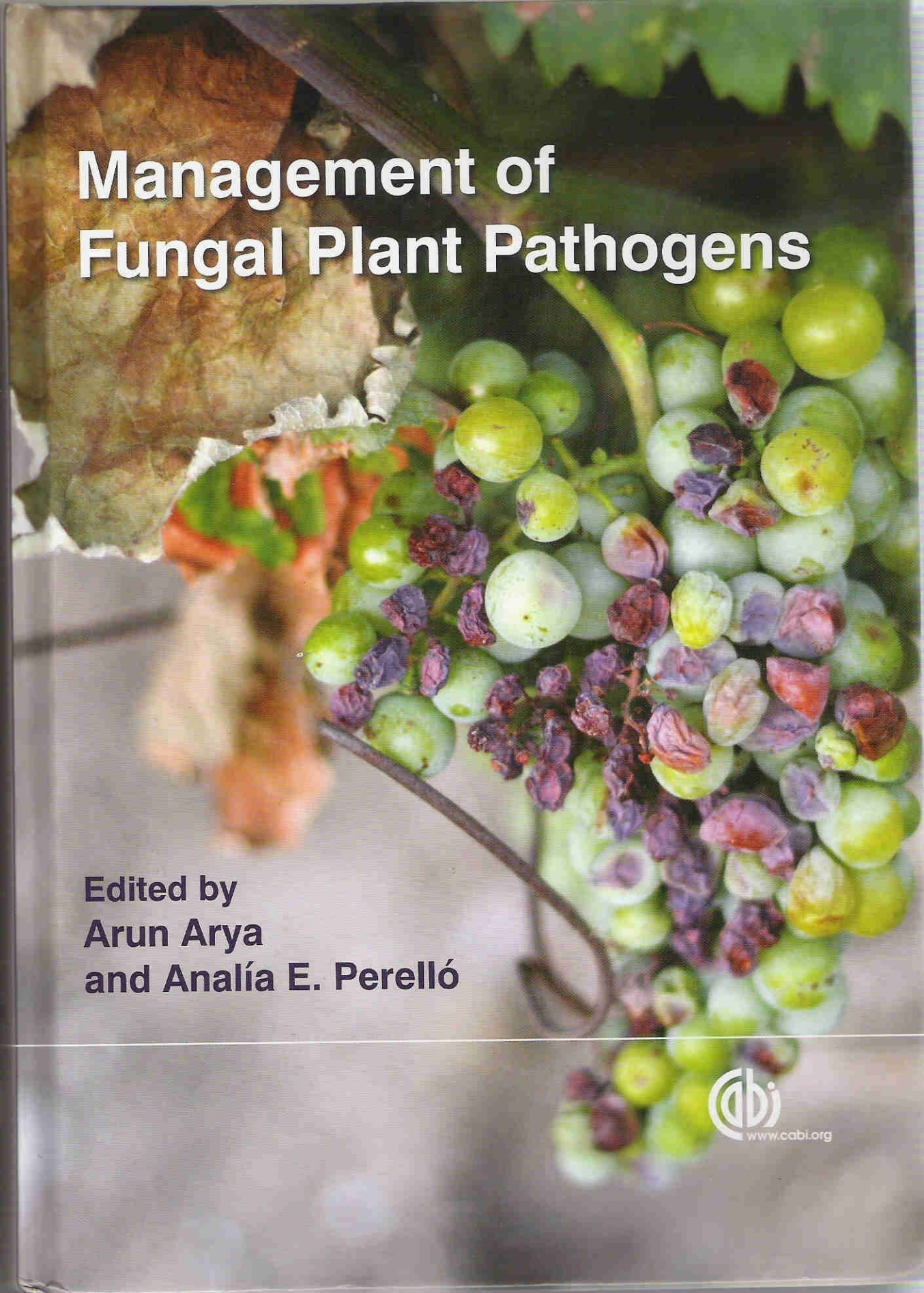
Management of Fungal Plant Pathogens



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13 Effect of Tillage Systems on the Arbuscular Mycorrhizal Fungi (AMF) Propagule Bank in Soils

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Abstract
In this chapter we discuss the effects of tillage and no-tillage systems on the characteristics of the arbuscular mycorrhizal fungi (AMF) propagule bank in soils. These fungi, which belong to the phylum *Glomeromycota*, are of great interest in agriculture. AMF are often assumed to be solely beneficial; however, in certain environmental conditions, growth depressions related to AMF have been observed. In soils under no-tillage, an intact hyphal network is present, whereas under conventional tillage, this network can be damaged and AMF spores may remain as propagule sources. Some direct effects of tillage on AMF propagules are: (i) disruption of the hyphal network; (ii) dilution of the propagule-rich topsoil; and (iii) accelerated root decomposition. Spore counts in soils should be considered as useful indicators for AMF activity *in situ*; however, the presence of spores does not always imply recent activity of AMF and mechanical disturbance may change their spatial distribution in the soil profile. Therefore, the information about spore numbers in agricultural systems needs to be analysed cautiously. The different environmental conditions and direct effects related with tillage and no-tillage on AMF communities generate shifts not only in the composition of the AMF soil propagule bank, but also in its diversity. If the differential use of the various types of propagules by the *Glomeromycota* families, as many authors suggest, is confirmed, the lack of disruption of the hyphal network in no-tillage can help to explain the differences in *Glomeromycota* diversity that are found in field experiments.

Importance of AMF in Agriculture

Arbuscular mycorrhizae (AM) show symbioses between plant roots and fungi belonging to the phylum *Glomeromycota* (Schübler *et al.*, 2001). These fungi are obligate biotrophs and form associations with most plant species (Trappe, 1987). AM associations are the most frequent symbioses in nature because of their broad association with plants and their cosmopolitan distribution (Harley and Smith, 1983). They have been found from the Antartic Peninsula to the tropics (Huante *et al.*, 1993; Cabello *et al.*, 1994). The wide host range of these fungi and their ability to grow in different environments are the reason why arbuscular mycorrhizal fungi (AMF) are usually considered 'generalists' with low host specificity (Smith and Read, 1997). Studies have confirmed that mycorrhizal

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fungi colonize most agricultural plants and that they can have a substantial impact on crop productivity (Johnson, 1993).

The interaction between the fungus and its host plant consists mainly in nutrient transfer: the plant provides the fungus with carbon compounds, while the fungus delivers nutrients to the plant. The increased nutrient uptake from the soil, particularly of phosphorus and nitrogen, is the main benefit attributed to mycorrhizal symbioses (Smith and Read, 1997; Govindarajulu *et al.*, 2005). Other benefits may include enhancement of resistance to root parasites (Borowicz, 2001), improvement of drought tolerance (Augé, 2001) and reduction of the impact of environmental stresses such as salinity (Ruiz-Lozano *et al.*, 1996). AMF also have an important role in the improvement of soil stability, which can possibly diminish erosion (Rillig *et al.*, 2002).

AM fungi are often assumed to be solely beneficial, since they are widely thought to function as mutualists. However, their effects on host growth often depend on environmental conditions such as nutrient availability and soil moisture (Peng *et al.*, 1993; Al-Karaki *et al.*, 1998; Graham and Abbott, 2000; Valentine *et al.*, 2001). As AMF draws C from the host, the overall effect on host growth depends on the cost–benefit relationship of the symbiosis (Johnson *et al.*, 1997; Grimoldi *et al.*, 2005). Consequently, in fertile soils, growth patterns of mycorrhizal plants often do not differ significantly from those of non-mycorrhizal ones (Newsham *et al.*, 1995) and even growth depressions related to AMF have been observed in many plant species (Johnson *et al.*, 1997; Allen *et al.*, 2003). In such plant–AMF interactions, only the fungal symbiont has a net benefit, and this has sometimes been interpreted as parasitism (Johnson *et al.*, 1997).

AM fungi are grouped into genera that encompass more than 150 species described to date and the effects that they have on their host plants, or 'effectivity', differ greatly between fungal strains or species (Miller *et al.*, 1985; Modjo and Hendrix, 1986). Since a single root can be colonized simultaneously by various *Glomeromycota* species, AMF root colonization is mediated by interspecific fungal interactions, such as competition, antagonism and dominance (Allen *et al.*, 2003). Because of the importance of AMF in agrosystems, their study is relevant both for the manipulation of indigenous AMF in the field through appropriate agricultural practices and for the development of a successful inoculation.

Agricultural Practices and Mycorrhizae

Agricultural practices for annual crops, such as crop rotations, tillage, sowing, fertilization, pest, weed and disease control, and harvest, generate changes that affect the microbial communities in the rhizosphere. Conventional tillage is characterized by the use of disc or mouldboard ploughs, followed by harrowing for seedbed preparation. In no-tillage, seeds are drilled directly into the soil with an appropriate planting machine (Crovetto, 1992). No-tillage systems are characterized by the accumulation of crop residues on the soil surface, leading to greater carbon, nitrogen and surface water, compared to conventional tillage (Doran and Linn, 1994). Several changes in soil properties have been reported with no-tillage management systems: improved aggregate stability, moisture availability with residue retention, changes in the distribution of organic matter residues down the soil profile, for example, a more even distribution of organic matter in cultivated soil as compared to that in non-tilled soil, where residues are concentrated on the surface (Alvarez *et al.*, 1998). One of the problems that may occur in no-tillage is the nutritional deficiency because of the reduced mineralization of the soil organic matter (Fox and Bandel, 1986).

In the case of AMF, the lack of soil physical disturbance in no-tillage might wrongly suggest that soils with annual crops under this system may be similar to those of natural grasslands. However, agroecosystems have particular characteristics which influence AMF activity. Natural ecosystems present various plant species hosting AMF,

at different phenological stages. Annual crops, however, inherently represent a change for AMF, because of the reduction in host biodiversity. In addition, cropped systems show two clearly different periods: a period with high density of host plants of the same species growing simultaneously and, after harvesting, the fallow period with no host or, in some cases, scarce presence of spontaneous vegetation (i.e. weeds). As obligate symbionts, *Glomeromycota* relies on the plant host for the supply of C assimilates required for its growth, maintenance and functioning. Therefore, dynamics and biodiversity are clearly affected by agricultural practices (Kurle and Pfleger, 1994).

Significance of the AMF Propagule Bank on Root Colonization

Effect of tillage

Colonization of roots by AM fungi can arise from three sources of inoculum: spores, colonized root fragments and hyphae. The propagules in soils therefore may be called a 'propagule bank' that is 'waiting' for suitable conditions to germinate, grow and eventually colonize new plant roots (Öpik, 2004; Schalamuk, 2005). Most of the host plant benefits obtained by AM symbiosis, mainly phosphorus acquisition, depend on the early colonization of roots. The rapid colonization is related to AMF propagule density and composition, i.e. the so-called propagule bank. A graph of the percentage of the root length colonized against time has a sigmoid form showing three phases: lag phase, linear phase and a plateau (Sieverding, 1991). A higher AMF propagule density often reduces the length of the lag phase and thereby accelerates the process of mycorrhizal colonization (Smith and Read, 1997).

Numerous studies have shown that mycorrhizal colonization is affected negatively by tillage (Douds *et al.*, 1995; McGonigle and Miller; 1996a; Kabir *et al.*, 1998; Mozafar *et al.*, 2000). Soil disturbance reduces AMF propagule density since tillage of soil breaks up the AM fungi hyphal network and consequently lowers mycorrhizal colonization (McGonigle and Miller, 1996a). At the final crop stages, the AMF colonization levels in no-tillage and conventional tillage often do not differ significantly; however, at the early stages, crop plants under no-tillage often show higher mycorrhizal colonization (Schalamuk *et al.*, 2004). As already mentioned, in no-tillage systems, the reduced mineralization of the soil organic matter often generates plant nutritional deficiencies. Nevertheless, a higher nutrient concentration related to a rapid AMF colonization has been observed under no-tillage systems (McGonigle and Miller, 1996a; Mozafar *et al.*, 2000; Schalamuk *et al.*, 2004). By using the method of Plenchette *et al.* (1989), we have previously found higher levels of mycorrhizal soil infectivity in no-tillage systems (Schalamuk *et al.*, 2004). As already pointed out, colonization of roots by AM fungi can arise from different sources of inoculum. Colonized root fragments (Rives *et al.*, 1980), spores (Gould and Liberta, 1981; Jasper *et al.*, 1987, 1988) and hyphae (Jasper *et al.*, 1989) lose their ability to initiate colonization with soil disturbance, which can be related to physical damage to the propagules by tillage and/or unfavourable conditions for germination or colonization after disturbance (Stahl *et al.*, 1988; Bellgard, 1993).

Mycorrhizal soil infectivity (MSI) (Plenchette *et al.*, 1989) compares the ability of different soils to induce colonization in plants and depends on the activity of all the propagule types in soil. It is difficult to distinguish the relative contributions of the different types of propagules to the colonization of root systems (Smith and Read, 1997), and mycorrhizal infectivity does not provide information about the relevance of each propagule type in any particular field situation. Although a number of different propagule types exist in the soil, they may not be equally effective at producing new infection units (Klironomos and Hart, 2002). In many habitats, the hyphal network in the soil, together with root fragments, is probably the main means by which plants become colonized, even when significant spore populations are also present (Hepper, 1981;

Tommerup and Abbott, 1981; Birch, 1986; Jasper *et al.*, 1992). Studies have shown that AMF extraradical hyphae are affected severely by soil disturbance at tillage (Fairchild and Miller, 1990; McGonigle and Miller, 1996b; Kabir *et al.*, 1997; Wright and Upadhyaya, 1998). Jasper *et al.* (1989) have stated that due to the importance of the AMF hyphal network as inoculum in undisturbed soil, a lower infectivity of soil propagules after the disturbance usually can be determined by the damage on the network, rather than on spores and colonized root fragments. Another effect of tillage on the AMF propagule bank, which occurs simultaneously with the disruption of the hyphal network, is the dilution of the topsoil rich in propagules, with the poorest part in the subsurface (Sieverding, 1991). Clearly, mechanical soil mixing affects all types of AMF propagules.

As a conclusion, it is suggested that tillage affects all types of AMF propagules directly, to a greater or lesser extent, through different mechanisms acting together: (i) disruption of the hyphal network; (ii) dilution of the propagule-rich topsoil; and (iii) accelerated root decomposition. Through all these direct effects, tillage may reduce soil mycorrhizal infectivity and thereby AM root colonization at the early stages of crop growth.

Effects of Tillage and Cropping on AMF Spore Densities in Soils

AMF spores are formed by differentiation of vegetative hyphae in soil or roots and appear to be long-term survival structures. In agricultural systems with annual crops, other propagule types (i.e. hyphae inside and outside the roots) seem to be more important to start colonization in particular conditions. Nevertheless, spore counts in soils should be considered as useful indicators for AMF activity *in situ*. Several studies have found higher spore numbers in no-tillage than in conventional tillage (Crovetto, 1985; Kabir *et al.*, 1998; Jansa *et al.*, 2002; Schalamuk *et al.*, 2003). In agroecosystems with annual crops, the number of spores generally increases during the growing cycle (Cabello, 1987) and sporulation is frequently linked to host phenology in the field (e.g. maximum spore production occurs near the middle or the end of a growing season) (Morton *et al.*, 2004). At the early stages of the crop, higher spore densities are usually found in untilled soils, in comparison with conventional systems, whereas at the more advanced phenological stages, differences between tillage systems are reduced (Schalamuk *et al.*, 2003).

It is well known that spores can survive in soils for several years (Sieverding, 1991). Thus, spore counts reflect both the sporulation and the action of many factors that affect their survival and accumulation in the soil. Consequently, spore density is a result of a complex balance and, while sporulation is probably related to the recent activity of the AMF, spore counts in the soil include structures formed at different times.

Spore production depends on carbon supply from the host to the fungus (Furlan and Fortin, 1977; Daft and El Giahmi, 1978). Douds *et al.* (1993) have indicated that the production of fungal AM spores can decrease when soils are tilled. Increases in spore numbers have been associated with root growth (Hayman, 1970) and/or with host maturity or senescence (Hayman, 1970; Koske and Halvorson, 1981; Giovannetti, 1985; Gemma *et al.*, 1989; Troeh and Loynachan, 2003). Agricultural practices generate disturbances that affect AMF colonization and, in turn, spore formation in soils (Kurle and Pfleger, 1994). Therefore, tillage, either through changes in mycorrhizal colonization or through indirect effects, such as changes in the soil environment and plant growth, largely affect AMF spore production in soils.

The survival of a spore depends on its morphological traits, determined mainly by the species of *Glomeromycota* to which it belongs, as well as on the characteristics of the soil environment. Spore survival is an important factor determining the variations in AMF spore counts in soils; however, information about spore survival is scarce as compared to that about sporulation (Lee and Koske, 1994a). In natural ecosystems, decreases in spore numbers have been

attributed mainly to their germination, the activity of macro and micro fauna and their destruction by other soil fungi and parasites (Gerdemann and Trappe, 1974; McIlveen and Cole, 1976; Ross and Ruttencutter, 1977; Ross and Daniels, 1982; Rabatin and Stinner, 1985, 1988). AMF spores are commonly infected either by other fungi (Daniels and Menge, 1980; Lee and Koske, 1994a; Rousseau *et al.*, 1996) or by *actinomycetes* (Lee and Koske, 1994b), and environmental conditions have a strong influence on these processes (Janos, 1980; Koske, 1988). In agricultural systems, another effect that directly reduces spore counts is the dilution of the topsoil rich in spores with the part in the subsurface poorer in propagules (Crovetto, 1985; Sieverding, 1991). For all these reasons, spore survival and accumulation may have a great influence on spore counts, and the largest spore numbers in no-tillage at the early stages may be the result of either higher or faster sporulation and/or the presence of residual spores produced during the fallow or the previous crop. As the presence of spores does not always imply recent activity of AMF, and mechanical disturbance may change their spatial distribution in the soil profile, the information about spore numbers in agricultural systems is useful, but needs to be analysed cautiously.

AMF Propagule Bank and Biodiversity

As already pointed out, tillage may alter the AMF propagule bank in several ways and the lack of disturbance in continuous no-tillage systems can generate accumulative effects. Therefore, in soils under no-tillage, an intact hyphal network can be present, whereas under conventional tillage, this network can be damaged and AMF spores may remain as propagule sources. Little information exists on the effect of tillage systems on *Glomeromycota* diversity (Jansa *et al.*, 2002; Schalamuk *et al.*, 2006). Several studies have shown that *Glomeromycota* taxa may vary in their colonization strategies and that these variations can be associated with the utilization of different propagule types by AMF families (i.e. *Acaulosporaceae*, *Gigasporaceae* and *Glomeraceae*) (Tommerup and Abbott, 1981; Biermann and Linderman, 1983; INVAM, 1993; Braunberger *et al.*, 1996; Brundrett *et al.*, 1999; Klironomos and Hart, 2002; Hart and Reader, 2002, 2004). Jansa *et al.* (2002), in an intensively used agricultural soil under long-term reduced tillage management, found that the presence of certain AMF species, especially those that did not belong to *Glomus* spp., had a tendency to increase. However, we have found that the contribution of species belonging to the *Glomeraceae* family increases in no-tillage plots, to the detriment of *Acaulosporaceae* and *Gigasporaceae* (Schalamuk *et al.*, 2006). In that experiment, the greatest contribution of *Glomeraceae* species in no-tillage indicated a lower equitability in the distribution among the families of *Glomeromycota*, and thereby a lower diversity, in comparison with conventional tillage. These findings differ from those of Jansa *et al.* (2002). Nevertheless, it is important to point out that mycorrhizal communities are site-specific and that each AMF species can be affected in several ways by different agricultural management practices; therefore, generalization is difficult.

De Souza (2005), based on life history strategy studies, suggested that members of the *Gigasporaceae* family were '*K*' strategists in contrast to single spore-producing '*Glomus*' species. Hart and Reader (2004) found that the *Gigasporaceae* family was less sensitive to soil disturbance than the *Glomeraceae*. The basis for this difference between both families is due probably to differences in their colonization strategies. AM fungi in the *Gigasporaceae* colonize primarily from spores, whereas those belonging to the *Glomeraceae* can colonize from hyphae (Tommerup and Abbot, 1981; Biermann and Lindermann, 1983). Hyphae are more sensitive to soil disturbance than spores and thus subsequent colonization of additional roots is affected more.

Tillage or the lack of disturbance in continuous no-tillage determine different

environmental conditions and direct effects on AMF communities, and thereby shifts in the composition of the AMF soil propagule bank. Consequently, if the differential use of the various types of propagules by the *Glomeromycota* families, as many authors suggest, is confirmed, the lack of disruption of the hyphal network in no-tillage for a period of several years can help to explain the higher proportions of *Glomeraceae* that have been found previously in the system (Schalamuk *et al.*, 2006).

Conclusions

Tillage and continuous no-tillage systems change the composition of the AMF propagule banks in the soil, whereas mechanical soil mixing affects all types of AMF propagules. Continuous no-tillage systems favour the presence of an intact hyphal network in soils. Possible differences in colonization strategies among *Glomeromycota* taxa might have a great influence on the impacts of tillage on AMF diversity.

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