

Root Interactions with Nonpathogenic *Fusarium oxysporum*

Hey *Fusarium oxysporum*, What Do You Do in Life When You Do Not Infect a Plant?

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Abstract In this review, we tried to present *Fusarium oxysporum* in an ecological context rather than to confine it in the too classic double play of the nonpathogenic fungus that protects the plant against the corresponding *forma specialis*. Moreover, *F. oxysporum* is sometimes one, sometimes the other, and only the fungus can reveal its hidden face, according to it is or not in front of the target plant. Despite the quality and richness of the studies conducted to date, molecular approaches highlight some of the evolutionary mechanisms that explain the polyphyletic nature of this species, but still they do not identify a nonpathogenic *F. oxysporum*.

This soilborne fungus has primarily an intense saprophytic life, and it finds its place in the functioning of the ecosystem of which it actively occupies all compartments, thanks to an impressive metabolic flexibility and a high enzyme potential. This adaptability is exploited by *F. oxysporum* first to get carbon from different organic sources and energy through variable strategies including nitrate dissimilation under severe anaerobic conditions and also to colonize extreme environments, some of which being dramatically anthropized. This adaptability is also exploited by man for bioremediation of polluted sites, for detoxification of xenobiotic compounds including pesticides, and furthermore for industrial and biotechnological processes. The presence of the fungus in water distribution networks of city stresses again the adaptable nature of the fungus, but more precisely, this highlights the presence of clonal populations worldwide and raises the question of the role of man in the transfer of biological resources.

We conclude in a provocative manner by asking if nonpathogenic *F. oxysporum* would not be the all-purpose fungal tool needed to ensure a good soil functioning.

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1 Introduction

If there are microorganisms, especially soilborne fungi, that fascinate mycologists, plant pathologists, doctors, and microbial ecologists, without forgetting evolutionists, geneticists and taxonomists, *Fusarium* or more precisely *Fusarium oxysporum* is one of those. We should probably also mention in the list that growers and horticulturists are equally concerned with survival, evolution, and activities of *F. oxysporum* Schlecht, but maybe they do not feel the same fascination as the aforementioned corporations. Indeed, *F. oxysporum* is primarily known for its ability to cause disease on a large number of host plants, while the predominant role of this fungus in soils is essentially determined by its saprophytic activity in raw and rhizospheric soils whether they are cultivated or not, by its biochemical activity in anthropic environments, and by its long survival in various environments (Burgess 1981; Bao et al. 2004; Christakopoulos et al. 1991; Holker et al. 1999).

2 To Be or Not to Be a Nonpathogenic *F. oxysporum*?

F. oxysporum is an ascomycete, belonging to the family of Nectriaceae and the order of Hypocreale. This is an asexual fungus whose teleomorph is unknown. Actually, the *F. oxysporum* species complex includes both pathogenic and non-pathogenic populations, the former being split into more than 100 *formae speciales*, each of them being specific of a plant species (Armstrong and Armstrong 1981; Correll 1991; Baayen et al. 2000). This morphological species is now recognized as a species complex because of its high level of phylogenetic diversity (O'Donnell et al. 2009). Phylogenetic analyses also revealed how diverse is the origin of the pathogenicity of most of the various *formae speciales*. Only a few of them such as *F. oxysporum* f. sp. *albedinis*, *ciceri*, and *loti* are monophyletic (Tantaoui et al. 1996; Wunsch et al. 2009; Demers et al. 2014). Therefore, a great effort of research is devoted to characterize the diversity of *formae speciales* of peculiar interest in agriculture (Elias and Schneider 1992; Kistler 1997; Abo et al. 2005; Lievens et al. 2008; Edel-Hermann et al. 2012) and in horticulture (Löffler and Rumine 1991; Lori et al. 2012; Canizares et al. 2015; Lecomte et al. 2016), in order to identify some specific molecular markers allowing to detect and monitor both pathogenic and nonpathogenic populations in the rhizosphere of host plants (Recorbet et al. 2003; Edel-Hermann et al. 2011). However, to date and despite these efforts, it is still not possible to generally discriminate nonpathogenic populations from pathogenic populations except by the fact that a strain is said to be nonpathogenic if it does not cause any symptom on the plant on which it has been inoculated, but even so it is not possible to say whether this strain is definitively nonpathogenic regardless of the plant species. Thus, the very definition of nonpathogen is blurred because it relies on the absence of a trait that can only be expressed by a pathogenic strain in the presence of the host plant on which it is

specifically subservient; we talk about compatibility. So, while highlighting that the polyphyletic nature of the origins of the pathogen status has been acquired in the course of evolution by a fungus that originally is not pathogenic, doubt always exists that a strain incapable of causing symptoms on a given plant is not pathogen of a plant species with which the compatibility was not tested. Nevertheless, the notion of risk associated to this doubt is limited and should not be considered as a foil to the positive role that *F. oxysporum* plays in the biological functioning of the soil and can also play in the protection of plants as a biocontrol agent. Indeed, the already mentioned polyphyletic nature of the origin of pathogenicity in most of the *formae speciales* can be explained especially by the presence and mobility of a large number of transposable or repetitive elements, responsible for timely and random mutations in the genomes of pathogenic strains, and by horizontal transfers of chromosomal regions (Daboussi and Langin 1994; Daviere et al. 2001; Ma et al. 2010; Inami et al. 2012; Schmidt et al. 2013). The presence of many transposable elements in *F. oxysporum*, as in other Deuteromycetes, is probably a consequence of the asexual lifestyle of these fungi and the resulting absence of the meiosis process that normally eliminates repetitive elements (Daboussi 1996). In the case of *formae speciales*, it can be assumed that the ongoing compatible interaction of the pathogen with the plant is an additional selection pressure that strengthens the interest for the phytopathogenic fungus to have generators of diversity and adaptation mechanisms to overcome the defense reactions opposed by the plant. In the case of the few nonpathogenic populations that have been studied so far on that point, it seems they harbor much less transposable elements than pathogenic strains (Migheli et al. 1999). Therefore, one could assume a greater genetic stability from a nonpathogenic population than from a pathogenic population. However, this putative genetic stability for a given population is probably compensated by an incredible diversity within the species giving *F. oxysporum* the ability to colonize a huge variety of environments (Edel et al. 2001; Lori et al. 2004; O'Donnell et al. 2004; Sautour et al. 2012). In addition, the host pathogen-plant compatibility is a mark enabling to appreciate the diversity and evolutionary history of a given *forma specialis*. This kind of reference is not available for the nonpathogenic populations, and although nonpathogenic strains are generally used as a control in the analyses of diversity of pathogenic populations, rare phylogenetic studies are dedicated to the evolutionary history of nonpathogenic populations; therefore, it is difficult to comment on their genetic stability (Inami et al. 2014).

3 Is *F. oxysporum* Only a Soilborne Fungus?

The geographic distribution of *formae speciales* is probably affected by that of host plants and by anthropogenic activities; however, all the various data in the literature for many years issuing from local surveys have shown that *F. oxysporum* occurs primarily in soils in most parts of the world without recourse to pathogenesis (Park 1963; McKenzie and Taylor 1983; Backhouse et al. 2001). Anyway, the

terminology “nonpathogenic” is a default appellation regarding the very likely initial saprotrophic status of this species complex, and studies on the ecology of *F. oxysporum* do not discriminate between pathogenic and nonpathogenic populations. So we will do the same. The places over the world where *F. oxysporum* can be found include natural extreme conditions such as saline soil habitats of the hot arid desert environment (Mandeeel 2006), tropical dry forests (Bezerra et al. 2013), Arctic circle (Kommedahl et al. 1988), and environments affected by human activities such as industrially polluted sediments (Massacesi et al. 2002), metal mine wastes (Ortega-Larrocea et al. 2010), biofilms in household appliances such as washing machines (Babic et al. 2015), and water system of hospitals (Anaissie et al. 2001; Steinberg et al. 2015). It is likely that the diversity hosted by *F. oxysporum* explains the adaptation of the fungi to various niches under various soil and climatic conditions, as well as in water and in the air. Their concentration was estimated to vary between 10^2 and 10^4 propagules per gram of soil (Park 1963; Alabouvette et al. 1984; Larkin et al. 1993,) while it is much less (a few propagules per liter) in seawater or springwater (Palmero et al. 2009). It can reach up to 10^3 propagules per mL when accidentally colonizing water pipes (Sautour et al. 2012). Spores of *F. oxysporum* have been found associated with rain dust (0.1–45 propagules per gram of dust) and transported over long distances including overseas (Palmero et al. 2011). Spores of *F. oxysporum* are also found in the air outdoor as well as in air-conditioned indoor environments (Debasmita et al. 2014; Khan et al. 2009). So clearly *F. oxysporum* is a ubiquitous fungus that is able to adapt to many types of environments, although it is more frequently encountered in the soil where its density is important both in cultivated and noncultivated ecosystems. Focus is generally made on the diversity of pathogenic populations to understand the origins of this particular trait (Baayen et al. 2000; Groenewald et al. 2006; Luongo et al. 2015; O’Donnell et al. 1998, 2004). However, many studies have revealed an incredible intraspecific diversity within *F. oxysporum* (Demers et al. 2015; Edel et al. 2001; Edel-Hermann et al. 2015; Laurence et al. 2012; Lori et al. 2004). It is not forbidden to think that this diversity, although it is often assessed by the analysis of noncoding DNA regions, could explain the ability of *F. oxysporum* to colonize such different environments, among which is the rhizosphere of putative host plants. Abundant and more or less specific exudates released by plant roots in the rhizosphere are a main food source for microorganisms and a driving force of their population density and activities. *F. oxysporum* populations are particularly affected by this privileged habitat, and they are actively involved in the colonization of the rhizospheric soil, the rhizosphere, and also root tissues (Fravel et al. 2003; Landa et al. 2001; Ling et al. 2012; Toyota and Kimura 1992). The selective nature of root exudates linked to the genotype of the host plant determines the composition of the populations of *F. oxysporum* associated with the plant (Edel et al. 1997; Demers et al. 2015). Actually, all the strains do not respond in the same way to released exudates, what explains that the abundance ratios between strains of the same population are different from one to another rhizosphere. This difference in ability to use root exudates of a given plant depends on the own characteristics of each strain but is not

linked to the pathogenicity or nonpathogenicity of the strains (Steinberg et al. 1999a, b). Consequently, the ability in using efficiently the root exudates determines the issue of the competition for trophic sources between pathogenic and nonpathogenic *F. oxysporum* and therefore the selection for efficient biocontrol agents (Eparvier and Alabouvette 1994; Olivain et al. 2006) (see below). Nonpathogenic strains of *F. oxysporum* can cross the epidermis cells of the root surface, but they are unable to cause disease (Olivain and Alabouvette 1997). They colonize the root cortex of a plant and may establish as endophytes (Belgrove et al. 2011; Demers et al. 2015), but the main point is that this narrow interaction between nonpathogenic *F. oxysporum* and the host-plant results in the so-called priming effect, i.e., the implementation of defense reactions of the plant that slow down their progress and prevent any further invasion by a pathogenic strain (Aime et al. 2013; Benhamou and Garand 2001). Similarly to the absence of preferential selection between pathogenic and nonpathogenic populations of *F. oxysporum* at the root surface of the host plant (Olivain et al. 2006), there is no clear genetic differentiation in the composition of endophyte populations and rhizosphere populations (Demers et al. 2015).

All these interactions in the rhizosphere of the host plant between pathogenic and nonpathogenic populations of *F. oxysporum* reveal protective ability of the latter against the pathogen and invite to consider the use of nonpathogenic strains in biocontrol strategy against *formae speciales* of *F. oxysporum* or other pests (Alabouvette et al. 2009; Vos et al. 2014).

4 Would There Be a New Robin Hood in the Rhizosphere of Plants to Be Protected?

Evidence of a possible role of nonpathogenic *Fusarium* spp. in controlling pathogens resulted from the observation that soils suppressive to *Fusarium* wilt harbored high populations of nonpathogenic *F. oxysporum* and *F. solani* whose involvement in the mechanism of soil suppressiveness was confirmed experimentally (Rouxel et al. 1979). Strains of *F. oxysporum* were much more efficient in establishing suppressiveness in soil than other species of *Fusarium* (Tamietti and Alabouvette 1986). Moreover, there is a great variability among soilborne nonpathogenic strains of *F. oxysporum* for their capacity to protect plants against their specific pathogens (Forsyth et al. 2006; Nel et al. 2006), and some effective strains have not been isolated from soil but from the stem of healthy plants (Ogawa and Komada 1984; Postma and Rattink 1992). In addition, it is well established that a pathogenic strain applied to a non-host plant is able to protect this plant against further infection by its specific *forma specialis*. A review was recently published by Alabouvette et al. (2009) describing the main modes of action of biological control agents in soil and listing a large number of situations in which selected strains of nonpathogenic *F. oxysporum* succeeded or not in protecting the plant against pathogenic

formae speciales. Since the publication of this review, many other examples of the protective potential of nonpathogenic *F. oxysporum* were also published (Belgrove et al. 2011; Morocko-Bicevska et al. 2014), and it would be tedious to list them all. Actually what is noticeable is the fact that nonpathogenic *F. oxysporum* have been shown to control not only pathogenic *F. oxysporum* but also *Verticillium dahliae* causing wilting of eggplant, pepper, and cotton (Gizi et al. 2011; Veloso and Díaz 2012; Zhang et al. 2015), nematodes causing damage on banana and tomato roots (Paparú et al. 2009; El-Fattah et al. 2007), and insects such as the sucking *Aphis gossypii* and the whitefly *Trialeurodes vaporariorum* affecting tomato (Martinuz et al. 2012; Menjivar et al. 2012). While in the case of *V. dahliae* on eggplant and cotton, volatile organic compounds produced by the strains of *F. oxysporum* control the pathogen; in the case of nematodes, weevils, and insects, the *F. oxysporum* strains are endophyte and elicit the plant defense reactions of the host plants.

It must be admitted that most of the examples cited here and in the review published in 2009 (Alabouvette et al. 2009) correspond to controlled situations that reveal the potential of nonpathogenic strains, but a very limited number of the most powerful strains are licensed, registered, and available in the market with a biocontrol allegation. The protective capacity in *F. oxysporum* is not a simple trait and many genes are likely to be involved. Identifying some traits linked to the protective capacity would help in differentiating pathogenic from protective strains and in screening among soilborne strains to identify potential protective strains. Success of microbiological control requires a sufficient understanding of the modes of action of the antagonist and also of its interactions with the plant, the pathogen, and the rest of the microbiota. All these studies take time, and most of the biocontrol agents other than *F. oxysporum* and already on the market have been studied for more than 20 years before registration. The work already done and the results obtained with nonpathogenic strains of *F. oxysporum* augur an imminent placing on the market of representatives of this species to control pathogens. It is however necessary to be wary of the too rapid interpretation found in recent papers (Schmidt et al. 2013) concerning the results of Ma et al. (2010). Ma et al. showed that under very special laboratory conditions, the nonpathogenic strain Fo47, isolated from the suppressive soil of Châteaurenard (France) and whose protective capability was already proved (Olivain et al. 2004), was likely to integrate by horizontal transfer, a fragment of chromosome 14, bearer genes involved in the pathogenicity of a strain of *F. oxysporum* f. sp. *lycopersici*. Actually, the experimental conditions were such that the likelihood of such a natural realization is zero; the authors simply wanted to show that the horizontal transfer was possible, which is different from likely. We can thus consider as reliable the strains of nonpathogenic *F. oxysporum* to be used in biological control strategies.

5 Dormant or Active Actor of the Biological Functioning of Soils?

5.1 Carbon Utilization

The distribution of *F. oxysporum* in numerous, complex, and varied environments is explained by the enzymatic machinery at its disposal and its ability to modify its metabolism within the constraints of these environments including microaerobic and very-low-oxygen conditions, which gives it this remarkable adaptability and an important role in the biodegradation of the organic matter. *F. oxysporum* produces indeed a large spectrum of extracellular oxidative enzymes of various types including cellulases, laccases, xylanases, lignin-degrading enzymes, and manganese peroxidases (Falcon et al. 1995; Rodriguez et al. 1996; Silva et al. 2009; Zhou et al. 2010; Xiros et al. 2011; Huang et al. 2015). Apart from study cases dedicated to the ability of *F. oxysporum* to metabolize a given C source or to denitrify a nitrogen-containing substrate (Rodriguez et al. 1996; Takaya and Shoun 2000; Ali et al. 2014), there is no global data to quantify the relative importance of the role of *F. oxysporum*, within the fungal community, in the decomposition, reorganization, and mineralization of organic matter in soils and litter. However, its ubiquitous presence and its high abundance mean that the contribution of this fungus in the carbon and nitrogen cycles must be significant. Beyond its ecological role in the saprophytic phase of *F. oxysporum*, this important enzymatic potential is usable in processes for bioproduction and/or biodegradation of natural resources under solid-state fermentation but also in bioremediation process and phytoextraction of heavy-metal under field conditions. For instance, *F. oxysporum* is used to produce ethanol from agricultural sources such as cereal straw, thanks to its ability to combine both the cellulose and hemicellulose degradation system and the capability to ferment hexoses and pentoses to ethanol (Christakopoulos et al. 1989; Ruiz et al. 2007; Anasontzis et al. 2011; Xiros et al. 2011; Ali et al. 2012). Similarly, *F. oxysporum* appears as an efficient biotechnological partner. It is grown in solid-state fermentation process to degrade by-products of the olive oil production or the citrus-processing industry (Sampedro et al. 2007; Mamma et al. 2008).

5.2 Nitrogen Utilization

Nitrogen sources in the environment including soil are variable in nature (organic and mineral) as in structural complexity. It is often difficult to separate the use of nitrogen from that of carbon, but it nevertheless appears that biomass production and secretion of hydrolytic enzymes to use carbon by *F. oxysporum* is strongly impacted by the nitrogen source at its disposal (Da Silva et al. 2001; Escobosa et al. 2009). This phenomenon has been mainly shown in biotechnology processes to solicit the enzyme potential of *F. oxysporum* to degrade a carbon substrate such

as lignin or agriculture by-products or to obtain a product of interest (Cheilas et al. 2000; Panagiotou et al. 2003, 2005; Lee et al. 2011). It is also noticeable that, thanks to the incredible flexibility of its metabolism, *F. oxysporum* adapts to moderately up to severe anaerobic conditions by replacing the energy-producing mechanism of O₂ respiration with the reduction of NO₃⁻ and NO₂⁻ to N₂O. Denitrification is a dissimilating metabolic mechanism for nitrate and was described in *F. oxysporum* not so long ago (Shoun and Tanimoto 1991). This dissimilatory nitrate reduction allows *F. oxysporum* to regenerate the cofactor NAD(+) during the denitrification process to then efficiently hydrolyze xylose to achieve its anaerobic growth (Panagiotou et al. 2006). *F. oxysporum* could not only denitrify nitrate through the classical sequential reactions of nitrate and nitrite reductases but it can also reduce nitrate to ammonium through ammonia fermentation (Takaya 2002; Takasaki et al. 2004; Zhou et al. 2010). A deep focus has been given to the specific pathways used by this fungus to denitrify nitrate and nitrite to gain energy. It was shown that *F. oxysporum* denitrification activities are localized in the mitochondria and are coupled to the synthesis of ATP (Kobayashi et al. 1996) and that cytochrome P-450, designated as P450nor, was involved in the respiratory nitrite reduction of *F. oxysporum*, while the equivalent NO reductase (NOR) system in bacteria is derived from cytochrome c-oxidase (Shoun and Tanimoto 1991; Takaya and Shoun 2000; Dalber et al. 2005). Recent studies related to the use of nitrogen by *F. oxysporum* help at explaining the role of soilborne fungi in the nitrogen cycle and more specifically in soils (Long et al. 2013; Mothapo et al. 2015). For instance, fungal denitrifiers including *F. oxysporum* generally do not have the gene encoding N₂O reductase (NosZ) as bacteria have and thus are incapable of reducing N₂O to N₂ (Shoun et al. 2012). Many studies dedicated to the fungal release of N₂O as a powerful greenhouse gas contributing both to global warming and ozone depletion underlined the contribution of *F. oxysporum* to this phenomenon (Shoun et al. 2012; Jirout et al. 2013; Chen et al. 2014; Maeda et al. 2015). An equivalent strategy allows *F. oxysporum* to reduce sulfur in anoxic condition to recover energy (still via NADH cofactor) and ensure efficient oxidation of the carbon source and subsequent fungal growth. As for nitrate dissimilation, the anaerobic sulfur reduction by *F. oxysporum* results in the release of a gas, the hydrogen sulfide (H₂S), but in amounts that are less than those noted for N₂O (Abe et al. 2007; Sato et al. 2011). This reveals how the fungus adapts to anaerobic conditions and replaces the energy-producing mechanism of O₂ respiration by a dissimilative strategy. This ability to reduce sulfide in anoxic conditions can confer a competitive advantage to populations of *F. oxysporum* when *Brassica*, rich in sulfur, are ground and incorporated into the soil to reduce densities of primary inoculums of plant pathogenic fungi (Larkin and Griffin 2007).

5.3 Bioremediation

As mentioned above, *F. oxysporum* has also attracted interest for bioremediation of soil and purification of water due to its capability to detoxify and colonize polluted environments. For instance, *F. oxysporum* excretes alkaline substances that increase the pH of the medium around its mycelium, which affects the status of certain minerals. Thus, by issuing chelators produced during its growth in the presence of glutamate, *F. oxysporum* hydrolyzes coal without producing specific enzymes. On the other side, *Trichoderma viride* produces enzymes attacking coal under alkaline conditions; therefore, these fungi combine solubilization of coal and ligninolysis of humic acids, which enables them to colonize mineral soils (Holker et al. 1999). In an iron ore area in Brazil, *F. oxysporum* associated with mycorrhizal fungi facilitates the solubilization of phosphorus, thus facilitating the installation of legumes to ensure revegetation of the soil (Matias et al. 2009). *F. oxysporum* was isolated from industrially polluted effluents highly contaminated with cadmium alone or cadmium and lead. Thanks to its ability to grow in the presence of heavy metals and its associated metabolic activity, *F. oxysporum* may, in aqueous medium, either sequester cadmium in its mycelial biomass (Massaccesi et al. 2002) or turn Pb^{2+} and Cd^{2+} metal ions into the corresponding carbonates that can then be recovered. Besides the removal of toxic heavy-metal ions from water, the crystals thus created have a specific morphology making them exploitable as biominerals for biological and materials sciences (Sanyal et al. 2005). Moreover, the capability of *F. oxysporum* to reduce extracellularly metal ions and in particular silver ions into silver nanoparticles which have an antibacterial effect has been proposed for the production of sterile clothing for hospitals to prevent infection with pathogenic bacteria such as *Staphylococcus aureus*. In this case, the bioremediation of water is ensured by the cyanogenic bacterium *Chromobacterium violaceum* (Duran et al. 2007). It may be admitted that despite the anthropogenic character of mining and the presence of heavy metals at industrial sites, pollutants, although toxic, are natural constituents of the environment that man has concentrated, certainly, but that *F. oxysporum* particularly ubiquitous fungus was confronted to and was able to adapt to their presence, tolerate them, and even exploit them. By cons, it is notable that the enzymatic equipment of *F. oxysporum* makes it capable of degrading synthetic molecules. So *F. oxysporum* was used to degrade and to detoxify a new chemical class of textile dyes called glycoconjugate azo dye and is proposed in the frame of remediation strategies of textile effluents (Porri et al. 2011). The ability of *F. oxysporum* to grow in the presence of arsenic and to volatilize this element present in polluted environments allows considering its exploitation for the bioremediation of As-contaminated soils, sediments, and effluents (Zeng et al. 2010; Feng et al. 2015). As well, the efficiency with which *F. oxysporum* is capable of extracting the iron from asbestos fibers due to a change of its metabolism and thereby reduce its toxicity makes the fungus a potential candidate for the bioremediation of contaminated sites. First, the internalization of asbestos fibers is prevented in *F. oxysporum*, thanks to its rigid cell wall. Then a

proteomic analysis revealed an upregulation of two proteins, homologous of already known proteins in *F. graminearum* and *Coccidioides immitis*, and a rerouting of *F. oxysporum* metabolism to the pentose-phosphate pathway to counteract the deleterious consequences of oxidative stress (Chiapello et al. 2010). Indirectly, *F. oxysporum* also contributes to the bioremediation of soils contaminated with zinc and cadmium or mining soils by facilitating the phytoextraction of heavy metals from the soils by plants introduced for that purpose in the areas concerned (Ortega-Larrocea et al. 2010; Zhang et al. 2012).

6 Adaptation to Human Activities

6.1 *A Ticket for the Degradation of Xenobiotics?*

With a stated goal of protecting crops, chemical control against pests, either weeds, insects, or plant pathogenic microorganisms, results in a spill of more or less complex molecules, most of which being xenobiotic compounds. The accumulation of these molecules can negatively impact human, animal, plant, and microbial populations under increasing pressure. The enzymatic equipment of *F. oxysporum* allows the fungus to degrade pesticides, including organophosphates such as malathion and fenitrothion which are neurotoxic insecticides (Hasan 1999; Peter et al. 2015). According to the initial concentration (400–1000 ppm) and to the availability of additional nutrients (carbon, nitrogen, phosphate), *F. oxysporum* was capable of degrading malathion in less than 8 days up to 3 weeks of incubation. The insecticide chlordecone is a contaminant found in most of the banana plantations in the French West Indies. Microbial communities were severely negatively affected by this organochlorine, but *F. oxysporum* was able to tolerate the presence of the toxic molecules in soil as well as some few other fungal genera belonging to the Ascomycota phylum (Merlin et al. 2013). However, *F. oxysporum* was the only species able to grow on chlordecone as only carbon source in controlled conditions and to dissipate up to 40% of chlordecone. So also there, the enzyme potential confers to the fungus a ubiquitous adaptability leading to exploit those skills to address the presence of xenobiotic pesticides in soil and water (Pinto et al. 2012).

6.2 *A Ticket for the Hospital?*

Nosocomial infections are more and more frequently attributed to the presence of *Fusarium* in hospital settings (Girmenia et al. 2000; Anaissie et al. 2001; Dignani and Anaissie 2004; Sautour et al. 2012). The diseases often affect dramatically immunocompromised patients (Nucci and Anaissie 2007) but can also target more specifically and less dramatically contact-lens wearers and patients with infectious

keratitis (Jureen et al. 2008). *F. oxysporum* and *F. solani* are the most dominant species involved among the various *Fusarium* species that have been detected so far (Anaissie et al. 2001; O'Donnell et al. 2007; Short et al. 2011; Scheel et al. 2013). An epidemiological investigation conducted over 2 years in hospital and nonhospital buildings in France revealed the existence of homogeneous populations of *F. oxysporum* and *F. dimerum* common to all contaminated hospital sites (Steinberg et al. 2015). The waterborne isolates tolerated higher concentrations of chlorine dioxide used to disinfect the hospital water distribution systems and of copper sulfate released by copper pipes and higher temperatures than did soilborne isolates but did not show any specific resistance to fungicides. These populations are present at very low densities in natural waters, making them difficult to detect, but they are adapted to the specific conditions offered by the complex water systems of public hospitals in France and probably other localities in the world (Steinberg et al. 2015). Molecular analyses on the genetic diversity of populations of *F. oxysporum* in hospitals brought evidence for the recent release of a clonal lineage geographically widespread (O'Donnell et al. 2004).

These studies conducted by doctors, mycologists, taxonomists, and ecologists led the different hospital departments to take measures to reduce the risk of spread of the fungus in the premises, including minimizing the effects of aerosolization to prevent nosocomial infections, what is quite good of course. They especially highlight the impact of man on the evolution of microorganisms and their distribution throughout the world because here are clonal populations of *F. oxysporum* adapted to urban water supply systems that are found in countries from different continents.

7 Conclusion

There is no doubt that nonpathogenic *F. oxysporum* interact firstly with pathogenic *formae speciales* of *F. oxysporum* or other pathogenic fungal species for the use of trophic resources and space in the rhizosphere of host plants and also with the plant, and they elicit defense reactions. These are the reasons why many strains of nonpathogenic *F. oxysporum* are proposed as biocontrol agents to control the infectious activity of pathogens or pests and reduce the severity of the disease even if not so many strains are actually registered and available on the market. Although this biocontrol activity is particularly important, it would be a shame to reduce *F. oxysporum* to a simple role-playing in the rhizosphere of a plant that distributes the game depending on its compatibility with one or the other of the strains. Indeed, only the interaction with the plant discriminates pathogenic strains from nonpathogenic ones. Molecular markers exist for a few number of *formae speciales*, but for most of the others, these markers, if any, are difficult to identify. The reasons are the very high genetic diversity within this species and the polyphyletic origin of the pathogenicity. In return, this diversity is a major asset for *F. oxysporum* that can colonize and exploit all the compartments of the terrestrial

ecosystem, even the most unexpected, whether they are extreme in nature or a result of excessive anthropization. Thanks to a diverse enzymatic equipment and a flexible metabolism, *F. oxysporum* is able to adapt to many environmental conditions and above all to actively contribute to the biochemical processes governing the functioning of the niches used by the fungus, whatever they are.

Beyond the biocontrol activity of *F. oxysporum*, the mechanisms of which are beginning to be elucidated, at least partially, the bioremediation of contaminated soils and the detoxification of harmful xenobiotics used in agriculture become particularly attractive, as well as the potential its enzymatic equipment offers for biotechnological processes including food processing. Finally, its ability to reduce nitrates makes *F. oxysporum* the preferred study model to understand the role of fungi in the denitrification process and particularly in their contribution to the production of N₂O and the resulting greenhouse gas. *F. oxysporum*, whether it is pathogenic or nonpathogenic *F. oxysporum*, deserves its qualification as a ubiquitous fungus because actually it is everywhere and it is active throughout. It appears as the multipurpose fungal toolbox that pathologists sometimes ignore but which nevertheless actively contributes to the global functioning of soil.

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