CHRISTIANO DA CONCEIÇÃO DE MATOS

INFLUÊNCIA DAS INTERAÇÕES PLANTA DANINHA-MICROBIOTA DO SOLO SOBRE A CAPACIDADE COMPETITIVA VEGETAL E A MINERALIZAÇÃO RIZOSFÉRICA DA MATÉRIA ORGÂNICA

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Fitotecnia, para obtenção do título de *Doctor Scientiae*.

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APROVADA: 20 de julho de 2017.

André Marcos Massenssini

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Ivan Francisco de Souza

Maurício Dutra Costa
(Coorientador)

Antonio Alberto da Silva
(Orientador)

“A tarefa não é tanto ver aquilo que ninguém viu,
mas pensar o que ninguém ainda pensou sobre
aquilo que todo mundo vê.”

Arthur Schopenhauer

A Deus, aos meus pais, Vinício e Laci, a meu irmão, Clayton, à minha namorada, Lívia, ao meu orientador, Antonio Alberto da Silva, e aos coorientadores, Maurício Dutra Costa e Ivo Ribeiro da Silva.

Dedico.

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BIOGRAFIA

CHRISTIANO DA CONCEIÇÃO DE MATOS, filho de Vinício Francisco de Matos e Laci dos Santos Cruz de Matos, nasceu em 18 de dezembro de 1987, no município de Belo Horizonte, Minas Gerais. Em fevereiro de 2006, completou o ensino médio e técnico em agropecuária na Central de Ensino e Desenvolvimento Agrário de Florestal (CEDAF/ UFV), em Florestal, Minas Gerais, Brasil. Em março de 2007, iniciou o curso de graduação em Agronomia na Universidade Federal de Minas Gerais (ICA/UFMG), Montes Claros, Minas Gerais, recebendo o título de Engenheiro Agrônomo em janeiro de 2012. Em março do mesmo ano, iniciou o curso de mestrado no Programa de Pós-Graduação em Produção Vegetal na Universidade Federal dos Vales do Jequitinhonha e Mucuri, submetendo-se à defesa de dissertação em julho de 2013. Em agosto do mesmo ano, iniciou o curso de doutorado no Programa de Pós-Graduação em Fitotecnia na Universidade Federal de Viçosa.

SUMÁRIO

CAPACIDADE COMPETITIVA E MINERALIZAÇÃO RIZOSFÉRICA DA MATÉRIA ORGÂNICA DURANTE AS INTERAÇÕES PLANTA DANINHA-MICROBIOTA DO SOLO

SOIL MICROORGANISMS CHANGE THE COMPETITIVE ABILITY OF MAIZE AND WEEDS

RHIZOSPHERE PRIMING EFFECT ON SOIL ORGANIC MATTER INDUCED BY CROP-WEED COMPETITION

INTERSPECIFIC COMPETITION CHANGES NUTRIENT STOICHIOMETRY BETWEEN WEEDS AND CROPS

RESUMO

MATOS, Christiano da Conceição de, D.Sc., Universidade Federal de Viçosa, julho de 2017. **Influência das interações planta daninha-microbiota do solo sobre a capacidade competitiva vegetal e a mineralização rizosférica da matéria orgânica**. Orientador: Antonio Alberto da Silva. Coorientadores: Maurício Dutra Costa e Ivo Ribeiro da Silva.

Interações entre plantas e micro-organismos do solo podem afetar a capacidade competitiva de plantas daninhas, bem como as propriedades físico-químicas do solo. Certas combinações de plantas podem estimular a mineralização da matéria orgânica do solo (MOS), alterando o armazenamento de carbono orgânico nesse ambiente. Além disso, quando em competição, as plantas podem mudar a estequiometria elementar de seus tecidos, sendo essa característica reflexo da capacidade das mesmas de competir com outras espécies em ambientes com variada disponibilidade de nutrientes. Assim, os objetivos deste trabalho foram: I) determinar como a microbiota do solo pode contribuir para o estabelecimento inicial e a capacidade competitiva de plantas daninhas e do milho; II) avaliar se a competição entre plantas daninhas e o milho pode estimular a decomposição da MOS; III) analisar a estequiometria elementar de plantas daninhas durante a competição interespecífica com o milho em experimentos de casa de vegetação. Para alcançar o primeiro objetivo, um experimento foi conduzido em casa de vegetação com *Bidens pilosa*, *Amaranthus viridis* e *Zea mays*. Avaliamos seis manejos de cultivo (monocultura de milho, coexistência entre plantas daninhas e milho, monoculturas de plantas daninhas e solo sem cultivo) em duas condições do solo (solo esterilizado e solo esterilizado com microbiota reconstituída). A reconstituição da microbiota do solo foi realizada pela aplicação de suspensão aquosa de solo fresco no solo esterilizado. A microbiota do solo desempenhou papel importante nas interações entre *B. pilosa*, *A. viridis* e milho, influenciando o crescimento da planta e a capacidade competitiva das mesmas. A reconstituição da microbiota do solo melhorou a capacidade do milho de competir com *A. viridis*, enquanto o inverso foi observado para *B. pilosa*. Para alcançar o segundo objetivo, as espécies de plantas *A. viridis*, *B. pilosa* e *Ipomoea grandifolia*, consideradas plantas daninhas, e *Z. mays* foram cultivadas em casa de vegetação. Foram avaliados oito tratamentos: monoculturas de milho e plantas daninhas, milho em competição com plantas daninhas e solo sem cultivo. A concentração total de CO_2 (solo + planta) foi determinada semanalmente. Nessas ocasiões, o efluxo de CO_2 e a composição isotópica de amostras gasosas ($\delta^{13}CO_2$) foram quantificados e o efeito *priming* rizosférico (EPR) sobre a MOS foi estimado. As plantas foram colhidas aos 60 dias após o plantio. Nessa ocasião, amostras de solo foram coletadas para medir o conteúdo de C e N da matéria orgânica particulada (MOP) e da matéria orgânica associada a minerais (MOAM). Todos os tratamentos de competição levaram a valores de EPR positivos. A monocultura de *I. grandifolia* e o milho vs. *B. pilosa* levaram às maiores perdas de C da MOAM e da MOP em comparação com os solos não cultivados. A competição entre o milho e *B. pilosa* aumenta a mineralização da MOS, enquanto a competição do milho com *A. viridis* e *I. grandifolia* retarda esse processo. Para alcançar o terceiro objetivo, os dados de conteúdo de nutrientes do experimento anterior foram coletados e as razões estequiométricas elementares foram calculadas para os tratamentos de monocultura e de competição. *Amaranthus viridis* apresentou baixa flexibilidade estequiométrica sob a mesma condição de pressão competitiva enfrentada por *B. pilosa* e *I. grandifolia*. A competição interespecífica alterou a estequiometria elementar das plantas, e a magnitude dessa alteração dependeu das espécies de plantas envolvidas. A competição interespecífica diminuiu a qualidade da biomassa vegetal, resultando em maiores relações C:N, C:P, C:K e N:P, principalmente para *B. pilosa* e *I. grandifolia*. Esse decréscimo de qualidade poderá reduzir a taxa de decomposição dos resíduos vegetais e levar à imobilização de nutrientes no solo.

ABSTRACT

MATOS, Christiano da Conceição de, D.Sc., Universidade Federal de Viçosa, July, 2017. **Influence of weed-soil microbiota interactions on plant competitive ability and rhizospheric organic matter mineralization**. Advisor: Antonio Alberto da Silva. Co-advisors: Maurício Dutra Costa and Ivo Ribeiro da Silva.

The interactions between plants and soil microorganisms can affect weed-crop competition as well as the physico-chemical properties of the soil. Certain plant combinations can stimulate the mineralization of soil organic matter (SOM), thereby changing the storage of organic carbon in the soil. Additionally, under competition, plants can change the elemental stoichiometry of their tissues and this may be a reflection of their ability to compete with other species in environments with distinct nutrient availability. Thus, the objectives of this work were: I) to determine how the soil microbiota may contribute to the initial establishment and competitive ability of weeds and maize; II) to evaluate whether competition between weeds and maize can stimulate SOM decomposition; III) to analyze weed-crop elemental stoichiometry during interspecific competition between weeds and crops in greenhouse experiments. To achieve the first objective, a research was conducted under greenhouse conditions with *Bidens pilosa, Amaranthus viridis*, and *Zea mays*. We evaluated six cultivation managements (maize monoculture, coexistence between weeds and maize, weed monocultures, and non-cultivated soil) under two soil conditions (sterilized soil and sterilized soil with reconstituted microbiota). Soil microbiota reconstitution was done by the application of a fresh soil suspension to the sterilized soil. The soil microbiota plays an important role in the interactions between *B. pilosa*, *A. viridis,* and maize, influencing plant growth and their competitive ability. Soil microbiota reconstitution improved the ability of maize to compete with *A. viridis*, while the reverse was observed with *B. pilosa*. To achieve the second objective, the plant species *A. viridis*, *B. pilosa*, and *Ipomoea grandifolia*, considered as weeds, and *Z. mays* were grown under greenhouse conditions. We evaluated eight treatments: maize and weed monocultures, maize in competition with weeds, and non-cultivated soil. Total CO_2 concentration (soil + plant) was determined weekly. On these occasions, the CO_2 efflux and isotopic composition of gaseous samples ($\delta^{13}CO_2$) were quantified and the rhizosphere priming effect (RPE) on soil organic matter was estimated. The plants were harvested at 60 days after planting. At that time, soil samples were collected to measure the C and N contents of particulate (POM) and mineral-associated organic matter (MAOM). All competition treatments led to positive RPE values. *Ipomoea grandifolia* monoculture and maize vs. *B. pilosa* led to the highest MAOM-C losses and reduced POM-C compared to those of non-cultivated soils. Competition between maize and *B. pilosa* increases SOM mineralization, while maize competition with *A. viridis* and *I. grandifolia* retards this process. To achieve the third objective, nutrient content data from the previous experiment were collected and the elemental stoichiometric ratios were calculated for the monoculture and competition treatments. *Amaranthus viridis* showed low stoichiometric flexibility under the same competitive pressure as that faced by *B. pilosa* and *I. grandifolia*. Interspecific competition changed the elemental stoichiometry of plants, and the magnitude of these changes was dependent on the plant species involved. Interspecific competition decreased plant biomass quality, leading to higher C:N, C:P, C:K, and N:P ratios, mainly for *B. pilosa* and *I. grandifolia*. This may subsequently reduce plant residue decomposition rate and lead to nutrient immobilization in the soil.

INTRODUÇÃO GERAL

INTRODUÇÃO GERAL

A interferência de plantas daninhas é um dos principais problemas limitantes à produtividade e à rentabilidade das atividades agrícolas. De maneira geral, a presença dessas plantas causa maiores perdas à produção das culturas do que a incidência de insetos pragas e patógenos (Oerk 2006). O manejo inadequado de plantas daninhas causa perdas severas no rendimento das culturas, podendo chegar a 90 % no algodoeiro (Manalil et al. 2017) e no milho (Mhlanga et al. 2016) e a 97 % no sorgo (Peerzada et al. 2017). Isso ocorre porque as plantas daninhas apresentam múltiplas estratégias de sobrevivência às diferentes condições de meio e de manejo agrícola, o que as tornam extremamente competitivas e persistentes.

A ciência das plantas daninhas focaliza, principalmente, o desenvolvimento de métodos químicos e mecânicos para minimizar a abundância dessas plantas, em detrimento dos mecanismos que conduzem às interações competitivas com as culturas (Ward et al. 2014; Johnson et al. 2017). Os micro-organismos do solo podem alterar a capacidade competitiva dessas plantas. A microbiota do solo, por manter interações de cooperação ou simbiose com as plantas daninhas, podem aumentar a sobrevivência das mesmas (Chen et al. 2012; Massenssini et al. 2014). Em conjunto, essas associações podem levar a um *feedback* planta-solo positivo para a planta daninha (Lee et al. 2012; Sardans et al. 2016).

As plantas desempenham papel importante no ciclo do C, tanto pelo sequestro de C pela fotossíntese quanto pela liberação do elemento por meio da decomposição de resíduos, da respiração radicular e, ou do efeito *priming* rizosférico (EPR) (Sardans e Penuelas 2012; Sardans et al. 2012; Kumar et al. 2016). O EPR é definido como o estímulo ou retardamento da decomposição da matéria orgânica do solo (MOS) em função da atividade de raízes e de organismos vivos associados à rizosfera (Kuzyakov 2002; Cheng et al. 2014). Embora a associação de plantas daninhas com a microbiota do solo possa interferir no rendimento das culturas e na qualidade do solo, poucos estudos têm avaliado os efeitos dessas associações sobre a dinâmica da MOS.

Por ser mecanismo que pode influenciar o balanço atmosférico de CO_2, o EPR tem se tornado parte importante da pesquisa em ecologia do solo, especialmente na Alemanha, França, EUA, Reino Unido e Itália (Kuzyakov 2010). No Brasil, os estudos ainda são incipientes. O termo “*rhizosphere priming*” está associado a pelo menos 57 trabalhos no portal Web of Science, 62 no Scopus e 1540 do Google Scholar. Além disso, já foram publicados pelo menos cinco revisões (Kuzyakov 2002, 2010; Blagodatskaya e Kuzyakov 2008; Dijkstra et al. 2013;

Cheng et al. 2014) e uma meta-análise (Huo et al. 2017) sobre o tema. Apesar disso, não temos conhecimento de estudos que investiguem os efeitos da competição entre culturas e plantas daninhas sobre o EPR, embora o conjunto de informações da literatura forneça fortes indícios de que a convivência entre tais plantas pode aumentar a mineralização da MOS.

A estequiometria elementar da biomassa vegetal tem sido amplamente aplicada a diversos processos ecológicos e usada com sucesso para explicar muitos fenômenos, a exemplo das mudanças de composição de espécies vegetais em função das alterações climáticas globais e da introdução de plantas invasoras (Ye et al. 2014). Mudanças na estequiometria elementar têm sido frequentemente associadas ao sucesso adaptativo e competitivo. Conhecer a estequiometria elementar, principalmente as relações C:nutrientes e a relação N:P dos tecidos da planta, permite fazer uma série de abordagens biológicas e ecológicas sobre determinada espécie, como por exemplo, seu potencial em se adaptar ou sobreviver em ambientes ricos ou pobres em nutrientes (Güsewell 2004; Yu et al. 2010; Wang et al. 2015). No entanto, os efeitos da competição entre culturas e plantas daninhas sobre a estequiometria dessas plantas permanece pouco explorado. Hipotetizamos, nesta tese, que plantas daninhas mais competitivas são mais aptas a promover alterações na estequiometria elementar de seus tecidos.

A melhor compreensão das complexas interações que podem ocorrer entre plantas daninhas e a microbiota do solo pode permitir o desenvolvimento de estratégias que visem reduzir os impactos negativos das mesmas sobre a qualidade do solo. Assim, os objetivos deste trabalho foram: I) determinar como a microbiota do solo pode contribuir para o estabelecimento inicial e a capacidade competitiva de plantas daninhas e do milho; II) avaliar se a competição entre plantas daninhas e o milho pode estimular a decomposição da MOS; III) analisar a estequiometria elementar de plantas daninhas durante a competição interespecífica com o milho em experimentos de casa de vegetação.

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CAPÍTULO 1

Capacidade competitiva e mineralização rizosférica da matéria orgânica durante as interações planta daninha-microbiota do solo

CAPACIDADE COMPETITIVA E MINERALIZAÇÃO RIZOSFÉRICA DA MATÉRIA ORGÂNICA DURANTE AS INTERAÇÕES PLANTA DANINHA-MICROBIOTA DO SOLO

RESUMO

A competição entre plantas daninhas e culturas é um dos principais fatores responsáveis por perdas de produtividade nos campos agrícolas. Essa revisão teve como objetivo apresentar e discutir como a interação entre plantas daninhas e micro-organismos podem 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 há fortes indícios de que as plantas daninhas sejam mais dependentes de associações com micro-organismos 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 capacidade das plantas daninhas em se 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 forneçam fortes indícios de que a convivência das culturas com plantas daninhas possa aumentar a mineralização da matéria orgânica do solo (MOS), não temos conhecimento de estudos que investiguem os efeitos da competição entre tais plantas sobre o EPR.

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

INTRODUÇÃO

As plantas daninhas são caracterizadas por seus efeitos negativos sobre o crescimento das culturas, principalmente, por serem fortes competidoras por recursos. A interferência dessas plantas não só causa grandes perdas na produtividade, como também aumentam os custos de produção. Desde os primórdios da agricultura, as plantas daninhas interferem no rendimento das lavouras. Essas plantas possuem múltiplas estratégias de sobrevivência que as tornam extremamente competitivas e persistentes no ambiente. Certas plantas daninhas, por exemplo, podem modificar a estrutura das comunidades microbianas e alteram a disponibilidade de nutrientes no solo, facilitando o próprio crescimento ao longo dos cultivos (Reinhart e Callaway 2006; Kulmatiski et al. 2008). Apesar disso, a contribuição das interações com a microbiota do solo para a capacidade competitiva das plantas daninhas é pouco conhecida.

A capacidade competitiva de uma dada espécie vegetal está associada, também, à sua habilidade intrínseca de modificar o metabolismo respondendo às condições do meio. Plantas com alta flexibilidade estequiométrica, ou seja, com alta capacidade de alterar a composição elementar de seus tecidos em reposta a condição de estresse apresentam, em geral, maior sucesso adaptativo e competitivo. O conhecimento da estequiometria elementar dos tecidos da planta permite fazer inferências biológicas e ecológicas sobre determinada espécie, a exemplo do seu potencial de se adaptar ou sobreviver em ambientes ricos ou pobres em nutrientes (Güsewell 2004; Yu et al. 2010; Wang et al. 2015b). No entanto, os efeitos da competição entre culturas e plantas daninhas sobre a estequiometria dessas plantas permanece pouco explorado.

O estabelecimento e a persistência de plantas daninhas em determinada área levam a mudanças químicas e biológicas nas propriedades do solo (Kulmatiski et al. 2006; Sanon et al. 2009; He et al. 2013). As plantas, por meio da liberação de exsudados radiculares, podem influenciar a atividade microbiana, aumentando ou retardando a decomposição da matéria orgânica do solo (MOS). Esse fenômeno é conhecido como efeito *priming* rizosférico (EPR) (Kuzyakov 2002). Os solos agrícolas desempenham papel central no que diz respeito às alterações climáticas globais, podendo atuar como reservatório de carbono (Lal 2011) ou como fonte de gases de efeito estufa (Smith 2012; Smith et al. 2013). Comumente, as plantas daninhas estão presentes nos campos agrícolas. Apesar disso, a influência da competição planta daninha-cultura sobre o EPR ainda não é conhecida. Compreender a real contribuição do EPR para o balanço global de C é importante para adoção de práticas de manejo mais sustentáveis.

Neste trabalho, revisamos os dados da literatura sobre a influência da microbiota do solo para a capacidade competitiva de plantas daninhas, bem como sobre a ocorrência de EPR durante a competição entre essas plantas e as espécies cultivadas. Adicionalmente, levantamos as informações de literatura sobre a estequiometria elementar da biomassa vegetal, relacionando-a à capacidade competitiva de plantas daninhas.

MICROBIOTA DO SOLO E CAPACIDADE COMPETITIVA DE PLANTAS DANINHAS

Uma planta só pode ser considerada daninha se estiver prejudicando, direta ou indiretamente, determinada atividade humana (Silva e Silva 2007). Desde os primórdios da agricultura há a ocorrência de plantas consideradas daninhas em lavouras (Randall 1997). O termo planta invasora é usado com mais frequência em estudos ecológicos, pois remete a plantas que foram introduzidas naturalmente ou antropicamente em habitats naturais ou seminaturais, interferindo na composição de espécies, estrutura ou nos processos dos ecossistemas (Randall 1997). A competição entre plantas pode ser vista como uma série de mudanças fisiológicas e morfológicas inter-relacionadas que ocorrem como resultado de processos dependentes e independentes de recursos (Ballaré 1999; Kiær et al. 2013). A capacidade competitiva das culturas e das plantas daninhas é determinada por atributos fisiológicos e morfológicos que lhes permitem capturar e explorar os recursos disponíveis do ambiente (Swanton et al. 2015). As espécies com demanda de nutrientes relativamente baixa, sistema radicular extenso e transportadores de membrana eficazes, por exemplo, terão vantagem competitiva em ambiente limitado em nutrientes (Swanton et al. 2015). A capacidade competitiva de uma dada espécie reflete a capacidade em adquirir e, ou fazer o melhor uso de recursos limitantes e, ou a capacidade de lidar com baixos níveis de recursos ou reduzir a disponibilidade dos mesmos para seus concorrentes (Gioria e Osborne 2014). Adicionalmente, as interações com a microbiota do solo podem ser importantes para a capacidade competitiva de plantas daninhas (Kulmatiski et al. 2006; Santos et al. 2013; Massenssini et al. 2014a; Fialho et al. 2016).

Há modelos de competição entre plantas que buscam explicar a diversidade vegetal por meio da identificação das circunstâncias sob as quais os competidores podem coexistir (Gurevitch et al. 2002). Modelos ecológicos de coexistência de espécies de plantas, com base na diferenciação de nicho e partilha de recursos, fornecem informações sobre como e porque as plantas daninhas competem com as culturas (Smith et al. 2010). O pressuposto da maioria desses modelos é que a convivência entre plantas exige espécies capazes de ocupar nichos diferentes, ou seja, espécies que apresentem diferenças nas necessidades e formas de aquisição de recursos (Gurevitch et al. 2002; Silvertown 2004). Na ausência de diferenças de nichos, diferenças de *fitness* entre plantas, ou seja, diferenças na capacidade reprodutiva ou de suscetibilidade a predadores e patógenos, levam à exclusão competitiva de certas espécies (Gioria e Osborne 2014).

Os microrganismos do solo têm papel fundamental na diferenciação de nicho e de *fitness* entre as espécies vegetais, uma vez que são capazes de interagir com as plantas de forma positiva ou negativa (Reinhart e Callaway 2006; Kulmatiski et al. 2008). A partição de recursos, mediada por associações microbianas, permite que espécies de plantas acessem diferentes *pools* de recursos, reduzindo assim a competição (Reynolds et al. 2003). A diferenciação na exploração de nichos por plantas também depende de características intrínsecas das espécies que irão permitir a aquisição de recursos, a exemplo da morfologia do sistema radicular (Gabriel et al. 2006). Plantas daninhas e culturas podem responder de forma diferente a determinado nível de recursos no solo (Blackshaw et al. 2003; Grant et al. 2007). A competição entre plantas será mais intensa, independente dos níveis de recurso ou da diversidade de nicho, quando as características de aquisição de recursos da cultura e da planta daninha forem semelhantes (Smith et al. 2010).

Associações entre plantas e microrganismos do solo podem promover aumento do crescimento vegetal, da resistência a patógenos e da tolerância a estresses ambientais (Rodriguez et al. 2009). Plantas daninhas são capazes de se associar, por exemplo, com fungos micorrízicos arbusculares (FMA) e dark septate endophytes (Santos et al. 2013; Massenssini et al. 2014b). Plantas que estabelecem esses tipos de associação podem adquirir vantagem competitiva sobre outras (Massenssini et al. 2014a). *Bidens pilosa* e *Eleusine indica* reduziram mais o crescimento e o acúmulo de nutrientes do milho do que *Urochloa decumbens* (Fialho et al. 2016). Provavelmente, essa resposta estava associada ao fato de *B. pilosa* e *E. indica* terem apresentado maior colonização micorrízica. De maneira geral, há forte indícios de que as plantas daninhas são mais dependentes de associações com micro-organismos do solo do que as culturas para o crescimento e a capacidade competitiva (Massenssini et al. 2014a).

O solo atua como componente interativo na competição entre plantas por recursos (Klironomos 2002; Callaway et al. 2004; Lee et al. 2012). A hipótese de *feedback* planta-solo propõe que mudanças nas comunidades microbianas ou na disponibilidade de recursos, durante os sucessivos ciclos de crescimento de uma dada espécie, podem proporcionar vantagem competitiva para essa espécie de planta sobre outras (Bever 1994; Reynolds et al. 2003). Se o desempenho de uma dada espécie no próximo ciclo de crescimento for estimulado, o *feedback* será positivo; por outro lado, se o crescimento for reduzido, o *feedback* será negativo (Hol et al. 2013). A competição por recursos pode ser de importância secundária quando algumas condições do solo, como a presença ou ausência de simbiontes, forem determinantes para o crescimento da planta (Kulmatiski et al. 2006; Lee et al. 2012).

A técnica que permite avaliar a influência da microbiota sobre o crescimento das plantas envolve a esterilização do solo. No entanto, todos os métodos de esterilização modificam as propriedades desse substrato, tais como o pH, CTC, N, Mn, etc. (Darbar e Lakzian 2007; Perkins et al. 2013). Tais modificações dificultam atribuir diferenças de crescimento de uma determinada planta a mudanças na comunidade microbiana do solo, quando cultivos em solos esterilizados e não esterilizados são comparados. Para contornar tal problema, a inoculação ou reconstituição da microbiota de um solo esterilizado por meio da aplicação de suspensão de solo fresco, por exemplo, tem sido frequentemente utilizada (Hol et al. 2013; Crawford e Knight 2017; Johnson et al. 2017). A comparação de cultivos em solos esterilizados e em solos esterilizados com a microbiota inoculada ou reconstituída permite observar a resposta das plantas a mudanças na comunidade microbiana do solo.

A hipótese de que plantas invasoras têm vantagem sobre as espécies nativas em função de *feedback* planta-solo positivo estimularam vários estudos (Suding et al. 2013). A maioria desses relatos avaliaram como o cultivo sucessivo de plantas invasoras e nativas influenciou o crescimento e a produtividade das gerações de plantas subsequentes (Suding et al. 2013). De maneira geral, as plantas invasoras e as plantas daninhas alteram as características químicas e biológicas do solo e produzem mais matéria seca (Kulmatiski et al. 2006, 2008; Lee et al. 2012), enquanto que, para a maioria das nativas ou culturas, o cultivo sucessivo em uma mesma área leva à redução da produtividade (Koike et al. 2013; Suding et al. 2013). Poucos estudos avaliaram se esses *feedbacks* positivos melhoraram ou não a capacidade competitiva de plantas invasoras com as nativas (Aguilera 2011), ou de daninhas com as culturas (Hol et al. 2013).

O crescimento do trigo foi maior em solos inoculados, principalmente, quando a biota reconstituída foi oriunda de sistemas orgânicos de cultivo em detrimento dos convencionais (Johnson et al. 2017). Tais efeitos foram explicados por provável mudança na abundância relativa de organismos mutualistas e patogênicos em função dos sistemas de cultivo. Adicionalmente, à medida que os *feedbacks* planta-solo se tornaram mais positivos, a competição do trigo com *Amaranthus retroflexus* ou *Avena fatua* diminuiu e a facilitação aumentou (Johnson et al. 2017). Por outro lado, a inoculação da microbiota do solo tornou o trigo mais sensível à competição com *Vicia villosa*, *Chenopodium album* e *Myosotis arvensis* (Hol et al. 2013). Isto pode ter sido devido a uma melhoria na capacidade competitiva das plantas daninhas em função de *feedback* positivo com o solo.

A inoculação de solo com a microbiota de áreas invadidas por *Lespedeza cuneata* melhorou significativamente o crescimento dessa planta em monocultivo, mas, curiosamente, na presença de competidores interespecíficos, o efeito positivo da origem do solo desapareceu (Crawford e Knight 2017). Similarmente, a planta invasora *Microstegium vimineum*, apesar de aumentar a disponibilidade de nitrato no solo, beneficiou-se de tal efeito somente na ausência de competição com espécies nativas (Lee et al. 2012). A persistência de plantas invasoras pode ser favorecida por *feedbacks* planta-solo positivos, mas a magnitude desses *feedbacks* pode depender de interações interespecíficas (Lee et al. 2012). Assim, o melhor crescimento de uma dada espécie em seu próprio solo não garante que a mesma terá sucesso competitivo (Crawford e Knight 2017).

Em trabalho com *Andropogon gerardii* e *Sorghastrum nutans*, os efeitos do *feedback* e da competição foram específicos para cada espécie de planta (Casper e Castelli 2007). Enquanto o *feedback* melhorou a capacidade competitiva de *A. gerardii*, a competição interespecífica eliminou os efeitos de *feedback* positivo para *S. nutans*. Mudança na importância do *feedback* planta-solo conforme o contexto competitivo também foi observada para *Microstegium vimineum* (Shannon et al. 2012). As interações de *feedback* podem reverter o resultado da competição e vice-versa. Os diferentes cenários de *feedback*, por sua vez, dependem da intensidade da competição entre plantas (Aguilera 2011). Essa dependência do contexto implica que o *feedback* planta-solo pode mudar quando as interações competitivas entre plantas mudam à medida que as infestações progridem (Shannon et al. 2012).

A contribuição das associações com micro-organismos para o sucesso competitivo de plantas é complexa. A espécie *Lolium arundinaceum*, por exemplo, depende da simbiose com o fungo endofítico *Neotyphodium coenophialum* para que consiga modificar a comunidade microbiana do solo a ponto de reduzir o crescimento de algumas espécies arbóreas sucessoras (Rudgers e Orr 2009). Essa simbiose tem potencial de alterar a sucessão de plantas e a futura composição florestal. No entanto, os efeitos são específicos para cada espécie arbórea.

A planta nativa *Quercus acutissima* reduziu o crescimento da invasora *Robinia pseudoacacia* em solo inoculado, porém, em solo esterilizado, os efeitos da competição foram menores para a invasora (Chen et al. 2012). Essa resposta foi associada a mudanças na comunidade microbiana do solo, principalmente, com o aumento de bactérias fixadoras de N. Por outro lado, a esterilização do solo reduziu o crescimento da planta nativa *Bouteloua gracilis* e da invasora *Bromus tectorum*, cultivadas em monocultivo. Os efeitos negativos da competição foram maiores para a invasora do que para *B. gracilis* (Emam et al. 2014), provavelmente, em decorrência da esterilização do solo eliminar os microrganismos deletérios à planta nativa.

Até o momento, alguns estudos demonstraram que não há consistência na relação entre competição e *feedback* (Callaway et al. 2004; Casper e Castelli 2007; Hol et al. 2013). Mesmo sem competição, os *feedbacks* planta-solo foram descritos como idiossincráticos (Jiang et al. 2010). No entanto, ainda há poucos trabalhos que avaliaram a contribuição da microbiota do solo para o sucesso competitivo de uma dada espécie em agroecossistemas. O desafio é identificar como a competição influencia o resultado das interações entre plantas e micro-organismos e vice-versa. Alguns estudos, mostraram que a composição da estrutura da comunidade microbiana do solo é alterada pela competição interespecífica de plantas (Massenssini 2014; Monteiro 2016) e que algumas espécies são mais hábeis em moldar a microbiota do solo que outras (Massenssini 2014). Possivelmente, plantas com tal habilidade podem ser favorecidas por um *feedback* positivo, mesmo em competição.

Interação planta daninha-cultura altera a estequiometria elementar da biomassa vegetal?

As plantas usam a radiação solar para fixar carbono enquanto absorvem nutrientes em quantidades adequadas para atender seus requerimentos. No entanto, a fotossíntese e a absorção de nutrientes não estão perfeitamente acopladas e, por isso, o conteúdo de nutrientes em relação ao de C varia dentro de cada espécie vegetal (Goldman et al. 1979; Rhee e Gotham 1981). Haja vista que o carbono e os nutrientes são essenciais para o funcionamento celular (Güsewell 2004; Ågren 2008) e que o equilíbrio C:nutriente geralmente afeta a produção das culturas e a dinâmica da cadeia alimentar nos ecossistemas, a estequiometria elementar tem sido um dos fatores mais investigados nas interações ecológicas (Elser et al. 2010; Sardans e Penuelas 2012; Ye et al. 2014).

Mudanças na estequiometria elementar têm sido frequentemente associadas ao sucesso da infestação de plantas invasoras (Sardans e Penuelas 2012). As plantas podem mudar a estequiometria elementar como resposta adaptativa à disponibilidade diferencial de nutrientes (Ventura et al. 2008; Liang et al. 2015). O sucesso de plantas invasoras em infestar ambientes ricos ou pobres em nutrientes normalmente está associado a características morfofisiológicas da espécie. Em ambientes com baixa disponibilidade de nutrientes, o crescimento é lento, a relação C:nutrientes da biomassa aumenta, e as plantas usam os nutrientes de forma mais eficiente (González et al. 2010). Em contraste, em condições de alta disponibilidade de nutriente, as plantas maximizam a síntese proteica e o crescimento como estratégias competitivas (González et al. 2010), resultando em diminuição da razão C:nutriente do tecido (Ågren 2008). No entanto, nem todas as plantas são capazes de modificar a estequiometria elementar em resposta à limitação de nutrientes (Elser et al. 2010; Yu et al. 2011). Assim, alterações adaptativas da razão C:nutriente podem levar ao aumento do sucesso da infestação, principalmente em ambientes pobres em nutrientes (Funk 2008). Adicionalmente, plantas invasoras que são capazes de aumentar ativamente a disponibilidade de nutrientes no ambiente, em particular por meio da fixação de N_2 ou mobilização de P no solo, superam os concorrentes em ambientes com baixa disponibilidade desses elementos. A infestação por plantas invasoras não é o agente principal que leva a mudanças na composição de espécies do ecossistema; essas mudanças refletem, também, as alterações na estequiometria elementar do solo (Sardans et al. 2016b), que podem estar ligadas ao EPR e à ciclagem biogeoquímica de resíduos vegetais.

A estequiometria elementar de plantas depende das características do ecossistema, das estratégias de crescimento vegetal, da composição de espécies da comunidade e da heterogeneidade dos nutrientes no solo (Sardans et al. 2016a). É questão difícil de se discernir se o sucesso competitivo de uma planta invasora é causa ou consequência da composição elementar do solo e da disponibilidade de nutrientes (Sardans et al. 2016b). Porém, algumas pesquisas sugerem que as mudanças no conteúdo de nutrientes nas plantas e no solo são mais consequência da infestação de plantas invasoras do que a causa (Sardans et al. 2016b). Assim, a infestação por plantas invasoras pode ser indicador de mudanças globais da composição elementar e estequiométrica das comunidades vegetais e do solo (Sardans et al. 2016b).

A estequiometria elementar de plantas tem sido particularmente bem estudada em abordagens ecológicas sobre a dinâmica de populações de plantas invasoras em ecossistemas naturais. Curiosamente, não encontramos estudos que investigassem se a competição influencia a estequiometria de plantas daninhas e das culturas.

MUDANÇAS NAS PROPRIEDADES DO SOLO DURANTE O ESTABELECIMENTO DE PLANTAS DANINHAS

Geralmente, o estabelecimento e a persistência de plantas invasoras e de plantas daninhas em determinada área estão associados a mudanças nas propriedades do solo. Além de aumentar a atividade e de alterar a estrutura da comunidade microbiana do solo (Sanon et al. 2009; Massenssini 2014; Souza-Alonso et al. 2015), essas plantas aumentam as atividades enzimáticas (He et al. 2013; Kuebbing et al. 2014; Wang et al. 2015a) e, consequentemente, a mineralização de nutrientes no solo (Li et al. 2006; Fickbohm e Zhu 2006; Elgersma et al. 2011; Si et al. 2013). Esses processos, normalmente, ocorrem de forma associada e possuem fortes implicações para a qualidade do solo, uma vez que podem alterar a composição e a estequiometria elementar desse ambiente (Sardans et al. 2016b). O impacto sobre o solo, decorrente da presença de plantas invasoras, não pode ser revertido mesmo após longo período de ocorrência da infestação, como relatado para *Acacia dealbata* (Souza-Alonso et al. 2015).

O sucesso da infestação por plantas daninhas em áreas agrícolas abandonadas pode correlacionar-se com aumentos nas concentrações de C, N e P do solo (Kulmatiski et al. 2006). Esse fato tem sido atribuído à capacidade das plantas daninhas de facilitarem o próprio crescimento ao longo das gerações por meio da manutenção de comunidades fúngicas benéficas e pelas rápidas taxas de ciclagem de nutrientes no solo.

Aumentos nas concentrações de nutrientes em solos infestados por plantas invasoras foram mais comuns em solos com baixas concentrações iniciais desses elementos, enquanto decréscimos na disponibilidade de nutrientes foram observados em condições opostas (Dassonville et al. 2008). Resultados semelhantes foram apresentados em uma meta-análise de 215 artigos em que diferenças na disponibilidade de C, N, P e K entre solos com plantas invasoras ou nativas diminuíram quando o ambiente era rico em nutrientes (Sardans et al. 2016b). De maneira geral, os solos infestados por plantas invasoras apresentam maiores concentrações de N, P, K, portanto, maior disponibilidade dos três macronutrientes mais importantes para o crescimento das plantas (Sardans et al. 2016b). Alguns exemplos de mudanças nas propriedades do solo em decorrência da infestação por plantas invasoras foram listados na Tabela 1. Deve-se ressaltar que algumas espécies desenvolveram estratégias de sobrevivência ou competitivas diferentes. Por exemplo, mudanças na mineralização de nutrientes não foram observadas em solos infestados por *Artemisia biennis*, *Centaurea stoebe*, *Tragopogon dubius*, *Bidens frondosa* e *Senecio inaequidens* (Meisner et al. 2011). Apesar disso, essas espécies foram mais competitivas que seus congêneres nativos por apresentarem maior capacidade em absorver nutrientes.

As enzimas são reconhecidas como os principais agentes das atividades que ocorrem na rizosfera (Gianfreda 2015). Enzimas produzidas e liberadas por raízes e micro-organismos alteram a disponibilidade de nutrientes na rizosfera, implicando na mineralização da MOS e das formas orgânicas de nutrientes. A atividade enzimática é importante por determinar a intensidade e direção do EPR (Gianfreda 2015). A liberação de exsudados radiculares pode ativar a síntese microbiana de enzimas intra- e extracelulares ou pode servir como fonte de energia para que os micro-organismos produzam enzimas extracelulares com o subsequente aumento na decomposição da MOS (Gianfreda 2015). Aumento da decomposição da MOS em solos cultivados com cevada foram associados a aumentos das atividades das enzimas quitinase e β-xilosidase (Pausch et al. 2016).

Tabela 1. Mudanças nas propriedades do solo pela presença de plantas invasoras.

Características do solo	Plantas invasoras ou daninhas
Aumento nos valores de atributos químicos	
N, P e K, MOS e pH	*Mimosa pudica* (Wang et al. 2015a)
C, N e P	*Acacia dealbata* (Souza-Alonso et al. 2015), *Amaranthus viridis* (Sanon et al. 2009)
K, Mg, Mn e N	*Fallopia japonica, Heracleum mantegazzianum, Impatiens glandulifera, Prunus serotina, Rosa rugosa, Senecio inaequidens, Solidago gigantea* (Dassonville et al. 2008)
pH e Ca	*Wedelia trilobata* (Si et al. 2013)
Aumentos da atividade enzimática	
Urease, invertase, protease, catalase e cellulase	*Mimosa pudica* (Wang et al. 2015a)
Urease, invertase e fosfatase ácida	*Bidens pilosa* (He et al. 2013)
Fosfatase ácida, β-glucosidase, urease e N-acetilglucosaminidase	*Acacia dealbata* (Souza-Alonso et al. 2015)
β -glucosidase, invertase, protease, urease, acid phosphatase, alkaline phosphatase e phenol oxidase	*Mikania micrantha* (Li et al. 2006)
Mudanças na estrutura da comunidade microbiana do solo	
Aumento das populações fúngicas e bacterianas no solo	*Bidens pilosa* (He et al. 2013)
Aumento da abundância bacteriana	*Amaranthus viridis* (Sanon et al. 2009)
Aumento de bactérias aeróbicas e redução das anaeróbicas	*Mikania micrantha* (Li et al. 2006)
Aumento da riqueza da comunidade fúngica do solo	*Wedelia trilobata* (Si et al. 2013)

Efeito *priming*

O efeito *priming* (EP) é definido como uma mudança na taxa de decomposição da MOS do solo devido à adição de substrato (Löhnis 1926; Kuzyakov et al. 2000). Quando esse fenômeno ocorre na rizosfera é definido como efeito *priming* rizosférico (EPR) e representa a alteração na decomposição da MOS causada pela atividade das raízes (Figura 1) (Kuzyakov 2002; Dijkstra et al. 2013). O EPR é positivo quando há aceleração da decomposição da MOS, e, negativo, quando há o retardamento da decomposição (Kuzyakov 2002). Esse fenômeno pode, por exemplo, retardar a decomposição da MOS em 79% (Thurgood et al. 2014) ou estimulá-la em mais de 500% (Shahzad et al. 2015). Em média, nos solos cultivados, a decomposição do C orgânico via EPR é cerca de 59% maior do que naqueles sem cultivo (Huo et al. 2017).

As plantas constituem uma das principais fontes de entrada de carbono no solo. Cerca de 40 a 60% do carbono fixado fotossinteticamente são direcionados para as raízes e para os micro-organismos delas associados por meio de rizodeposições (Clemmensen et al. 2013). As rizodeposições correspondem a substâncias orgânicas liberadas pelas raízes das plantas, tais como exsudatos, mucilagens, secreções e lizados celulares (Kuzyakov 2002). Esses compostos possuem diferentes propriedades estequiométricas e energéticas (Dijkstra et al. 2013), sendo importantes fontes de energia para a produção microbiana de enzimas extracelulares capazes de quebrar a MOS (Blagodatskaya e Kuzyakov 2008). Portanto, o EPR é fenômeno comum nas interações planta-solo. As plantas, por meio de exsudatos radiculares, fornecem energia para os microrganismos do solo, controlando a mineralização da MOS para o próprio suprimento de nutrientes (Kuzyakov 2010; Shahzad et al. 2015; Bernal et al. 2017).

O EPR não pode ser atribuído somente a rizodeposições (Kuzyakov 2002; Blagodatskaya e Kuzyakov 2008; Cheng et al. 2014). O desenvolvimento radicular pode desestabilizar agregados do solo e, assim, disponibilizar ou facilitar o acesso de micro-organismos ao carbono orgânico do solo (Kuzyakov 2002; Cheng et al. 2014). Outros fatores do solo, a exemplo da umidade, da temperatura, do pH e de características físicas, interferem na magnitude e direção do EPR (Cheng et al. 2014; Huo et al. 2017).

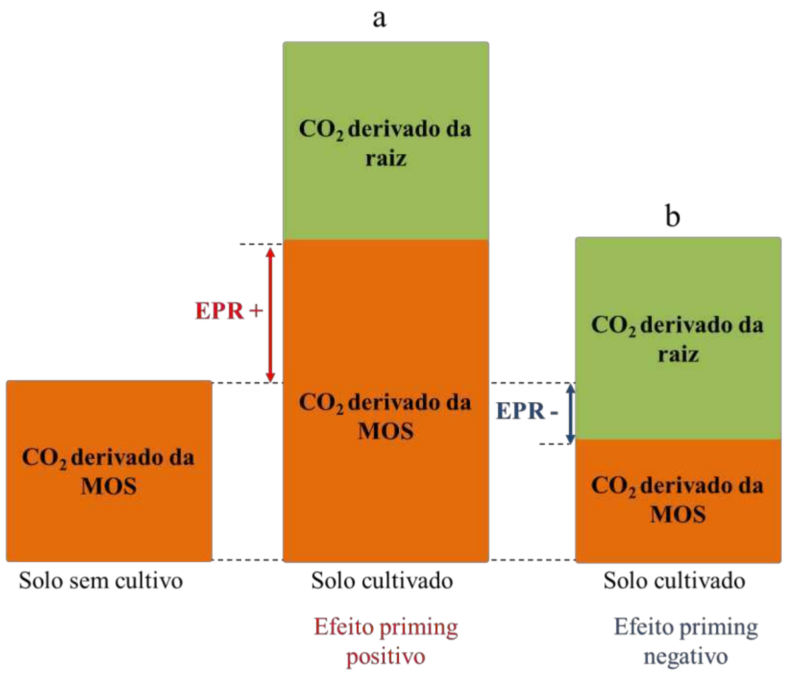

Figura 1. Esquematização do efeito *priming* rizosférico (EPR) - Interações não aditivas entre o crescimento da raiz e a decomposição da matéria orgânica do solo (MOS): (a) aceleração da decomposição da MOS - EPR positivo; (b) retardamento da decomposição da MOS - EPR negativo.

Fonte: (Kuzyakov 2002).

Em geral, acredita-se que o EPR a curto prazo, isto é, dias a semanas, seja principalmente relevante para a mudança na dinâmica da MOS lábil, enquanto que o EPR a longo prazo, ou seja, meses a décadas, possa influenciar a MOS estabilizada (Rousk et al. 2015). Globalmente, algumas evidências indicam que o EPR pode persistir por anos em cultivos de plantas perenes (Huo et al. 2017), como relatado para as espécies arbóreas *Pinus ponderosa* e *Populus fremontii* (Dijkstra e Cheng 2007).

Mecanismos do efeito *priming* rizosférico

Há evidências de que os fatores biológicos, em detrimento dos físicos, são os principais responsáveis pelo EPR (Cheng e Kuzyakov 2002). As hipóteses de (a) ativação microbiana, (b) utilização de substrato preferencial e (c) competição pelo N entre plantas e microrganismos correspondem aos mecanismos mais importantes do EPR (Kuzyakov 2002). O conteúdo de carbono orgânico e nitrogênio disponível no solo determinam a presença e a magnitude desses mecanismos (Kuzyakov 2002, 2010; Dijkstra et al. 2013). As três hipóteses citadas estão simplificadas na figura 2, segundo a perspectiva de disponibilidade de nutriente no solo, proposta por Dijkstra et al. (2013).

A liberação de exsudatos radiculares estimula o crescimento e a atividade de micro-organismos, aumentando, assim, o potencial fisiológico geral da comunidade de decompositores para mineralização de carbono por cometabolismo (Kuzyakov 2002). Outros fatores, como o aumento da demanda microbiana por nitrogênio ou mudanças sucessionais na estrutura da comunidade, podem também contribuir para o aumento das taxas de mineralização.

Há forte ligação entre a exsudação radicular e a mineralização bruta de N, sugerindo que as plantas tornam-se progressivamente menos limitadas pelo elemento quando ocorrem altas taxas de exsudação radicular (Bengtson et al. 2012). O EPR positivo pode melhorar o suprimento de N para as plantas em solos com baixa disponibilidade desse nutriente (Dijkstra e Cheng 2007). No entanto, resultados experimentais sobre a fertilização com N indicaram papel inconsistente do status desse elemento no solo na regulação do EPR (Liljeroth et al. 1994; Cheng et al. 2003; Kumar et al. 2016; Zang et al. 2016; Studer et al. 2016). O EPR de solos cultivados com soja e trigo variaram de 0% a 383% e não foram influenciados pelo nível de N, P e K (Cheng et al. 2003). Já a limitação de N em solo cultivado com milho levou a aumento de 35% para 126% no EPR da MOS (Kumar et al. 2016).

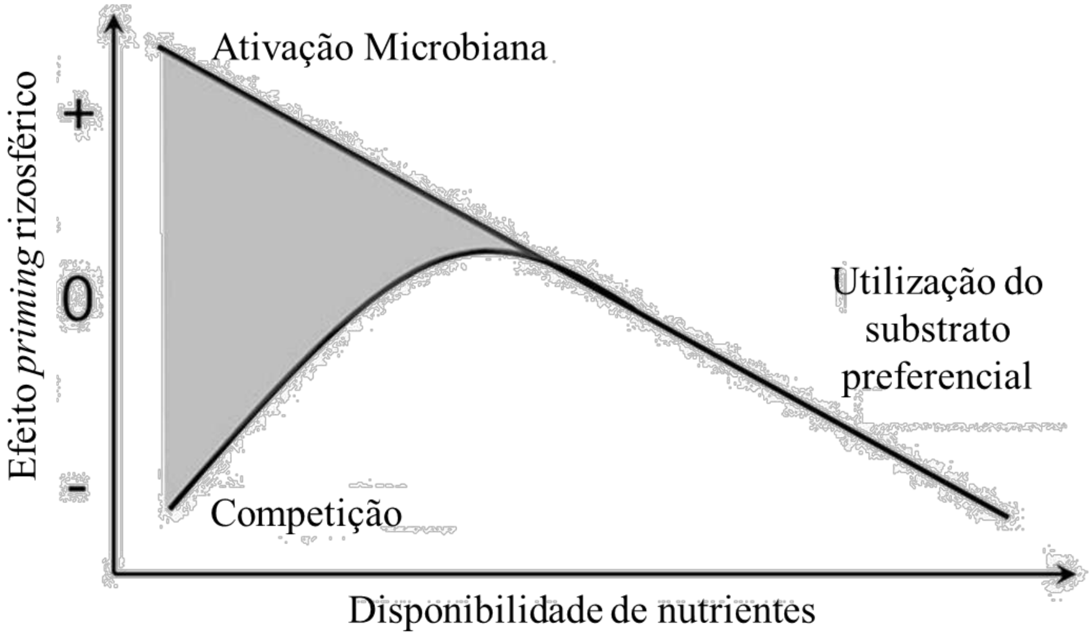

Figura 2. "Relação hipotética entre a disponibilidade de nutrientes do solo e o EPR. Foram apresentadas três hipóteses centradas na disponibilidade de nutrientes: (a) ativação microbiana ou mineralização microbiana: os microrganismos utilizam rizodeposições para mineralizar os nutrientes na MOS, causando EPR positivo quando a disponibilidade de nutrientes é baixa; (b) Utilização do substrato preferencial: os microrganismos preferem utilizar primeiramente as rizodeposições, pois estão facilmente disponíveis e, em seguida, a MOS, quando a disponibilidade de nutrientes é alta; (c) Competição pelo N: os microrganismos competem por nutrientes com plantas causando um EPR negativo, pois o crescimento microbiano e a decomposição da MOS são limitados pela disponibilidade de nutrientes. Ambos os efeitos, positivos e negativos, podem ocorrer sob baixa disponibilidade de nutrientes (área cinza)".

Fonte: (Dijkstra et al. 2013)

É notório que a maioria dos estudos relataram EPR negativo com o aumento da adubação nitrogenada do solo. Isso nos leva a acreditar que o fornecimento de N facilita o sequestro de C no solo pela redução da decomposição da MOS na rizosfera, conforme inferido para o cultivo do trigo (Zang et al., 2016).

O EPR é fenômeno complexo e a adubação nitrogenada pode não reduzir as taxas de decomposição da MOS para todos os cultivos. Possivelmente, a presença de plantas daninhas pode interferir na magnitude e na direção do EPR pela modificação das propriedades físicas, químicas e biológicas do solo, mesmo em áreas adubadas.

Diante da perspectiva de que a baixa disponibilidade de N aumenta o EPR, é provável que a competição de plantas daninhas com as culturas pelos nutrientes do solo tenda a aumentar a decomposição da MOS. Ainda, o melhoramento das culturas, ao selecionar plantas para a produção de grãos em solos férteis, pode ter reduzido a capacidade dessas plantas em estimular a decomposição da MOS para o suprimento nutricional, diminuindo assim o EPR (Huo et al. 2017). Nesse contexto, é provável que plantas daninhas tenham maior potencial em estimular a decomposição da MOS. Colabora com essa hipótese o fato de que, geralmente, culturas agrícolas causam menor EPR do que gramíneas e espécies arbóreas (Huo et al. 2017).

Os exsudatos radiculares com baixos teores de C e N têm maior potencial de acelerar as perdas de C do solo, estimulando os micro-organismos a extraírem N da MOS. A magnitude desse efeito depende da recalcitrância da MOS, da disponibilidade de N e das comunidades microbianas do solo (Huajun et al. 2016). O sucesso de certas plantas daninhas pode estar mais associado à sua capacidade em formar associações com micro-organismos do solo do que com a competição ou disponibilidade de nutrientes, como relatado para *Bidens pilosa* (Cui e He 2009). Mudanças na biomassa e na estrutura da comunidade microbiana do solo podem ser mecanismos que ajudam a explicar o EPR (Fontaine et al. 2003; Blagodatskaya e Kuzyakov 2008).

A biomassa microbiana não é apenas reservatório de C, mas, também, agente de ciclagem da MOS (Blagodatskaya et al. 2010). O EPR está associado com mudanças na composição microbiana do solo (Blagodatskaya e Kuzyakov 2008). Bactérias são o primeiro grupo a capturar e a metabolizar a maior parte das substâncias orgânicas facilmente disponíveis no solo (Moore-Kucera e Dick 2008). Isso, por sua vez, acelera a ciclagem da biomassa microbiana, especialmente, dos estrategistas r, desencadeando o EPR aparente. Nesse caso, o aumento da mineralização de C e N em resposta à elevação da taxa de ciclagem da biomassa microbiana ocorre sem que haja aumento concomitante na decomposição da MOS (Fontaine et al. 2003; Blagodatskaya e Kuzyakov 2008; Kuzyakov 2010).

Sequencialmente, outros grupos de microrganismos, a exemplo dos fungos, que preferencialmente utilizam substratos mais recalcitrantes como a MOS, beneficiam-se da biomassa bacteriana morta remanescente após o esgotamento dos compostos orgânicos facilmente disponíveis (Fontaine et al. 2003). Esses organismos, que são predominantemente estrategistas k (Fontaine et al. 2003; Blagodatskaya et al. 2007), são estimulados pela biomassa morta, o que aumenta a decomposição da MOS (EPR real).

Alguns grupos específicos de micro-organismos do solo foram associados ao EPR real. Bactérias gram-negativas são capazes de assimilar C da MOS (Nottingham et al. 2009). Fungos ectomicorrízicos, além de aumentarem a exsudação de C no solo, podem sintetizar enzimas extracelulares, enquanto os micorrízicos arbusculares, apesar de não produzirem enzimas extracelulares, foram capazes de aumentar o EPR, possivelmente pela exsudação de C (Phillips e Fahey 2006; Brzostek et al. 2015). O aumento das taxas de decomposição da MOS em ecossistemas de carvalho foi atribuído a maior abundância relativa de fungos no solo (Carney et al. 2007).

Em solo com baixa disponibilidade de N, a espécie nativa *Fragaria vesca* aumentou o crescimento e a exsudação radicular, o que estimulou o crescimento e a ciclagem da biomassa microbiana. Em contraste, a planta infestante *Duchesnea indica* aumentou a absorção e o acúmulo de N sem alocar maior matéria seca nas raízes. Isto resultou em deficiência de N, retardando o crescimento e a ciclagem microbiana na rizosfera (Blagodatskaya et al. 2014). Assim, a maior capacidade competitiva de *D. indica* pelo N permite que essa planta controle a comunidade microbiana na rizosfera, favorecendo o crescimento de micro-organismos estrategistas k (Fontaine et al. 2003). Portanto, a capacidade de algumas plantas daninhas em moldar a comunidade microbiana do solo (Massenssini 2014) pode ser considerada indício do potencial das mesmas em aumentar a mineralização da MOS.

Hipóteses de mecanismos que independem da ação direta da microbiota do solo

Contrariando os mecanismos mencionados acima, a hipótese do "*Regulatory Gate*" assume que a mineralização da MOS é independente do tamanho, da composição ou da atividade específica da microbiota do solo (Kemmitt et al. 2008). O processo é abiótico e ocorre por meio de oxidação e hidrólise química, ação de enzimas estabilizadas extracelularmente, dessorção de matéria orgânica sorvida ou difusão de substratos dentro de agregados (Kemmitt et al. 2008). Somente após a desestabilização da MOS por tais processos é que o C estaria disponível para ser utilizado pela microbiota. Algumas pesquisas corroboram essa hipótese (Wertz et al. 2006; Rousk et al. 2011, 2015).

Na hipótese tradicional, exsudatos radiculares aceleram a mineralização da MOS, sendo ela usada como cometabólito, isto é, a MOS é mineralizada fortuitamente em função do catabolismo de fontes de carbono e de energia mais biodisponíveis, a exemplo dos exsudados radiculares. Portanto, a adição de glicose, substrato energeticamente favorável, deveria causar maior EPR do que substratos menos favoráveis, a exemplo do ácido oxálico. No entanto, o inverso é observado. O ácido oxálico estimulou mais a decomposição da MOS por liberar compostos orgânicos protegidos em frações minerais do solo (Keiluweit et al. 2015). Em vez da via cometabólica, os ligantes orgânicos com capacidade de complexação de metais aceleraram a mineralização microbiana de C na rizosfera por meio de mecanismo indireto (Keiluweit et al. 2015).

O mecanismo alternativo proposto leva em conta que grandes quantidades de C no solo são inacessíveis à microbiota em função da associação com a fase mineral. A ligação forte aos metais protege o material orgânico de ser imediatamente alcançado e decomposto (Clarholm et al. 2015). Os exsudatos radiculares que podem atuar como ligantes, por exemplo, os ácidos orgânicos, desprendem C por reações de complexação e dissolução da fase mineral, promovendo a acessibilidade da MOS aos microrganismos e acelerando a sua perda do sistema através da mineralização microbiana (Keiluweit et al. 2015).

Um processo de três etapas, por meio do qual os ácidos orgânicos de baixa massa molecular e as enzimas hidrolíticas agem em série para desestabilizar as supramóleculas de MOS (Figura 2), foi proposto por Clarholm et al. (2015). Nesse modelo, os ácidos orgânicos de baixa massa molecular, como o ácido oxálico, são liberados por plantas vasculares, fungos de vida livre, ectomicorrizas, bem como por bactérias (Clarholm et al. 2015; Keiluweit et al. 2015). A interação entre plantas e fungos conduz o mecanismo biótico ao nível de agregado supramolecular e determina o *priming* da MOS, onde a etapa de desestabilização é condição prévia para a liberação subsequente de nutrientes (Clarholm et al. 2015).

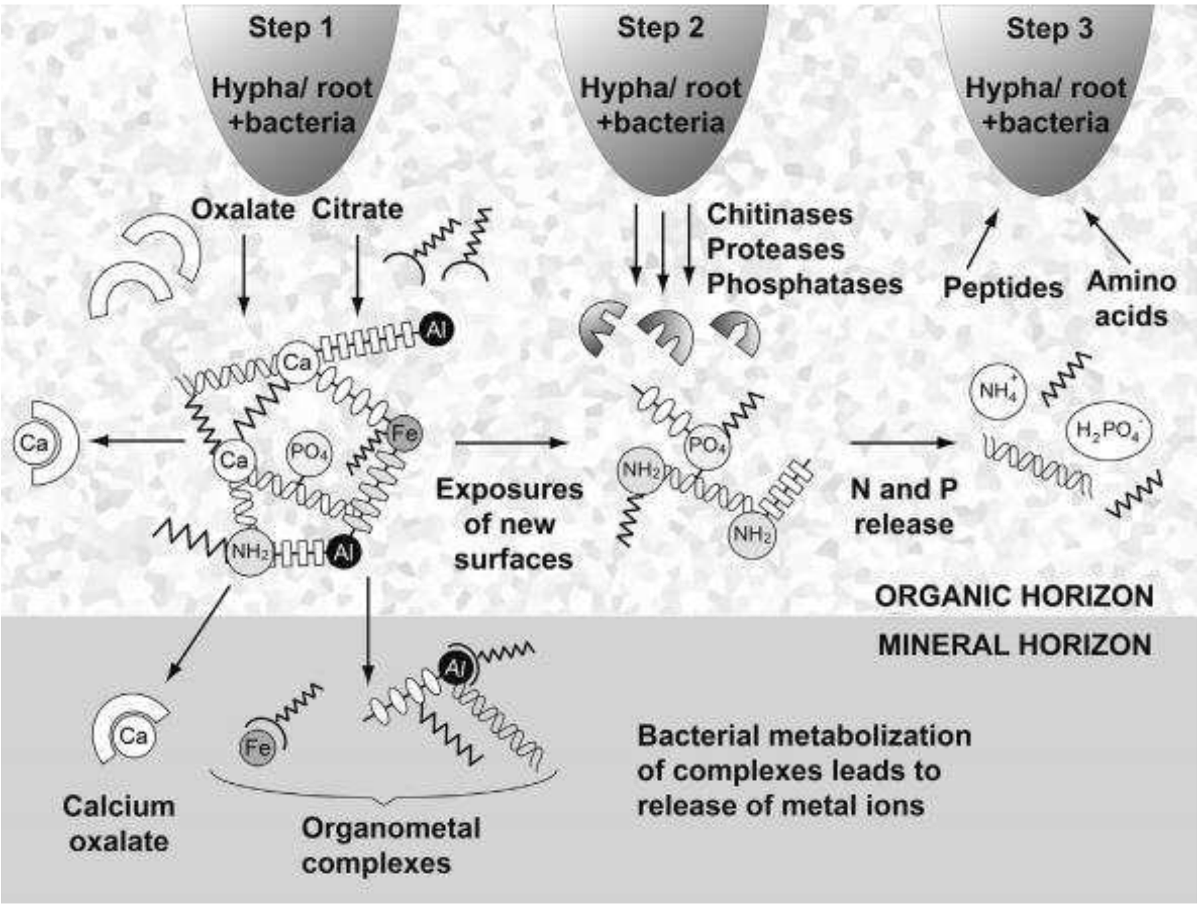

Figura 2. Descrição de mecanismo de decomposição da MOS em três etapas, induzido por plantas. Os principais blocos de construção da MOS são polissacarídeos, polipeptídios, cadeias de carbono alifáticas e fragmentos aromáticos (lignina) combinados de forma secundária em agregados supramoleculares e mantidos em conjunto por forças de van der Waals, ligações de H e pontes metálicas envolvendo Ca, Al e Fe (Simpson et al. 2002). A massa dos agregados supramoleculares varia entre 10^3 e 10^5 Da (Lehmann et al. 2007) e de seus múltiplos Primeira etapa: o oxalato liberado de hifas ou raízes (à esquerda) ou, alternativamente, a liberação de moléculas de citrato (direita) quelatam e removem o metal (símbolo redondo) do agregado supramolecular. Segunda etapa: A liberação de enzimas hidrolíticas por hifas fúngicas ou bactérias disponibiliza moléculas de N ou P do material orgânico recém-exposto na solução do solo. Terceira etapa: a absorção das moléculas de N ou P por hifas fúngicas ou raízes. A descrição completa está disponível na fonte: Clarholm et al. (2015).

O efeito *priming* pode não estar relacionado com a dinâmica de crescimento de microrganismos estrategistas r e k, uma vez que a adição de fonte de C lábil pode iniciar a mineralização da MOS sem que haja prazo suficiente para a sucessão de r para k (Rousk et al. 2015). A mineralização da MOS pode ser devido à ação de enzimas extracelulares durante a degradação do C lábil. O cultivo do híbrido arbóreo *Populus deltoides x nigra,* em solo com baixa disponibilidade de nutrientes, estimulou o EPR da MOS (Studer et al. 2016). A quantidade de C liberado pela raiz dessa espécie foi menor do que a quantidade total de C respirado do solo, e ambos foram menores do que a biomassa microbiana. Isso indica EPR aparente. No entanto, houve mineralização da MOS. Provavelmente, as plantas com maior limitação de crescimento aumentaram ativamente à liberação de compostos específicos, tais como ácidos orgânicos e enzimas extracelulares, para aumentar a aquisição de nutrientes.

Em vista dos resultados controversos sobre os mecanismos que induzem o EPR da MOS, esse fenômeno deve ser visto como a soma de mecanismos diretos e indiretos (Keiluweit et al. 2015; Studer et al. 2016).

A infestação de plantas daninhas pode influenciar o EPR da MOS?

Certas plantas daninhas ou invasoras podem influenciar o teor de MOS (Tabela 1). No entanto, os trabalhos que avaliaram tais efeitos não abordaram se a competição entre plantas daninhas e cultivadas pode modificar a magnitude de tais mudanças. Além disso, estudos que avaliaram impactos da infestação de plantas daninhas nas frações de C mais e menos estáveis do solo são escassos.

Apesar de todas as evidências de que a presença de plantas daninhas ou invasoras podem influenciar o EPR da MOS, curiosamente, encontramos apenas dois estudos que mediram tal efeito. Em um desses estudos, o crescimento do sistema radicular da planta invasora *Phragmites australis* aumentou a decomposição da MOS apenas nas camadas mais profundas do solo, o que pode alterar a dinâmica da MOS e levar à perdas de C estável em áreas infestadas por essa planta (Bernal et al. 2017). A decomposição da MOS, provavelmente, foi devido ao aumento do fornecimento de recurso limitante, a exemplo do O_2 e, ou substratos orgânicos lábeis para o crescimento de micro-organismos nas camadas mais profundas do solo. A MOS antiga mais estável estava sendo substituída por MOS nova, derivada de *P. australis* (Bernal et al. 2017). Por outro lado, a planta invasora *Bromus tectorum*, tanto em monocultivo quanto em competição com *Elymus elymoides,* levou a um EPR negativo quanto à mineralização de N, tanto em solos infestados quanto naqueles não infestado por essa espécie (Concilio et al. 2015).

Isso sugere redução na decomposição da MOS por *B. tectorum*. Ambas as pesquisas estudaram os efeitos das plantas invasoras em solos de ecossistemas naturais e mostram que o estímulo ou não da decomposição da MOS pode estar relacionado às diferenças nas estratégias de infestação dessas plantas.

Não encontramos relatos sobre a interferência de plantas daninhas no EPR da MOS em agroecossistemas. Nesses ambientes, as práticas de manejo, por influenciarem os reservatórios de recursos do solo, podem afetar diretamente a intensidade da competição das culturas com as plantas daninhas, como prevê a hipótese de "*The resource pool diversity*" (Smith et al. 2010). Essa hipótese propõe que a competição entre culturas e plantas daninhas diminui com o aumento da diversidade dos reservatórios de recursos do solo. Nas comunidades vegetais, a intensidade da competição interespecífica irá depender do grau de diferenciação de nicho e da partilha de recursos entre as espécies. Conhecer as possíveis implicações da presença de plantas daninhas sobre a MOS é essencial para direcionar práticas de manejos sustentáveis.

Além de conhecer a direção e magnitude do EPR é importante avaliar possíveis mudanças na qualidade da MOS. EPR positivo não significa, necessariamente, perda no conteúdo total de carbono da MOS, pois, simultaneamente, pode ocorrer estabilização de C, proveniente de plantas ou microrganismos (Kuzyakov 2002). Essa substituição de parte do C antigo pode aumentar a ciclagem da MOS ao longo dos cultivos, dependendo da qualidade do novo C (Bernal et al. 2017). Não é correto afirmar que EPR positivo contribui para o aumento de CO_2 na atmosfera, haja vista que, na maioria das vezes, o balanço completo de C não é conhecido (Kuzyakov 2010).

Competição entre plantas interfere no EPR?

Embora as plantas cresçam em comunidades, estudos que avaliem a influência da convivência interespecífica vegetal no EPR são raros. Encontramos apenas três relatos que fizeram tal abordagem (Dijkstra et al. 2010; Pausch et al. 2013; Concilio et al. 2015).

Os efeitos da rizosfera na decomposição da MOS variaram de positivo a negativo entre o monocultivo e os tratamentos de convivência de cinco espécies de gramíneas, sendo que os efeitos negativos prevaleceram ao final do cultivo e foram menores nos consórcios (Dijkstra et al. 2010). De maneira semelhante, o cultivo misto de plantas agrícolas reduziu o EPR em comparação aos monocultivos (Pausch et al. 2013). Possivelmente, a complementaridade no uso de recursos, como água (Verheyen et al. 2008) e N (Hooper e Vitousek 1997), pelas plantas nos cultivos consorciados, reduziu a atividade microbiana e diminui os efeitos da rizosfera sobre a decomposição da MOS (Dijkstra et al. 2010).

A redução no EPR pode contribuir, a longo prazo, para o aumento de C orgânico no solo no cultivo consorciado (Pausch et al. 2013). Todavia, a convivência entre plantas daninhas e cultura pode levar a mudanças na comunidade microbiana do solo (Massenssini 2014; Trognitz et al. 2016), estimulando o crescimento de micro-organismos com maior capacidade em decompor a MOS (Blagodatskaya e Kuzyakov 2008). Adicionalmente, é possível que plantas em competição por nutrientes liberem compostos, tais como os ácidos orgânicos, para mobilização ou solubilização de nutrientes, e enzimas extracelulares, para a decomposição da MOS.

Plantas em competição podem alterar a quantidade e a composição dos exsudados radiculares liberados (Carvalhais et al. 2013), o que altera a comunidade de micro-organismos no solo, como relatado para os cultivos de *B. pilosa* vs. *Ipomoea ramosíssima* e milho vs. *B. pilosa*, que mostraram estruturas distintas da comunidade microbiana em comparação com as do solo com monocultivos (Massenssini 2014). No entanto, houve maior similaridade da estrutura da comunidade microbiana dos solos cultivados com milho vs. *I. ramosissima* com aquela observada no monocultivo do milho (Massenssini 2014). A análise metagenômica mostrou domínio de bactérias na comunidade microbiana dos solos cultivados com milho vs. *I. ramosissima*, enquanto que para a competição dessa cultura com *B. pilosa* prevaleceram as populações fúngicas (Monteiro 2016). Portanto, mudanças na estrutura da comunidade microbiana provocadas pela alteração da composição de espécies vegetais podem levar a diferenças na magnitude e direção do EPR. Se essas mudanças na comunidade microbiana do solo, em decorrência da convivência entre plantas daninhas e cultura, são capazes de estimular a degradação da MOS é hipótese que ainda resta a ser investigada.

CONCLUSÕES E PERSPECTIVA

A contribuição de micro-organismos para o sucesso competitivo das espécies vegetais é complexa. As pesquisas sobre a importância da microbiota para o sucesso competitivo de plantas daninhas ainda são incipientes. O número limitado de estudos sobre a influência de micro-organismos durante a competição não permite concluir se há padrões de resposta para a capacidade competitiva das espécies envolvidas.

O estudo da estequiometria elementar dos tecidos das plantas tem sido recentemente utilizado para definir concentrações ótimas de nutrientes durante o desenvolvimento das culturas e, assim, contribuir para o uso eficiente de fertilizantes (Greenwood et al. 2008). Há ainda, a possibilidade de explorar informações sobre a estequiometria elementar de plantas para conhecer a capacidade de uma dada espécie em se adaptar a diferentes manejos agrícolas. Conhecer a flexibilidade estequiométrica de plantas daninhas pode ser ferramenta importante para o manejo integrado dessas espécies. Além de ampliar o rol de estratégias competitivas das plantas daninhas, alterações na estequiometria elementar podem interferir na ciclagem de nutrientes dos resíduos vegetais.

Não há dúvidas de que as plantas, por processos rizosféricos, controlam a disponibilidade de nutrientes e a qualidade da MOS. Curiosamente, apesar de o EPR ser largamente estudado, não encontramos estudos que avaliassem a interferência de plantas daninhas nesse fenômeno. Diferentemente das culturas agrícolas, as plantas daninhas mantêm maior dependência da microbiota do solo como estratégia adaptativa e competitiva. É provável que essas plantas levem a maior EPR.

Diante disso, algumas questões ainda precisam ser respondidas para melhorar a compreensão do papel dos micro-organismos do solo nas interações entre as plantas nos ambientes agrícolas. O aumento da intensidade competitiva pode influenciar as respostas de *feedback* planta daninha-solo? A fertilização influencia a interação entre plantas daninhas e micro-organismos do solo? Plantas daninhas podem alterar a estequiometria de seus tecidos em resposta a competição com as culturas? As plantas mais competitivas são mais aptas a promover alterações na estequiometria elementar de seus tecidos? A competição entre plantas daninhas e culturas influencia a taxa de mineralização da MOS? Mudanças na estrutura da comunidade microbiana do solo em função da competição entre culturas e plantas daninhas podem interferir na magnitude do EPR? A fertilidade do solo influencia o EPR durante a competição planta daninha-cultura?

As plantas daninhas sempre estiveram presentes nos agroecossistemas e, certamente, sempre estarão. Representam número expressivo de espécies vegetais que evoluem com os manejos agrícolas e, frequentemente, desafiam a ciência a aprimorar e a buscar novos métodos de manejo. É cada dia mais urgente o estabelecimento de medidas sustentáveis para a produção agrícola. Para isso, conhecer a biologia de plantas daninhas pode ser fundamental para a elaboração de estratégias de manejo integrado das mesmas.

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CAPÍTULO 2

Soil microorganisms change the competitive ability of maize and weeds

SOIL MICROORGANISMS CHANGE THE COMPETITIVE ABILITY OF MAIZE AND WEEDS

ABSTRACT

The interactions between plants and soil microorganisms are not considered in most researches about weed-crop competition. The aim of this study was to evaluate if the soil microbiota contributes to the initial establishment and the competitive ability of weeds and maize. The research was conducted under greenhouse conditions with *Bidens pilosa, Amaranthus viridis*, and *Zea mays*. We evaluated six cultivation managements (maize monoculture, coexistence between weeds and maize, weed monocultures, and non-cultivated soil) under two soil conditions (sterilized soil and sterilized soil with reconstituted microbiota). Soil microbiota reconstitution was done by the application of a fresh soil water suspension to the sterilized soil. Soil microbiota reconstitution reduced dry matter production and nutrient content in maize cultivated in monoculture and in competition with *B. pilosa*, but did not affect the growth of maize in competition with *A. viridis*. Soil microbial reconstitution did not influence *A. viridis* growth, but reduced *B. pilosa* total dry matter accumulation. The soil microbial activity was influenced by the cultivated plant species and by soil microbiota reconstitution. Maize showed greater competitive ability against *B. pilosa* in sterilized soil and against *A. viridis* in soil with reconstituted microbiota. Soil microbiota reconstitution did not affect the weeds´ ability to compete with maize. The lower maize and *B. pilosa* dry matter production when grown in soils with reconstituted microbiota can be attributed to the addition, via reconstitution, of microorganisms with negative relationship with the plants. The soil microbiota plays an important role in the interactions between *B. pilosa*, *A. viridis* and maize, influencing plant growth and competitive ability. Soil microbiota reconstitution improves the ability of maize to compete with *A. viridis*, while the reverse was observed with *B. pilosa*.

Keywords: *Amaranthus viridis*, *Bidens pilosa*, competitive capacity, invasive plant, microbial reconstitution, soil microbiota.

INTRODUCTION

Soil microorganisms are responsible for nutrient cycling, affects plant nutrition, transformation of xenobiotic compounds, and beneficial or antagonistic interactions with other organisms that inhabit the soil (Kremer and Li 2003; Reinhart and Callaway 2006; Rout and Callaway 2009). Soil microorganisms may reduce or improve plant growth and compete for or make available soil resources for plants (Shah et al. 2008; Veiga et al. 2011).

Some weeds are able to associate with mycorrhizal fungi and dark septate endophytes (Santos et al. 2013; Massenssini et al. 2014). Plants that establish these associations can gain competitive advantages over others (O'Connor et al. 2002; Shah et al. 2008; Rout and Callaway 2009). Furthermore, the soil biota is important in plant invasion dynamics, in invasive plant adaptation at new sites, and in competition with native plants (Emam et al. 2014). The association degree between microorganisms and plants can be changed by plant competition (Massenssini 2014; Liao et al. 2015). Interactions between weeds, crops, and soil microorganisms can influence the growth and competitiveness of plants (Pausch et al. 2013; Massenssini 2014; Melo et al. 2014). This phenomenon depends on the plant species and associated microorganisms, season, plant growth stage, and soil type.

Amaranthus viridis L. (Amaranthaceae) is a native annual weed in Central America; it is fast-growing and yields high number of seeds (Bensch et al. 2003). Same Amaranthaceae, as *A. viridis*, are characterized by their nitrophily and the C_4 photosynthesis pathway. *A. viridis* infestation can influence nutrient availability, bacterial abundance, and soil microbial activities (Bensch et al. 2003). Hence, *A. viridis* can reduce the growth of native or cultivated plants, as observed for species of the genus *Acacia* (Sanon et al. 2009). *Bidens pilosa* L. (Asteraceae) is an annual plant with a height of up to 1.0 m and often infests agricultural areas in tropical regions (Santos and Cury 2011; Hsiao-Mei and Wen-Yuan 2014). The species produces large amounts of seeds and has a high resource efficiency use, especially in terms of water and nutrients, with a high ability to compete with crops (Procópio et al. 2004; Santos and Cury 2011). In addition, *B. pilosa* is capable of forming associations with the soil microbiota, which can increase its competitive capacity (Massenssini et al. 2014; Melo et al. 2014) and facilitate invasion of new areas, making it difficult to control (Santos and Cury 2011).

Studies on the competition between plants provide information on the potential of each individual to modify the soil microbiota composition for their own support (Hart et al. 2003; Massenssini 2014) and enable the determination of plant species and microorganisms which are most affected (Callaway et al. 2002; Kulmatiski et al. 2008; Massenssini 2014). Nevertheless, most researches involving weed-crop competition do not explore how interactions between plants and soil microorganisms can contribute effectively to the competitive success of a species. In addition, the weed potential to influence the soil microbial communities is not well understood (Li and Kremer 2000; Smith et al. 2011).

The aim of this study was to investigate how the soil microbiota influences the initial growth of weeds and maize and their competitive ability.

MATERIAL AND METHODS

Experimental design

The influence of the total soil microbiota in the initial establishment and coexistence between plants was evaluated between two weed species (*Bidens pilosa* L. and *Amaranthus viridis* L.) and hybrid maize BG 7049 (*Zea mays* L.). These plants were selected due to their different interactions with the soil microbial community, showing varied degrees of dependence on soil microorganisms for their growth (Santos et al. 2012; Massenssini 2014). We used a completely randomized design in a factorial 6 x 2 scheme with four replications in a greenhouse experiment. We evaluated six cultivation managements (maize in monoculture, coexistence between weeds and maize, weeds in monoculture, and non-cultivated soil) with two soil conditions: sterilized soil and sterilized soil with the reconstituted microbiota.

Soil sterilization

The soil was collected to 0-20 cm depth in an area frequently cultivated with maize, located at an experimental site of Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil. Soil samples were air-dried, sieved through a 4-mm-screem sieve, and used to fill plastic pots for plant cultivation (22.0 cm diameter and 17.0 cm height). The soil mass used was 3.8 kg per pot. The pots were autoclaved twice at 0.2 MPa and 121°C for 1 h, with 48 hours between each autoclaving. The chemical soil analyses, after autoclaving, resulted in pH 4.8; 18.61 g kg^{-1} organic content; 4.2 mg dm^{-3} $P_{Mehlich-1}$, 75 mg dm^{-3} K; 2.0, 1.1, 0.2, 3.96, and 3.49 $cmol_c$ dm^{-3} Ca, Mg, Al, H + Al, and effective CEC, respectively, 45 % base saturation. Physical analysis showed 32% clay, 10% silt, and 58% sand.

Soil microbiota reconstitution

Reconstitution of soil microorganisms was carried out via soil suspension. The suspension was made by mixing soil in distilled water at the ratio of 1:5 (w:w). This mixture was stirred for 6 min and leached through synthetic fiber gauze. Part of this suspension was placed in Erlenmeyer flasks and autoclaved at 0.2 MPa and 121°C for 20 minutes. Subsequently, 200 ml of soil suspension were added to each pot as follows: 24 pots containing autoclaved soil received autoclaved suspension constituting the treatment "sterilized soil" and the other 24 pots received the un-autoclaved suspension, characterizing the treatment "soil with reconstituted microbiota".

Seed disinfestation and planting

Maize and weed seeds were dipped in 70% ethyl alcohol solution, maintained under stirring for 1 min, rinsed with autoclaved distilled water, and immersed in 20% H_2O_2 solution for 6 min under stirring. Then, the seeds were washed five times in autoclaved distilled water and kept in a sterilized Petri dish until planting.

Three maize and 20 weed seeds were sown per pot. After seed germination, one plant of each species was kept per pot and the others were removed, according to the treatments. The pots were irrigated on a daily basis to maintain 80 % field capacity.

Fertilization was performed after planting by adding 100 ml of 20% strength Hoagland nutrient solution every seven days (Hoagland and Arnon 1950). The pots were kept under non-aseptic conditions. Microbial succession in the autoclaved soil was not controlled. The observed effects of soil sterilization and soil microbiota reconstitution reflect different soil microbial community structures obtained along microbial ecological succession.

Plant harvest

Forty-three days after planting, plants were removed from the pots, separated into roots and shoots, and washed in water. All plant tissues were placed in paper bags and oven-dried under forced air circulation at 65°C until constant weight. Subsequently, the plant material was milled in an analytical mill IKA® A11 Basic for quantification of plant nutrient concentrations.

Plant tissue nutrient analyses

Phosphorus, potassium, calcium, magnesium, zinc, iron, copper, and manganese were measured after digestion with a mixture of nitric and perchloric acids and nitrogen was determined after sulfuric solubilization (Jones Junior et al. 1991). Phosphorus concentration was determined via molecular absorption spectrophotometry, K by flame emission spectrometry, Ca, Mg, Zn, Fe, Cu, and Mn by atomic absorption spectrophotometry (Jones Junior et al. 1991), and nitrogen by the Kjeldahl method (Kjeldahl 1883). The concentration of

B was determined colorimetrically using the azomethine-H method (Gaines and Mitchell 1979). The N and B contents were not quantified for *B. pilosa* because there was not enough plant tissue for analysis.

The total nutrient content of plant tissue (mg) was calculated by multiplying the N, P, K, Ca, Mg, Zn, Fe, Cu, Mn, and B concentrations (mg nutrient per mg of dry matter) by the total plant dry matter.

Competition index

The competition effects for the plants grown in sterilized soil or in the soil with reconstituted microbiota were evaluated by the relative interaction index (RII). This index was calculated as described in Armas et al. (2004): RII = (total dry matter of plant growing with competitor - total dry matter of plant growing in monoculture)/(total dry matter of plant growing with competitor + total dry matter of plant growing in monoculture).

Soil microbiota analyses

Respiratory rate (RR)

The C-CO_2 evolved from soil was estimated by the respirometric method (Stotzky, 1965). For this, 100 g of sieved soil with moisture at 60% field capacity were incubated for 15 days in tightly closed pots. The C-CO_2 released from the soil was transported by continuous flow of CO_2-free air to Erlenmeyer flasks containing 100 mL of NaOH solution (0.5 mol L^{-1}). The C-CO_2 was estimated by titrating 10 mL of NaOH solution with 0.5 mol L^{-1} HCl solution.

Microbial biomass carbon (MBC)

After 15 days of incubation, 18 g of soil were taken from each pot to determine microbial biomass carbon (MBC), using the method described by Vance et al. (1987) and modified by Islam and Wright (2006), in which samples were treated with microwave radiation during previously calculated time. The extraction efficiency coefficient used for calculation of the MBC was 0.33 (Sparling and West 1988). From the C-CO_2 evolution and MBC values, the metabolic quotient (qCO_2) was determined (Anderson and Domsch 1993).

Statistical analysis

Maize and weed dry matter, RR, MBC, qCO_2, and RII data were subjected to analysis of variance and the means were compared by the Tukey´s test ($p < 0.05$).

We used multivariate canonical analyses to evaluate the effects of the treatments on maize and weed nutrient contents. For this, macro- (N, P, K, Ca, and Mg) and micronutrient

(Zn, Fe, Cu, Mn, and B) contents were reduced by a data set through linear combinations, generating the canonical variable scores. When the first canonical variable was able to account for over 80 % of the total data variance (Cruz and Regazzi 1994), these canonical variable scores were subjected to variance analysis followed by the Tukey´s test ($p < 0.05$).

RESULTS

We observed a significant interaction ($p < 0.05$) between cultivation managements and growing conditions (sterilized soil or sterilized soil with reconstituted microbiota) for shoot, root, and total dry matter, first canonical variable scores for macro- and micronutrients in maize, RIIs for maize competitive response, P content in *B. pilosa*, K and Mg contents in *A. viridis*, respiratory rate (RR), microbial biomass carbon (MBC), and metabolic quotient ($q\text{CO}_2$). Unpacking these interactions allowed us to compare means within each cultivation management and growing condition.

Microbiota reconstitution decreased root, shoot, and total dry matter (Figs. 1A, 1B and 1C) and macro- and micronutrient contents (Figs. 2A and 2B) of maize in coexistence with *B. pilosa*. Microbiota reconstitution also decreased total dry matter (Fig. 1C) and macro- and micronutrient contents (Figs. 2A and 2B) when maize was grown in monoculture. Microbiota reconstitution did not influence the growth and nutrient content of maize coexisting with *A. viridis* (Figs. 1 and 2).

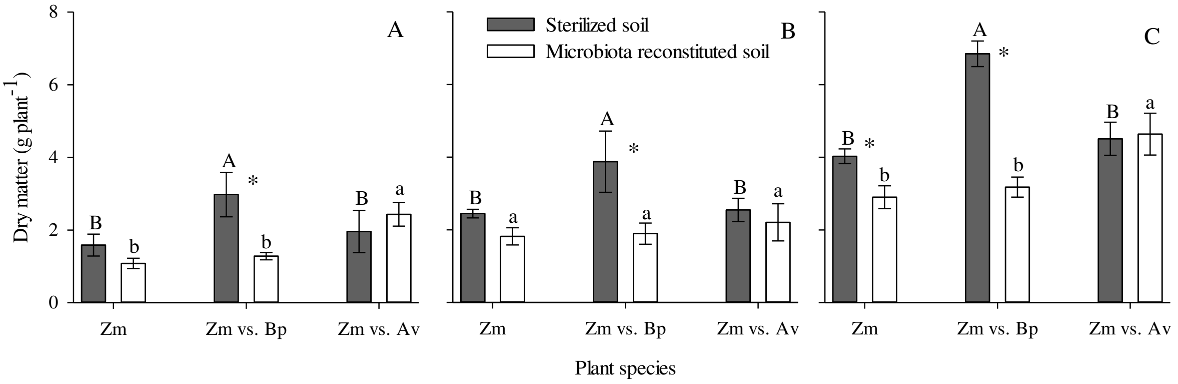

Figure 1. Root (A), shoot (B), and total (C) *Zea mays* (Zm) dry matter production after growth for 43 days in sterilized soil and in sterilized soil with reconstituted microbiota under interspecific competition with *Bidens pilosa* (Bp) and *Amaranthus viridis* (Av). Bars represent standard deviation of means (n = 4). Different capital and lowercase letters within a soil condition indicate significant difference between means based on the Tukey´s test ($p < 0.05$). Asterisks indicate that dry matter was different between paired bars by the Tukey´s test ($p < 0.05$).

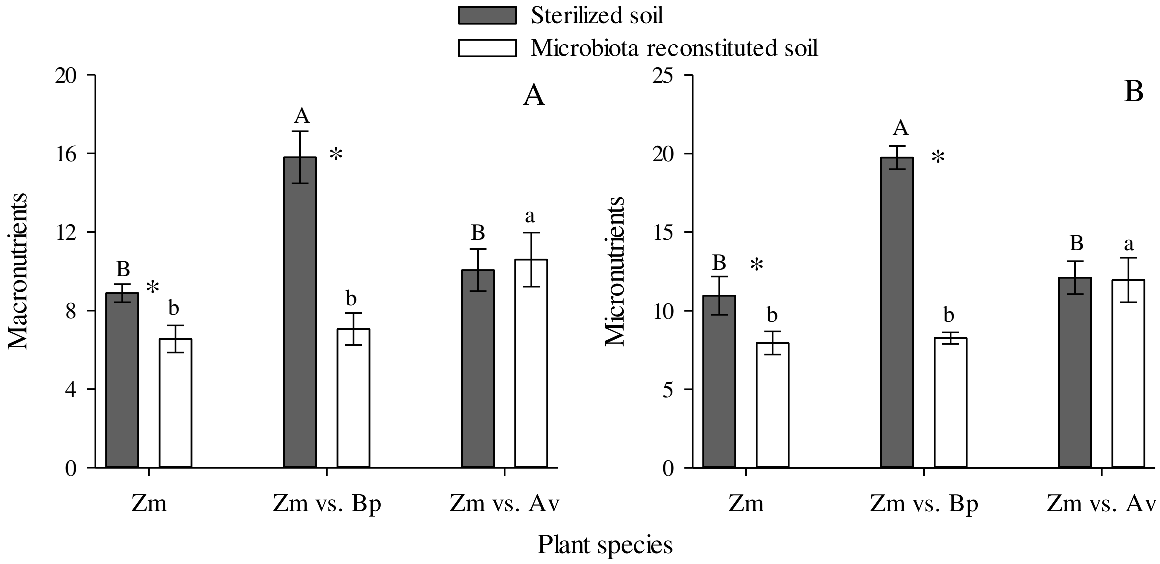

Figure 2. Canonical variable scores of macro- (A) and micronutrient contents (B) in *Zea mays* (Zm) after growth for 43 days in sterilized soil and in sterilized soil with reconstituted microbiota under interspecific competition with *Bidens pilosa* (Bp) and *Amaranthus viridis* (Av). Bars represent standard deviations of means (n = 4). Different capital and lowercase letters within a soil condition indicate significant differences between means based on the Tukey´s test (p < 0.05). Asterisks indicate canonical variable score was different between paired bars by the Tukey´s test (p < 0.05).

Coexistence with *A. viridis* in the soil with reconstituted microbiota and coexistence with *B. pilosa* in sterilized soil increased root and total dry matter of maize as well as its nutrient content (Figs. 1A, C, and 2). In contrast, coexistence with both weed species, in soil with reconstituted microbiota, did not affect the shoot dry matter of maize (Fig. 1B).

Coexistence with maize and cultivation in soil with reconstituted microbiota decreased the total dry matter of *B. pilosa* (Tab. 1). On the other hand, these treatments did not influence root, shoot and total dry matter of *A. viridis* (Tab. 1).

Microbial reconstitution reduced P and K content in *Bidens pilosa* and *A. viridis* grown alone (Tab. 2). It also increased Mn content in both weeds.

Coexistence with maize reduced P and K content in *B. pilosa* and *A. viridis*, respectively, grown in sterilized soil (Tab. 2). Moreover, the coexistence reduced K and Zn content in *B. pilosa* for both soil conditions. Ca, Mg, Fe, Mn, and Cu contents in *B. pilosa* and N, P, Ca, Zn, Fe, Cu, and B contents in *A. viridis* were not influenced by the treatments. *A. viridis* showed a high Mg content in coexistence with maize.

Maize competitive capacity was influenced by the growing conditions (Fig. 3A). The soil microbiota reconstitution did not affect the capacity of weeds to compete with maize (Fig. 3B). Maize was more competitive than weeds in both soil conditions (Fig. 3). Maize competed better with *B. pilosa* in sterilized soil and with *A. viridis* in soil with reconstituted microbiota (Fig. 3A). Soil microbiota reconstitution reduced the ability of maize to compete against *B. pilosa* (menor RII), but improved it against *A. viridis*.

Soil microbial activity was influenced by the cultivated species and by the soil microbiota reconstitution (Fig. 4). Exposure of sterilized soil to environmental conditions and plant cultivation were sufficient for reestablishing part or all of the soil microbial populations.

Soil microbiota reconstitution reduced RR and qCO_2 for the soil cultivated with *B. pilosa* (Fig. 4a). This treatment increased MBC in *B. pilosa* monoculture and in maize vs *B. pilosa* coexistence (Fig. 4b). It also increased qCO_2 in *A. viridis*-cultivated and in non-cultivated soils (Fig 4c).

The coexistence between maize and *B. pilosa* provided the smallest RR and qCO_2 in sterilized and reconstituted soils (Figs. 4A, C). In contrast, the highest qCO_2 values were observed for *B. pilosa* monoculture in sterilized soil and for *A. viridis* in reconstituted soil (Fig. 4C).

Table 1. Root, shoot, and total dry matter production of *Bidens pilosa* and *Amaranthus viridis* after growth for 43 days in sterilized soil and in sterilized soil with reconstituted microbiota under interspecific competition with maize. Values are means ± standard deviations (n = 4).

	Cultivation managements					
	B. pilosa	*B. pilosa* vs. maize	Mean	*A. viridis*	*A. viridis* vs. maize	Mean
Soils	Root dry matter (g plant^{-1})					
Sterilized	0.11 ± 0.05	0.10 ± 0.04	0.10	0.43 ± 0.10	0.27 ± 0.09	0.35
Reconstituted	0.06 ± 0.02	0.02 ± 0.003	0.04	0.46 ± 0.15	0.43 ± 0.10	0.44
Mean	0.08	0.06		0.45	0.35	
CV (%)		81.92			28.31	
	Shoot dry matter (g plant^{-1})					
Sterilized	0.28 ± 0.05	0.16 ± 0.06	0.22	2.29 ± 0.40	1.76 ± 0.23	2.03
Reconstituted	0.20 ± 0.04	0.17 ± 0.03	0.19	2.20 ± 0.53	2.06 ± 0.31	2.13
Mean	0.24^{a}	0.17^{b}		2.25	1.91	
CV (%)		23.42			18.34	
	Total dry matter (g plant^{-1})					
Sterilized	0.39 ± 0.09	0.26 ± 0.01	0.32^{a}	2.72 ± 0.39	2.03 ± 0.18	2.37
Reconstituted	0.26 ± 0.10	0.19 ± 0.03	0.22^{b}	2.66 ± 0.67	2.49 ± 0.28	2.58
Mean	0.32^{a}	0.22^{b}		2.69	2.26	
CV (%)		20.49			16.99	

Different letters indicate significant differences between means based on the F test ($p < 0.05$). CV = coefficient of variation.

Table 2. Total nutrient contents in *Bidens pilosa* and *Amaranthus viridis* after growth for 43 days in sterilized soil and in sterilized soil with reconstituted microbiota under interspecific competition with maize. Values are means ± standard deviations (n = 4).

	Cultivation managements					
	B. pilosa	*B. pilosa* vs. Maize		*A. viridis*	*A. viridis* vs. Maize	
Soils	P (mg)		Mean	K (mg)		Mean
Sterilized	0.87^{Aa} ± 0.19	0.38^{Ba} ± 0.21	0.63	75.56^{Aa} ± 14.62	38.38^{Ba} ± 5.32	56.98
Reconstituted	0.51^{Ab} ± 0.20	0.42^{Aa} ± 0.08	0.47	55.70^{Ab} ± 11.80	45.03^{Aa} ± 6.00	50.37
Mean	0.69	0.4		65.63	41.71	
CV(%)		32.73			19.03	
	K (mg)			Mg (mg)		
Sterilized	9.60 ± 2.03	4.09 ± 2.19	6.84	16.62^{Aa} ± 4.60	13.13^{Ab} ± 0.92	14.88
Reconstituted	6.57 ± 2.60	4.90 ± 1.07	5.73	14.56^{Aa} ± 3.18	18.64^{Aa} ± 3.35	16.60
Mean	8.08^{a}	4.49^{b}		15.59	15.88	
CV(%)		32.63			20.93	
	Zn (mg)			Mn (mg)		
Sterilized	0.15 ± 0.03	0.07 ± 0.03	0.11	72.36 ± 9.74	57.81 ± 11.88	65.08^{b}
Reconstituted	0.10 ± 0.03	0.06 ± 0.02	0.08	80.56 ± 22.27	86.26 ± 16.29	83.41^{a}
Mean	0.12^{a}	0.06^{b}		76.46	72.03	
CV(%)		31.04			21.67	

Values followed by the same lowercase letter within each column and uppercase letter in each row are not significantly different by the Tukey´s test ($p < 0.05$). When interactions were not significant, the means of the individual factors were compared by F test ($p < 0.05$). CV = coefficient of variation.

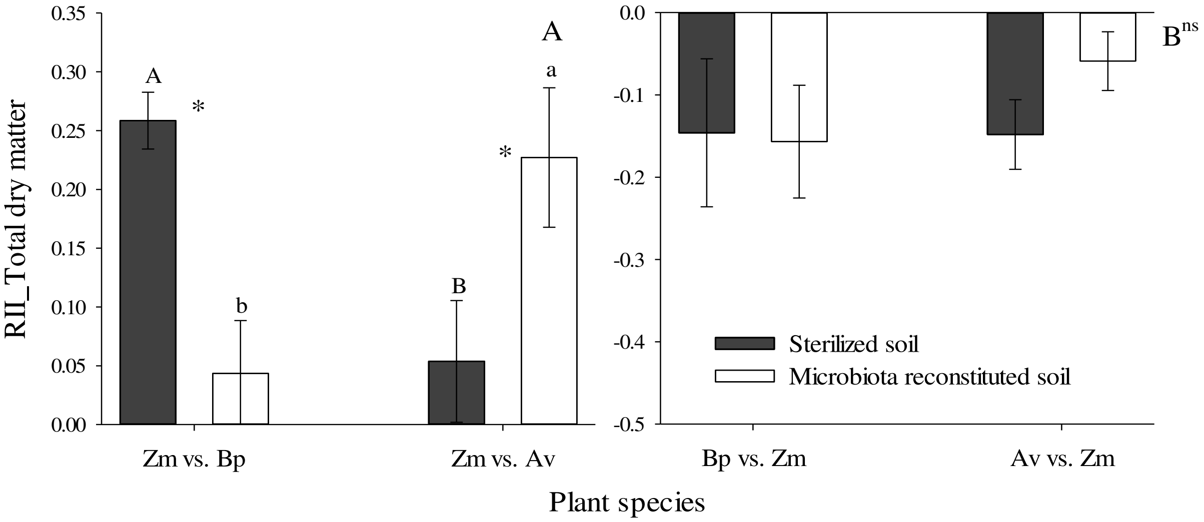

Figure 3. Effect of soil sterilization and soil microbiota reconstitution on the competitive ability (measured as the relative interaction index –RII) for *Bidens pilosa* (Bp) and *Amaranthus viridis* (Av) in competition with *Zea mays* [Zm] (A) and for *Zea mays* in competition with *Bidens pilosa* and *Amaranthus viridis* (B) after 43 days of growth. Bars represent standard deviations of means (n = 4). Different capital and lowercase letters within a soil condition indicate significant differences between means based on the Tukey´s test ($p < 0.05$). Asterisks indicate RII was different between paired bars by the Tukey´s test ($p < 0.05$). ^{ns} not significant by the F test ($p < 0.05$).

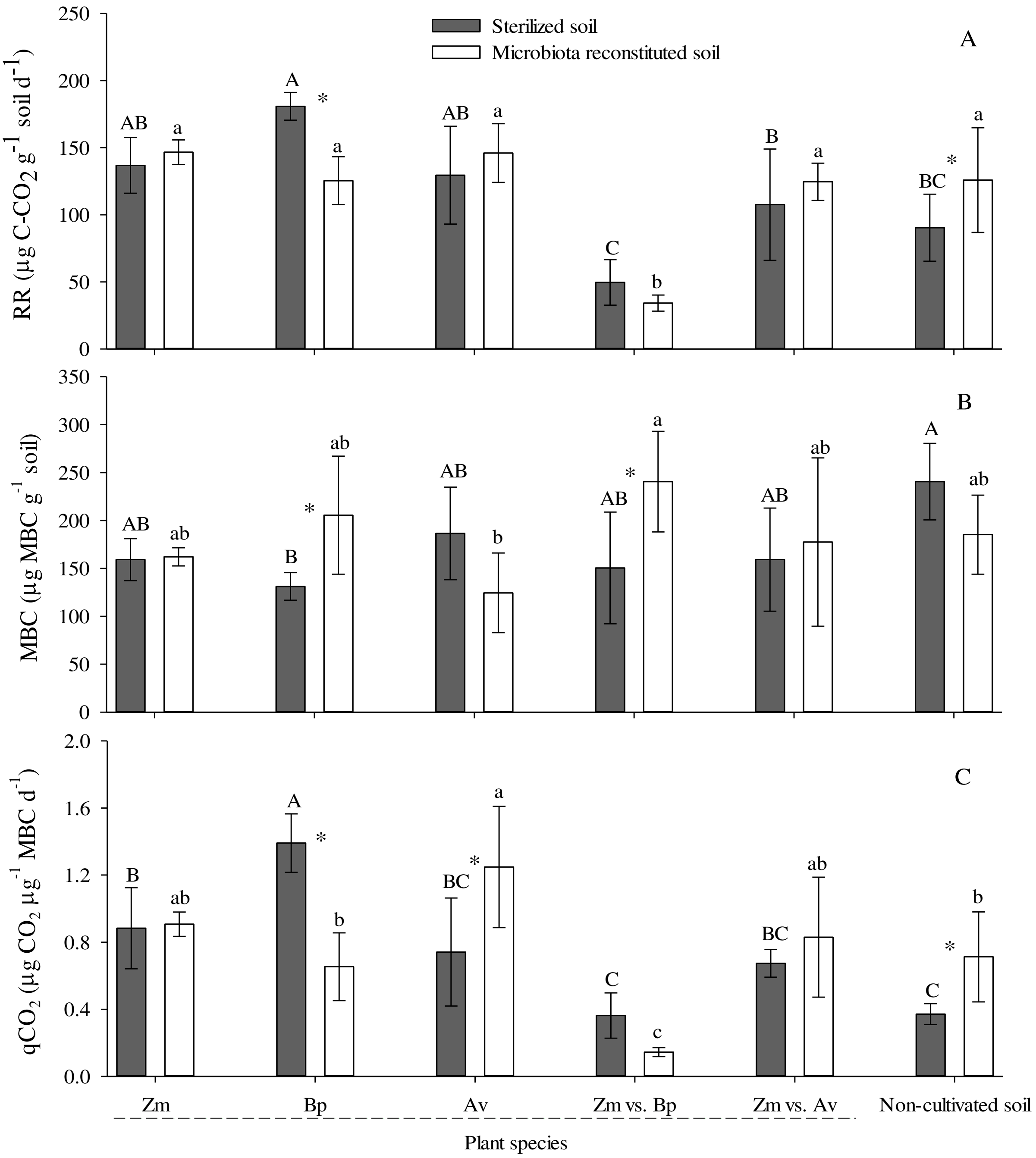

Figure 4. Respiratory rate – RR (A), microbial biomass carbon – MBC (B), and metabolic quotient – $q\mathrm{CO_2}$ (C) of sterilized soil and sterilized soil with reconstituted microbiota cultivated for 43 days with *Zea mays* (Zm), *Bidens pilosa* (Bp), *Amaranthus viridis* (Av) and non-cultivated soil (control). Bars represent standard deviations of means (n = 4). Different capital and lowercase letters within a soil condition indicate significant differences between means based on the Tukey´s test ($p < 0.05$). Asterisks indicate that RII was different between paired bars by the Tukey´s test ($p < 0.05$).

DISCUSSION

Soil microbiota reconstitution reduced the dry matter production in both maize and *B. pilosa* grown in monoculture and in coexistence conditions. In our work sterilized non-cultivated soil showed similar chemical properties to those of non-cultivated soil with reconstituted microbiota (Tab. S1, Suppl. data). This indicates that plant growth differences were due solely to changes in plant interactions with soil microorganism. Thus, soil reconstitution may have introduced microorganisms that maintain negative relationships with maize and *B. pilosa*. The soil used in our experiments had a history of maize cultivation. Successive planting of one crop or low plant species diversity in an area may favor pathogen development, thereby reducing plant performance (Reinhart and Callaway 2006; Liao et al. 2015). Native or cultivated plants grown frequently in the same area tend to show more negative feedback with soil microbes, which increases over time due to the accumulation of deleterious microorganisms in the soil (Hawkes et al. 2013) as reported for soil pathogens of the genus *Pythium* (Mills and Bever 1998).

The frequent cultivation of maize in an area infested with *B. pilosa*, such as in the case of this work, may select soil microorganisms that exert negative feedback on both species. This explains the poor performance of maize and *B. pilosa* grown in the soil with reconstituted microbiota. Nevertheless, weeds, such as *B. pilosa,* change the soil microbial community structure by selecting microorganisms that establish positive feedback interactions with them, thereby increasing their survival capacity and infestation area over time (Kulmatiski et al. 2008; Massenssini 2014; Emam et al. 2014). Soil sterilization reduced the growth of the native plant *Bouteloua gracilis* and of the invasive *Bromus tectorum*, both cultivated in monoculture. However, the competition effects among these plants were higher in *Bromus* than in *Bouteloua* (Emam et al. 2014), possibly because soil sterilization eliminated harmful microorganisms.

Amaranthus viridis and *B. pilosa* reduce crop yields, as reported for maize (Faria et al. 2014) and *Cicer arietinum* (Amaral et al. 2015). Nevertheless, in our work, maize coexistence with *A. viridis* in soil with reconstituted microbiota and with *B. pilosa* in sterilized soil improved maize growth and nutrition. Changes in soil microbial communities driven by changes in weed community composition and diversity potentially lead to positive or negative feedbacks on crop growth and competitive ability (Smith et al. 2011). Crops can benefit from coexistence with non-cultivated plants if they occur at low densities or if coexistence occurs only during a specific period of the crop development cycle (Sturz et al. 2001). In a similar study, the weeds

Spergula arvensis L. and *Lolium multiflorum* L. increased the biodiversity of plant growth-promoting rhizobacteria in the soil, which favored potato development (Sturz et al. 2001).

The change in maize competitive ability and growth caused by soil microbiota reconstitution showed that the interactions between maize and weeds are dependent on soil microorganisms. Although maize vs. *B. pilosa* and maize vs. *A. viridis* showed similar microbial biomass values in both soil conditions, we assume that different microorganisms were recolonizing the sterilized soil when compared to the soil with reconstituted microbiota. Plants in competition can change the amount and composition of root exudates released in the soil (Carvalhais et al. 2013), leading to changes in the soil microbial community. This has been reported for *B. pilosa* vs. *Ipomoea ramosissima* and *Z. mays* vs. *B. pilosa* (Massenssini 2014). Furthermore, the carbon released by plant roots can influence soil nutrient availability (Cheng et al. 2014). In soil with low N availability, the native species *Fragaria vesca* increased its growth and root exudation, stimulating microbial biomass growth and turnover and increasing its own N content (Blagodatskaya et al. 2014).

Less negative values for RII indicate a stronger competitive ability of plants (Liao et al. 2015). The similar growth and competitive ability (RII) of *A. viridis* cultivated in both soil conditions showed that this weed is less dependent on the soil microbiota than maize and *B. pilosa*. On the other hand, soil microbiota reconstitution reduced K content, but improved Mg and Mn content in *A. viridis*. In our work, soil microbiota reconstitution increased $q\mathrm{CO}_2$ during *A. viridis* monoculture. These greater $q\mathrm{CO}_2$ values suggest that this weed stimulated soil microbial community activity, and therefore, soil organic matter mineralization to meet its nutritional requirements.

Bidens pilosa grown in monoculture, in the soil with reconstituted microbiota, showed a decrease in the P content, which reinforces the hypothesis of negative interactions with the soil microbiota. *Amaranthus retroflexus* and *B. pilosa* grown individually increased soil phosphate solubilization (Santos et al. 2013). *Bidens pilosa* shows a high ability to take up and accumulate phosphorus (Santos and Cury 2011). Furthermore, this weed is efficient at phosphorus use, which represents an advantage when in competition with other plant species (Procópio et al. 2005). Nevertheless, in other works, soil sterilization decreased *B. pilosa* P content (Santos et al. 2012), indicating that it may be more dependent on soil microorganisms for P acquisition than the other plants tested. Soil reconstitution or microbial recolonization after soil autoclaving may not have provided the set of microorganisms that benefit *B. pilosa* at P uptake.

The soil microbiota is extremely sensitive to soil management strategies and most of the microbial activity is dependent on the carbon released by plant roots (Shemesh et al. 2015). Thus, plants not only provide energy to soil microorganisms via root exudates, but also seem to control the way the energy is used in order to maximize soil organic matter mineralization and to drive their own nutrient supply (Shahzad et al. 2015). Therefore, changes in RR, MBC, and $q\mathrm{CO}_2$ in soils with maize and weeds may be associated with differences in root-derived carbon released by these plants. Soil microbiota reconstitution also changed the soil microbial activity and influenced the competitive ability of plants. This shows that, although plants are pivotal at controlling soil microbial activity, the established soil microbiota after soil sterilization may also impact respiration, microbial biomass, and the ecological interactions between plants.

CONCLUSION

Our data show that soil microbiota reconstitution after soil sterilization plays an important role in the interactions between maize and weed plants, influencing plant growth and competitive ability.

The greater or lower ability of maize to compete with weeds is associated with the soil microbial community. Soil microbial reconstitution improves the ability of maize to compete with *A. viridis*, while the reverse is observed with *B. pilosa.*

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SUPPLEMENTARY DATA

Table S1. Concentration of phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), zinc (Zn), iron (Fe), manganese (Mn), copper (Cu), boron (B), hydrogen potential (pH_{H2O}), hydrogen + aluminum (H + Al), base sum (BS), effective cation exchange capacity (CEC t), potential cation exchange capacity (CEC T), base saturation (V), organic matter (OM), and, remaining phosphorus (P rem) in sterilized soil and in sterilized soil with reconstituted microbiota kept uncultivated for 43 days. Values are means ± standard deviations (n = 4).

	Soil conditions	
Soil proprieties ^{ns}	Sterilized	Reconstituted
$P_{Mehlich-1}$ (mg dm^{-3})	4.60 ± 0.20	4.70 ± 0.70
K (mg dm^{-3})	83.33 ± 7.09	81.33 ± 3.21
Ca (cmolc dm^{-3})	2.13 ± 0.15	2.13 ± 0.06
Mg (cmolc dm^{-3})	1.10 ± 0.10	1.03 ± 0.06
Zn (mg dm^{-3})	1.53 ± 0.23	1.30 ± 0.10
Fe (mg dm^{-3})	26.47 ± 2.80	23.46 ± 3.95
Mn (mg dm^{-3})	255.40 ± 23.65	241.73 ± 13.86
Cu (mg dm^{-3})	1.00 ± 0.10	1.17 ± 0.06
B (mg dm^{-3})	0.23 ± 0.06	0.20 ± 0.00
pH	5.43 ± 0.21	5.17 ± 0.12
H+ Al (cmolc dm^{-3})	4.02 ± 0.25	4.13 ± 0.0
BS (cmolc dm^{-3})	3.45 ± 0.27	3.37 ± 0.13
CEC(t) (cmolc dm^{-3})	3.45 ± 0.27	3.44 ± 0.16
CEC(T) (cmolc dm^{-3})	7.46 ± 0.24	7.50 ± 0.13
V (%)	46.33 ± 3.06	44.67 ± 1.15
OM (dag kg^{-1})	2.90 ± 0.07	2.98 ± 0.12
P rem (mg L^{-1})	30.70 ± 1.10	31.8 ± 0.00

^{ns} indicate soil property was not different between soil conditions by the t test ($p < 0.05$).

CAPÍTULO 3

Rhizosphere priming effect on soil organic matter induced by crop-weed competition

RHIZOSPHERE PRIMING EFFECT ON SOIL ORGANIC MATTER INDUCED BY CROP-WEED COMPETITION

ABSTRACT

Certain plant combinations can stimulate the mineralization of soil organic matter (SOM), thereby changing the storage of soil organic carbon and affecting the physical and chemical soil properties. This reduces the sustainability of agricultural systems and can increases the atmospheric CO_2 concentration. Many studies have found that crop plants increase the priming effect of SOM. However, no study has assessed how competition between weeds and crops can influence this priming effect. The aim of this study was to evaluate whether competition between weeds and maize can stimulate SOM decomposition. In this research, the plant species *Amaranthus viridis*, *Bidens pilosa*, and *Ipomoea grandifolia*, considered as weeds, and *Zea mays* were grown under greenhouse conditions. We evaluated eight treatments: maize and weed monocultures, maize in competition with weeds, and non-cultivated soil. The experiment was conducted in a randomized block design with five replications. Total CO_2 concentration (soil + plant) was determined weekly. On these occasions, the CO_2 efflux and isotopic composition of gaseous samples ($\delta^{13}CO_2$) were quantified and the rhizosphere priming effect (RPE) on soil organic matter was estimated. The plants were harvested at 60 days after planting. At that time, soil samples were collected to measure the C and N contents of particulate (POM) and mineral-associated organic matter (MAOM). Competition between plants did not influence maize growth, but reduced dry matter production by weeds. All competition treatments led to positive RPE. From the 43rd day of cultivation onwards, the coexistence between maize and *B. pilosa* led to the highest RPE values, while maize vs. *A. viridis* showed negative RPE. The soil organic C and N and the C:N ratio varied with the cultivation management. The POM- and MAOM-C contents were similar between maize monoculture and the non-cultivated soil. Maize vs. *A. viridis* and maize vs. *I. grandifolia* increased MAOM-C, but reduced the POM-C contents. *Ipomoea grandifolia* monoculture and maize vs. *B. pilosa* led to the highest MAOM-C losses and reduced POM-C compared to those of non-cultivated soils. We conclude that competition between maize and *B. pilosa* increases SOM mineralization, while competition between maize and *A. viridis* or *I. grandifolia* retards this process.

Keywords: CRDS, corn, invasive plant, microbiota, SOM mineralization.

INTRODUCTION

One of the main goals of weed management programs is to reduce the competition effects these plants have on crops. Weed science has been an effective discipline for the development, evaluation, and improvement of strategies to control or reduce weed abundance in agricultural areas (Monaco et al. 2002; Christoffoleti et al. 2007; Bajwa 2014). However, the ecological factors that affect interactions between weeds and crops are still poorly known (Smith et al. 2010).

Among these factors, soil microorganisms play a key role in the competitive ability of different plant species and can directly affect plant productivity and nutrient acquisition (van der Heijden et al., 2003; see chapter 2). Some combinations of different plant species can possibly stimulate soil microbial community to increase SOM mineralization to meet their nutritional requirements. This hypothesis, however, has not been tested for weed-crop competition.

Most interactions between plants and soil microorganisms occur in the rhizosphere. On a global scale, these interactions can control up to 50 % of total CO_2 released from terrestrial ecosystems (Hopkins et al. 2013) and regulate practically all soil nutrient cycling processes (Kuzyakov 2002). The influence of the interactions between plants and microorganisms on the soil organic matter (SOM) dynamics can be studied by evaluating the rhizosphere priming effect (RPE). This phenomenon is defined as the stimulation or retardation of SOM decomposition by live roots and associated rhizosphere organisms when compared to SOM decomposition from bulk soils under the same environmental conditions (Cheng et al. 2014). The priming effect is positive when SOM decomposition is accelerated and negative when the decomposition is retarded (Kuzyakov 2002).

The RPE is an important regulator of SOM decomposition, providing nutrients to plants or sequestering soil C (Bengtson et al. 2012). The RPE depends on the soil microbial community, exudate quality and stoichiometry, and soil nutrient availability, particularly nitrogen and phosphorus (Dijkstra et al. 2013). Plants can shape the soil microbial community structure (Broeckling et al. 2008; Massenssini 2014) by controlling rhizodeposition quality and quantity in the rhizosphere (Grayston et al. 1997; Broeckling et al. 2008). Therefore, it is important to study how different plant species and their interactions can influence the RPE (Shahzad et al. 2015). Several studies have found that plants can increase or retard SOM decomposition (Dijkstra et al. 2013; Shahzad et al. 2015; Mwafulirwa et al. 2016). However, most of these studies assessed only the effects of monocultures or intraspecific competition on RPE.

The association between plants and microorganisms may increase, decrease, or not affect the soil organic carbon content. Even small changes in soil organic carbon storage can have a profound impact on the atmospheric CO_2 concentrations (Manlay et al. 2007). However, it is still not well understood how RPE may be influenced by interactions between crops and weeds. It is already known that plant-plant interactions can shape plant functions, such as exudate release and nutrient absorption (Pausch et al. 2013). There are few studies about the influence of interspecific competition on RPE (Dijkstra et al. 2010; Pausch et al. 2013). Therefore, studies on the interactions between weeds and crops and their impact on SOM dynamics are needed. The aim of this study was to determine whether the competition between weeds and maize can stimulate RPE and, therefore, SOM degradation.

MATERIAL AND METHODS

Soil sampling and conditioning

The experiment was conducted in a greenhouse at the Universidade Federal de Viçosa, Viçosa city, Minas Gerais State, Brazil. The soil was sampled from a plough horizon (top 20 cm) of a Xanthic Ferralsol (*Latossolo Amarelo*) from a farm in Guarapari, Espírito Santo State, Brazil. The results of the chemical soil analyses are as follows: pH 5.77, 8.8 g kg^{-1} organic carbon content, 6.8 mg dm^{-3} P (Mehlich-1), 67 mg dm^{-3} K, 3.17, 0.97, 0.10, 2.00, and 4.41 cmolc dm^{-3} Ca, Mg, Al, H + Al, and effective CEC, respectively, 68.3 % base saturation. Physical analyses showed 22% clay, 4% silt, and 74% sand. The soil contained $\delta^{13}C\text{-}CO_2$ value of -20.0‰, measured by spectroscopy using a cavity ring-down spectrometer analyzer (CRDS, G2131-i, Picarro, Sunnyvale, CA). We therefore selected this soil because of its intermediate isotopic composition, commonly found in soils cultivated with C_3 and C_4 plants. Pots (18 cm height, 22 cm diameter) were filled with 7.1 kg of air-dried and sieved (< 4 mm) soil. Prior to planting, fertilization was performed by mixing 0.21 g dm^{-3} of P_2O_5 into the soil. A polyvinyl chloride tube (PVC) of 10.0-cm height x 5.0-cm diameter was fixed in the center of each pot at a soil depth of 5 cm (see Fig. S1, Suppl. data).

Experimental set-up

The experiments consisted of *Amaranthus viridis* L., *Bidens pilosa* L., *Ipomoea grandifolia* (Dammer) O'Donell, and *Zea mays* L. (maize) monocultures and cultivation systems of maize vs. *A. viridis*, maize vs. *B. pilosa*, and maize vs. *I. grandifolia*. Additionally, non-cultivated pots with soil were prepared. All treatments were conducted under greenhouse conditions. We used a complete randomized block design with five replicates.

Although there is intraspecific competition between plants grown in monoculture, our purpose with this study was to evaluate the interspecific competition effects on SOM degradation. Thus, the possible intraspecific competition effects were not reported.

Seed planting and cultivation

For all treatments with plant coexistence, we used four maize and seven weed plants of each species per pot. For maize and weed monocultures, we used four and seven individual plants per pot, respectively. To obtain one individual plant, two seeds of maize and 20 seeds of each weed species were planted. After emergence, seedlings were thinned to one. Soil moisture content was measured gravimetrically and daily adjusted to 80 % of the field capacity.

Ammonium nitrate and potassium chloride solutions containing 50 mg dm^{-3} of N and K, respectively, were applied at 12 and 32 days after planting the seeds (DAP). At 19 DAP, we applied 0.2 g L^{-1} of acetamiprid (Mospilan®) to control whiteflies (*Bemisia tabaci* Gennadius, 1889).

Rhizosphere priming effect (RPE) determination

CO_2 efflux and isotopic composition ($\delta^{13}C$)

Soil-plant system measurements

The CO_2 efflux measurements were carried out by coupling PVC chambers (24.0-cm height x 5.2-cm diameter), on previously installed fixed PVC bases (see Fig. S1, Suppl. data). The PVC chambers were built with a rubber septum on the top. Air sampling was performed using 60-mL syringes introduced into the septum at 0, 5, 10, and 15 minutes after coupling the chambers to the PVC base. Seven samples of CO_2 were taken from the eighth DAP with an interval of seven days between samplings.

$\delta^{13}C$ of root-respired CO_2

At 60 DAP, plants were carefully removed from the soil and their roots washed in water. The samples were then placed in plastic pots with deionized water; the roots remained submerged (see Fig. S1, Suppl. data). The pots were covered with plastic bags that were tied to the plant stems, thus keeping the roots in a closed environment. The CO_2 samples were captured using 60-mL syringes at 1:00, 1:30, 2:00, and 2:30 hours after tying the plastic bags to the stems. Holes left by the syringe needle were immediately sealed with adhesive tape after CO_2

sampling. Plastic pots with water and without plants were evaluated as described above. The gas samples were used to quantify the natural ^{13}C abundance of root-respired CO_2 (Tab. S1, Suppl. data).

C-CO_2 efflux and $\delta^{13}C$ quantification

The CO_2 concentrations and $\delta^{13}C$ of the gaseous samples stored in the syringes were quantified by spectroscopy using the CRDS analyzer. Natural ^{13}C abundance of CO_2 was expressed as ‰, compared to standard Pee Dee Belemnite - PDB (Clapp et al. 2000). The $\delta^{13}C$-CO_2 values were estimated by the Keeling Plot method, wherein the intercept of a linear regression with the y-axis ($\delta^{13}C$ vs. $1/[CO_2]$) corresponded to the $\delta^{13}C$-CO_2 value (Pataki et al. 2003; Kayler et al. 2010).

The CO_2-C effluxes were calculated from the concentration changes after coupling the chamber to the base during sampling times, using Equation 1:

$$F = [(\Delta Q/ \Delta t) \text{ x } (M \text{ x } P \text{ x } V)]/ (R \text{ x } T \text{ x } A), \quad (1)$$

Where F: CO_2-C efflux ($\mu g\ s^{-1}\ m^2$), ($\Delta Q/ \Delta t$): variation in the gas concentration by the evaluated time interval, equivalent to the slope of a linear regression obtained by Q ($\mu g\ g^{-1}$) versus t (s), M: C molar mass, P: chamber pressure, taken as 1 atmosphere (atm), V: chamber volume (L), T: chamber's internal temperature in degrees Kelvin, R: universal gas constant (0.0821 L atm K^{-1} mol^{-1}), and A: chamber area (m^2).

Partitioning the CO_2 of the soil-plant system

The term 'root-derived CO_2' is used here to describe the sum of root respiration and CO_2 evolved by microbial decomposition of rhizodeposition and root litter, while 'root-respired CO_2' represents only CO_2 released by root respiration (Tab. S1, Suppl. data). For CO_2 partitioning, we considered that $\delta^{13}C$ of root-derived CO_2 is the same as root-respired CO_2.

Soil-derived CO_2 was separated from plant-derived CO_2 using the mass balance equations 2 and 3 (Shahzad et al. 2015):

$$C_{Total} = C_{SOM\text{-}derived} + C_{Root\text{-}derived} \quad (2)$$

$$C_{SOM\text{-}derived} = C_{Total} \text{ x } [(\delta^{13}C_{Total} - \delta^{13}C_{Root\text{-}respired})/ (\delta^{13}C_{SOM\text{-}derived} - \delta^{13}C_{Root\text{-}respired})] \quad (3)$$

$$C_{Root\text{-}derived} = C_{Total} - C_{SOM\text{-}derived} \quad (4)$$

where C_{Total} was the total CO_2-C emitted by the soil-plant system, $C_{SOM\text{-}derived}$ was the soil-derived CO_2-C released as result of microbial mineralization of SOM, $C_{Root\text{-}derived}$ was the CO_2-C from plants, rhizodeposits, and root litter, $\delta^{13}C_{SOM\text{-}derived}$ was the ^{13}C abundance of soil-derived carbon, $\delta^{13}C_{Root\text{-}respired}$ was the ^{13}C abundance of respective plant root C, and $\delta^{13}C_{Total}$ was the ^{13}C abundance of total CO_2 emitted from the plant-soil system.

Plant-induced RPE was calculated as suggested by (Kuzyakov 2002):

RPE (%) = 100 x [$C_{\text{SOM-derived}}$ (cultivated soil) – $C_{\text{SOM-derived}}$ (non-cultivated soil)]/ $C_{\text{SOM-derived}}$ (non-cultivated soil) (5)

Based on the RPE values for each sampling time, we calculated the average rhizosphere priming effect (average % RPE) for each treatment.

Plant dry matter determination

Immediately after the capture of root-respired CO_2, all plants were removed from the plastic pots and separated into roots and shoots. The samples were placed in paper bags and oven-dried with forced air circulation at 65°C until constant weight to determine dry matter (g pot^{-1}). Subsequently, root and shoot tissues were ground in an analytical mill (IKA® A11 basic grinder) for quantification of plant nutrient concentrations and root and shoot $\delta^{13}C$.

Plant tissue analyses

Concentrations of phosphorus, potassium, calcium, and magnesium were measured after digestion with a mixture of nitric and perchloric acids; nitrogen was determined after sulfuric digestion (Jones Junior et al., 1991). Phosphorus concentration was determined by molecular absorption spectrophotometry, K by flame emission spectrometry, Ca and Mg by atomic absorption spectrophotometry (Jones Junior et al. 1991), and N by the Kjeldahl method (Kjeldahl 1883).

Total nutrient content of plant tissues (g pot^{-1}) was calculated by multiplying the N, P, K, Ca, and Mg concentrations (g nutrient per g of dry matter) with the root and shoot dry matter.

Root and shoot $\delta^{13}C$ was determined by isotope ratio mass spectrometry (ANCA-GSL, Sercon, Crewe, UK).

Microbial biomass carbon (MBC)

Values of MBC were obtained by the irradiation-incubation method (Islam and Weil 1998; Islam and Wright 2006). For this, 5-g soil subsamples from each treatment were placed in a Petri dish and treated with microwave radiation over a previously calculated period (Islam and Weil 1998). Both irradiated and non-irradiated soils were inoculated with 0.1 g of fresh soil and then incubated for 10 days at 25°C and 60% water holding capacity in glass tubes sealed with a rubber septum screw-cap. Tubes without soil were also sealed for atmospheric CO_2 concentration measurements and served as controls. The CO_2 samples were taken using 60-mL syringes introduced into the septum at 48, 96, 144, 192, and 240 hours after closing the tubes. The CO_2 concentrations of the gaseous samples taken in the syringes were quantified by spectroscopy using the CRDS analyzer. The MBC was estimated by subtracting total organic carbon in the non-irradiated samples from that in the irradiated ones. The extraction efficiency coefficient used for MBC calculations was 0.33 (Sparling and West 1988).

Microbial biomass nitrogen (MBN)

Microbial biomass nitrogen (MBN) was determined using 20 g of fresh soil by the method described by Vance et al. (1987) and modified by Islam and Weil (1998), in which samples were treated with microwave radiation over a previously calculated period. The MBN was estimated based on the differences in total organic nitrogen by subtracting non-irradiated sample values from those of irradiated ones. The extraction efficiency coefficient used for MBN calculations was 0.54 (Jenkinson et al. 2004).

Physical SOM fractionation

Five-gram soil subsamples from each treatment and from the soil before cultivation (SBC) were dispersed in 15 mL of 5 g L^{-1} sodium hexametaphosphate by shaking constantly at 120 rpm for 16 h on a horizontal shaker. The dispersed soil samples were passed through a 53-µm (270 mesh) sieve and, after rinsing several times with water, the material was separated into two parts: particulate organic matter (POM), which was retained on the sieve and associated with the sand fraction, and organic matter associated with silt and clay minerals (MAOM) (Cambardella and Elliott 1992). The fractions were dried at 65°C in an oven with forced air circulation and the dried sample was ground until all material passed through a 149-µm (100 mesh) sieve. The C and N contents and $\delta^{13}C$ of POM and MAOM fractions were measured by isotope ratio mass spectrometry (ANCA-GSL 20-20, Sercon, Crewe, UK). The $\delta^{13}C$ values were calculated in relation to the international standard PDB - Pee Dee Belemnite (δ_{PDB}) (Bernoux et al. 1998) and expressed in parts per 1,000 (‰).

Plants contribution to C input in POM and MAOM

Carbon in POM and MAOM was partitioned into old C, or original C that was present in the non-cultivated soil, and new C, derived from plants grown during the experiment. We partitioned POM-C and MAOM-C into old C and new C present in these SOM fractions using the following equations (Balesdent 1987):

$$C_{fn} = (\delta^{13}C_{CS} - \delta^{13}C_{NCS}) / (\delta^{13}C_{Root} - \delta^{13}C_{NCS}) \quad (6)$$

$$C_{o} = (1 - C_{fn}) \times C_{e} \quad (7)$$

Where C_{fn} is the fraction of C from the plants; $\delta^{13}C_{CS}$ is the $\delta^{13}C$ of the MAOM or POM carbon after soil cultivation; $\delta^{13}C_{NCS}$ is the $\delta^{13}C$ of MAOM or POM carbon in the non-cultivated soil; $\delta^{13}C_{Root}$ is the $\delta^{13}C$ of plant root inputs to soil. C_o is the MAOM-C or POM-C (old soil organic matter); C_e is the total soil organic carbon (old C + new C).

In the soil with the coexistence treatments, we calculated a root biomass weighted $\delta^{13}C_{Root}$ value (eq. 8) adapted from Pausch et al. (2013). We did not use the *f* factors in our calculations because, differently from Pausch et al. (2013), the root tissue isotopic composition was measured.

$$\delta^{13}C_{Root} = \sum(\delta^{13}C_{Root,i}) \text{ x } \alpha_i \qquad (8)$$

where α_i is the percentage of root dry weight of species i on total root dry weight per pot.

Statistical analysis

Maize dry matter production, N, P, K, Ca, and Mg content in maize, MBC, MBN, and $C{:}N_{mic}$ data were subjected to variance analyses and the means were compared by Tukey´s test at 5% probability. The competition effects of maize on weed dry matter production and nutrient content were compared by t-test at 5% probability. The data of root-derived CO_2, SOM-derived CO_2, and RPE were not normally distributed, thus, they were represented by the mean data for each evaluation period. Average % RPE data was represented by mean + standard error. The total POM and MAOM C and N contents and their C:N ratio data were subjected to variance analyses and the means were grouped by the Scott–Knott test at 5% probability. Carbon in POM and MAOM partitioned into old C, were also subjected to variance analysis and the means were grouped by the Scott–Knott test at 5% probability.

RESULTS

Plant dry matter production and nutrient content

Coexistence with weeds did not influence shoot and root dry matter production of maize (Fig. 1). On the other hand, competition with maize reduced weed growth.

Except for P and K, shoot and root nutrient content in maize were not influenced by competition with weeds (Fig. 2). Among the weeds, *A. viridis* grown in monoculture was the plant with the highest nutrient content in its tissues, particularly P and Ca (Figs. 2B, 2D). However, competition with maize reduced the contents of all nutrients for this species (Fig. 2). Competition with maize reduced shoot N, P, K, and Ca contents in *B. pilosa* and *I. grandifolia* (Fig. 2). Lower root N and P contents were observed in *B. pilosa* under the same treatment (Fig.

2). Competition with maize reduced P and K contents in the roots of *I. grandifolia*, with no effect on the other nutrients.

Microbial biomass C and N

Microbial biomass carbon in soils with maize in monoculture or in coexistence with the weeds did not differ from that in the non-cultivated control soil (Fig. 3A), while soils under weed monocultures showed lower MBC (Fig. 3A). Among the cultivated soils, those with maize monoculture, maize vs. *B. pilosa*, and maize vs. *I. grandifolia* showed higher MBC than the ones grown with *B. pilosa* and *I. grandifolia* monocultures.

Generally, the cultivated soils had MBN similar to that of the non-cultivated control soil (Fig. 3B). The exception corresponded to the soils cultivated with maize vs. *I. grandifolia*, that had MBN values higher than the control (Fig. 3B).

Among the cultivated soils, MBN for maize vs. *I. grandifolia* was higher than that for maize vs. *A. viridis* (Fig. 3B).

The different cultivation managements, monocultures or plant coexistence, did not affect the $C:N_{mic}$ ratio (Fig. 3C). Interestingly, soils with weed monocultures had lower $C:N_{mic}$ than the non-cultivated control soil.

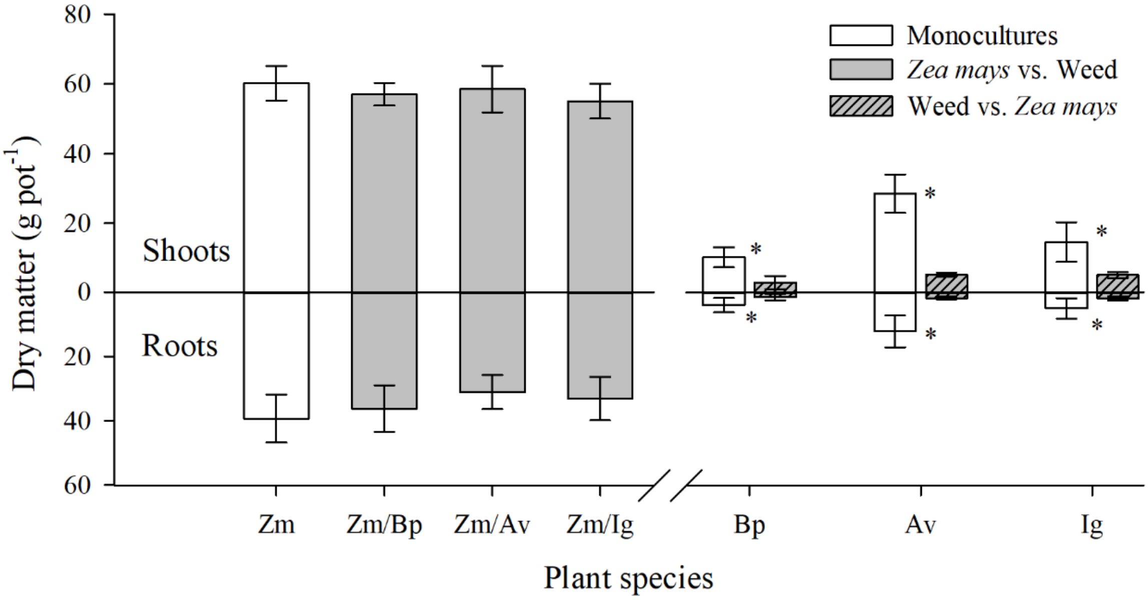

Figure 1. Shoot and root dry matter (±SDM) of *Zea mays* (Zm), *Bidens pilosa* (Bp), *Amaranthus viridis* (Av), and *Ipomoea grandifolia* (Ig) grown for 60 days in monoculture or in interspecific competition. Asterisks indicate that shoot and root dry matter were different between paired bars by t test ($p < 0.05$).

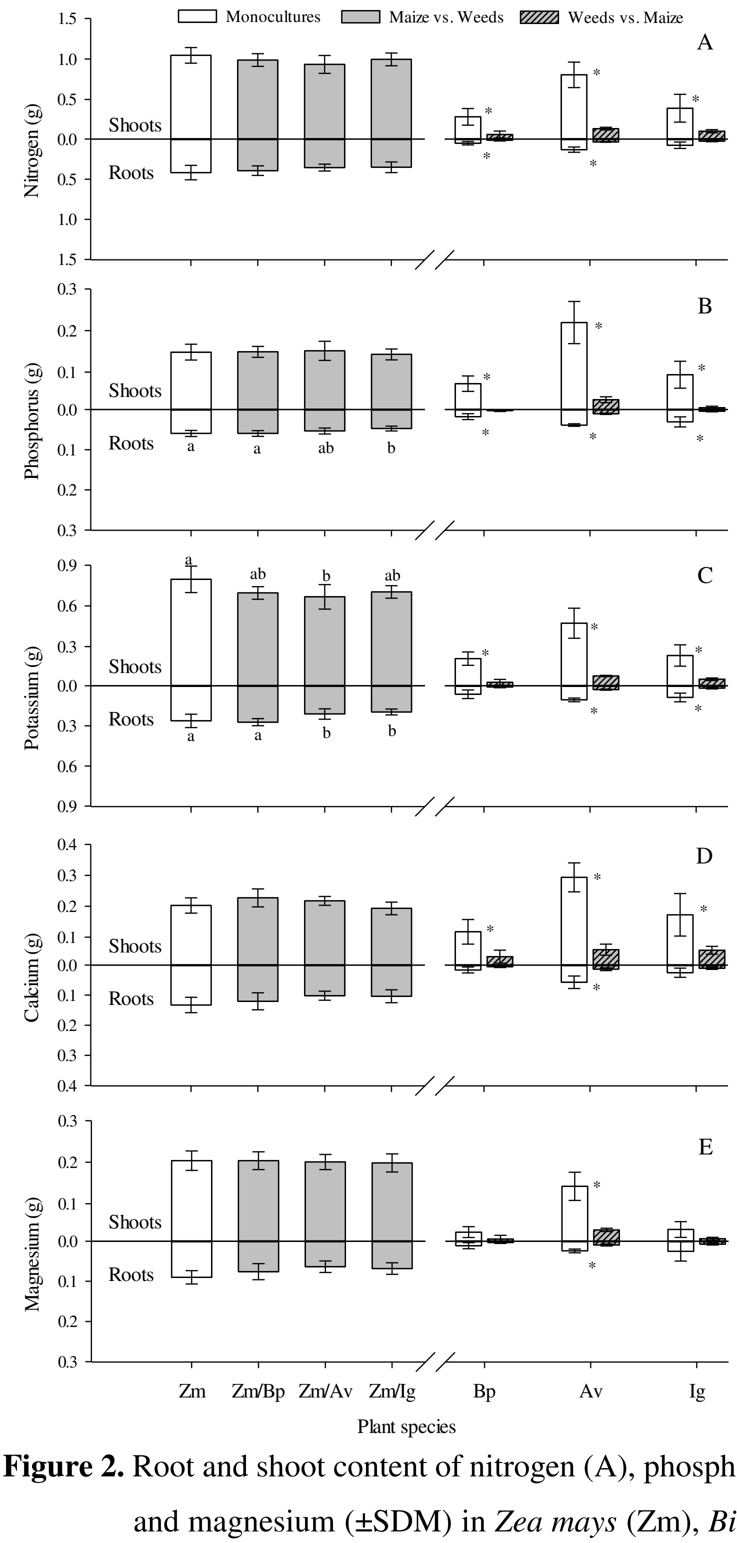

Figure 2. Root and shoot content of nitrogen (A), phosphorus (B), potassium (C), calcium (D), and magnesium (±SDM) in *Zea mays* (Zm), *Bidens pilosa* (Bp), *Amaranthus viridis* (Av), and *Ipomoea grandifolia* (Ig) grown for 60 days in monoculture or in interspecific competitions. Different letters for nutrient content in maize indicate significant differences between means by the Tukey´s test (p < 0.05). Asterisks indicate that shoot and root nutrient content were different between weed monocultures and competition by the t test (p < 0.05).

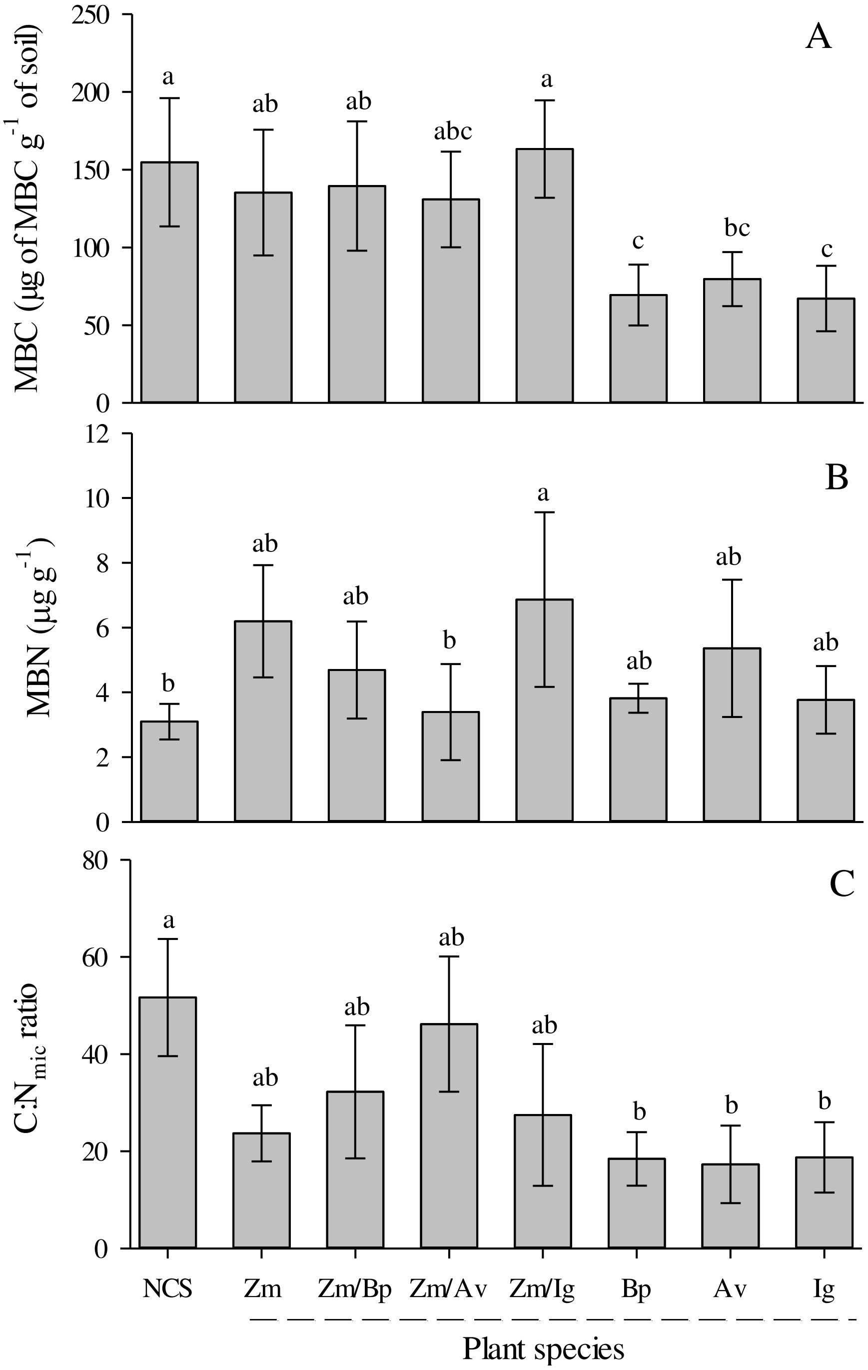

Figure 3. Microbial biomass carbon – MBC (A), microbial biomass nitrogen – MBN (B), and microbial biomass C:N ratio – C:N$_{mic}$ (B) (±SDM) of non-cultivated soil (NCS) and soils cultivated for 60 days with *Zea mays* (Zm), *Bidens pilosa* (Bp), *Amaranthus viridis* (Av), and *Ipomoea grandifolia* (Ig) in monoculture or in interspecific competition. Bars followed by different lowercase letters indicate significant differences between the treatments by the Tukey´s test ($p < 0.05$).

Plant δ^{13}C, CO_2 efflux partitioning, and RPE

Shoot and root dry matter of *I. grandifolia* and *B. pilosa* (C_3 plants) were more depleted in ^{13}C than those of maize and *A. viridis* (C_4 plants) (Tab. S1, Suppl. data). Plants with the same metabolism type showed a similar shoot isotopic composition. The root-respired CO_2 from plants in monoculture showed an isotopic composition similar to that observed in their root tissues. However, the similarity between these values varied according to the plant species. The treatments with C_3 weeds and maize coexistence showed δ^{13}C of root-respired CO_2 values closer to the isotopic composition of maize tissues.

Both root- and SOM-derived CO_2 varied between treatments and cultivation periods (Fig. 4). The CO_2 efflux in both root and SOM was low until 22 DAP. Thereafter, root-derived CO_2 increased in the treatments with *B. pilosa* and maize in monoculture and in those with maize-weed coexistence (Fig. 4A). In contrast, at 50 DAP, *A. viridis* and *I. grandifolia* monocultures reduced root CO_2 efflux. The highest SOM-derived CO_2 effluxes were observed in the soils with *A. viridis* at 36 DAP and in those with maize vs. *B. pilosa* in the 43-50 DAP interval (Fig. 4B).

The RPE varied during the cultivation period and was influenced by the plant species (Fig. 5A). The highest RPE among treatments was observed in soils grown with maize vs. *B. pilosa* from the 43rd day of cultivation onwards. On the other hand, maize vs. *A. viridis* showed negative RPE values after 36 days of cultivation, while *A. viridis* monoculture showed higher RPE values between 36 and 43 DAP.

Soils cultivated with maize in monoculture showed similar RPE to that of the soil with maize vs. *I. grandifolia* throughout the growing period. Comparing the cultivations (maize vs. *I. grandifolia* and *I. grandifolia* alone), the greatest RPE was observed between 23 and 36 DAP in monoculture soils (Fig. 5A). However, the average RPE was higher in soils with maize vs. *B. pilosa* and lower in those soils with *B. pilosa* in monoculture (Fig. 5B).

Carbon and nitrogen contents in particulate and in mineral-associated organic matter

The SOM C and N contents and the SOM C:N ratio varied among treatments (Fig. 6). The POM-C contents were similar among the treatments soil before cultivation, non-cultivated soil, and soils cultivated with maize and *A. viridis* in monoculture (Fig. 6A). *Bidens pilosa* and *I. grandifolia* grown in monoculture or in competition with maize reduced POM-C content compared to the other treatments.

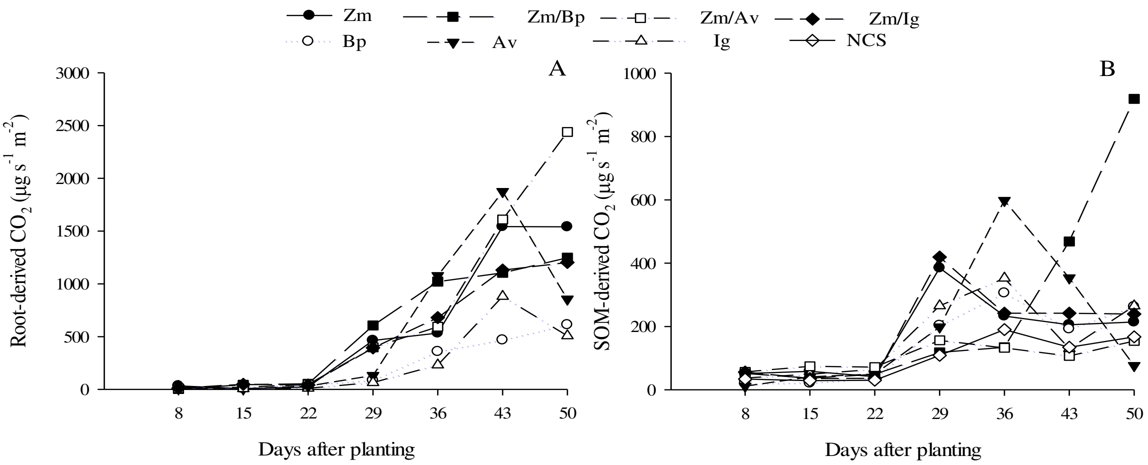

Figure 4. Root- (A) and SOM-derived CO_2 (B) of non-cultivated soil (NCS) and *Zea mays* (Zm), *Bidens pilosa* (Bp), *Amaranthus viridis* (Av) and *Ipomoea grandifolia* (Ig) in monoculture or in interspecific competitions during 50 days of plant cultivation.

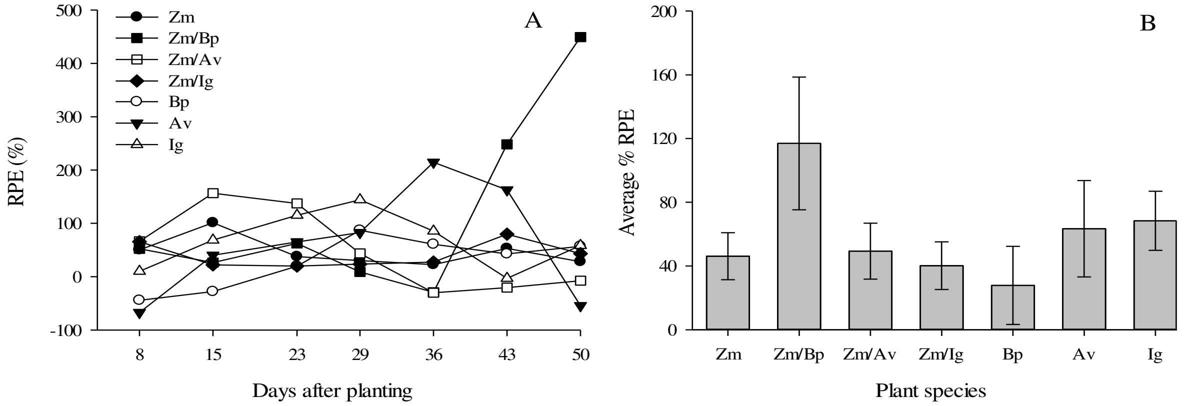

Figure 5. Rhizosphere priming effect – RPE (A) and average % RPE (±SEM) (B) in soils grown with *Zea mays* (Zm), *Bidens pilosa* (Bp), *Amaranthus viridis* (Av), and *Ipomoea grandifolia* (Ig) in monocultures or in interspecific competition during 50 days of plant cultivation.

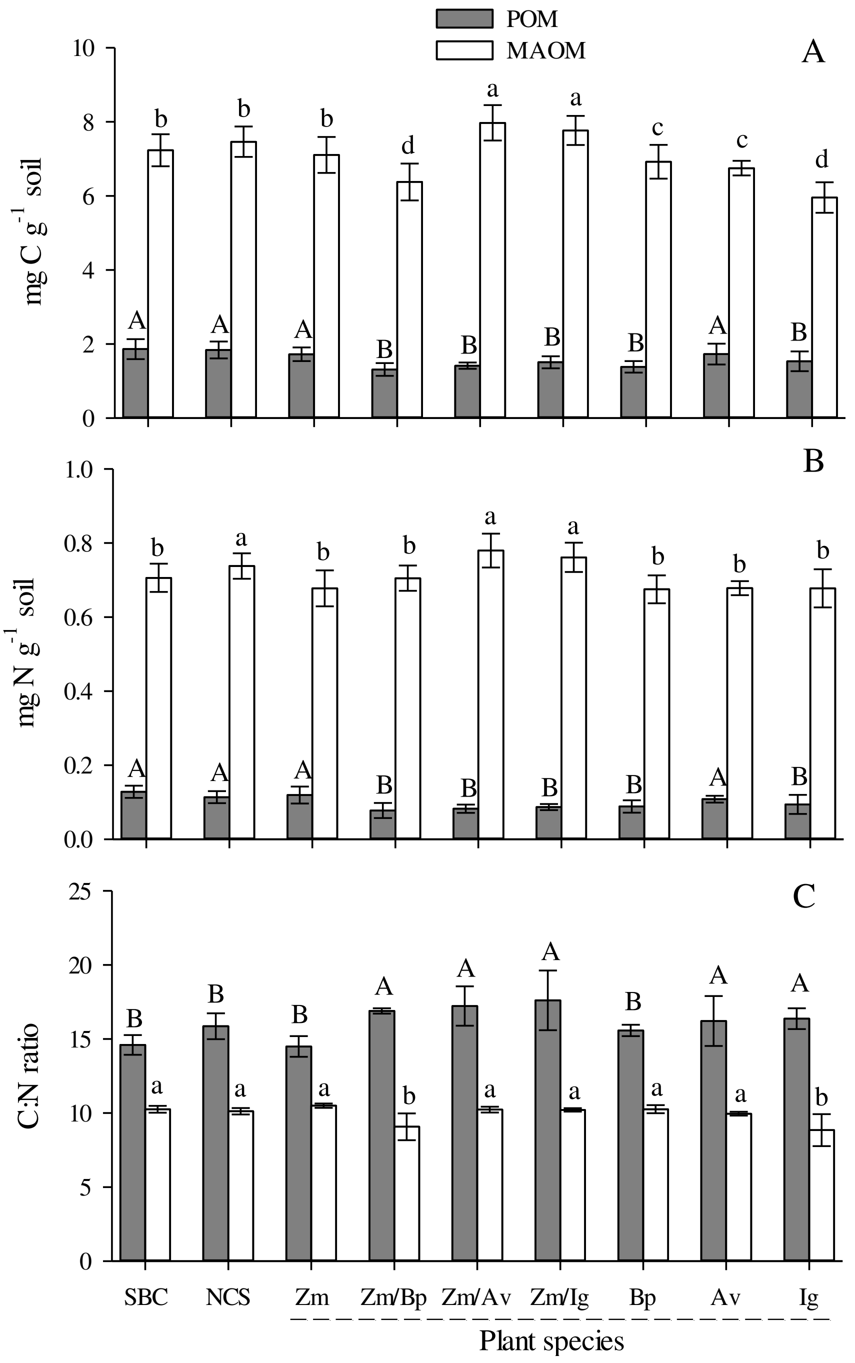

Figure 6. Carbon (A), nitrogen content (B), and carbon:nitrogen ratio (C) (±SDM) of particulate (POM), and mineral-associated organic matter (MAOM) in soils before cultivation (SBC), non-cultivated soil (NCS), and soils cultivated for 60 days with *Zea mays* (Zm), *Bidens pilosa* (Bp), *Amaranthus viridis* (Av), and *Ipomoea grandifolia* (Ig) in monocultures or in interspecific competition. Same color bars followed by different capital or lowercase letters indicate significant differences between the treatments based on Scott-Knott test ($p < 0.05$).

MAOM-C in the soil with maize monoculture was similar to that in the non-cultivated soil (Fig. 6A). The greatest MAOM-C losses were observed for the soils grown with *I. grandifolia* monoculture and with maize vs. *B. pilosa*. *A. viridis* and *I. grandifolia* monocultures also led to MAOM-C reductions when compared to the non-cultivated soil. In contrast, for soils with maize vs. *A. viridis* and maize vs. *I. grandifolia*, higher MAOM-C values were recorded.

The POM-N contents did not differ among soils with maize and *A. viridis* monocultures, soil before cultivation, and non-cultivated soil (Fig. 6B). In contrast, the other cultivation managements showed similar POM-N contents which were lower than that of the non-cultivated soil. The highest MAOM-N contents were observed in the soils with maize vs. *A. viridis* and maize vs. *I. grandifolia* as well as in the non-cultivated soil. Moreover, compared to the soil before cultivation, only soils grown with maize vs. *A. viridis*, maize vs. *I. grandifolia,* and non-cultivated soil had significant increases in MAOM-N.

Soils grown with maize and *B. pilosa* monocultures presented similar POM C:N ratios when compared to the soil before cultivation and to the non-cultivated soil (Fig. 6C). However, soils with *A. viridis* and *I. grandifolia* monocultures and the soils grown with maize and weeds in coexistence showed higher POM C:N ratios than the non-cultivated soils. Among the cultivated soils, those with maize and *B. pilosa* monocultures showed lower C:N ratios than soils from the other treatments. Only *I. grandifolia* monoculture and maize vs. *B. pilosa* reduced the MAOM C:N ratio. The other cultivation managements showed MAOM C:N ratios similar to those of the soil before cultivation and of the non-cultivated soil.

The root-derived C input to MAOM and POM C was affected by the cultivation managements (Fig. 7A and B). Root-derived C from maize, *B. pilosa* and *I. grandifolia* monocultures contributed to MAOM-C, while only maize vs. *A. viridis* allocated C from their roots to MAOM (Fig. 7A). After analyzing root contribution to MAOM-C, we observed that soil with maize monoculture showed the smaller old C content in MAOM (Fig. 7A) followed by maize vs. *A. viridis* and the *I. grandifolia*.

There was no contribution of root-derived C to POM-C in soils cultivated with weeds in monoculture and in that with maize vs. *B. pilosa* (Fig. 7B). Soils grown with maize, *B. pilosa,* and *I. grandifolia* monocultures showed the highest old C content in POM.

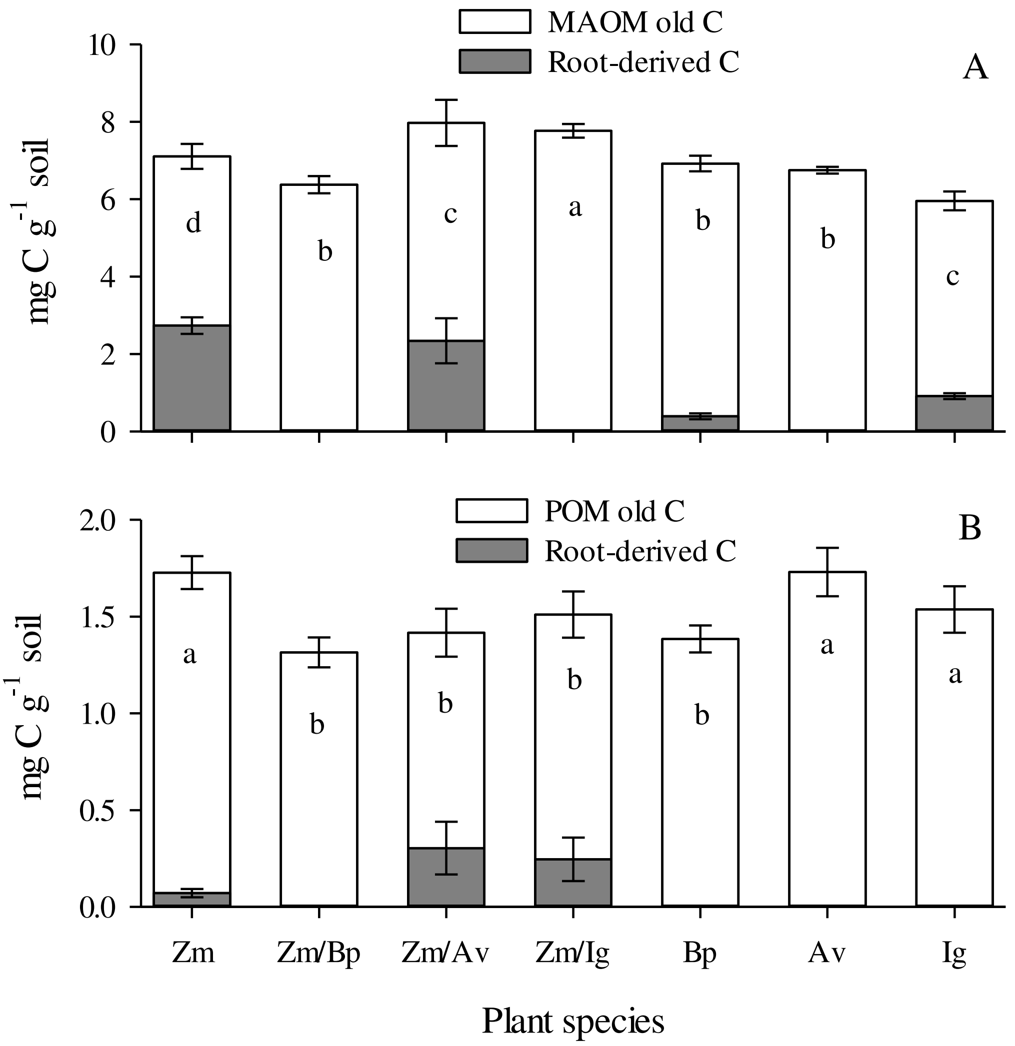

Figure 7. Contribution of root-derived C to particulate (POM), and mineral-associated organic matter (MAOM) (±SEM) in soils before cultivation (SBC), non-cultivated soil (NCS), and soils cultivated for 60 days with *Zea mays* (Zm), *Bidens pilosa* (Bp), *Amaranthus viridis* (Av), and *Ipomoea grandifolia* (Ig) in monoculture or in interspecific competition. For bars with the same color, lowercase letters indicate significant differences between treatments by the Scott-Knott test ($p < 0.05$).

DISCUSSION

Plant interspecific competition

Lower root P and K contents in maize grown with *I. grandifolia* and lower shoot and root K contents in maize in competition with *A. viridis* indicate that these weeds have a greater competitive capacity than *B. pilosa*. On the other hand, the reduction in maize P and K contents did not affect maize growth. Competition with maize reduced the growth and macronutrient content in all weeds. This rather negative effect of competition on weeds is probably due to the faster seed germination and early growth of maize (Andrew et al. 2015), thereby favoring resource uptake by this crop and allowing it to shade out the weeds. In our work, maize and *A. viridis* emergence was observed at the fourth day after planting, while for *B. pilosa* and *I. grandifolia* this occurred on the seventh day. Response of crops to weed interference depends on the weed community, crop type, and environmental conditions for plant development (Zanine and Santos 2004; Andrew et al. 2015). Competition for soil resources often reduces plant performance more effectively than competition for light, particularly for smaller competitors, and also when the competitor is a wild rather than a domesticated species (Kiær et al. 2013).

Plant species and plant growth effects on RPE

The plants showed different isotopic composition in their tissues (Tab. S1, Suppl. data) in comparison to that observed in the soil ($\delta^{13}C = -20.00$). The similar isotopic composition between plant tissues and root-respired CO_2 shows that the method used to capture and quantify the $\delta^{13}C$ of root-respired CO_2 was efficient. Also, it must be considered that there is a consistent depletion in ^{13}C of CO_2 from rhizosphere respiration related to C_3 and C_4 plant root tissues (Zhu and Cheng 2011), which was confirmed in maize, *B. pilosa*, *A. viridis*, and *I. grandifolia*. These differences in the isotopic composition of CO_2-C and plant tissues may increase uncertainty and lead to erroneous conclusions when the $\delta^{13}C$ of the plant tissues are used to calculate SOM-derived and root-derived CO_2 (Zhu and Cheng 2011; Pausch et al. 2013). Thus, root-respired CO_2 was used to calculate the contributions of SOM- and root-derived sources to total soil CO_2.

The increase in root-derived CO_2 efflux during the plant cultivation period (Fig. 4A) can be explained by the growth of their root system. The positive correlation ($R^2 = 0.74$, $N = 35$, $p < 0.05$) between root-derived CO_2 and root dry matter supports this affirmative. Similar results were observed for sunflower, wheat, soybean (Pausch et al. 2013), *Artemisia frigida*, *Linaria dalmatica*, *Bouteloua gracilis*, *Hesperostipa comate,* and *Pascopyrum smithii* (Dijkstra et al.

2010). Furthermore, increased root-derived CO_2 efflux may be associated with larger RPE, as reported for *Lolium perenne*, *Trifolium repens*, and *Poa trivialis* (Shahzad et al. 2015). This suggests that SOM degradation is stimulated by plant root growth. However, the RPE in monocultures or in maize coexisting with weeds varied from positive to negative during the cultivation period (Fig. 5A) and caused different effects on POM and MAOM C contents (Fig. 6A). These differences in the RPE response in terms of root growth, besides being associated with the environmental conditions and the intrinsic characteristics of a given plant species, can be attributed to the fact that this research evaluated the growth of C_3 and C_4 plants and the coexistence between them, while Shahzad et al. (2015) studied only C_3 plants in monocultures.

We observed changes in RPE with plant age and cultivation management (Fig. 5A). Similar results were also observed for sunflower, wheat, and soybean in monoculture and mixed systems, which showed a positive RPE, with an increase from 43 to 136 % in SOM decomposition rate compared to the unplanted soil (Pausch et al. 2013). These changes in RPE magnitude during plant growth may be due to differences in requirements and strategies for environmental resource access and distinct plant–soil–microorganism interactions (Kuzyakov 2002; Pausch et al. 2013; Shahzad et al. 2015). Still, the amount of rhizodeposition C varies widely among plant species, plant age, soil types, and nutrient availabilities (Nguyen 2003; Jones et al. 2009), which contributed to the different SOM mineralization rates between the treatments.

The average RPE was positive for all cultivated soils (Fig. 5A). This suggests an increase in SOM decomposition rates with cultivation. However, there was no reduction in the POM- and MAOM-C contents in soils with maize in monoculture compared to the non-cultivated soils (Fig. 6A). Moreover, the treatments maize vs. *A. viridis* and maize vs. *I. grandifolia* increased the MAOM-C content. In the other cultivated treatments, there was a decrease in POM and MAOM-C contents, except for *A. viridis* monoculture, which showed POM-C similar to that of non-cultivated soils. The absence of correlation between the average RPE and MAOM- and POM-C contents may be due to the input of C from plant roots to these SOM fractions (Fig. 7).

Plant interspecific interactions modify SOM-C content

The negative RPE in the soil cultivated with maize vs. *A. viridis* and the positive RPE in the soil with maize vs. *B. pilosa*, after 36 DAP (Fig. 5A), suggest that the interactions between maize and these weeds were different. The RPE on SOM decomposition ranged from positive to negative between the monocultures and five kinds of grass species mixes, wherein the negative effects prevailed at the end of the cultivation period and were smaller in the mixed cultivations (Dijkstra et al. 2010). Similarly, mixed crop cultivation reduced the RPE compared to monocultures (Pausch et al. 2013). With the coexistence between plant species, the belowground resources, such as water (Verheyen et al. 2008) and N (Hooper and Vitousek 1997), are being complementarily used. This may reduce belowground resource availability and thus limit microbial activity, consequently reducing RPE on SOM decomposition more significantly than in monocultures (Dijkstra et al. 2010). This reduction in RPE may contribute to long-term increases in soil organic C in mixed crops compared to monocultures (Pausch et al. 2013). Despite the short cultivation period, complementarity in resource use by maize vs. *A. viridis* and also by maize vs. *I. grandifolia* may have contributed to the increase in MAOM-C content (Fig. 6A). In contrast, competition between maize and *B. pilosa* led to higher SOM-derived CO_2 efflux and losses in MAOM-C, both of which probably be attributed to changes in the interactions with soil microorganisms.

Competition between maize and *Bidens pilosa* may have stimulated exudate release that induced SOM degradation. The similar MBC values and $C:N_{mic}$ ratios of soils with maize monocultures and soils with maize in coexistence with weeds (Fig. 3) reinforces this hypothesis. Nevertheless, changes in the soil microbial community composition driven by the interactions between plant species cannot be ruled out. Root exudation is the main way by which plants stimulate the RPE on SOM mineralization, followed by root litter, as reported for *Poa trivialis*, *Trifolium repens*, and *Lolium perene* (Shahzad et al. 2015). Exudates induced RPE without increasing soil microbial biomass, whereas root litter increased soil microbial biomass and raised the RPE, mediating saprophytic fungi growth (Shahzad et al. 2015). In this context, positive correlations between root exudates and SOM decomposition were observed in *Pinus ponderosa*, *Picea sitchensis*, and *Tsuga heterophylla*, wherein each milligram of exuded C resulted in the decomposition and release of 6 mg bioavailable C from SOM (Bengtson et al. 2012). In general, exudates that lead to more alkalinity during their decomposition or that are richer in N usually cause greater RPE, as reported for acetic, malic, citric, ferulic and benzoic acids in a Podosol and a Tenosol (Rukshana et al. 2012).

Changes in the microbial community structure caused by plant species composition may explain the retardation of SOC decomposition in soils cultivated with maize vs. *A. viridis* and with maize vs. *I. grandifolia*, as well as the stimulus of SOC decomposition in soils with maize vs. *B. pilosa* compared to the respective monocultures. We assume that there was a predominance of "k-strategists" in soils cultivated with maize vs. *B. pilosa*, which increased the RPE and led to POM and MAOM C losses (Fig. 6A), while maize vs. *A. viridis* and maize vs. *I. grandifolia* favored the growth of "r-strategists" (Fontaine et al. 2003). The predominance of one particular microbial group can determine whether rhizodeposition results in negative or positive RPE, particularly in soils with low nutrient availability (Dijkstra et al. 2010). Each soil microbial group has a different ability to decompose SOM. While rhizodepositions can significantly increase the growth and activity of fast-growing microbes such as bacteria (r-strategists), a part of it may be used by slow-growing microbes, especially fungi, decomposing recalcitrant organic matter (k-strategists), particularly when nutrient availability is low (Fontaine et al. 2003). Plant competition can change the amount and composition of exudates released into the soil (Carvalhais et al. 2013), which changes the soil microbial community. This could be shown for *B. pilosa* vs. *Ipomoea ramosissima*, *Glycine max* vs. *Ageratum conyzoides*, *G. max* vs. *A. conyzoides*, maize vs. *A. conyzoides* and maize vs. *B. pilosa*, which showed a distinct soil microbial community structure in comparison to monoculture conditions for the same plant species (Massenssini 2014). However, there was a greater similarity of the microbial community structure of the soil cultivated with maize vs. *I. ramosissima* with those observed for maize when compared to the *I. ramosissima* (Massenssini 2014). Nevertheless, metagenomic analyses showed bacterial predominance in the microbial community of soils cultivated with maize vs. *I. ramosissima*, while for the competition of maize with *Bidens pilosa*, fungal growth prevailed (Monteiro 2016).

The lower MAOM-C in soils with monocultures of *A. viridis*, *B. pilosa*, and *I. grandifolia* (Fig. 6A) shows that weed-soil microbiota interactions, as well as weed exudation and root litter, stimulate SOM mineralization more significantly than maize. Physiological differences between C_3 and C_4 plants can influence rhizosphere processes (Kuzyakov 2002). Compared to C_3 plants, C_4 plants use nutrients more efficiently and exudes less carbon in the rhizosphere (Kuzyakov 2002). The higher root exudation of C_3 plants, i.e. *B. pilosa* and *I. grandifolia* in monoculture, may have contributed to more significant losses in soil C. On the other hand, increases in SOM mineralization by *A. viridis* (Fig. 6A) compared to that caused by maize, both C_4 plants, may be due to differences in the quality and quantity of rhizodepositions and in the structure of soil microbial communities associated with each species. Maize caused greater losses of old C from MAOM than *A. viridis* (Fig. 7A), but, while the first contributed to the input of new C into SOM, the second did not. Additionally, growing roots may destruct soil aggregates, thereby exposing SOM to microbial attack (Kuzyakov 2002). The dicot *A. viridis* has a tap root system, while the monocot maize has fasciculate roots, each with different growth and branching patterns in the soil. Thus, the distinct types of roots of *A. viridis* and maize may have contributed to their distinct capacity of mineralizing SOM.

Bidens pilosa and *I. grandifolia* grown in monoculture showed the lowest nutrient contents in their tissues, suggesting that the amounts of nutrients left in the soil after cultivation of these plants was higher. Thus, as suggested by the preferential substrate utilization hypothesis (Cheng 1999; Dijkstra et al. 2013), these weeds would have caused negative RPE. However, they increased SOM mineralization. This shows the potential of *B. pilosa* and *I. grandifolia* to stimulate SOM mineralization even in fertilized soils and that factors, other than nutrient availability, may play a significant role in SOM mineralization via RPE.

The increase in MAOM-C in the soil cultivated with maize vs. *A. viridis* can be explained by the stabilization of root-derived C in the soil (Fig. 7A). This was also observed for soils cultivated with barley (Mwafulirwa et al. 2016), with rapid allocation and stabilization of root-derived C in protected soil fractions. The increase in MAOM-C in soils cultivated with maize vs. *I. grandifolia* may be due to POM decomposition and subsequent carbon transfer to MAOM, since no transfer of plant C to this fraction could be detected.

We did not observe the contribution of root-derived C to MAOM in soils cultivated with maize vs. *B. pilosa* and maize vs. *I. grandifolia* (Fig. 7A). It is possible that the coexistence of C_3 and C_4 plants would have maintained MAOM isotopic composition close to that of the non-cultivated soil. This could be due to a probable contribution of both plants to MAOM-C. If this is the case, while the C derived from maize roots increased the soil isotopic composition, the C derived from *B. pilosa* and *I. grandifolia* roots did the reverse. The fact that the monocultures of these plants allocated C to MAOM corroborates this hypothesis (Fig. 7A).

The carbon within the silt-and-clay fraction is more stable compared to that in the coarse one (von Lützow et al. 2007). All cultivations, except maize monoculture, affected the MAOM-C levels in the soil. The *I. grandifolia* monoculture and maize vs. *B. pilosa* were the treatments that better stimulated SOM mineralization, reducing MAOM C:N ratio. Therefore, infestation with these weeds can cause significant physical and chemical soil damage. We therefore suggest the use of suitable weed management strategies not only to ensure crop productivity, but also to improve SOM conservation.

Our results provide evidence that the presence of a given weed can lead to losses of organic C from the soil. It remains to be quantified whether these losses of C will be mitigated by the inputs from the decomposition of plant residues. We still should consider that in some cases, such as maize cultivation for silage, crop residues remaining in the field may be lower. In our study, although competition with weeds did not reduce maize growth, there were C losses in soils grown with maize vs. *B. pilosa*. If this response is confirmed in the field, it may be interesting to control weeds even in periods when their coexistence with crops does not interfere with crop productivity.

CONCLUSIONS

The interspecific interactions between weeds and crops influences RPE, which varies with plant age and species coexistence.

Our data provide clear evidence that distinct weed-crop combinations influences the magnitude of SOM mineralization.

Competition between maize and *B. pilosa* increases SOM degradation; on the other hand, competition between maize and *A. viridis* and between maize and *I. grandifolia* retards SOM loss.

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SUPPLEMENTARY DATA

Table S1. Isotopic composition of plant tissues, particulate organic matter carbon (POM-C), mineral-associated organic matter carbon (MAOM-C), and root-respired CO_2-C.

	Treatments	Species	$\delta^{13}C$ (‰)					
			POM*	MAOM*	Shoot*	Root*		Root-respired CO_2**
Monoculture	SBC		-25.29	-23.71				
	NCS		-25.78	-22.86				
	Zm	*Z. mays*	-25.41	-20.26	-11.10	-12.47		-9.85
	Bp	*B. pilosa*	-24.84	-23.04	-29.70	-28.63		-26.85
	Av	*A. viridis*	-26.03	-22.21	-11.93	-14.27		-12.62
	Ig	*I. grandifolia*	-24.03	-22.90	-28.63	-27.06		-26.85
Coexistence	Zm/Bp	*Z. mays*	-25.25	-23.65	-11.24	-11.80	-12.24	-13.94
		B. pilosa			-29.57	-24.31		
	Zm/Av	*Z. mays*	-26.12	-20.33	-10.98	-11.55	-11.57	-10.78
		A. viridis			-12.48	-12.00		
	Zm/Ig	*Z. mays*	-25.25	-23.99	-11.18	-12.58	-13.19	-10.62
		I. grandifolia			-27.72	-24.61		

* Measured by isotope ratio mass spectrometry (ANCA-GSL, Sercon, Crewe, UK); ** measured by spectroscopy using cavity ring-down spectrometer analyzer (CRDS, G2131-i, Picarro, Sunnyvale, CA).

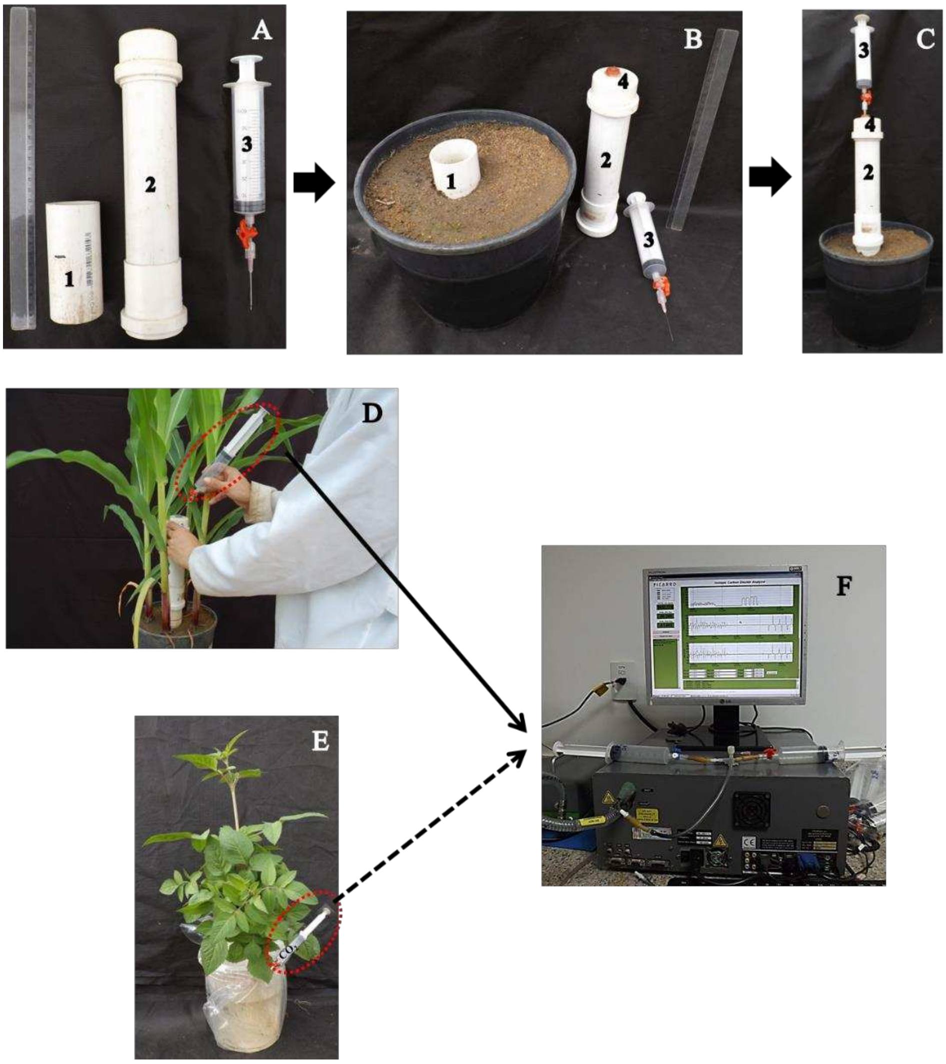

Figure S1. Sequence of processes to sample CO_2 from the soil-plant system and root-respired CO_2. PVC bases (10.0-cm height x 5.0-cm diameter) were fixed in the center of each pot (**1A e 1B**). The CO_2 efflux measurements were carried out by coupling PVC chambers, 24.0-cm height x 5.2-cm diameter, (**2A, 2B e 2C**) on previously installed fixed PVC bases (**C**)**.** Air sampling was performed using 60-mL syringes (**3A, 3B e 3C**) introduced into the septum (**4B e 4C**)**.** See the example where the CO_2 of the soil cultivated with maize was taken (**D**). Plants with roots washed in water were placed in plastic pots with deionized water; the roots remained submerged (**E**). The pots were enveloped with plastic bags that were tied to the plant stems, thus keeping the roots in a closed environment. (**E**). The CO_2 samples were captured using 60-mL syringes after tying the plastic bags to the stems. The gas samples were used to quantify the natural ^{13}C abundance of root-respired CO_2. The CO_2 concentrations and $\delta^{13}C$ of the gaseous samples stored in the syringes were quantified by spectroscopy using the CRDS analyzer (**F**).

CAPÍTULO 4

Interspecific competition changes nutrient stoichiometry between weeds and crops

INTERSPECIFIC COMPETITION CHANGES NUTRIENT STOICHIOMETRY BETWEEN WEEDS AND CROPS

ABSTRACT

The elemental stoichiometry (nutrient:nutrient and carbon:nutrient ratios) of plant tissues has been widely evaluated in ecological studies and is associated with the adaptive and competitive success of a plant species in the ecosystem. So far, no study has evaluated if and how crop-weed competition influences elemental stoichiometry of competing populations, although such information is important to understand weed infestation dynamics and to improve weed management techniques in agroecosystems. The objective of this study was to analyze weed-crop elemental stoichiometry during interspecific competition between weeds and crops in greenhouse experiments. For this, the plant species *Amaranthus viridis*, *Bidens pilosa*, and *Ipomoea grandifolia*, considered as weeds, and *Zea mays* were grown under seven treatments: maize and weed monocultures, maize in competition with weeds. The experiment was conducted in a randomized block design with five replications. Competition between plants practically did not influence growth and nutrient content of maize, but reduced weed growth and nutrient uptake. Maize showed slight changes in elemental stoichiometry. In contrast, *B. pilosa* and *I. grandifolia* were very sensitive to competition and showed significant increases in C:N, C:P, C:K, N:P, and N:K ratios and decreases in the C:Mg, N:Ca, P:Ca, K:Ca, N:Mg, P:Mg and K:Mg ratios when grown in coexistence with maize. *A. viridis* showed low stoichiometric flexibility under the same competitive pressure as that faced by *B. pilosa* and *I. grandifolia*. The interspecific competition led to increases only in the C:P ratio of *A. viridis* shoots, while the other C:nutrient and nutrient:nutrient ratios either decreased or remained unchanged. Therefore, interspecific competition changes the elemental stoichiometry of plants, and the magnitude of this change seems to be dependent on the plant species involved. Interspecific competition decreases plant biomass quality (higher C:N, C:P, C:K and N:P ratio), mainly for *B. pilosa* and *I. grandifolia*. This may subsequently reduce plant residue decomposition rate and lead to nutrient immobilization in the soil.

Keywords: *Amaranthus*, *Bidens*, corn, *Ipomoea*, invasive plant, interspecific competition.

INTRODUCTION

Plants assimilate carbon and take up nutrients in adequate amounts to maintain their biological integrity. However, photosynthesis and nutrient uptake are not perfectly coupled, and thus, C:nutrient ratios of the plant biomass can change within the same species (Ågren 2008; Zheng 2009). The stoichiometries between carbon and nutrients in plants are flexible, as observed in phytoplankton communities (Striebel et al. 2009) and in vascular plants (Elser et al. 2010; Yu et al. 2010; Ye et al. 2014). The degree of stoichiometric flexibility changes with the environmental condition and stress situations, such as competition, probably as an adjustment between flexibility and homeostasis (Yu et al. 2010). The magnitude of the change in nutrient stoichiometry in plants depends on a set of conditions to which they are exposed and on the species plasticity in taking up and using nutrients (Güsewell 2004; Sardans et al. 2016a).

Nutrient concentrations and elemental stoichiometry, mainly N:P, C:N, C:P and C:K ratios, of plant biomass have been evaluated in ecological studies because they reflect a plant's capacity to adapt to changes in edaphoclimatic conditions and species composition (Güsewell 2004; Elser et al. 2010; Sardans et al. 2016a). In addition, changes in stoichiometric ratios influence ecological relations, including herbivory and the decomposition of plant residues by decomposers (Hall 2009; Hessen et al. 2013). Elemental stoichiometry of plant tissues can successfully explain many phenomena in ecosystems, because of this, it is the most investigated factor in ecological interactions (Ye et al. 2014).

In agroecosystems, crop-weed competition decreases the economic and productive yield of crops (Kiær et al. 2013). Each plant species has its own mechanisms of adaptation and survival that provide greater capacity to compete or to interfere in the development of neighboring plants (Gioria and Osborne 2014). Changes in nutrient stoichiometry have often been associated with the adaptive and competitive success of weeds in ecosystems (Sardans and Penuelas 2012; Sardans et al. 2016b).

Most of the studies that have evaluated the influence of competition between crops and weeds focused on growth, nutrient accumulation, competitive capacity, dry matter allocation, productivity, etc. (Kiær et al. 2013; Faria et al. 2014; Gioria and Osborne 2014; Poffenbarger et al. 2015). However, whether or not weed-crop competition can influence elemental stoichiometry remains poorly exploited. Information on nutrient concentration and biomass stoichiometric composition of weeds are required for understanding the contribution of such plants to soil nutrient cycling during the fallow period (Sakonnakhon et al. 2006; Harre et al. 2014).

The study of plant tissue stoichiometry may help in the elaboration of management strategies for the production of agricultural crops (Greenwood et al. 2008; Ye et al. 2014). Evaluating the elemental stoichiometry allows agronomists to know the optimal concentrations of nutrients in the plant and, thus, contributes to the efficient use of fertilizers (Sadras 2006; Greenwood et al. 2008). For example, the leaves and shoot C:P ratios of crops, such as corn (Bélanger et al. 2011, Ziadi et al. 2007), wheat (Bélanger et al. 2011), rice (Bélanger et al. 2012) and the grass *Phleum pratense* L. (Bélanger et al. 2017), have been studied with the aim of establishing an indicator of P deficiency during plant growth.

Crops and weeds play an important role in the C cycle, both in C sequestration via photosynthesis and C release from plant residue decomposition, root respiration and/or rhizosphere priming effect (Sardans and Penuelas 2012; Sardans et al. 2012; Kumar et al. 2016). Agricultural management practices influence plant development, affecting C sequestration and emission as observed in areas planted with rice (Ye et al. 2014) and corn (Kumar et al. 2016). However, whether and how the interspecific competition can influence the elemental stoichiometry of crops and weeds remains unknown.

Though at least 16 elements are necessary for plant development, most researches on plant nutrition and stoichiometry studied only N and P, since both are considered the most limiting nutrients for crop growth and production (Weih et al. 2016) and the development of ecosystems (Sardans et al. 2016a, b). Therefore, studies that take into account other nutrients, including K, Ca and Mg, are needed (Weih et al. 2016; Yan et al. 2016). We are not aware of studies investigating the effects of competition between crops and weeds on elemental stoichiometry, including several nutrients in addition to N and P. The objective of this study was to analyze weed-crop elemental stoichiometry during interspecific competition between weeds and crops in greenhouse experiments.

MATERIAL AND METHODS

Soil sampling and conditioning

The experiment was conducted in a greenhouse at the Universidade Federal de Viçosa, in Viçosa, Minas Gerais State, Brazil. The soil was sampled from a plough horizon (top 20 cm) of a Xanthic Ferralsol (*Latossolo Amarelo*) from a farm in Guarapari, Espírito Santo State, Brazil. The results of the chemical soil analysis are as follows: pH 5.77, 8.8 g kg^{-1} organic carbon content, 6.8 mg dm^{-3} P Mehlich-1, 67 mg dm^{-3} K, 3.17, 0.97, 0.10, 2.00, and 4.41 cmolc dm^{-3} Ca, Mg, Al, H + Al, and effective CEC, respectively, 68.3 % base saturation. Physical analysis showed 22% clay, 4% silt, and 74% sand. Pots (18 cm height, 22 cm diameter) were filled with 7.1 kg of air-dried and sieved (< 4 mm) soil. Prior to planting, fertilization with simple superphosphate was performed by mixing 0.21 g dm^{-3} of P_2O_5 into soil.

Experimental set-up

The experiments consisted of *Amaranthus viridis* L, *Bidens pilosa* L., *Ipomoea grandifolia* (Dammer) O'Donell, and *Zea mays* L. (maize) monocultures and maize vs. *A. viridis*, maize vs. *B. pilosa*, and maize vs. *I. grandifolia*. All treatments were performed under greenhouse conditions. We used a complete randomized block design with five replicates.

Seed planting and cultivation

For all treatments using plant coexistence, we used four maize and seven weed plants of each species per pot. For maize and weed monocultures, we used four and seven individual plants per pot, respectively. To obtain one individual plant, eight seeds of maize and 20 seeds of each weed species were planted and thinned to one plant after seedling emergence. Soil moisture content was measured gravimetrically and adjusted daily to 80% of the field capacity.

Ammonium nitrate and potassium chloride solutions containing 50 mg dm^{-3} of N and K, respectively, were applied at 12 and 32 days after planting the seeds (DAP). At 19 DAP, we applied 0.2 g L^{-1} of acetamiprid (Mospilan®) to control whiteflies (*Bemisia tabaci* Gennadius, 1889).

Plant dry matter determination

All plants were removed from the plastic pots at 60 days after planting (DAP) and separated into roots and shoots. The samples were placed in paper bags and oven-dried with forced air circulation at 65°C until constant weight to determine dry matter (g pot^{-1}). Subsequently, root and shoot tissues were ground in an analytical mill (IKA® A11 basic grinder) for quantification of plant carbon and nutrient concentrations.

Competition Balance Index (Cb)

The total dry matter (root and shoot), in grams per pot, data were used to calculate a Competition Balance Index (Cb) between the plant species, according to equation 1 (Wilson 1988).

$$Cb = \ln[(W_{AB}/W_{BA})/(W_{AA}/W_{BB})] \quad (1)$$

W_{AB} = dry weight of plant species ‘A’ grown together with plant species ‘B’; W_{BA} = dry weight of plant species ‘B’ grown together with plant species ‘A’; W_{AA} = dry weight of plant species ‘A’ grown in monoculture and W_{BB} = dry weight of plant species ‘B’ grown in monoculture.

Cb values > 0 indicate a higher competitive ability of plant species ‘A’ relative to plant species ‘B’; Cb values = 0 indicate an equal competitive ability between the plant species, and Cb values < 0, indicates a higher competitive ability of plant species ‘B’ relative to plant species ‘A’ (Wilson 1988).

Plant tissue analyses

The concentrations of phosphorus, potassium, calcium, and magnesium were measured after digestion of a subsample of ground tissue with a mixture of nitric and perchloric acids; nitrogen was determined after sulfuric digestion. Phosphorus concentration was determined by molecular absorption spectrophotometry, K by flame emission spectrophotometry, Ca and Mg by atomic absorption spectrophotometry (Jones Junior et al. 1991), and N by the Kjeldahl method (Kjeldahl 1883).

Root and shoot C concentrations were determined by isotope ratio mass spectrometry (ANCA-GSL, Sercon, Crewe, UK).

Nutrient stoichiometry

Total nutrient and carbon contents (g plant^{-1}) of shoots and roots were calculated by multiplying the N, P, K, Ca, and Mg concentrations (g nutrient or carbon per g of dry matter) by root and shoot dry matter, respectively. The C:nutrient and nutrient:nutrient ratios (C:N, C:P, C:K, C:Ca, C:Mg and N:P, N:K, N:Ca, N:Mg, P:K, P:Ca, P:Mg, K:Ca, K:Mg, Ca:Mg) were calculated for roots and shoots. The ratios between nutrients can be expressed as mass ratios or as atomic ratios. The use of molar proportions is more common in physiological research because it reflects the real stoichiometric ratios (Güsewell 2004). Nevertheless, most of the papers in the literature report mass relations to facilitate comparisons. The data of our research were expressed as mass relations between the elements (g g^{-1}).

Nutrient utilization efficiency (NUE)

The macronutrient utilization efficiency for N, P, K, Ca, and Mg was calculated using the following equation: NUE= (total dry matter)^2 / (total nutrient content in the plant) (Siddiqi and Glass 1981).

Statistical analysis

Maize dry matter production, N, P, K, Ca, and Mg contents, nutrient stoichiometry (N:P, N:K, N:Ca, N:Mg, P:K, P:Ca, P:Mg, K:Ca, P:Mg,and Ca:Mg ratios), C:nutrient ratios (C:N, C:P, C:K, C:Ca, and C:Mg) in maize tissue and NUE were subjected to variance analyses and the means were compared by the Tukey´s test at 5% probability. The competition effects of maize on weed dry matter production, nutrient content, nutrient stoichiometry, C:nutrient ratio and NUE were compared by t-test at 5% probability. The Cb values were submitted to statistical analyses to test the null hypothesis Cb=0 (Wilson 1988) by One-Sample t-test at 5% probability.

RESULTS

Plant dry matter production and nutrient content

Competition with weeds did not influence shoot and root dry matter production of maize (Fig. 1). On the other hand, coexistence with maize reduced shoot and root growth of the weeds tested.

Shoot and root N, Ca, and Mg contents in maize were not influenced by competition with weeds (Figs. 2A, 2D, and 2E). In contrast, despite the similar shoot P content in maize grown in monoculture or in coexistence with weeds, competition with *I. grandifolia* reduced root P content in this crop (Fig. 2B). The lowest maize root K content was observed in maize vs. *A. viridis* and maize vs. *I. grandifolia*. However, shoot K content in maize was lower only when grown in competition with *A. viridis* compared to the monoculture conditions (Fig. 2C).

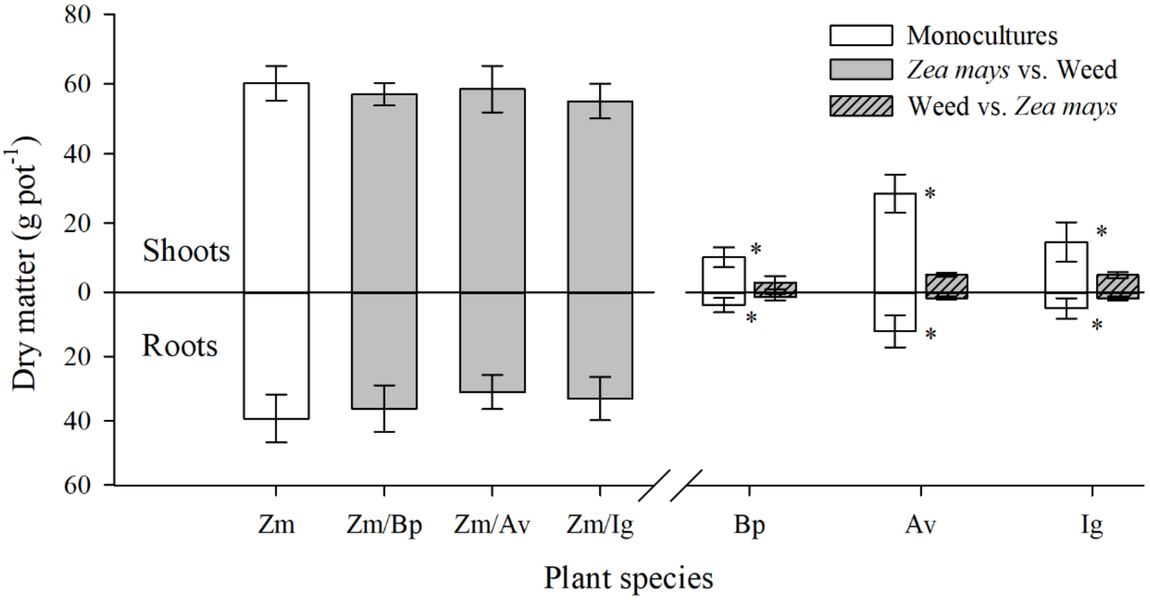

Figure 1. Shoot and root dry matter (±SDM) of *Zea mays* (Zm), *Bidens pilosa* (Bp), *Amaranthus viridis* (Av), and *Ipomoea grandifolia* (Ig) grown for 60 days in monoculture or in interspecific competition. Asterisks indicate that shoot and root dry matter were different between paired bars by the t test ($p < 0.05$).

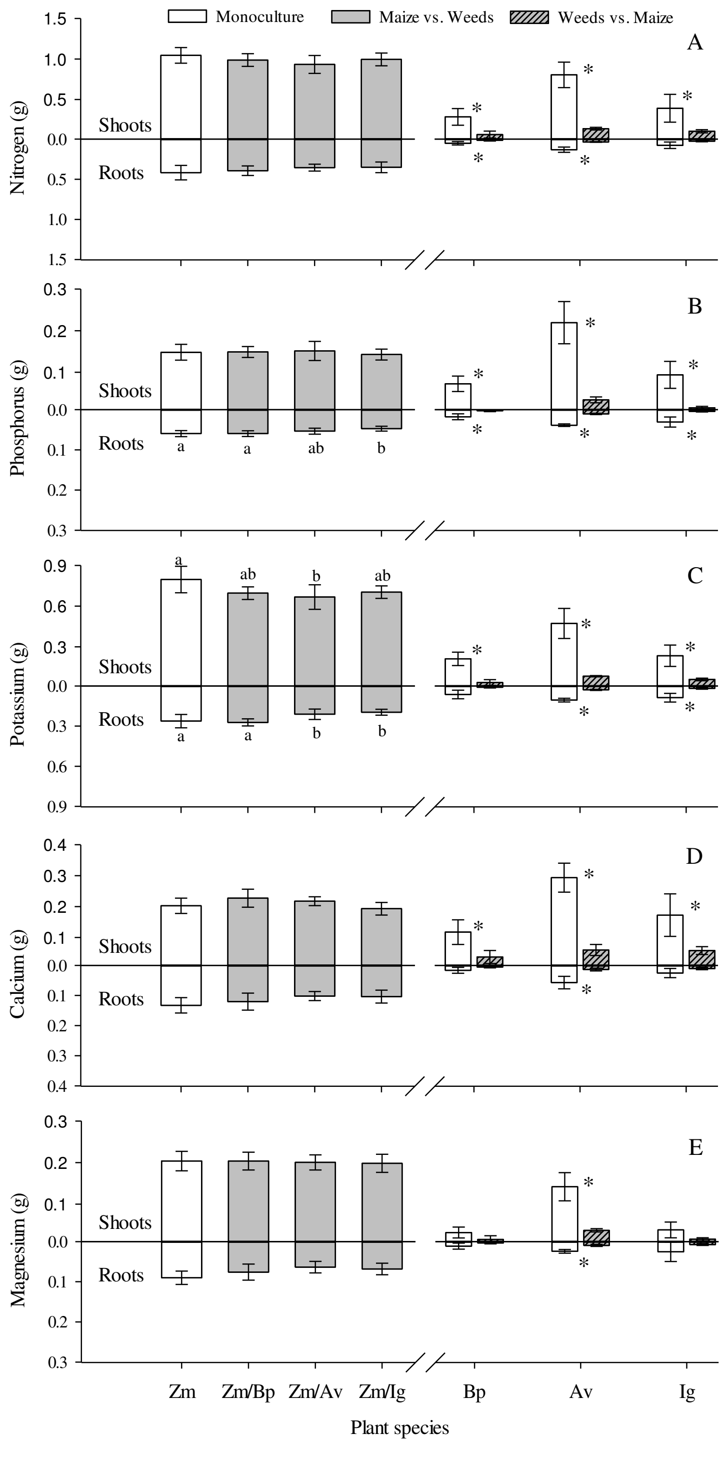

Figure 2. Root and shoot content of nitrogen (A), phosphorus (B), potassium (C), calcium (D), and magnesium (±SDM) for *Zea mays* (Zm), *Bidens pilosa* (Bp), *Amaranthus viridis* (Av), and *Ipomoea grandifolia* (Ig) grown for 60 days in monoculture or in interspecific competition. Different letters within maize nutrient content indicate significant differences between means based on the Tukey´s test ($p < 0.05$). Asterisks indicate that shoot and root nutrient content were different between weed monocultures and competition by t test ($p < 0.05$).

Competition with maize reduced shoot N, P, K, and Ca content in *B. pilosa* and *I. grandifolia*, but did not influence Mg content in these weeds (Fig. 2). In addition, lower root N and P contents were observed for *B. pilosa* grown in competition with maize, but root P, Ca, and Mg content in this weed was not affected by the treatments (Fig. 2). Competition with maize reduced root P and K contents in *I. grandifolia*, but did not influence root N, Ca, and Mg contents. In contrast, competition with maize reduced root and shoot N, P, K, Ca, and Mg contents in *A. viridis* (Fig. 2). Nevertheless, among the weeds, *A. viridis* grown in monoculture was the plant with the highest nutrient contents in its tissues, particularly P and Ca.

The Cb values showed that maize had a higher competitive ability than *B. pilosa*, *A. viridis* and *I. grandifolia* (Tab. 1).

Carbon:nutrient stoichiometries

Competition with *A. viridis* increased maize shoot C:N, while the presence of *B. pilosa* and *I. grandifolia* did not influence this stoichiometry (Fig. 3). Maize shoot C:P, C:Ca and C:Mg were similar between the monoculture and the coexistence treatments. The competition with weeds increased C:K in maize shoots. In contrast, C:N, C:P, C:K, C:Ca and C:Mg of maize roots was not influenced by competition with weeds.

The weed-crop competition changed the C:N, C:P and C:K of *B. pilosa* and *I. grandifolia*, and C:P and C:Mg of *A. viridis* (Fig. 3).

Bidens pilosa increased root C:N, C:P, and C:K and shoot C:P and C:K, but reduced shoot C:Mg when grown in coexistence with maize (Fig. 3). *I. grandifolia* increased the shoot and root C:N, C:P, and C:K, but decreased the shoot C:Mg in coexistence with maize. On the other hand, among the weeds, *A. viridis* was the one that showed less stoichiometric flexibility. This species changed only the shoot C:P and root and shoot C:Mg when grown in competition with maize (Fig. 3).

Table 1. Competitive balance (Cb) for *Zea mays* grown for 60 days in monoculture or in interspecific competitions with *Bidens pilosa, Amaranthus viridis*, and *Ipomoea grandifolia*

Competition treatments	Cb
Zea mays vs. *Bidens pilosa*	1.03 ± 0.63 *
Zea mays vs. *Amaranthus viridis*	1.54 ± 0.15 **
Zea mays vs. *Ipomoea granfifolia*	1.12 ± 0.50 *

* 5% significance; ** 1% significance by the t test. Positive significant values indicate that the first species have higher competitive ability, while negative significant values indicate that the second species is more competitive. No significant values indicate a similar competitive ability between species.

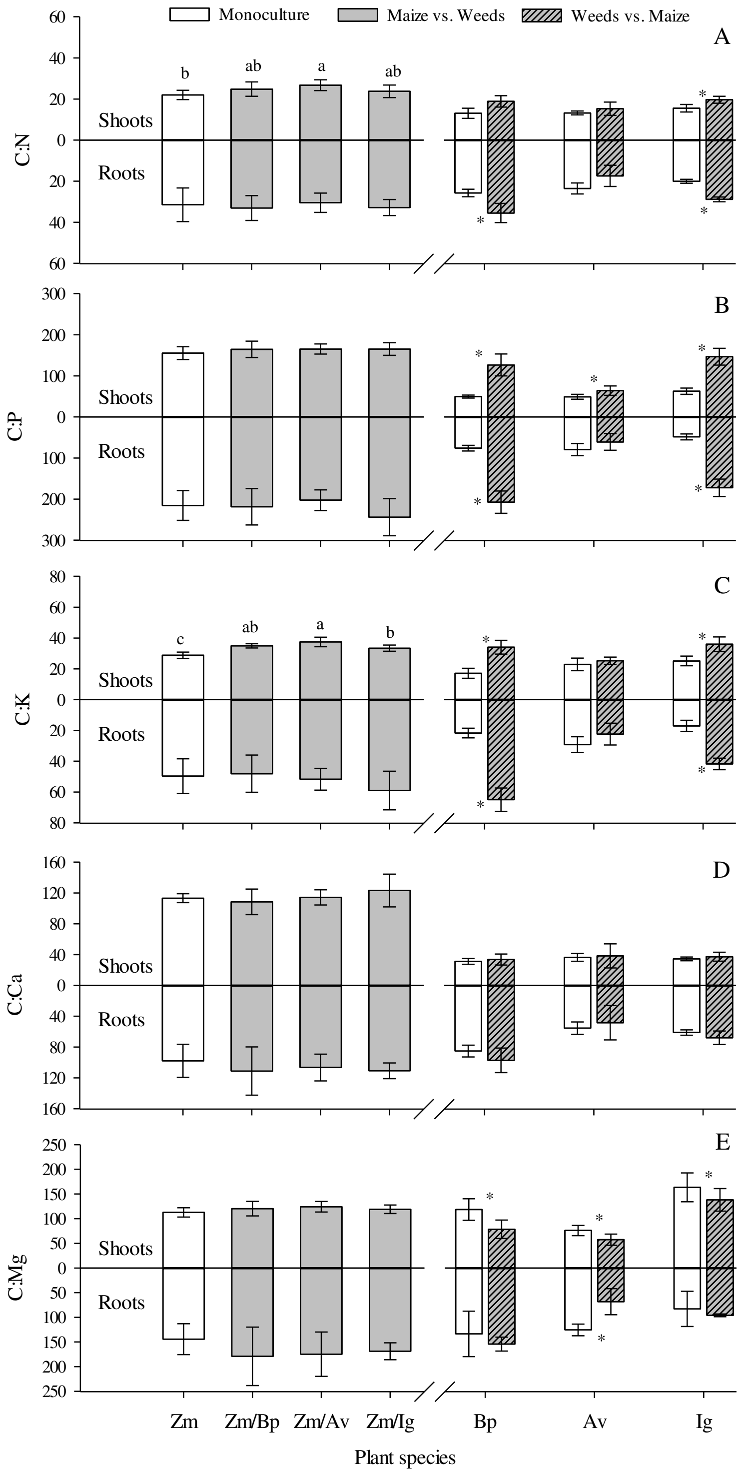

Figure 3. Root and shoot carbon-nutrient stoichiometry, C:N (A), C:P (B), C:K (C), C:Ca (D) and C:Mg (±SDM) for *Zea mays* (Zm), *Bidens pilosa* (Bp), *Amaranthus viridis* (Av), and *Ipomoea grandifolia* (Ig) grown for 60 days in monoculture or in interspecific competition. Different letters within maize nutrient stoichiometry indicate significant differences between means by the Tukey´s test (p < 0.05). Asterisks indicate that shoot and root nutrient contents were different between weed monocultures and competition treatments by the t test (p < 0.05).

Nutrient stoichiometry

Maize showed lower nutrient stoichiometric flexibility in its tissues than weeds (Fig. 4). The interspecific competition influenced only N:Ca and P:K. The N:Ca was higher for maize grown with *I. grandifolia* than for that with *B. pilosa* or *A. viridis* (Fig. 4). When grown in competition with *A. viridis*, we observed an increase in the P:K of maize compared to that obtained for maize monoculture or for maize vs. *I. grandifolia*.

The weeds *B. pilosa* and *I. grandifolia* showed greater changes in the stoichiometric ratios of macronutrients than those of *A. viridis*. The coexistence with maize increased N:P and N:K of *B. pilosa* and *I. grandifolia* (Fig. 4) and decreased the N:Ca, N:Mg, P:Ca, P:Mg, K:Ca and K:Mg of these plants.

Nutrient utilization efficiency

Competition with weeds did not influence maize NUE (Fig. 5). The opposite was observed for the weed species. *Amaranthus viridis* was the most sensitive to interspecific competition (Fig. 6). Its nutrient efficiency utilization for N, P, K, Ca and Mg was strongly reduced in the presence of maize. *Bidens pilosa* and *I. grandifolia* in competition showed lower utilization efficiencies for N, Ca and Mg than their respective monocultures. For these plants, the utilization efficiencies for P and K were similar in all competition treatments.

DISCUSSION

The effects of interspecific competition on the elemental stoichiometry depends on the plant species. The smallest stoichiometric flexibility was observed for maize, while *Bidens pilosa* and *I. grandifolia* were shown to be the most flexible. These weeds increased their C:N:P:K, N:P and N:K ratios, but decreased the C:Mg, N:Ca, P:Ca, K:Ca, N:Mg, P:Mg, and K:Mg ratios in response to competition with maize. *A. viridis* showed low stoichiometric flexibility under the same competitive pressure as that faced by *B. pilosa* and *I. grandifolia*.

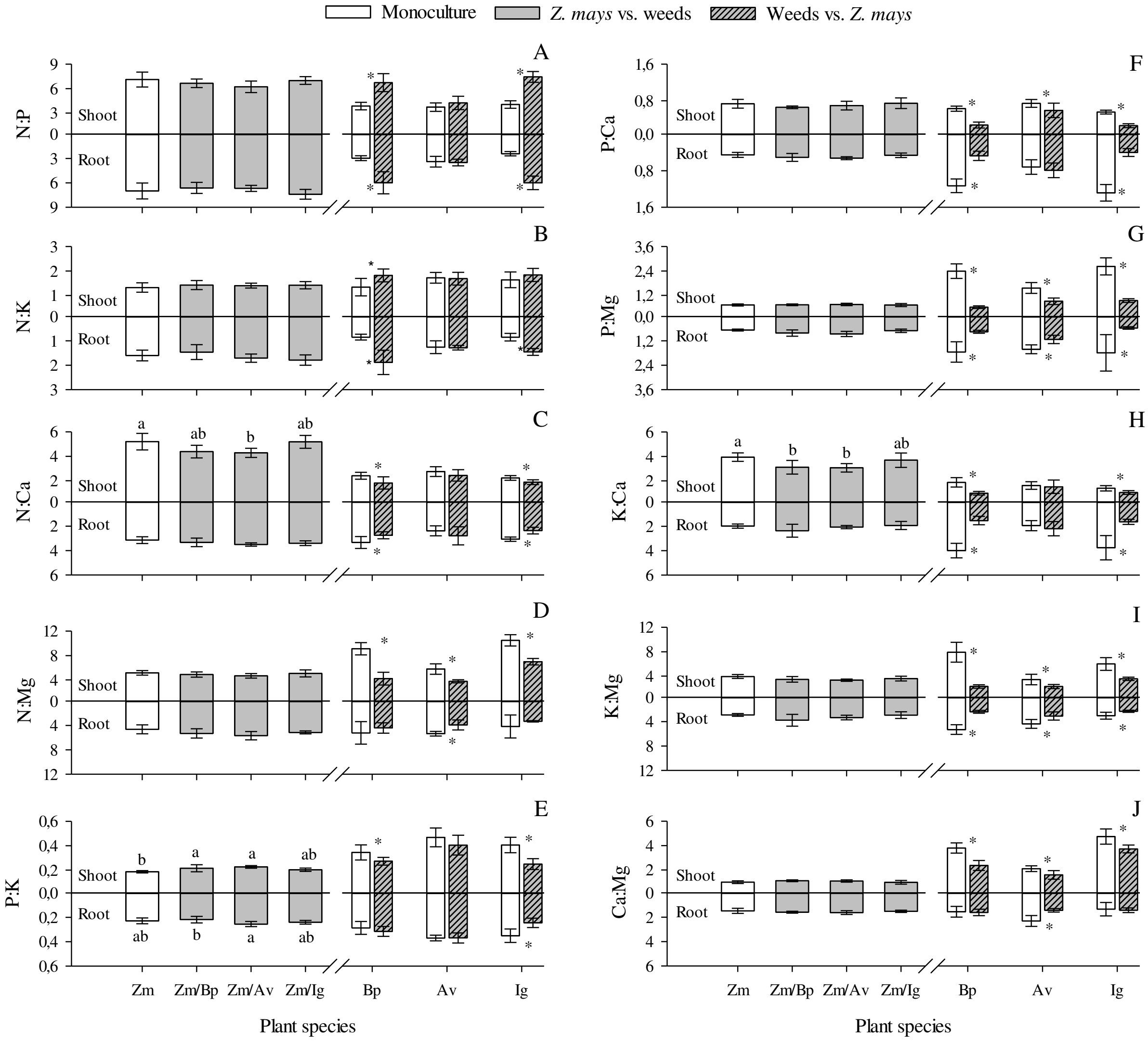

Figure 4. Root and shoot nutrient stoichiometries, N:P (A), N:K (B), N:Ca (C), N:Mg (D), P:K (E), P:Ca (F), P:Mg (G), K:Ca (H), K:Mg (I), and Ca:Mg ratios (J) (±SDM) for *Zea mays* (Zm), *Bidens pilosa* (Bp), *Amaranthus viridis* (Av), and *Ipomoea grandifolia* (Ig) grown for 60 days in monoculture or in interspecific competition. Different letters within maize nutrient stoichiometry indicate significant differences between means based on the Tukey´s test ($p < 0.05$). Asterisks indicate that shoot and root nutrient content were different between weed monoculture and competition by the t test ($p < 0.05$).

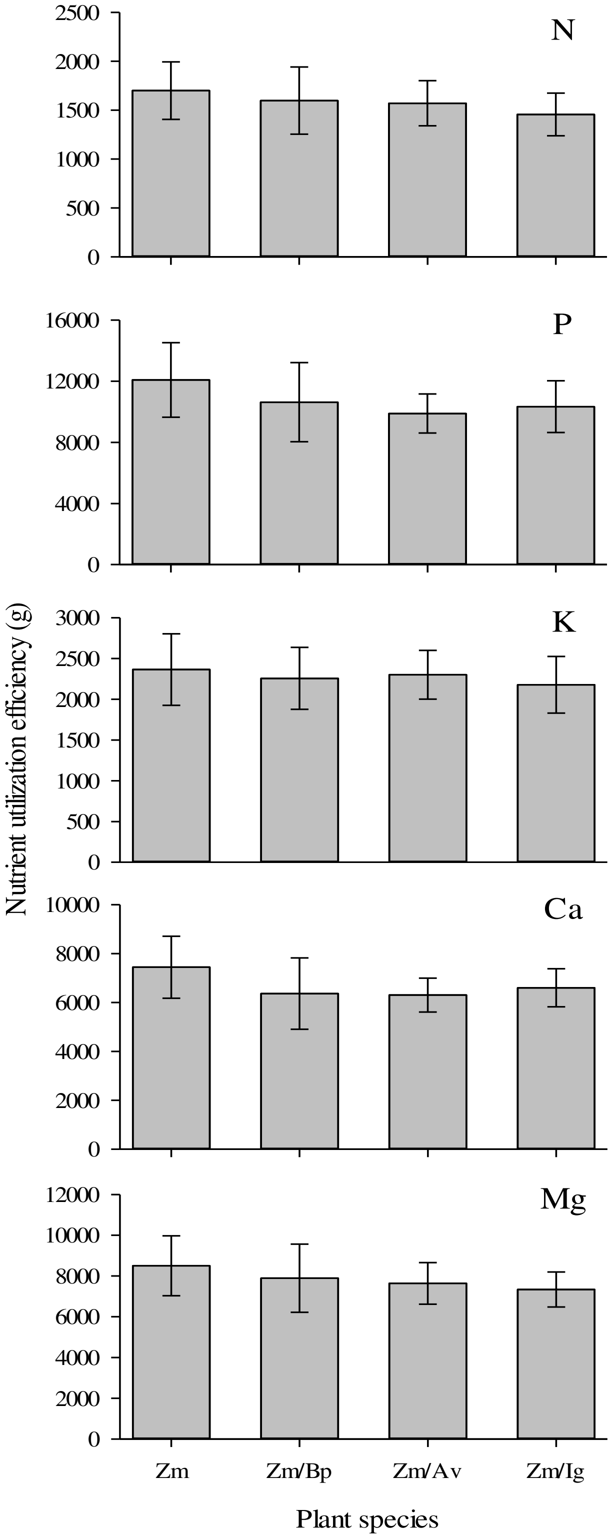

Figure 5. Utilization efficiency of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) (±SDM) by *Zea mays* (Zm) grown for 60 days in monoculture or in interspecific competitions with *Bidens pilosa* (Bp), *Amaranthus viridis* (Av), and *Ipomoea grandifolia* (Ig).

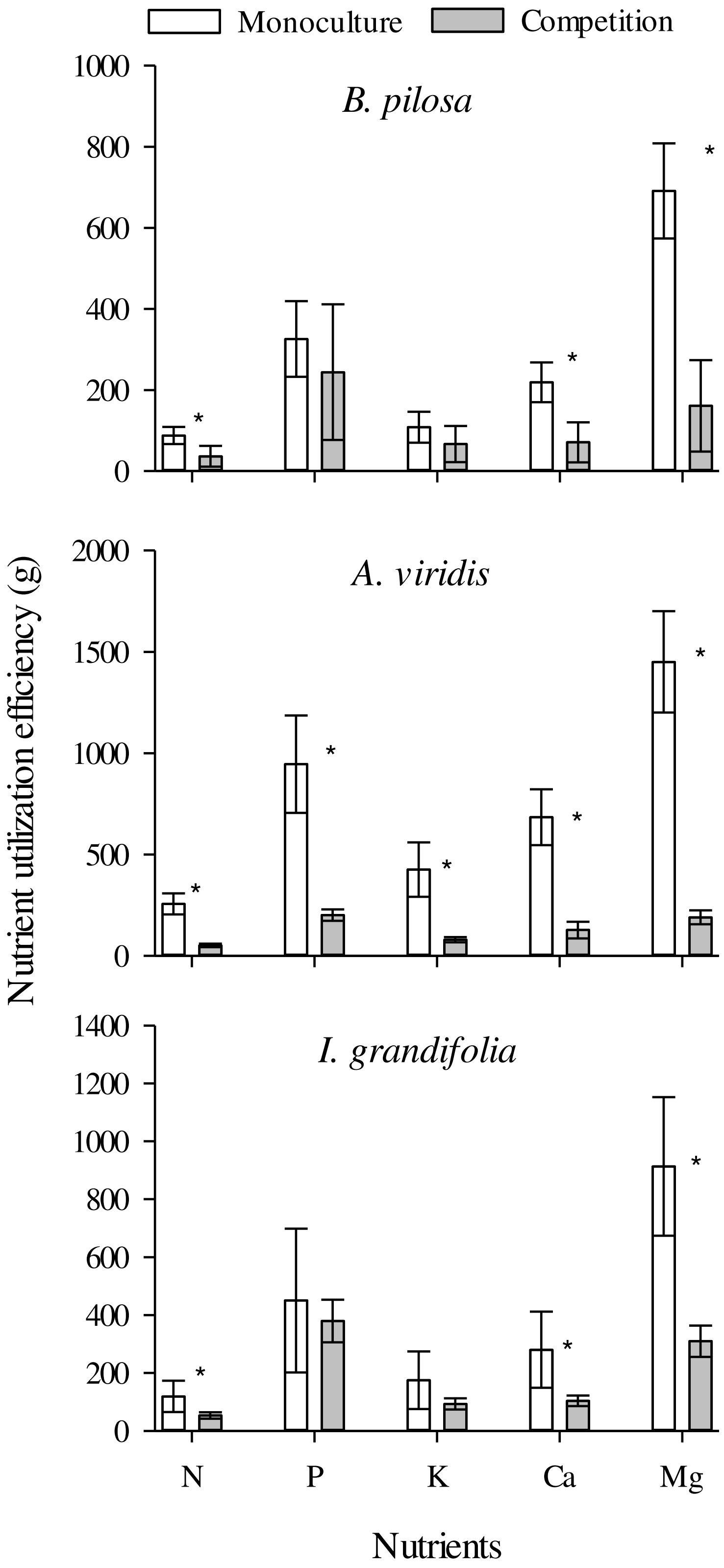

Figure 6. Utilization efficiency of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) (±SDM) for *Bidens pilosa*, *Amaranthus viridis,* and *Ipomoea grandifolia* grown for 60 days in monoculture or in interspecific competition with *Zea mays*. Asterisks indicate that nutrient utilization efficiencies were different between weed monocultures and competition by the t test ($p < 0.05$).

Plant interspecific competition

Lower root P and K content in maize grown with *I. grandifolia* and lower shoot and root K content in maize in competition with *A. viridis* indicate that these weeds have a greater competitive capacity than *B. pilosa*. However, this decrease in maize P and K contents did not affect maize growth. The NUE for N, P, K, Ca, and Mg utilization were similar for maize grown in monoculture or in interspecific competition. The evaluation of NUE considers several morphological, physiological and biochemical factors (including genetics) (Siddiqi and Glass 1981). Therefore, NUE is more effective in determining the plant´s ability to adapt to a competitive stress situation than the simple ratio of total dry matter to total plant nutrient content. Maize had a higher competitive ability than weeds. The greater capacity of maize to compete with weeds was also observed when it coexisted with *Setaria faberi* and *Amaranthus hybridus* during 48 days in soil with N limitation (Poffenbarger et al. 2015). This negative effect of maize competition on weeds is due to the faster seed germination and early growth of this crop observed in this work, thereby favoring resource uptake by maize and allowing it to shade out the weeds (Andrew et al. 2015). In our work, maize and *A. viridis* emergence was observed at the fourth day after planting, while for *B. pilosa* and *I. grandifolia* this occurred on the seventh day. Moreover, maize was more efficient in using nutrients than weeds, a fact that probably contributed to the greater competitive capacity of this plant, as reported earlier in competition experiments with *A. hybridus* (Poffenbarger et al. 2015). Our results showed that interspecific competition may have led to larger resource limitations for weeds than for maize and this may have contributed to the greater changes in the elemental stoichiometry of the weeds.

Elemental stoichiometry

The differences in elemental stoichiometry between maize, *B. pilosa*, *A. viridis* and *I. grandifolia* are probably due to the intrinsic morphophysiological characteristics of these species. As proposed by Wang et al. (2015), interspecific differences in stoichiometric ratios, such as C:N, C:P and N:P, may reflect differences in plants morphology, nutrient use efficiency and photosynthetic capacity, as observed for *Phragmites australis* e *Cyperus malaccensis*.

The increase in the C:N ratio of *B. pilosa* and *I. grandifolia* tissues in response to competition with maize may be due to physiological and genetic adjustments of these weeds to adapt to competition. Plants have mechanisms that allow them to detect and respond to changes in the metabolic levels of carbon and nitrogen. These mechanisms regulate the gene expression and protein activities involved in C and N transport and metabolism, allowing plants to optimize the use of energy resources (Coruzzi and Zhou 2001; Zheng 2009; Elser et al. 2010). Thus, the

C:N regulation mechanism allows plants to activate genes involved in N-assimilation when C-skeletons are abundant and internal organic N levels are low, or disrupt N-uptake when photosynthesis levels are low or the internal organic N levels are high (Coruzzi and Zhou 2001). C metabolism influences the N metabolism and vice versa (Vidal and Gutie 2008; Pérez-delgado et al. 2016). Plants can develop mechanisms to detect the N status of the root system and soil and, thus, coordinate responses in their leaves that will influence photosynthetic yield (Zheng 2009; Elser et al. 2010; Pérez-delgado et al. 2016). Out of the total N applied to the soil, maize cultivations (monoculture or in coexistence with the weeds) extracted about 205%, while the monoculture of *B. pilosa* extracted 47% and that of *I. grandifolia* 66% (Tab. S1 – Suppl. data). Therefore, maize was more efficient to extract N from the soil than the weeds. Less N was left in the soil cultivated with mixed plants than in those cultivated with monocultures. This suggests that both *B. pilosa* and *I. grandifolia*, grown in competition with maize, increased their C:N ratio as a physiological adjustment to the lower N availability in the soil as a consequence of N uptake by maize.

The stoichiometric composition probably reflects plant physiological restrictions, such as reduced activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (RUBISCO) and ribosomes (Elser et al. 2010). Thus, plant nutrient status may reflect differences in soil nutrient supply and the physiological mechanisms that determine how nutrients are used for growth (Elser et al. 2010; Wang et al. 2015). In certain cases, the C:N, C:P and N:P ratios of plants are positively correlated with the carbon:nutrient ratios of the soil (Fan et al. 2015). The increase in the C:P of weeds grown in competition with maize may be due to restrictions in P uptake, since the faster seed germination and early growth of maize allowed it to get an advantage over the weeds in the competition for P. Phosphorus is taken up by plants mainly by diffusion, thus, root interception may be fundamental to ensure and/or increase plant P uptake (Gerke 2015). The fast growth of maize may have allowed its roots to occupy most of the soil volume, which favored maize nutrients uptake (Fig. S2, Suppl. data) and, making it difficult for the weed roots to grow in the same location. Thus, despite the P supply in the soil, less root growth led to reduced P uptake by *B. pilosa* and *I. grandifolia* (Fig. S2, Suppl. data). Under these conditions, both species showed a high capacity to adjust their C:P ratios in the roots and shoots, with a 2.8-fold increase in P assimilation per unit of C. Therefore, *B. pilosa* and *I. grandifolia* optimized P use in their biochemical and physiological processes

The similar shoot and root C:Ca ratios of maize, *B. pilosa*, *I. grandifolia*, and *A. viridis*, grown in monoculture or in interespecific competition, show that these plants have low stoichiometric C:Ca flexibility. Calcium is important for plant cell wall structural rigidity and cell membrane permeability (White and Broadley 2003; Hepler 2005). Furthermore, Ca^{2+} is recognized as a crucial messenger in signaling pathways that connect the perception of environmental stimuli (temperature, salt stress, drought, etc.) to adaptive plant cellular responses (Ranty et al. 2016). Although Ca plays an important role in plant response to stress, high Ca soil supply probably contributed to the similarities in C:Ca ratios in maize and weeds. The lower growth of weeds grown in coexistence with maize seems to be more related to N, P, and K limitations in the soil than to Ca or Mg deficiency. Besides, the structural role of Ca may render the C:Ca ratios less flexible, since this nutrient cannot be re-translocated in the plant tissues to allow physiological adjustments when plants are grown in competition.

We observed the lowest nutrient:Mg ratios for the weeds grown in coexistence with maize. Magnesium is the central atom of the chlorophyll molecule and is essential for many cellular enzymes and for ribosome aggregation (Shaul 2002). This element is involved in several plant physiological and biochemical processes, such as the activation of ATPase enzymes, ribulose-1,5-bisphosphate carboxylase (RuBP), and RNA polymerase (Shaul 2002; Cakmak and Kirkby 2008). Furthermore, in C_4 plants, phosphoenolpyruvate (PEP) carboxylase, an enzyme responsible for incorporating CO_2 into PEP, is also activated by Mg^{2+} (Cakmak and Kirkby 2008). Thus, increases in Mg content in the weeds under competition may be a reflection of less photosynthetic activity, and therefore, lower nutrient utilization efficiency (Fig. S2 – Suppl. data), because of shading by maize or other nutrient deficiency. Competition between plants may decrease their photosynthetic capacity as observed for coffee seedlings in competition with *Mucuna aterrima* or *Brachiaria decumbens* (sin *Urochloa decumbens*) (Matos et al. 2013). The NUE for Mg was more affected by plant competition than those of other nutrients (Fig. S3, Suppl. data), mainly in *A. viridis*, which contributed to the observed changes in the nutrient:Mg ratios.

In our research, the elemental stoichiometry for maize was practically unaffected by competition with weeds. Limitations to weed growth and competition for N with maize probably led to increased N:P, C:N, and C:P ratios in *B. pilosa* and *I. grandifolia*. We have assumed, based on N uptake data (Tab. S1, Suppl. data), that this element was the most limiting for maize and weeds in competition. The plant biomass N:P ratio are mainly regulated by the adjustment of the N and P uptake rates (Elser et al. 2010; Ma et al. 2016). Plants with N deficiency increase N uptake and decrease that of P, whereas P deficient plants do the reverse (Bélanger et al. 2011; Ye et al. 2014). Both N and P can stimulate plant growth. Therefore, the supply of one of these elements influences the efficiency with which the other is uptaken and used (Güsewell 2004). Stoichiometry in cereal, legume, and oilseed crops, for example, indicate that the uptake of P instead of N is the main source of variation in the N:P ratios (Sadras 2006). Cereal N:P ratios ranged from 1 to 20 mainly due to variations in N and P supply to crops. Crops tend to take up much more P than is necessary to meet their immediate requirements (Sadras 2006). The N:P ratios in corn shoots were positively correlated with N application rates (Ma et al. 2016). That is, corn adjusted the N:P ratio of its tissues in response to soil N availability. In addition, N may influence the concentration of various other elements in plant tissues, as observed for wheat (Weih et al. 2016).

Bidens pilosa and *I. grandifolia* in competition with maize showed higher N:P and P:K ratios in their tissues. The coexistence between plants may have increased the demand for water per pot and this may have led to more severe water restriction intervals for the plants. There is a positive relation between plant N:P and N:K ratios and its water use efficiency (Sardans et al. 2015; Yan et al. 2016). The low soil water availability decreased P:K ratios of leaves of *Erica multiflora*, and this was explained by the role of K in plant osmotic regulation. This *E. multiflora* adjustment coincided with an increase of compounds related to water stress tolerance in its tissues (Rivas-Ubach et al. 2012). In this perspective, *B. pilosa* and *I. grandifolia* may have adjusted their stoichiometry (N:P and P:K ratios) due to a probable water stress. Alternatively, the higher solubility of K compared to N and P allows a greater absorption of K when its availability in the soil is not limiting (Sardans et al. 2012). This may also explain the lower P:K ratio of *I. grandifolia* grown in competition with maize. C_4 metabolism plants, such as *A. viridis* and maize, tend to be more efficient at water use than C_3 plants (Way et al. 2014; Von Caemmerer et al. 2017). This may have contributed to a lack of stoichiometric adjustments in these plants.

The degree to which adjustments in plant stoichiometry occur depends on the stoichiometric homeostasis of each species, as reported for *Andropogon gerardii*, *Schizachyrium scoparium,* and *Salvia azurea* (Yu et al. 2015). Thus, the nutrient concentrations in plants may reflect the nutritional variation of the substrate on which they are growing, or may reflect values genetically determined and physiologically required to their development, regardless of the substrate (Elser et al. 2010).

There is a positive correlation between the N:P ratio of the plant biomass and its homeostatic regulation coefficient (H), as observed for three grass species, *Leymus chinensis*, *Cleistogenes squarrosa*, and *Chenopodium glaucum* (Yu et al. 2011). Higher H values indicate greater stoichiometric homeostasis, that is, plants with greater capacity to change the nutrient composition in their tissues (Elser et al. 2010). Species with strong homeostasis (> H) are dominant and stable in the community (Yu et al. 2010). The increase in the N:P ratios of *B.*

pilosa and *I. grandifolia* grown in competition with maize suggests that these weeds have a higher H than *A. viridis*, so that they would be better able to adapt to resource limitations in the soil and persist in the area than *A. viridis*.

The ability to change the stoichiometric characteristics confers an survival advantage to plants (González et al. 2010; Sardans and Penuelas 2012; Wang et al. 2015). Plants with greater competitive ability in nutrient-poor environments are able to modify their biomass nutritional content and increase their NUE (higher C:nutrients ratios) without major reductions in their growth and/or reproductive rates (Funk 2008; González et al. 2010). The success of weed plants in nutrient-rich environments is mainly linked to their high growth rates and nutrient acquisition (less C:nutrient ratio) (Funk 2008; Gioria and Osborne 2014). Plastic responses enable organisms to express advantageous phenotypes in a wider range of environments (Richards et al. 2006). Thus, adaptive changes may lead to increased weed infestation success (Funk 2008; Gioria and Osborne 2014; Ens et al. 2015). Together, data from this research provide scientific evidence that *A. viridis* is likely to have greater restrictions for infesting nutrient poor areas than *B. pilosa* and *I. grandifolia*.

We hypothesize that coexistence with maize tends to reduce the decomposition rates of weed residues, mainly for *B. pilosa* and *I. grandifolia*, which increased the C:N:P:K ratios of their respective biomasses. Probably, the decomposition of these plants tends to have greater losses of organic C via microbial respiration. The K, Ca, Mg, and, especially the N and P concentrations are positively related to the decomposition rate of organic materials (Enriquez et al. 1993; Zhang et al. 2008; Manzoni et al. 2010). Thus, increases in C:N and C:P ratios of the weeds tested in our work may decrease the decomposition rate of their residues. In addition, the microbial carbon use efficiency is lower in C-rich plant residues (higher C:nutrients ratios), which increases respiratory losses of organic C, while nutrients are retained more efficiently (Mooshammer et al. 2014). Residues with similar structure and chemical composition, but with different C:N:P stoichiometries may have different decomposition rates (Manzoni et al. 2010). Thus, changes in elemental stoichiometry of weeds influence nutrient cycling, organic carbon content, and, consequently, soil fertility (Manzoni et al. 2010; Zechmeister-Boltenstern et al. 2015). The higher C:N and C:P ratio of *B. pilosa* and *I. grandifolia* grown in competition with maize are indications that the residues of these weeds tend to immobilize nutrients in the soil for longer periods. Residues with C:N ratio greater than 19 immobilize N longer than those with smaller C:N ratios (Lindsey et al. 2013).

CONCLUSIONS

Interspecific competition changes the elementary stoichiometry of the plant tissues, and the magnitude of this change depends on the species and the nutrient of interest.

Bidens pilosa and *I. grandifolia* have a greater ability to adjust the balance of carbon and nutrients in their tissues than *A. viridis* and maize. This suggests that these weeds are more able to adapt to stress situations than *A. viridis*. The greater stoichiometric flexibility of *B. pilosa* and *I. grandifolia*, in response to competition indicate that these plants have a higher capacity to infest nutrient poor soils than *A. viridis*. These weeds seem to have distinct survival strategies: while *B. pilosa* and *I. grandifolia* are able to utilize a resource more efficiently, *A. viridis* tends to extract and accumulate nutrients in its tissues.

Interspecific competition decreases residue quality (higher C:N, C:P, C:K and N:P ratios) for *B. pilosa* and *I. grandifolia*.

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SUPPLEMENTARY DATA

Table S1. Percentage of nutrients extracted from the soil by the plants (total per pot), considering the amount supplied (via fertilizer) and the amount that was already in the soil. For N, only the amount of nutrient supplied (via fertilizer) was considered

	% nutrients extracted from soil				
	N	P	K	Ca	Mg
Zea mays	205.96	13.48	89.26	7.44	35.09
Z. mays vs. *B. pilosa*	206.11	14.33	85.46	8.65	35.61
Z. mays vs. *A. viridis*	205.80	16.03	83.07	8.68	36.96
Z. mays vs. *I. grandifolia*	207.87	13.51	82.03	8.06	34.39
Bidens pilosa	47.40	5.83	23.07	2.97	5.15
Amaranthus viridis	131.74	16.76	48.67	7.78	19.85
Ipomoea grandifolia	65.87	8.09	27.01	4.39	7.61

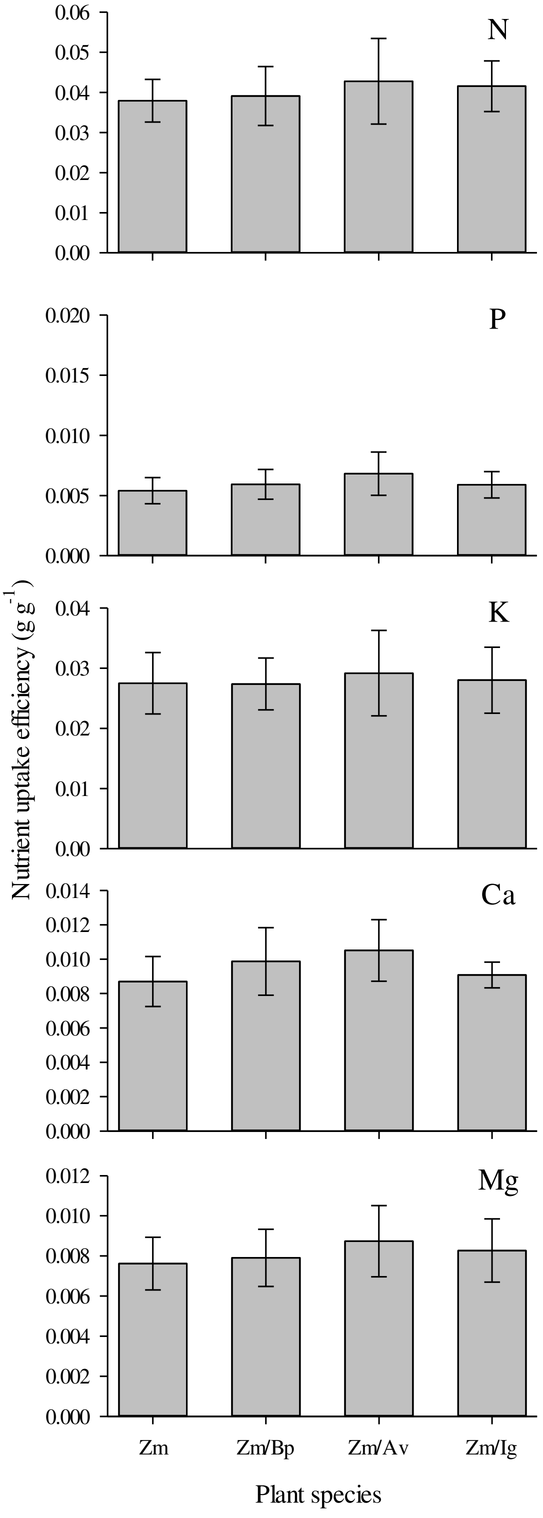

Figure S1. Uptake efficiency of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) (±SDM) for *Zea mays* (Zm) grown for 60 days in monoculture or in interspecific competition with *Bidens pilosa* (Bp), *Amaranthus viridis* (Av), and *Ipomoea grandifolia* (Ig). Nutrient uptake efficiency was calculated using the following equation: NUpE= (total nutrient content in the plant)/ (total root dry matter).

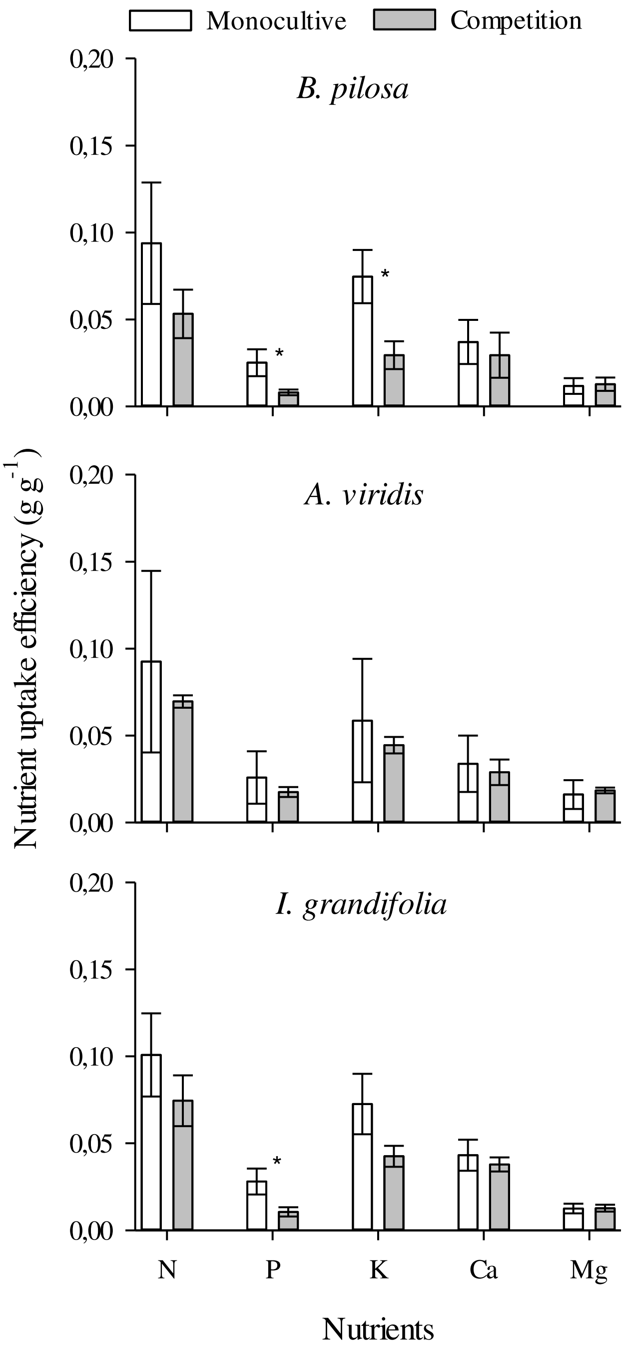

Figure S2. Uptake efficiency of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) (±SDM) for *Bidens pilosa*, *Amaranthus viridis* and *Ipomoea grandifolia* grown for 60 days in monocultures or in interspecific competitions with *Zea mays*. Asterisks indicate that nutrient utilization efficiency were different between weed monoculture and competition by t test ($P < 0.05$). Nutrient uptake efficiency was calculated using the following equation: NUpE= (total nutrient content in the plant)/ (total root dry matter).

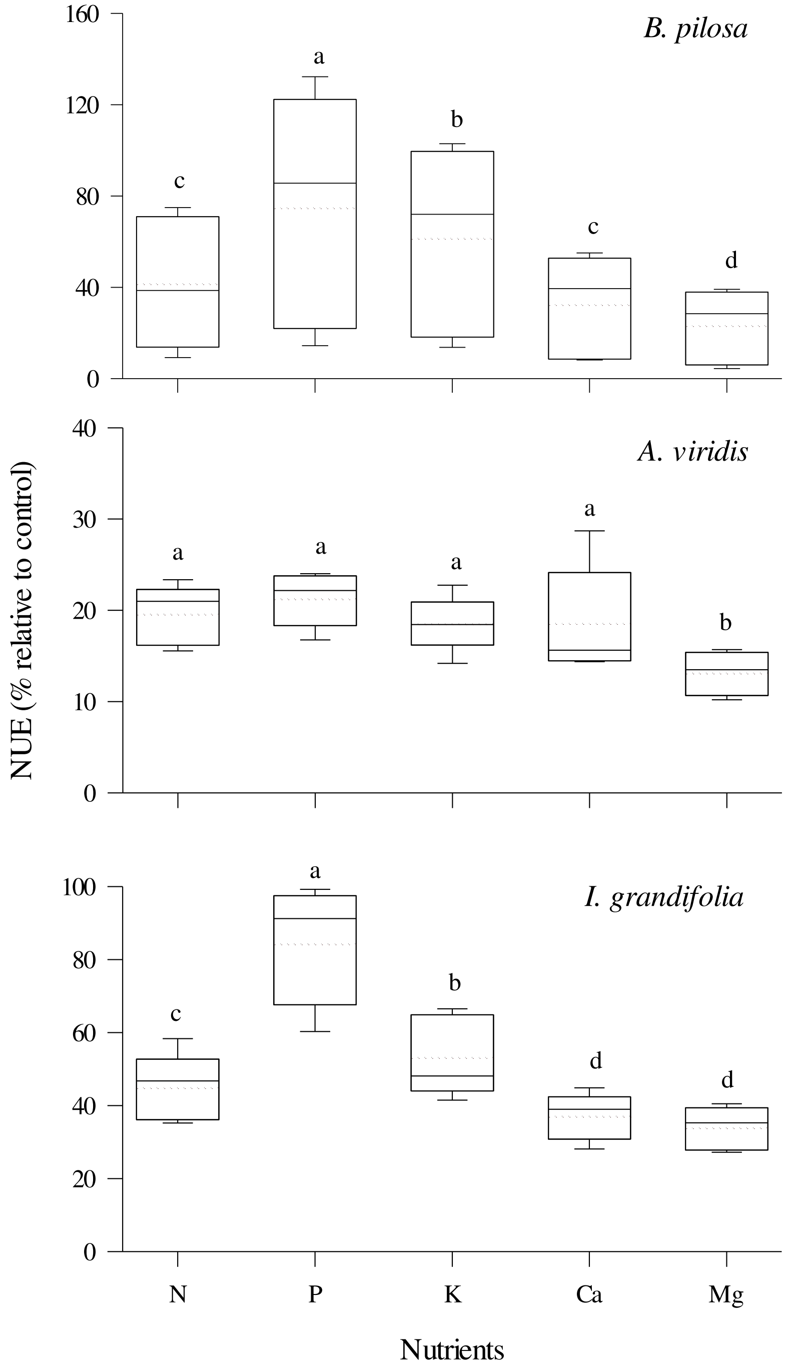

Figure S3. Relative Percentage of nutrient utilization efficiency (NUE) for nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) (±SDM) for *Bidens pilosa*, *Amaranthus viridis,* and *Ipomoea grandifolia* grown for 60 days in monoculture or in interspecific competition with *Zea mays*. Data were subjected to Friedman repeated measure analysis of variance on ranks and the means were compared by the Student-Newman-Keuls test at 5% probability. Different letters of box plot indicate significant difference between means based on the Student-Newman-Keuls test ($p < 0.05$).

CONCLUSÕES GERAIS

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I. A microbiota do solo desempenha papel importante nas interações entre *B. pilosa*, *A. viridis* e milho, influenciando o crescimento das plantas e a capacidade competitiva das mesmas.

II. A reconstituição da microbiota do solo melhora a capacidade do milho de competir com *A. viridis*, enquanto o inverso é observado para *B. pilosa*.

III. A competição entre milho e *B. pilosa, I. grandifolia* ou *A. viridis* leva a valores médios positivos de efeito *priming* rizosférico.

IV. A monocultura de *I. grandifolia* e o milho vs. *B. pilosa* leva a maiores perdas de C da MOAM e da MOP em comparação com os solos não cultivados.

V. A competição entre o milho e *B. pilosa* aumenta a mineralização da MOS, enquanto a competição do milho com *A. viridis* e *I. grandifolia* retarda esse processo.

VI. A competição interespecífica altera a estequiometria elementar das plantas, e a magnitude dessa alteração depende das espécies vegetais envolvidas.

VII. *Amaranthus viridis* apresenta baixa flexibilidade estequiométrica sob as mesmas condições de pressão competitiva enfrentada por *B. pilosa* e *I. grandifolia*.

VIII. A competição interespecífica diminuiu a qualidade da biomassa vegetal, principalmente para *B. pilosa* e *I. grandifolia*. Essa diminuição de qualidade pode reduzir a taxa de decomposição dos resíduos vegetais e levar à imobilização de nutrientes no solo.