropping Systems. J. Crop Prod. 8, 75–125.

Ritpitakphong, U., Falquet, L., Vimoltust, A., Berger, A., Métraux, J.-P., and L’Haridon, F. (2016). The microbiome of the leaf surface of Arabidopsis protects against a fungal pathogen. New Phytol. 210, 1033–1043.

Sapkota, R., Knorr, K., Jørgensen, L.N., O’Hanlon, K.A., and Nicolaisen, M. (2015). Host genotype is an important determinant of the cereal phyllosphere mycobiome. New Phytol. 207, 1134–1144.

Sengeløv, G., Kowalchuk, G.A., and Sørensen, S.J. (2000). Influence of fungal-bacterial interactions on bacterial conjugation in the residuesphere. FEMS Microbiol. Ecol. 31, 39–45.

Shaw, M.W., and Royle, D.J. (1989). Airborne inoculum as a major source of Septoria tritici (Mycosphaerella graminicola) infections in winter wheat crops in the UK. Plant Pathol. 38, 35–43.

Smil, V. (1999). Crop Residues: Agriculture’s Largest HarvestCrop residues incorporate more than half of the world’s agricultural phytomass. BioScience 49, 299–308.
Soubeyrand, S., Garreta, V., Monteil, C., Suffert, F., Goyeau, H., Berder, J., Moinard, J., Fournier, E., Tharreau, D., and Morris, C.E. (2017). Testing differences between pathogen compositions with small samples and sparse data. Phytopathology 107, 1199–1208.

Suffert, F., and Sache, I. (2011). Relative importance of different types of inoculum to the establishment of Mycosphaerella graminicola in wheat crops in north-west Europe: Wheat debris as local source of M. graminicola inoculum. Plant Pathol. 60, 878–889.

Suffert, F., Delestre, G., and Gélisse, S. (2018). Sexual reproduction in the fungal foliar pathogen Zymoseptoria tritici is driven by antagonistic density-dependence mechanisms.

Summerell, B.A., and Burgess, L.W. (1989). Factors influencing survival of Pyrenophora tritici-repentis: stubble management. Mycol. Res. 93, 38–40.

Thompson, S., Tan, Y., Shivas, R., Neate, S., Morin, L., Bissett, A., and Aitken, E. (2015). Green and brown bridges between weeds and crops reveal novel Diaporthe species in Australia. Persoonia Mol. Phylogeny Evol. Fungi 35, 39.

Vayssier-Taussat, M., Albina, E., Citti, C., Cosson, J.-F., Jacques, M.-A., Lebrun, M.-H., Le Loir, Y., Ogliastro, M., Petit, M.-A., Roumagnac, P., et al. (2014). Shifting the paradigm from pathogens to pathobiome: new concepts in the light of meta-omics. Front. Cell. Infect. Microbiol. 4.

Verhulst, N., Govaerts, B., Verachtert, E., Castellanos-Navarrete, A., Mezzalama, M., Wall, P., Deckers, J., and Sayre, K.D. (2010). Conservation agriculture, improving soil quality for sustainable production systems. Adv. Soil Sci. Food Secur. Soil Qual. CRC Press Boca Raton FL USA 137–208.

Vero, D., and Murray, T.D. (2016). Occurrence and Survival of Apothecia of the Eyespot Pathogens Oculimacula acuformis and O. yallundae on Wheat Stubble in the U.S. Pacific Northwest. Plant Dis. 100.

Vorholt, J.A. (2012). Microbial life in the phyllosphere. Nat. Rev. Microbiol. 10, 828–840.

Wagner, M.R., Lundberg, D.S., Tijana, G., Tringe, S.G., Dangl, J.L., and Mitchell-Olds, T. (2016). Host genotype and age shape the leaf and root microbiomes of a wild perennial plant. Nat. Commun. 7, 12151.

Figure captions

**Figure 1.** Disease triangle, serving as a conceptual model, presenting the factors that interact to cause a plant disease epidemic, completed by microbiota as a “fourth node”.
Figure 2. Positioning of the crop residues in relation to the other compartments constituting the different ecological niches of an agrosystem.

Figure 3. Representation of the most significant dynamic relationships – flow of microorganisms, biotic interactions, abiotic or cropping effects – between the crop residue, plant and soil compartments in an agrosystem.
Figure 2

- Non-buried plant residues
- Buried plant residues
- Detritusphere
- Soil bulk
- Rhizosphere
- Phyllosphere
- Endosphere
- Dead roots
- Living roots
Plant microorganisms

Residue microorganisms

Effect of plant exudates

Flow of microorganisms

Biotic interactions

Abiotic or cropping effects

Soil microorganisms

Soil properties (texture, structure, pH)

Effect of residue degradation (e.g. green manure)

Abiotic stresses

Host properties (species, genotype)

Effect of cropping system (rotation, soil management)

Effect of abiotic environment (temperature, rainfall, etc.)

Effect of soil management (from tillage to direct drilling)

Effect on plant physiology

Figure 3