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LITERATURE REVIEW

Competitive Capacity and Rhizosphere Mineralization of Organic Matter During Weed-Soil Microbiota Interactions

Capacidade Competitiva e Mineralização Rizosférica da Matéria Orgânica Durante as Interações Planta Daninha-Microbiota do Solo

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ABSTRACT The competition between weeds and crops is one of the main factors responsible for productivity losses in agricultural fields. This review aimed at presenting and discussing how the interactions between weeds and microorganisms can affect the competitive capacity of weeds and soil physicochemical properties. We also discuss how changes in the elemental stoichiometry of weeds can reflect their competitive and adaptative capacity. Although weeds are more dependent on associations with soil microorganisms than crops for growth, few studies have assessed the contribution of the soil microbiota to their competitive success in agroecosystems. When in competition, plants can change the elemental stoichiometry of their tissues in environments with varied nutrient availability. Elemental stoichiometry of plants has been particularly well studied using ecological approaches on the dynamics of weed populations in natural ecosystems, being a promising tool for understanding weed capacity to adapt to different agricultural managements. Plants control the biogeochemical cycles of carbon (C) and nitrogen (N) in the rhizosphere through a phenomenon known as the rhizosphere priming effect (RPE). Although this review has found some information in the literature that provides strong indications that the coexistence of weeds and crops may increase soil organic matter mineralization, we are not aware of studies investigating the effects of competition among these plants on RPE.

Keywords: rhizosphere priming, elemental stoichiometry, soil quality, agricultural sustainability.

RESUMO - A competição entre plantas daninhas e culturas é um dos principais fatores responsáveis por perdas de produtividade nos campos agrícolas. Esta revisão teve como objetivo apresentar e discutir como a interação entre plantas daninhas e microrganismos pode afetar a capacidade competitiva de plantas daninhas, bem como as propriedades físico-químicas do solo. Ainda, abordamos como as mudanças na estequiometria elementar de plantas daninhas podem refletir a capacidade competitiva e adaptativa das mesmas. Embora as plantas daninhas sejam mais dependentes de associações com microrganismos do solo do que as culturas para o crescimento, há poucos trabalhos que avaliaram a contribuição da microbiota do solo para o sucesso competitivo dessas plantas em agroecossistemas. Quando em competição, as plantas podem mudar a estequiometria elementar de seus tecidos em ambientes com variada disponibilidade de nutrientes. A estequiometria elementar de plantas tem sido particularmente bem estudada em abordagens ecológicas sobre a dinâmica de populações de plantas invasoras em ecossistemas naturais e parece ser ferramenta promissora para conhecer a

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capacidade das plantas daninhas para adaptar a diferentes manejos agrícolas. As plantas controlam os ciclos biogeoquímicos do carbono e do nitrogênio na rizosfera por meio de um fenômeno denominado efeito priming rizosférico (EPR). Embora esta revisão tenha levantado um conjunto de informações da literatura que fornecem fortes indícios de que a convivência das culturas com plantas daninhas pode aumentar a mineralização da matéria orgânica do solo (MOS), não se tem conhecimento de estudos que investiguem os efeitos da competição entre tais plantas sobre o EPR.

Palavras-chave: *priming* rizosférico, estequiometria elementar, qualidade do solo, sustentabilidade agrícola.

INTRODUCTION

Because of being strong competitors for resources, weeds are characterized by their negative effects on crop growth. In addition to causing large productivity losses, weed interference also increases production costs. Weeds have developed multiple evolutionary and/or adaptative strategies that made them extremely competitive and persistent in the environment. Some weeds, for instance, modify the structure of microbial communities and alter the availability of soil nutrients, facilitating their own growth (Reinhart and Callaway, 2006; Kulmatiski et al., 2008). Nevertheless, the contribution of interactions with the soil microbiota to the competitive capacity of weeds is poorly known.

The competitive capacity of a given plant species is also associated with its intrinsic ability to modify the metabolism to adapt to changing environmental conditions. Plants with a high stoichiometric flexibility, i.e. with a high capacity to alter the elemental composition of their tissues in response to stress conditions, present, in general, a greater adaptative and competitive success. The knowledge of elemental stoichiometry of plant tissues allows biological and ecological inferences on a particular species, such as its potential to adapt or survive in nutrient-rich or nutrient-poor environments (Güsewell, 2004; Yu et al., 2010; Wang et al., 2015a). However, the effects of competition between crops and weeds on their stoichiometry remain little explored.

The establishment and persistence of weeds in a given area lead to chemical and biological changes in soil properties (Kulmatiski et al., 2006; Sanon et al., 2009; He et al., 2013). Plants can influence microbial activity through the release of root exudates, increasing or retarding the decomposition of soil organic matter (SOM). This phenomenon is known as the rhizosphere priming effect (RPE) (Kuzyakov, 2002). Agricultural soils play a central role in global climate change and can act as a C reservoir (Lal, 2011) or source of greenhouse gases (Smith, 2012; Smith et al., 2013). Weeds are commonly present in agricultural fields. Despite this, the influence of weed-crop competition on RPE is yet to be elucidated. Understanding the real contribution of RPE to global C balance is important for adopting more sustainable management practices.

In this work, we reviewed literature data on the influence of soil microbiota on the competitive capacity of weeds, as well as on the occurrence of RPE during the interspecific competition. In addition, we collected literature information on the elemental stoichiometry of plant biomass, relating it to the competitive capacity of weeds.

SOIL MICROBIOTA AND COMPETITIVE CAPACITY OF WEEDS

A plant can only be considered a weed if it is, directly or indirectly, impairing a certain human activity (Silva and Silva, 2007). The occurrence of plants considered as weeds in crops has been observed since the beginning of agriculture (Randall, 1997). The term invasive plant is more commonly used in ecological studies and refers to plants naturally or anthropically introduced into natural or semi-natural habitats, interfering with the composition, structure or processes of the ecosystems (Randall, 1997). The competition between plants can be seen as a series of interrelated physiological and morphological changes that occur as a result of resource-dependent and independent processes (Ballaré, 1999; Kiær et al., 2013). The competitive capacity of crops and weeds is determined by physiological and morphological attributes that allow them to capture and exploit the resources available in the environment (Swanton et al., 2015). Species with relatively low nutrient demand, extensive root system, and effective membrane carriers, for instance, have a competitive advantage in a nutrient-limited environments (Swanton et al., 2015). The competitive capacity of a given species reflects its ability to acquire and/or make the best use of limiting resources and/or its ability to cope with low levels of resources or reduce their availability to its competitors (Gioria and Osborne, 2014). Additionally, the interactions with the soil microbiota may be important for competitive relations (Kulmatiski et al., 2006; Santos et al., 2013; Massenssini et al., 2014a; Fialho et al., 2016).

Some competition models among plants seek to explain plant diversity by identifying the circumstances under which competitors can coexist (Gurevitch et al., 2002). Ecological models of the coexistence of plant species based on niche differentiation and resource sharing provide information on how and why weeds compete with crops (Smith et al., 2010). The assumption of most of these models is that the coexistence between plants requires species capable of occupying different niches, i.e. species that present differences in the needs and ways of acquiring resources (Gurevitch et al., 2002; Silvertown, 2004). In the absence of niche differences, fitness differences, i.e. differences in reproductive capacity or susceptibility to predators and pathogens, lead to the competitive exclusion of certain species (Gioria and Osborne, 2014).

Soil microorganisms play a key role in niche and fitness differentiation among plant species since the microbiota is capable of interacting with plants either in a positive or negative way (Reinhart and Callaway, 2006; Kulmatiski et al., 2008). The partition of resources, mediated by microbial associations, allows plant species to access different pools of resources, thus avoiding competition (Reynolds et al., 2003). The differentiation in niche exploitation by plants also depends on the intrinsic characteristics of the species related to acquiring resources, such as the root system morphology (Gabriel et al., 2006). Weeds and crops may respond differently to the same level of soil resources (Blackshaw et al., 2003; Grant et al., 2007). Plant competition will be more intense, regardless of the resource levels or niche diversity, when the characteristics of resource acquisition of crops and weeds are similar (Smith et al., 2010).

Plant-soil microorganism associations may promote increased plant growth, pathogen resistance, and tolerance to environmental stresses (Rodriguez et al., 2009). Weeds are able to associate, for instance, with arbuscular mycorrhizal fungi (AMF) and dark septate endophytes (Santos et al., 2013; Massenssini et al., 2014b). Plants that establish these types of association can gain a competitive advantage over others (Massenssini et al., 2014a). *Bidens pilosa* and *Eleusine indica* reduced corn growth and nutrient accumulation more than *Urochloa decumbens* (Fialho et al., 2016). This response was probably because *B. pilosa* and *E. indica* had a higher mycorrhizal colonization. In general, weeds are more dependent on associations with soil microorganisms when compared to crops for growth and competitive ability (Massenssini et al., 2014a).

Soils act as an interactive component in the competition for resources between plants (Klironomos, 2002; Callaway et al., 2004; Lee et al., 2012). The plant-soil feedback hypothesis proposes that changes in microbial communities or resource availability during successive growth cycles of a given species may provide it with a competitive advantage over other plants (Bever, 1994; Reynolds et al., 2003). If the performance of a given species in the next growth cycle is stimulated, the feedback will be positive; on the other hand, if growth is reduced, the feedback will be negative (Hol et al., 2013). The competition for resources may have secondary importance when some soil conditions, such as the presence or absence of symbionts, are determinant for plant growth (Kulmatiski et al., 2006; Lee et al., 2012).

Most of the technique that allows assessing the influence of the soil microbiota on plant growth involves soil sterilization. However, all sterilization methods modify the properties of the soil, such as pH, CEC, N, Mn, etc. (Darbar and Lakzian, 2007; Perkins et al., 2013). These modifications make it difficult to attribute growth differences of a given plant to changes in the soil microbial community when cultivation on sterile and non-sterile soils are compared. To circumvent this problem, microbial inoculation or microbiota reconstitution of a sterilized soil by applying a fresh soil suspension, for example, has been frequently used (Hol et al., 2013; Crawford and Knight, 2017; Johnson et al., 2017). The comparison of crops in sterilized soils and in sterilized soils with inoculated or reconstituted microbiota allows observing the response of plants to changes in the soil microbial community.

The hypothesis that invasive plants have an advantage over the native species as a function of positive plant-soil feedback has stimulated several studies (Suding et al., 2013). Most of the reports assessed how the successive cultivation of invasive and native plants influence growth and productivity of subsequent plant generations (Suding et al., 2013). In general, invasive plants and weeds alter soil chemical and biological characteristics and lead to higher dry matter production (Kulmatiski et al., 2006, 2008; Lee et al., 2012), whereas for most native plants or crops, the consecutive cultivation in the same area reduces productivity (Koike et al., 2013, Suding et al., 2013). Few studies have assessed whether positive feedbacks improve the competitive capacity of invasive plants when growing together with native plants (Aguilera, 2011) or of weeds with crops (Hol et al., 2013).

Wheat growth was higher in inoculated soils, especially when the reconstituted microbiota was originally from organic cultivation systems rather than conventional ones (Johnson et al., 2017). These effects were explained by a probable change in the relative abundance of mutualistic and pathogenic organisms as a function of the cultivation systems. In addition, as plant-soil feedback became more positive, wheat competition with *Amaranthus retroflexus* or *Avena fatua* declined and facilitation increased (Johnson et al., 2017). On the other hand, the inoculation with the soil microbiota turned wheat more susceptible to competition with *Vicia villosa*, *Chenopodium album*, and *Myosotis arvensis* (Hol et al., 2013). This might have been due to an improvement in the competitive capacity of weeds as a result of positive feedbacks with the soil.

Soil inoculation with the microbiota from areas invaded by *Lespedeza cuneata* significantly improved plant growth in monoculture, but curiously, in the presence of interspecific competitors, this positive effect was eliminated (Crawford and Knight, 2017). Similarly, the invasive plant *Microstegium vimineum*, despite increasing nitrate availability in the soil, benefited from this effect only in the absence of competition with native plants (Lee et al., 2012). The persistence of invasive plants may be favored by positive plant-soil feedbacks, but the magnitude of the benefits gained may depend on interspecific interactions (Lee et al., 2012). Thus, a better growth of a given plant species in its original soil does not guarantee that it will be competitively successful during interactions with other plants (Crawford and Knight, 2017).

In a study with *Andropogon gerardii* and *Sorghastrum nutans*, the effects of feedback and competition were specific to each plant species (Casper and Castelli, 2007). While feedback improved the competitive capacity of *A. gerardii*, interspecific competition eliminated the effects of positive feedback for *S. nutans*. A change in plant-soil feedback according to the competitive context was also observed for *Microstegium vimineum* (Shannon et al., 2012). Feedback interactions can reverse the competition outcome and vice versa. The different feedback scenarios also depend on the intensity of competition between plants (Aguilera, 2011). This dependence on context means that plant-soil feedback can shift as competitive interactions between plants constantly change along infestation progress (Shannon et al., 2012).

The species *Lolium arundinaceum*, for instance, depends on the symbiosis with the endophytic fungus *Neotyphodium coenophialum* to modify the soil microbial community to the point of reducing the growth of successor tree species (Rudgers and Orr, 2009). This symbiosis has the potential to alter plant succession and forest composition.

The native plant *Quercus acutissima* reduced the growth of the invasive *Robinia pseudoacacia* in a soil previously inoculated with microorganisms (Chen et al., 2012). However, in sterilized soil, growth decrease of the invasive plant were smaller. This response was associated to changes in the soil microbial community, especially to an increase in N-fixing bacteria. On the other hand, soil sterilization reduced the growth of both the native plant *Bouteloua gracilis* and the invasive plant *Bromus tectorum* cultivated in monoculture. The negative effects of competition were higher for the invasive plant than for *B. gracilis* (Emam et al., 2014), probably because soil sterilization eliminated deleterious microorganisms to the native plant.

To date, some studies have shown that there is no consistency in the relationship between competition and feedback (Callaway et al., 2004; Casper and Castelli, 2007; Hol et al., 2013). Even without competition, plant-soil feedbacks were described as idiosyncratic (Jiang et al., 2010). However, few studies have assessed the contribution of the soil microbiota to the competitive success of a given species in agroecosystems. The challenge is to identify how competition influences the outcome of the interactions between plants and microorganisms and vice versa. Some studies have shown that the structure of the soil microbial community is altered by interspecific competition (Massenssini, 2014; Monteiro, 2016) and that some plant species are more dominant in shaping the soil microbiota than others (Massenssini, 2014). Plants with such dominance can possibly be favored by positive feedbacks, even when in interspecific competition.

Do weed-plant interactions alter the elemental stoichiometry of plant biomass?

Plants use solar radiation to fix C while absorbing nutrients in adequate amounts to meet their requirements. However, photosynthesis and nutrient absorption are not perfectly coupled and, therefore, nutrient contents in relation to that of C vary within each plant species (Goldman et al., 1979; Rhee and Gotham, 1981). Considering that C and nutrients are essential for cellular functioning (Güsewell, 2004; Ågren, 2008) and that C:nutrient balance generally affects crop production and the dynamics of the ecosystem food chain, elemental stoichiometry has been one of the most investigated factors in ecological interactions (Elser et al., 2010; Sardans and Penuelas, 2012; Ye et al., 2014).

Changes in nutrient stoichiometry have often been associated with the success of invasive plants (Sardans and Penuelas, 2012), which can change the elemental stoichiometry of their tissues as an adaptive response to variations in nutrient availability (Ventura et al., 2008; Liang et al., 2015). The success of invasive plants in infesting nutrient-rich or nutrient-poor environments is usually associated with their morpho-physiological characteristics. In environments with low nutrient availability, growth is slow, biomass C:nutrient ratio increases and plants use nutrients more efficiently (González et al., 2010). In contrast, under conditions of high nutrient availability, plants maximize protein synthesis and growth as competitive strategies (González et al., 2010), resulting in decreases in the C:nutrient ratios of their tissues (Ågren, 2008). However, not all plants are capable of modifying the tecidual elemental stoichiometry in response to nutrient limitation (Elser et al., 2010; Yu et al., 2011). Thus, adaptive changes of the C:nutrient ratios may lead to an increased infestation success, especially in nutrient-poor environments (Funk, 2008). Besides, invasive plants capable of actively increasing nutrient availability in the environment, especially through N_2 fixation or P mobilization in the soil, outperform competitors in environments with low N and P availability. Invasive plant infestation is one of the factors that shape species composition of ecosystems; the structure of plant communities may also reflect changes in the elemental stoichiometry of the soil (Sardans et al., 2016b), which may be linked to RPE and the biogeochemical cycling of plant residues.

The elemental stoichiometry of plants depends on ecosystem characteristics, plant growth strategies, community species composition, and soil nutrient heterogeneity (Sardans et al., 2016a). It is difficult to discern whether the competitive success of an invasive plant is a cause or consequence of the soil elemental composition and nutrient availability (Sardans et al., 2016b). Some studies suggest that changes in the nutrient content of plants and of the soil are more a consequence than the cause of invasive plant infestation (Sardans et al., 2016b).

Plant elemental stoichiometry has been particularly well studied in ecological research on the dynamics of invasive plant populations in natural ecosystems. Interestingly, we haven´t found any study investigating whether competition influences weed and crop stoichiometry.

CHANGES IN SOIL PROPERTIES DURING WEED ESTABLISHMENT

In general, the establishment and persistence of invasive plants and weeds in a given area are associated with changes in soil properties. In addition to increasing the activity and altering the structure of the soil microbial community (Sanon et al., 2009; Massenssini, 2014; Souza-Alonso et al., 2015), these plants increase soil enzymatic activities (He et al., 2013; Kuebbing et al., 2014; Wang et al., 2015b) and, consequently, nutrient mineralization (Li et al., 2006; Fickbohm and Zhu, 2006; Elgersma et al., 2011; Si et al., 2013). Soil changes are usually associated and have strong implications for soil quality by altering soil composition and elemental stoichiometry (Sardans et al., 2016b). In some cases, the impact of invasive plants on the soil may not be reversed even long after infestation, as reported for *Acacia dealbata* (Souza-Alonso et al., 2015). The infestation by this plant led to changes in soil nutrient availability, enzyme activity, and microbial community structure.

Weed infestation success in abandoned agricultural areas correlate with increases in soil C, N, and P (Kulmatiski et al., 2006). This has been attributed to the ability of weeds to facilitate their own growth over generations through the maintenance of beneficial fungal communities and the rapid rates of nutrient cycling in the soil.

Increases in nutrient concentrations in soils infested by invasive plants were more common in those with low nutrient levels, while decreases in nutrient availability were observed under opposite conditions (Dassonville et al., 2008). Similar results were presented in a meta-analysis of 215 articles, for which differences in C, N, P, and K availability between soils with invasive or native plants decreased in nutrient-rich environments (Sardans et al., 2016b). In general, soils infested with invasive plants have higher N, P, and K concentrations (Sardans et al., 2016b). Some examples of changes in soil properties due to infestation by invasive and weed plants are listed in Table 1. In this sense, some species have developed different adaptive or competitive strategies. For example, changes in nutrient mineralization have not been observed in soils infested by *Artemisia biennis*, *Centaurea stoebe*, *Tragopogon dubius*, *Bidens frondosa*, and *Senecio inaequidens* (Meisner et al., 2011). In spite of this, these species were more competitive than their native congeners because of their greater ability to take up nutrients.

Table 1 - Changes in soil properties due to the presence of invasive or weed plants

Soil characteristics	Invasive and weed plants
Increased values of chemical attributes	
N, P, K, SOM, and pH	*Mimosa pudica* (Wang et al., 2015b)
C, N, and P	*Acacia dealbata* (Souza-Alonso et al., 2015), *Amaranthus viridis* (Sanon et al., 2009)
K, Mg, Mn, and N	*Fallopia japonica*, *Heracleum mantegazzianum*, *Impatiens glandulifera*, *Prunus serotina*, *Rosa rugosa*, *Senecio inaequidens*, *Solidago gigantea* (Dassonville et al., 2008)
pH and Ca	*Wedelia trilobata* (Si et al., 2013)
Increased enzymatic activity	
Urease, invertase, protease, catalase, and cellulase	*Mimosa pudica* (Wang et al., 2015b)
Urease, invertase, and acid phosphatase	*Bidens pilosa* (He et al., 2013)
Acid phosphatase, β-glucosidase, urease, and N-acetylglucosaminidase	*Acacia dealbata* (Souza-Alonso et al., 2015)
β-glucosidase, invertase, protease, urease, acid phosphatase, alkaline phosphatase, and phenol oxidase	*Mikania micrantha* (Li et al., 2006)
Changes in the structure of the soil microbial community	
Increase of fungal and bacterial populations in the soil	*Bidens pilosa* (He et al., 2013)
Increase of bacterial abundance	*Amaranthus viridis* (Sanon et al., 2009)
Increase of aerobic bacteria and reduction of anaerobic bacteria	*Mikania micrantha* (Li et al., 2006)
Increase of richness of the soil fungal community	*Wedelia trilobata* (Si et al., 2013)
Change in the abundance of fungi, bacteria, and arches. Recruiting of specific microorganisms	*Ageratum conyzoides*, *Ipomoea ramosissima*, *Bidens pilosa* (Monteiro, 2016)

Enzymes are recognized as responsible for the activities occurring in the rhizosphere (Gianfreda, 2015). Enzymes produced and released by roots and microorganisms alter rhizosphere nutrient availability, leading to the mineralization of SOM. Enzyme activity determines the intensity and direction of RPE (Gianfreda, 2015). The release of root exudates activate the microbial synthesis of extracellular enzymes. Leading to subsequent SOM decomposition (Gianfreda, 2015). An increased SOM decomposition in soils cultivated with barley was associated with a higher activity of chitinase and β-xylosidase (Pausch et al., 2016).

Priming effect

Priming effect (PE) is defined as a change in SOM decomposition rate due to substrate addition (Löhnis, 1926; Kuzyakov et al., 2000). When this phenomenon occurs in the rhizosphere, it is defined as the rhizosphere priming effect (RPE) and represents the change in SOM decomposition caused by root activity (Kuzyakov, 2002; Dijkstra et al., 2013). RPE is positive when SOM decomposition is accelerated and negative when SOM decomposition is delayed (Kuzyakov, 2002). RPE may retard SOM decomposition rates by 79 % (Thurgood et al., 2014) or stimulate it up to more than 500 % (Shahzad et al., 2015). On average, organic C decomposition in cultivated soils via RPE is about 59 % higher than that observed in non-cultivated soils (Huo et al., 2017).

Plants are one of the main sources of C entry into the soil. About 40 to 60% of the photosynthetically fixed C is directed to roots and associated with microorganisms by means of rhizodepositions (Clemmensen et al., 2013). Rhizodepositions are organic substances such as exudates, mucilages, secretions, and cell lysates released by plant roots (Kuzyakov, 2002). These compounds have different stoichiometric and energetic properties (Dijkstra et al., 2013), being important energy sources for the microbial production of extracellular enzymes capable of breaking down SOM (Blagodatskaya and Kuzyakov, 2008). Therefore, RPE is a common phenomenon in plant-soil interactions. Plants provide energy to soil microorganisms through root exudates, controlling SOM mineralization and, therefore, nutrient availability (Kuzyakov, 2010; Shahzad et al., 2015, Bernal et al., 2017).

The RPE cannot be attributed only to rhizodepositions (Kuzyakov, 2002; Blagodatskaya and Kuzyakov, 2008; Cheng et al., 2014). Root development may destabilize soil aggregates and provide or facilitate access of microorganisms to soil organic C (Kuzyakov, 2002; Cheng et al., 2014). Other soil factors such as moisture, temperature, pH, and physical properties interfere with the magnitude and direction of RPE (Cheng et al., 2014; Huo et al., 2017).

In general, the short-term RPE, i.e. days to weeks, is believed to be mainly relevant for changing the dynamics of the labile SOM, whereas long-term RPE, i.e. months to decades, may influence the stabilized SOM (Rousk et al., 2015). Overall, some evidence indicates that RPE may persist for years in perennial crops (Huo et al., 2017), as reported for *Pinus ponderosa* and *Populus fremontii* (Dijkstra and Cheng, 2007).

Rhizosphere priming effect mechanisms

There is evidence that biological rather than physical factors are especially responsible for RPE (Kuzyakov, 2002). The hypotheses of microbial activation, preferential substrate use, and competition for N between plants and microorganisms correspond to the most important mechanisms proposed for RPE (Kuzyakov, 2002). The C and N content in the soil determines the operation and magnitude of one or more of these mechanisms (Kuzyakov, 2002, 2010; Dijkstra et al., 2013). These three hypotheses focusing on nutrient availability perspective propose the: (a) microbial activation or microbial mineralization: microorganisms use rhizodepositions to mineralize nutrients in SOM, causing a positive RPE when nutrient availability is low; (b) use of preferential substrate: microorganisms prefer to use rhizodepositions first since they are readily available and then SOM, when nutrient availability is high; (c) competition for N: microorganisms compete for nutrients with plants, causing a negative RPE because microbial growth and SOM decomposition are limited in nutrients. Both positive and negative effects may occur under a low nutrient availability (Dijkstra et al., 2013).

The release of root exudates stimulates microbial growth and activity, thus increasing the general physiological potential of the community of decomposers for C mineralization by co-metabolism (Kuzyakov, 2002). Other factors, such as an increased microbial demand for N or successional changes in the microbial community structure, may also contribute to increased SOM mineralization rates.

There is a strong connection between root exudation and gross N mineralization, suggesting that plants become progressively less limited by the element when high rates of root exudation occur (Bengtson et al., 2012). Thus, a positive RPE can improve N supply to plants in soils with a low availability of this nutrient (Dijkstra and Cheng, 2007). However, experimental results from N fertilization indicated an inconsistent role of this nutrient in the regulation of RPE (Liljeroth et al., 1994; Cheng et al., 2003; Kumar et al., 2016; Zang et al., 2016; Studer et al., 2016). The RPE of soils cultivated with soybean and wheat ranged from 0 to 383 % and was not influenced by N, P, and K levels (Cheng et al., 2003). However, N limitation in a soil cultivated with corn increased RPE from 35 to 126% (Kumar et al., 2016).

Most of the studies report a negative RPE with increasing N fertilization. This suggests that N supply facilitates soil C sequestration by reducing SOM decomposition in the rhizosphere, as inferred for wheat cultivation (Zang et al., 2016).

The RPE is a complex phenomenon and N fertilization may not reduce SOM decomposition rates for all crops. Possibly, the presence of weeds can interfere with the magnitude and direction of RPE by modifying soil physical, chemical, and biological properties, even in fertilized areas.

Considering that low N availability favors RPE, competition for soil nutrients between weeds and crops is likely to enhance SOM decomposition. Contrarily, by selecting plants for grain production in high-fertility soils, crop breeding may have favored plants that are less capable of stimulating SOM decomposition (Huo et al., 2017). In fact, agricultural crops have been reported to cause lower RPE compared to grasses and tree species (Huo et al., 2017). Thus, it is likely that weeds have a greater potential to decompose SOM than crops.

Root exudates with low C and N contents have a greater potential to accelerate soil C losses, stimulating soil microorganisms to extract N from SOM. The magnitude of this effect depends on SOM recalcitrance, N availability, and the soil microbial communities (Huajun et al., 2016). The success of certain weeds in the agricultural fields may be associated with their ability to form associations with soil microorganisms, as reported for *Bidens pilosa* (Cui and He, 2009). Changes in soil microbial biomass and in the structure of soil microbial communities brought about by weed may be a common strategy for favoring RPE (Fontaine et al., 2003; Blagodatskaya and Kuzyakov, 2008).

Microbial biomass is not only a C reservoir but also a cycling agent for SOM (Blagodatskaya et al., 2010). RPE is associated with changes in soil microbial composition (Blagodatskaya and Kuzyakov, 2008). Bacteria are the first group to take up and metabolize most of the organic substances readily available in the soil (Moore-Kucera and Dick, 2008). This, in turn, accelerates microbial biomass cycling, especially that of r-strategists, triggering the apparent RPE. In this case, an increase of C and N mineralization, in response to a higher cycling rate of the microbial biomass, occurs without concomitant increases in SOM decomposition (Fontaine et al., 2003; Blagodatskaya and Kuzyakov, 2008; Kuzyakov, 2010).

Sequentially, other groups of microorganisms, such as fungi, which preferentially use more recalcitrant substrates, such as SOM, benefit from the remaining dead bacterial biomass after depletion of the readily available organic compounds (Fontaine et al., 2003). Fungi, which are predominantly k-strategists (Fontaine et al., 2003; Blagodatskaya et al., 2007), are stimulated by the dead biomass, increasing SOM decomposition (real RPE).

Some specific groups of soil microorganisms are associated with real RPE. Gram-negative bacteria are capable of assimilating C from SOM (Nottingham et al., 2009). Ectomycorrhizal fungi, in addition to increasing C exudation in the soil, can synthesize extracellular enzymes, while arbuscular mycorrhizal fungi enhance RPE possibly by C exudation (Phillips and Fahey, 2006; Brzostek et al., 2015). Increased rates of SOM decomposition in oak ecosystems have been attributed to a higher relative abundance of fungi in the soil (Carney et al., 2007).

In soils with low N availability, the native species *Fragaria vesca* increased root growth and exudation, stimulating microbial biomass growth and cycling. In contrast, the invasive plant *Duchesnea indica* increased N uptake without allocating additional dry matter to the roots. This resulted in N deficiency in the soil, delaying microbial growth and biomass cycling in the rhizosphere (Blagodatskaya et al., 2014). The greater competitive capacity of *D. indica* for N allows this plant to control microbial communities in the rizosphere, favoring k-strategist (Fontaine et al., 2003). Therefore, the capacity of some weeds to shape the soil microbial community (Massenssini, 2014) may be an indicator of their potential to increase SOM mineralization.

Soil microbiota-independent mechanisms

In contrast to the aforementioned mechanisms, the Regulatory Gate hypothesis assumes that SOM mineralization is independent of the size, composition, or specific activity of the soil microbiota (Kemmitt et al., 2008). The process is abiotic and occurs through oxidation and chemical hydrolysis, catalysis by extracellularly stabilized enzymes, desorption of sorbed organic matter or diffusion of substrates within aggregates (Kemmitt et al., 2008). Only after SOM destabilization by these processes, C would be available for use by the microbiota. Some works corroborate this hypothesis (Wertz et al., 2006; Rousk et al., 2011, 2015).

In the traditional hypothesis, root exudates accelerate SOM mineralization, being used as co-metabolites, i.e., SOM is mineralized fortuitously during the catabolism of readily bioavailable C and energy sources, such as root exudates. Therefore, glucose addition, an energetically favorable substrate, should cause higher RPE than less favorable substrates, such as oxalic acid. However, the inverse is observed. Oxalic acid stimulates more SOM decomposition by releasing protected organic compounds from the soil mineral fractions (Keiluweit et al., 2015). Instead of a co-metabolic pathway, organic binders with metal complexing capacity accelerates C mineralization by rhizosphere microbes through an indirect mechanism (Keiluweit et al., 2015). The proposed alternative mechanism suggests that large amounts of C in the soil are inaccessible to the microbiota due to C association to the mineral phase. A strong binding to Fe and Al minerals protects organic materials from being immediately reached and decomposed (Clarholm et al., 2015). Root exudates that can act as Fe and Al binders, such as organic acids, release C by complexation and dissolution reactions of soil minerals, promoting SOM accessibility to microorganisms and accelerating its loss from the system through microbial mineralization (Keiluweit et al., 2015).

A three-step process whereby low molecular weight organic acids and hydrolytic enzymes act in series to destabilize SOM supra-molecules was proposed by Clarholm et al. (2015). In this model, low molecular weight organic acids, such as oxalic acid, are released by vascular plants, free-living fungi, ectomycorrhizas, as well as by bacteria (Clarholm et al., 2015; Keiluweit et al., 2015). The interaction between plants and fungi leads the biotic mechanism to the supramolecular aggregate level and determines the priming of SOM, in which the destabilization step is a precondition for the subsequent release of nutrients (Clarholm et al., 2015).

The priming effect may not be related to the growth dynamics of r- and k-strategists since the addition of a labile C source can initiate SOM mineralization without sufficient time for the succession from r to k (Rousk et al., 2015). SOM mineralization may be due to the action of extracellular enzymes during labile C degradation. The cultivation of the hybrid tree *Populus deltoides x nigra* in soils with a low nutrient availability stimulated RPE (Studer et al., 2016). The C released by roots was lower than the total soil C respired, and both were lower than the microbial biomass C. This indicates an apparent RPE. However, there was SOM mineralization. Probably, plants under higher growth limitation have actively increased the release of specific compounds, such as organic acids and extracellular enzymes, to increase nutrient uptake.

In view of the reported results from the experiments on the mechanisms that induce RPE, this phenomenon should be seen as the sum of direct and indirect mechanisms (Keiluweit et al., 2015; Studer et al., 2016).

Does interspecific plant competition influence RPE?

Although plants grow in communities, studies that assess the influence interspecific competition on RPE are rare. We have found only three reports that focused on this issue (Dijkstra et al., 2010; Pausch et al., 2013; Concilio et al., 2015).

Rhizosphere effects on SOM decomposition ranged from positive to negative when five grass species were grown in monoculture or in competition; the negative effects prevailed at the end of cultivation and were lower in the intercrops (Dijkstra et al., 2010). Similarly, mixed cultivation reduced RPE when compared to monocultures (Pausch et al., 2013). The complementarity in the use of resources, such as water (Verheyen et al., 2008) and N (Hooper, 1997), by plants in the intercrop systems possibly reduced microbial activity and decreased rhizosphere effects on SOM decomposition (Dijkstra et al. al., 2010).

Minimizing RPE may contribute, in the long-term, to increase soil organic C in intercrop cultivation systems (Pausch et al., 2013). Contrarily, the coexistence between weeds and crops can lead to changes in the soil microbial community (Massenssini, 2014; Trognitz et al., 2016), stimulating microorganisms with higher capacity to decompose SOM (Blagodatskaya and Kuzyakov 2008). In addition, it is possible that plants competing for nutrients release exudates, such as organic acids, for nutrient solubilization and extracellular enzymes for SOM decomposition.

Plants in competition may change the amount and composition of root exudates (Carvalhais et al., 2013), altering the soil microbial community in the rhizosphere, as reported for *B. pilosa* vs. *Ipomoea ramosissima* and corn vs. *B. pilosa* (Massenssini, 2014). These plant combinations showed distinct structures of the microbial community at the end of the experiment when compared to their monocultures (Massenssini, 2014). Metagenomic analyses showed a dominance of bacteria in the soil microbial communities for the treatment with corn vs. *I. ramosissima*, while for corn vs. *B. pilosa*, fungal populations prevailed (Monteiro, 2016). Therefore, these changes in the microbial community structure as a function of interspecific competition may lead to differences in the magnitude and direction of RPE. Yet, it remains to be investigated if such changes in soil microbial community, provoked by crop-weed competition, are able to stimulate SOM degradation.

Can weed infestation influence RPE?

Certain weeds or invasive plants may influence SOM content (Table 1). However, studies assessing this issue have not addressed whether crop-weed competition can modify SOM dynamics. In addition, studies assessing weed infestation impacts on soil C fractions are scarce.

Despite the evidence that the presence of weeds or invasive plants can influence RPE, interestingly we have found only two studies that measured this effect. In one of them, it is reported that root system growth of the invasive plant *Phragmites australis* increased SOM decomposition only at deeper soil layers, changing SOM dynamics and leading to stable C losses in areas infested with this species (Bernal et al., 2017). SOM decomposition was probably due to an increase in the supply of limiting resources, such as O_2 and/or labile organic substrates, for microorganism at the deepest soil layers. The most stable and old SOM was replaced by C derived from *P. australis* (Bernal et al., 2017). On the other hand, the invasive plant *Bromus tectorum*, either in monoculture or in competition with *Elymus elymoides*, led to negative RPE based N mineralization measurements, in both infested and non-infested soils (Concilio et al., 2015). This suggests a reduction in SOM decomposition by *B. tectorum*. The authors studied the effects of invasive plants on soils of natural ecosystems and showed that the stimulation of SOM decomposition may be related to differences in the infestation strategies of *B. tectorum* and *E. elymoides*.

We have not found reports on weed influence on the RPE in agroecosystems. In these environments, management practices can directly affect the competition intensity between crops and weeds by influencing the pools of soil resources, as predicted by the “The resource pool diversity” hypothesis (RPDH) (Smith et al., 2010). RPDH proposes that crop-weed competition decreases as the diversity of soil resource pools increases. In plant communities, the intensity of interspecific competition depends on the degree of niche differentiation and resource sharing between species. Knowledge on the possible implications of weeds on SOM is essential for sustainable management practices.

In addition to knowing the direction and magnitude of RPE, it is important to assess possible changes in SOM quality. A positive RPE does not necessarily mean decreases in SOM since plant and microbial C stabilization can compensate C losses (Kuzyakov, 2002). The replacement of old by recently added C can increase SOM cycling along cultivations and this will depend on the quality of plant residues and soil microbial biomass (Bernal et al., 2017). If a positive RPE contributes to increased atmospheric CO_2 is yet to be elucidated and depends on a better knowledge on C balance (Kuzyakov, 2010).

CONCLUSIONS AND PERSPECTIVES

The contribution of microorganisms to the competitive success of plants is complex. Research on the influence of the soil microbiota on the competitive success of weeds is still incipient. The limited number of studies available points to an urgent need for advances in this area.

Studies on the elemental stoichiometry of plant tissues has been used to determine the optimal nutrient concentrations for crop growth, contributing to a more efficient use of fertilizers (Greenwood et al., 2008). The relation between plant tissue elemental stoichiometry and the capacity of a given plant species to adapt to different environmental conditions must be investigate. Knowledge on the stoichiometric flexibility of weeds can be an important tool for an integrated weed management. In addition to expanding the competition strategies of weeds, changes in the elemental stoichiometry may influence plant residue and nutrient cycling in the environment.

There is no doubt that plants control nutrient availability and SOM quality by rhizosphere processes. Interestingly, although RPE has been extensively studied, we have not found any reports that assessed weed influence on this phenomenon. Unlike agricultural crops, weeds maintain a greater dependence on the soil microbiota as an adaptive and competitive strategy. It is likely that these plants provoke significant RPE.

Some questions still need to be answered for a better understanding of the role of soil microorganisms in the interactions between plants in agricultural environments. Can competition intensity influence weed-soil feedback responses? Does fertilization influence the interaction between weeds and soil microorganisms? Can weeds change the stoichiometry of their tissues in response to the competition with crops? Are the most competitive plants more apt to promote changes in the elemental stoichiometry of their tissues? Does competition between weeds and crops influence SOM mineralization? Can changes in the soil microbial community structure due to crop-weed competition be determinant to RPE magnitude? Does soil fertility influence RPE during weed-crop competition?

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