SOIL MICROORGANISMS AND THEIR ROLE IN THE INTERACTIONS BETWEEN WEEDS AND CROPS[1]

Microorganismos do Solo e suas Funções nas Interações entre Plantas Daninhas e Culturas

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ABSTRACT - The competition between weeds and crops is a topic of great interest, since this interaction can cause heavy losses in agriculture. Despite the existence of some studies on this subject, little is known about the importance of soil microorganisms in the modulation of weed-crop interactions. Plants compete for water and nutrients in the soil and the ability of a given species to use the available resources may be directly affected by the presence of some microbial groups commonly found in the soil. Arbuscular mycorrhizal fungi (AMF) are able to associate with plant roots and affect the ability of different species to absorb water and nutrients from the soil, promoting changes in plant growth. Other groups may promote positive or negative changes in plant growth, depending on the identity of the microbial and plant partners involved in the different interactions, changing the competitive ability of a given species. Recent studies have shown that weeds are able to associate with mycorrhizal fungi in agricultural environments, and root colonization by these fungi is affected by the presence of other weeds or crops species. In addition, weeds tend to have positive interactions with soil microorganisms while cultures may have neutral or negative interactions. Competition between weeds and crops promotes changes in the soil microbial community, which becomes different from that observed in monocultures, thus affecting the competitive ability of plants. When grown in competition, weeds and crops have different behaviors related to soil microorganisms, and the weeds seem to show greater dependence on associations with members of the soil microbiota to increase growth. These data demonstrate the importance of soil microorganisms in the modulation of the interactions between weeds and crops in agricultural environments. New perspectives and hypotheses are presented to guide future research in this area.

Keywords: competition, agriculture, mycorrhizal fungi, PGPR, ecology.

RESUMO - A competição entre plantas daninhas e culturas é um tópico de grande interesse, uma vez que essa interação pode causar grandes perdas na agricultura. Apesar de alguns estudos nesse tema, pouco se sabe sobre a importância dos microrganismos do solo na modulação dessa interação. As plantas competem por água e nutrientes presentes no solo e a capacidade das espécies em absorver esses recursos pode ser diretamente afetada pela presença de alguns grupos microbianos comumente encontrados no solo. Os fungos micorrízicos arbusculares (FMA) são capazes de se associar com as raízes das plantas, o que afeta a capacidade das diferentes espécies em absorver água e nutrientes do solo, promovendo alterações no crescimento. Outros grupos podem promover alterações positivas ou negativas no crescimento das espécies vegetais, a depender da identidade das espécies microbianas e vegetais envolvidas nas diferentes interações, alterando a capacidade competitiva de cada uma delas. Estudos recentes têm demonstrado que as plantas daninhas são capazes de se associar com fungos micorrízicos arbusculares nos ambientes agrícolas, e que a colonização das raízes por esses fungos é afetada pela presença de outras plantas daninhas ou de culturas. Além disso, as plantas daninhas tendem a apresentar interações positivas com a microbiota do solo, ao passo que as culturas apresentam interações neutras ou negativas. A competição entre plantas daninhas e culturas promove alterações na comunidade microbiana do solo, que se torna diferente daquelas observadas nas monoculturas, afetando a capacidade competitiva das espécies

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vegetais. Quando colocadas em competição, plantas daninhas e culturas apresentam diferentes comportamentos relacionados à microbiota do solo, sendo que as plantas daninhas apresentam maior dependência de associações com microorganismos do solo, em relação às culturas, para aumentar seu crescimento. Esses dados demonstram a importância dos microorganismos do solo na modulação das interações entre plantas daninhas e culturas nos ambientes agrícolas. Novas perspectivas e hipóteses são apresentadas para guiar as futuras pesquisas nessa área.

Plavras-chave: competição, agricultura, fungo micorrízico, PGPR, ecologia.

INTRODUCTION

Competition between weeds and crops is responsible for significant yield losses in agricultural ecosystems, which may vary depending on the species analyzed and the prevailing environmental conditions (Carvalho et al., 2007). The high competitive ability of weeds is partially explained by the biological characteristics of these plants, which have morphological and physiological adaptations in their root systems, allowing for greater absorption of water and nutrients from the soil (Carvalho et al., 2011). Furthermore, associations between weeds and soil microorganisms can promote increases in growth as well as resistance to pathogens (Brundrett, 2004; Massenssini et al., 2014). On the other hand, commercial crops tend to have lower competitive ability due to the selection process of cultivars, based on the control of competitors and high nutrient inputs through fertilization, leading to the selection of those less dependent on ecological processes and highly adapted to artificial conditions (Altieri, 1999).

Physical and chemical characteristics of the environment can change the intensity and balance of these interactions. Resources availability is an important modulator of competition among plants, since competition is more intense with lower resource levels (Berger et al., 2008). Extreme climatic conditions can also alter the balance of interactions between plants, with positive interactions, such as facilitation, being prevalent. Under such conditions, the availability of resources is not the main limiting factor in the environment (Callaway et al., 2002). Furthermore, biological aspects of the habitat may change the intensity of interactions between plants. The association of plants with arbuscular mycorrhizal fungi can alter the partition of resources among plants, promoting their coexistence (van der Heijden et al., 2003). Interactions with other groups of microorganisms can also alter the intensity of competition between plants, determining the population density of each species (Klironomos, 2002).

Although several studies have demonstrated the detrimental effect of competition between weeds and crops on agricultural productivity, few have given attention to the microbiological aspects involved. Plants are able to promote changes in the soil microbial community through the exudation of different combinations of organic compounds by the roots depending on environmental conditions (Bais et al., 2006). Plants cultivated under optimal conditions or in low P or N availability tend to exhibit significant differences in the composition of root exsudates (Carvalhais et al., 2011), which in turn cause changes in the population density of microbial groups in the soil (Eilers et al., 2010). Soil microorganisms play a central role in determining the competitive ability of weeds and crops, potentially altering the outcome of competition (Massenssini, 2014). In this study, we have reviewed the existing data on the interactions between plants and the main factors that affect them. We have also assessed the role of soil microorganisms on plant growth and on the competitive ability of weeds. Finally, we have focused on the influence of the soil microbiota on the competition between weeds and crops, and highlighted perspectives on this interaction.

Interactions between plants in natural environments

The composition of plant communities is a constant theme of scientific works due to the great importance of these organisms for terrestrial ecosystems (Bruno et al., 2003). Plants are the main terrestrial primary producers, essential for the flow of energy in these environments (Odum, 2001). In addition, plants interact in various ways with the diverse components of the ecosystem, controlling and having their biomass controlled by organisms that inhabit the terrestrial environment (Callaway, 1998b; Dýìaz & Cabido, 2001). Thus, knowledge on plant populations is of great value to ecological studies, since their fluctuations may determine the population densities of other species at different trophic levels.

Plants undergo the direct influence of biotic and abiotic factors, acting at different levels and synergistically, that will ultimately determine which species will be able to colonize a given environment (Zobel, 1997; Lortie et al., 2004). On a first level, stochastic factors related to evolutionary and biogeographic events initially determine which species will have access to a given location. Among them, the dispersion process and the distance that individuals must overcome to reach a new location are paramount (Dalling et al., 2002; Cannon & Leighton, 2004). On a second level, the abiotic environmental conditions select the tolerant species. Thus, only plants able to survive under the new prevalent climatic and soil conditions will establish themselves (Zobel, 1997; Sollins, 1998). On the last level, organisms able to establish at a particular site will interact with each other directly or indirectly, positively or negatively, selecting the species that will effectively colonize the site (Callaway et al., 2002; Zavaleta & Hulvey, 2004; Michalet et al., 2006). In addition, biological interactions modulate the density of plant populations both reciprocally and interdependently (Miller, 1994; Weigelt et al., 2007).

Generally, the first two levels participate in the determination of compositional variations in plant communities primarily at larger scales (Tuomisto et al., 2003), while the interactions between species are more important for determining the composition of plant communities at a local or regional scale (Zobel, 1997). This does not mean that environmental abiotic factors do not act at the local or regional scale, but that their importance increases with increasing spatial scales (Sollins, 1998; Tuomisto et al., 2002; Jones et al., 2008).

There are examples where climate and soil variations are responsible for part of the variation encountered in plant communities of certain environments, especially when these factors show a wide variation, such as soil fertility, slope, and precipitation (Duque et al., 2002; Tuomisto et al., 2003; John et al., 2007). Tuomisto et al. (2002) observed that, although there was no clear correlation between species richness or diversity of two plant families and the variations in base saturation of the soil, species composition was influenced by cation availability. However, interactions between different species are still responsible for much of the variation observed in plant community composition (John et al., 2007; Jones et al., 2008).

Interactions between individuals are the major factors responsible for variations in plant community composition at a local and regional scale. For example, positive interactions may allow that a weak competitor be present in a given environment, increasing its survival (Miller, 1994; Choler et al., 2001) and/or resistance to environmental factors (Cavieres et al., 2005). Conversely, negative interactions may reduce growth (Weigelt et al., 2007) or survival of a species (Choler et al., 2001; Holzapfel et al., 2006), potentially leading to its exclusion from a given location (Grime, 1973). Furthermore, there are indirect interactions, where one plant species alters the population density of another through competition or the direct facilitation of an intermediate species (Miller, 1994; Wootton, 1994; Liancourt et al., 2005).

Plant community populations interact with each other either directly or indirectly, positively or negatively. It is believed that competition for resources is the main process capable of shaping the floristic composition of an environment (Weigelt et al., 2007). However it is important to remember that other interactions play very important roles since they can modulate the intensity with which two populations compete, as well as interfere with the performance of one or more species, directly or indirectly, potentially altering the final result of competition (Miller, 1994).

In recent decades there has been a growing body of experimental evidence supporting the importance of positive interactions among plants in determining the composition of plant communities. Since the discovery of nurse plants (Went, 1942; Holmgren et al., 1997; Choler et al., 2001), the occurrence of positive interactions has been found in many different environments (Callaway et al., 2002; Liancourt et al., 2005; Holzapfel et al., 2006). The hypothesis of facilitation, which suggests that one species may favor the establishment of another, is already recognized (Brooker et al., 2008), and its inclusion in ecological models seeks to explain the variations observed in plant communities (Travis et al., 2005; Michalet et al., 2006; Travis et al., 2006).

Despite its importance, evidence indicates that facilitation between organisms is often not dependent on the specific interaction between two species, but instead the result of microclimatic changes promoted by one species that makes a determined environment inhabitable by another (Choler et al., 2001; Callaway et al., 2002; Liancourt et al., 2005). Greenlee & Callaway (1996) found that the positive effects promoted by some plant species on the survival and growth of *Lesquerella carinata* var. *languida* Rollins can be mimicked by the installation of baffles that provide shade. In another experiment, it was observed that the positive effect promoted by *Pinus albicaules* Engelm. on *Albies lasiocarpa* (Hooker) Nuttallis was mainly due to protection against extreme environmental factors such as wind and low temperature (Callaway, 1998b). However, when facilitation involves the escape from herbivores, *i.e.* one palatable species is protected by another unpalatable one due to the presence of specific morphological and chemical characteristics, the positive interaction is highly species-specific (Callaway, 1998a).

Abiotic factors of the environment, besides playing a major direct role on the composition of plant communities, may also have an indirect role by modulating the interactions among plant populations. The stress-gradient hypothesis is an example of how one or more abiotic factors can change the profile of biological interactions of a plant community (Greenlee & Callaway, 1996). This hypothesis suggests that along an increasing gradient of a stressful abiotic factor, the profile of interactions is changed from a net negative effect, where competition has a greater weight among biological interactions, to a net positive effect, where facilitation predominates (Callaway et al., 2002). Thus, a species tolerant to some degree of stress promotes the establishment of a non-tolerant species beyond the environmental limits that would be reached if the latter was growing alone (Michalet et al., 2006).

Several experiments have shown changes in the net effect of plant-plant interactions along different stress gradients. Choler et al. (2001) observed that various species in the French Alps showed changes from competition, in habitats with low elevation and protected from the wind, to facilitation, in environments with high elevation where the wind causes damage to the plants. In a study conducted in several alpine regions distributed over the globe, it was observed that with decreasing temperature, there was a change from prevalent negative interactions to positive ones among individuals (Callaway et al., 2002). The same was observed for plant communities in Israel along an aridity gradient with decreases in average annual precipitation between sampling sites (Holzapfel et al., 2006).

The stress-gradient hypothesis suggests that negative interactions predominate in environments where abiotic factors do not offer severe limitations to plant growth, while positive interactions predominate in high stressful environments (Liancourt et al., 2005). Although this trend has been confirmed in various environments, evidence indicates that it is not the rule. Works conducted in subalpine environments, where resource availability is not a stress factor, report changes from negative to positive interactions with an intensification of stress factors (Choler et al., 2001; Callaway et al., 2002). However, interactions among plants subjected to drought stress in Spain show a more complex scenario (Maestre & Cortina, 2004). The authors suggested that competition prevails at both ends of the stress gradient, but at intermediate conditions, there is a prevalence of facilitation. When the limiting factor is a vital resource for plant growth and becomes extremely scarce, plants tend to compete intensely for it, causing facilitation to have a marginal effect (Maestre & Cortina, 2004).

Influence of soil microorganisms on plant growth

Microorganisms in the soil may play a fundamental role in determining the composition of plant communities. They can alter the physico-chemical characteristics of the environment, directly participating in the transformations of nitrogen, phosphorus, and sulfur, and forming mutualistic associations with plants, all of these activities resulting in greater plant growth (Sylvia et al., 2005). Soil microorganisms are generally found in greater numbers near plant roots, where a greater content of organic compounds exuded by the root are available. The quality of root exudates can promote differential recruitment of microorganisms present in the soil (Wolfe & Klironomos, 2005). The recruited microbiota will interact intensively with the plant and can have a positive, neutral, or negative interference on plant growth and, thus, potentially determining the composition of plant communities (Klironomos, 2002).

Symbiotic associations between fungi and plants are present in a broad range of terrestrial ecosystems and involve a large proportion of plant taxa (Brundrett, 2009). It is believed that at least 85% of plant species are able to establish symbiotic associations with fungi, of which 70% are associated with individuals of the phylum Glomeromycota, forming the arbuscular mycorrhizas (Wang & Qiu, 2006). Thus, mycorrhizal associations are extremely important for terrestrial ecosystems due to their wide geographical distribution and the large proportion of plant taxa involved.

Throughout evolution, some plants families lost the ability to associate with mycorrhizal fungi due to the development of specializations for nutrient acquisition, such as the development proteoid roots, carnivorism or parasitism on other plants (Brundrett, 2009). For a long time, it was believed that the family Cyperaceae was not able to associate with mycorrhizal fungi (Brundrett, 2009), but recent evidence has shown otherwise (Bohlen, 2006). Species of the family Cyperaceae are able to associate with arbuscular mycorrhizal fungi and dark septate endophytes (DSE), but the intensity of root colonization may vary depending on the environment in which the samples were collected, the season of the year or the phenological stage of the plant (Wang & Qiu, 2006). These variations in colonization intensity or in the structures present in the association are those primarily responsible for the mistakes regarding the ability of members of the family Cyperaceae to form symbiotic associations (Wang & Qiu, 2006).

Thus, the inclusion of soil microorganisms in studies on interactions between plants and on the dynamics of plant communities is interesting because plant-microorganism interactions can be decisive for the establishment of a species in a given environment (Klironomos, 2002; Callaway et al., 2004; van Grunsven et al., 2009).

Mycorrhizal associations play a major role in determining the composition of plant communities, since plants that establish this type of association can obtain competitive advantages (O’connor et al., 2002; Shah et al., 2008) or facilitate the establishment of other species (Chen et al., 2004). Experimental evidence suggests that mycorrhizal associations can determine the coexistence of different plants (van der Heijden et al., 2003). The latter authors showed that plants inoculated with arbuscular mycorrhizal fungi (AMF) grew, on average, 11.8 times more than those uninoculated, and that the distribution of nitrogen and phosphorus between the species varied depending on the AMF present. Thus, arbuscular mycorrhizal fungi can redistribute resources among plants of different species, allowing their coexistence (van der Heijden et al., 2003).

Just as AMF can determine the composition of plant communities, the contrary may also be true (Eom et al., 2000). According to the authors, depending on the plant species cultivated in a soil, the final composition of AMF species varies greatly. Mummey & Rillig (2006) found that in areas dominated by the invasive species *Centaurea maculosa* Lam., the diversity of AMF was much smaller than in areas dominated by native species. Thus, the composition of plant communities and AMFs are influenced by feedback interactions in each community (Bever, 2003; Hart et al., 2003).

Another important group of soil microorganisms are the DSEs, which are able to associate with the roots of several plant species (Grünig et al., 2002; Weishampel & Bedford, 2006). Sometimes, DSEs are found colonizing roots containing AMF (Rains et al., 2003; Weishampel & Bedford, 2006). However, the importance of DSE appears to increase with the increasing severity of environmental conditions, since in high-stress environments the occurrence of plant associations with DSE is much more frequent than the associations with AMFs (Barrow, 2003; Postma et al., 2007). Thus, these two groups of fungi appear to have similar and complementary roles in various terrestrial ecosystems (Jumpponen, 2001; Postma et al., 2007).

DSEs can also play an important role in determining the composition of plant communities, since they can alter the performance of colonized plants (Grünig et al., 2008). The effect of root colonization by these fungi varies depending on the fungal and plant species evaluated. Some plants colonized by DSE have advantages compared to those not inoculated, among which we can list increases in biomass production and absorption of phosphorus from the soil (Barrow & Osuna, 2002). However, root colonization by DSE can bring disadvantages to the plant, such as decreases in biomass production (Grünig et al., 2008). Thus, the interaction of DSEs with plants seems to vary from mutualism to parasitism (Grünig et al., 2008), and may thus alter the competitive relations between plants.

Besides fungi, several groups of soil bacteria are important due to their role in plant growth. Certain bacteria are known for their ability to fix atmospheric nitrogen and form symbiotic associations with plants (Franche et al., 2009). Phosphate-solubilizing microorganisms are also very important, especially in tropical soils. They are able to indirectly provide phosphorus to plants by solubilizing P precipitated with iron, aluminum and calcium (Gyaneshwar et al., 2002). A large group of bacteria called PGPR (plant growth promoting rhizobacteria) also plays an important role, since they can promote plant growth by different mechanisms (Saharan & Nehra, 2011). By participating in key ecosystem processes or acting specifically on certain plant species, bacteria can also play a central role in the composition of plant communities in different environments.

Nitrogen-fixing bacteria belong to different phyla of the domain Eubacteria and may associate with the roots of plants in a more or less specific manner (Franche et al., 2009). Bacteria capable of symbiotically associating with the roots of plants, leading to the formation of structures called nodules, have a higher specificity in relation to the host (Masson-Boivin et al., 2009). However, some bacteria may inhabit the root surface or the plant rhizosphere, forming associations with low degree of specificity with the host (Bhattacharjee et al., 2008). Plants associated with these bacteria benefit themselves due to the increased nitrogen supply, and in the case of symbiotic associations, over 90% of nitrogen contained in the plant can be fixed by bacteria (Franche et al., 2009). Thus, the presence of N-fixing bacteria in the rhizosphere of plants can improve plant growth in nitrogen-poor environments, as well as promote increased nitrogen content in the soil, which is often related to the facilitative effect that legume species have on other plant species (Walker et al., 2003).

Phosphate-solubilizing microorganisms are naturally present in soils associated or not with plant roots (Rodrýìguez & Fraga, 1999; Gyaneshwar et al., 2002). These microorganisms solubilize phosphorus adsorbed by soil minerals by means of various mechanisms and have great potential to promote plant growth (Gyaneshwar et al., 2002). Some studies have shown that inoculation of this group of microorganisms in the rhizosphere of many plant species led to increased uptake of phosphorus by the plants, besides higher growth (Pal, 1998; Kumar & Narula, 1999; Peix et al., 2001). However, the benefits provided by these microorganisms are indirect, since soluble phosphorus is available in the soil solution and is not directly transferred to the plant (Rodrýìguez & Fraga, 1999). In this case plants able to recruit greater populations of these microorganisms can gain a competitive advantage over others, especially in soils where phosphorus is scarce.

The bacteria termed PGPR are able to promote plant performance by means of a wide variety of mechanisms (Saharan & Nehra, 2011). Studies have shown that inoculation of plants with PGPR can increase nutrient content (Orhan et al., 2006; Karthikeyan et al., 2010) and resistance to pathogens (Saravanakumar et al., 2007; Maksimov et al., 2011). Moreover, some PGPR are able to produce phytohormones, increase the population of other beneficial microorganisms and control the population of harmful ones in the rhizosphere (Saharan & Nehra, 2011). Thus, plants able to recruit greater populations of these microorganisms into their rhizospheres present greater survival, growth, and reproduction (Gholami et al., 2009), and consequently higher competitive ability.

In general, the interactions between plants and soil microorganisms show feedback responses where the influences promoted by plants on certain members of the soil microbiota are reflected in plant growth (Bever, 2003; Schröter et al., 2004). Alterations in the plant community composition are accompanied by changes in the composition of the soil microbial community (Balser & Firestone, 2005) which, in turn, can influence plant performance due to a number of factors, such as the accumulation of pathogens and changes in microbial populations involved in important ecological processes (Bohlen, 2006), potentially decreasing or increasing the performance of a certain plant species in relation to others. Thus, the success of some species to rapidly colonize a given environments may be directly associated with alterations in the soil microbial community.

Role of soil microorganisms on the success of invasive plants

Many studies have shown significant changes in the composition of the rhizosphere microbiota of invasive plants when they colonize a new ecosystem (Klironomos, 2002; Kao-Kniffin & Balser, 2008; Wan-Xue et al., 2010). These changes may have positive effects on the invasive species, when they involve the accumulation of mycorrhizal fungi, nitrogen fixing microorganisms, and other beneficial microbial partners, or negative effects, when pathogens, herbivores, or parasites accumulate (Reinhart & Callaway, 2006). The effects of such changes on the invasive species will determine its success in a given environment.

It is believed that the maintenance of plant communities with high species diversity is mainly due to the prevalence of negative interactions, which allows various species to live together without the dominance of a single one or a few (Bever, 2003). Changes in plant communities by invasive plants typically generate positive feedback interactions with the soil microbiota of the invaded environments (Klironomos, 2002). In their original sites, however, feedback interactions with soil microorganisms are negative (Klironomos, 2002). Thus, invasive plants acquire a great competitive advantage over native species, changing their interaction with soil biota from negative to positive.

Studies have shown that, in some cases, the escape of pathogens is an important mechanism by which invasive plants gain a competitive advantage over native species (Zhang et al., 2009). Van Grunsven et al. (2009) observed that the success of species of the genus *Carpobrotus* to invade areas of the Mediterranean basin is due to the lower negative effect caused by the soil microbiota present in the new habitat. The authors concluded that escape from pathogens in the new environment was an important factor for the plant´s competitive success (van Grunsven et al., 2009). The species *Solidago canadensis*, in turn, is able to inhibit pathogens in the new environment due to the presence of allelopathic compounds in its root exudates (Zhang et al., 2009). The presence of allelopathic compounds is also an important mechanism for the success of some invasive plants. Besides directly inhibiting the growth of pathogens and native plants (Zhang et al., 2009), these compounds may reduce the viability and infectivity of AMFs of the new environment, generating a competitive advantage for the invasive plant over the native ones, which are dependent on the association with these fungi (Callaway et al., 2008). However, some species may alter the composition of the AMF community of the new environment, reducing the diversity so as to promote the dominance of species that favor their growth (Mummey & Rillig, 2006). Thus, the strategy used by invasive plants varies as a function of the species and the environment in which they are located, but all strategies ultimately promote a greater competitive advantage for the invasive species (Bever, 2003).

The role of soil microorganisms on the interactions between weeds and crops

Weeds are wild plants that grow spontaneously in agricultural soils and that have some traits that allow their establishment in various environments, such as large competitive aggressiveness, large seed production, facility at dispersing seeds and increased seed longevity (Brundrett, 2008). Among these characteristics, the large competitive aggressiveness is the most related to yield losses, since weeds have greater ability to extract soil nutrients in relation to crops (Carvalho et al., 2007). Weeds have a similar behavior to that of invasive plants found in various natural ecosystems (Reinhart & Callaway, 2006).

Recent studies have demonstrated that weeds are able to associate with arbuscular mycorrhizal fungi (Santos et al., 2013; Massenssini et al., 2014) and that the effects of this association may vary from positive to negative, depending on the environmental conditions (Massenssini, 2014). Furthermore, the presence of a competing plant may alter weed root colonization by AMF. Fialho (2013) observed that *Bidens pilosa* and *Eleusine indica* showed higher mycorrhizal colonization when cultivated in competition with *Zea mays*. The author attributed this increase in AMF colonization to the competitive strategy of these weeds. In other work, mycorrhizal colonization of the weeds *Ipomoea ramosissima*, *Ageratum conyzoides*, and *B. pilosa* varied depending on the identity of the competitor species (Massenssini, 2014). This suggests that weeds may have different competitive strategies and may have positive interactions with different microbial groups.

The soil microbial biomass and activity may vary depending on the crop species as well as the presence or absence of competitor plants (Melo, 2012). Moreover, the structure of the soil microbial community may change depending on the crop species, and these changes are directly linked to the prevailing soil conditions (Massenssini, 2014). Studies have shown that the relationships of weeds and crops with the soil microbiota may be different. Weeds seem to show higher dependence on interactions with soil microorganisms. Santos et al. (2012) observed that among eight weed species studied, four showed reduced growth when cultivated in fumigated soil. The authors also found that the two crops analyzed showed increased growth in fumigated soil. In another work, the greater competitive ability of *Z. mays* in relation to *A. conyzoides* was related to a reduction in the microbial biodiversity of the soil when these plants were grown in competition (Massenssini, 2014).

The structure of the soil microbial community is responsive to competition between plants. In general, competition promotes changes in the structure of the soil microbial community, making it different from that found when plants are grown in monoculture (Massenssini, 2014). These differences are mainly related to archaeal and bacterial communities, suggesting a closer relationship between the plants evaluated and these microbial groups (Massenssini, 2014), supporting the idea that, in disturbed environments, with high fertility, there is a soil microbial food web based on bacterial populations (Kramer et al., 2012). Furthermore, weeds tend to have positive feedback interactions with soil microorganisms, while crops may present neutral or negative feedback interactions (Massenssini, 2014).

PERSPECTIVES

In agricultural environments, with a high level of disturbance and fertility, there are favorable conditions for the establishment of plants with rapid growth and short life cycles, such as weeds. Cultivation of the species of interest, whose main biological traits were selected in artificial environments with elevated human intervention, is negatively affected by the presence of weeds due to competition for resources. Allied with this, the greater ability of weeds to establish positive interactions with soil microbes, in relation to crops, allows them to acquire greater competitive ability in these environments.

In this context, the soil microbial community plays a central role in modulating the interactions between weeds and crops, potentially resulting in increases in the competitive ability of different plants depending on the prevalent environmental conditions. The management of soil microbial populations should be taken into account for the implementation of a sustainable agricultural model. Therefore, some issues still need to be investigated to better understand the role of soil microorganisms in the interactions between plants in agricultural environments. What is the minimum range required for the operation of the ecological functions performed by soil microorganisms? What are the effects of diversity loss of different soil microbial groups on plant growth? How does the diversity of the soil microbial community interfere with interactions between weeds and crops? Which microbial groups are directly involved with these interactions and what are the ecological functions they perform? What mechanisms are responsible for the changes in the competitive relationships between weeds and crops? How can these mechanisms interfere to reduce the damage caused by weeds, or even use them to improve agricultural productivity? Future studies should address these issues so that a new agricultural model, with less human intervention and greater productivity can be developed, reducing the dependence on inputs and greater participation of soil microorganisms in promoting plant growth.

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