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Farming system effects on biologically mediated plant–soil feedbacks

Uriel D. Menalled[1], Tim Seipel[2] and Fabian D. Menalled[2]

[1]Soil and Crop Sciences Section, School of Integrative Plant Science, Cornell University, Ithaca, NY 14853, USA and [2]Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, MT 59717, USA

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Author for correspondence:
Uriel D. Menalled, E-mail: udm3@cornell.edu

Abstract

Cropping system characteristics such as tillage intensity, crop identity, crop-livestock integration and the application of off-farm synthetic inputs influence weed abundance, plant community composition and crop-weed competition. The resulting plant community, in turn, has species-specific effects on soil microbial communities which can impact the growth and competitive ability of subsequent plants, completing a plant–soil feedback (PSF) loop. Farming systems that minimize the negative impacts of PSFs on subsequent crop growth can increase the sustainability of the farming enterprise. This study sought to assess the individual and combined impact of the cropping system (certified organic-grazed, certified organic till and conventional no-till) and crop sequence [pairwise rotations with safflower (*Carthamus tinctorius*), yellow sweet clover (*Melilotus officinalis*) and winter wheat (*Triticum aestivum*)] on the PSF magnitude and direction. All cropping systems followed the same 5-year rotation and had completed one full rotation before soil was sampled. In a greenhouse setting, a sterile soil mix was inoculated with field soil collected from all systems and three crops. The PSF study consisted of two stages (conditioning and response phases) that mimicked the rotation stages occurring in the field. PSFs were calculated by comparing the biomass of the response phase plants grown in inoculated and uninoculated soils. The farm management system affected PSFs, inferring that tillage reduction can encourage more positive PSFs. Crop sequence did not affect PSF but interacted strongly with the farm system. As such, the effects of the farming system on PSFs are best illustrated when taken into account with the identity of the previous and current crops of a cropping sequence.

Introduction

Understanding the ecological underpinnings of sustainable farming systems is essential for meeting long-term food, fiber and bioenergy demands (Robertson, 2015). Farm management systems modify plant communities (Barroso *et al.*, 2015; Adhikari and Menalled, 2018; Bàrberi *et al.*, 2018; Adhikari *et al.*, 2019), soil microbial communities (Zuber and Villamil, 2016; Ishaq *et al.*, 2017; Lori *et al.*, 2017) and reciprocal plant–microbe interactions (Brinkman *et al.*, 2010). In agroecosystems, weed and crop species influence soil micro-organisms, affecting soil-borne pathogens, beneficial symbionts and saprotrophs (Zuber and Villamil, 2016; Ishaq *et al.*, 2017; Lori *et al.*, 2017). These micro-organisms can influence crop performance (Miller and Menalled, 2015), crop-weed competition (Johnson *et al.*, 2017) and overall system resilience (Seipel *et al.*, 2019); completing a plant–soil feedback (PSF, henceforth) loop (Mariotte *et al.*, 2018).

The direction and magnitude of PSFs can have strong impacts on plant population and community dynamics. Negative PSFs can arise from the accumulation of pathogenic microbes, whereas positive PSFs are symbiotic plant–microbe relationships that facilitate plant growth (van der Putten *et al.*, 2016). Generally, PSFs between conspecific species are negative whereas feedbacks between heterospecific species are positive (Kulmatiski *et al.*, 2008; Van de Voorde, *et al.*, 2011). In agricultural settings, this principle manifests in the accumulation of soil specific pathogens after repeated monocultures, a phenomenon colloquially known as 'soil sickness' or 'soil fatigue' (Mariotte *et al.*, 2018). Conversely, crop rotation with phylogenetically distant species can establish positive PSFs (Miller and Menalled, 2015) and promote higher yields (Wang *et al.*, 2017). Farm practices that promote positive PSFs could increase system resilience by maximizing internal regulation of ecosystem function.

In agroecosystems, soil microbial communities can influence productivity by modifying soil pathogen pressure and crop-weed competition. Studies have shown that over-yielding in polycultures is facilitated by reduced soil pathogenesis (Maron *et al.*, 2011; Schnitzer *et al.*, 2011; Wang *et al.*, 2017). Wang *et al.* (2017) postulated that intercrops reduce pathogen pressure through dilution of soil pathogens relative to monocrops. Changes to soil pathogenicity influence PSFs and effect plant community competition. Soils that harbor higher PSFs for weedy plants can facilitate their establishment and persistence. For example, Kulmatiski *et al.* (2004)

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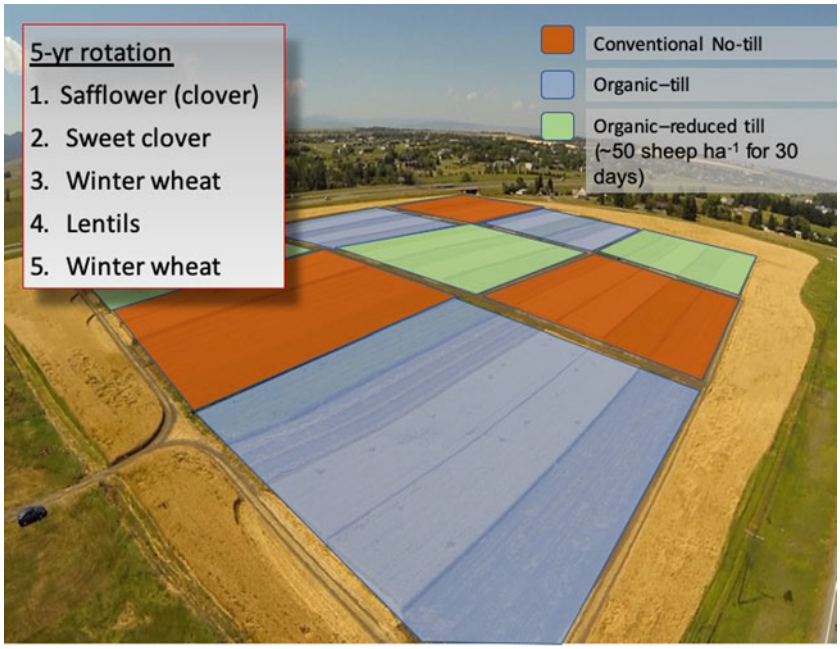


Fig. 1. Field experiment design. Conventional-no till, organic till and organic reduced till systems were replicated three times in 90 × 75 m plots. Within each plot, all stages of a 5-year crop rotation were present in 90 × 13 m sub-plots. The field experiment started in 2012 and we sampled it for our PSF experiment in 2017, after each subplot had gone through one full rotation. Figure adapted from Lehnhoff *et al.*, (2017).

found greater weed-promoting PSFs in disturbed soils and hypothesized that soil disturbance can reduce soil-based weed control.

Organic agriculture systems tend to have longer and more diverse crop rotations, greater plant-based weed suppression through cover crops, more biologically-based pest regulation and improved nutrient cycling relative to conventional chemical systems (Reganold and Wachter, 2016). Greater microbial abundance, activity (Lori *et al.*, 2017) and diversity (Lupatini *et al.*, 2017) have been reported in organic systems. In a meta-analysis of 149 organic and conventional chemical farm-pairs, organic systems had 32 to 84% greater microbial biomass, nitrogen, phospholipid fatty-acids, dehydrogenase, urease and protease than their conventional counterparts (Lori *et al.*, 2017). Johnson *et al.* (2017) compared PSFs between organic and chemical farming systems. While this work reported that PSFs were more positive in organic systems than in chemical systems, it failed to control for rotational diversity and cropping history. Doing so is warranted because the identity of the previous crop in a cropping sequence is responsible for over 80% of variation in the PSF direction and magnitude (Miller and Menalled, 2015). While organic farming systems do not rely on synthetic off-farm inputs such as chemical fertilizers and pesticides, the sustainability of organic farming is put to question by excessive reliance on tillage (Lehnhoff *et al.*, 2017). Tillage results in erosion and alters soil microbial communities. Integrated crop and livestock production systems can facilitate tillage reduction (Franzluebbers, 2007), increase soil carbon (Drinkwater *et al.*, 1998) and microbial carbon and nitrogen biomass (Acosta-Martinez *et al.*, 2004). Thus, PSFs in agricultural soils are likely a product of the combined effects of crop sequence, tillage intensity and crop-livestock integration.

An assessment of how different farming systems influence PSFs is required to better understand the ecological relevance of PSFs in crop production. This study assesses the impact of three farm systems: (1) a chemical no-till system, (2) a USDA-certified organic system reliant on tillage and (3) a USDA-certified organic system that included sheep grazing with the overall goal of minimizing tillage intensity on the PSFs of different cropping sequences. We ask: do PSFs vary as a function of the farm system, crop sequence or their interaction?

Materials and methods

Field experiment and site description

Soil was collected from a field experiment in Montana State University's Fort Ellis Research Center (45°40′N, 111°2′W). The field site has an ambient mean monthly air temperature between −5.7 to 18.9°C, the mean annual temperature is approximately 7.5°C and the site receives an average of 465 mm of precipitation a year. The experimental site has a slope of 0 to 4% and the predominant soil type is a Blackmore silt loam.

The field experiment followed a randomized split-plot design with the farming system as the main plot (90 × 75 m) and crop identity as the split-plot (90 × 13 m); each farming system was replicated three times (Fig. 1). Farming systems were: (1) a chemical no-till system, which was managed using synthetic fertilizer, herbicide and fungicide applications (referred to as conventional no-till, hereafter), (2) a USDA-certified tilled organic system that relied on cover crops and tillage for nutrient management and weed control (referred to as tilled organic, hereafter) and (3) a USDA-certified organic system where sheep (*Ovis aries*) grazing was used to control weeds and reduce tillage intensity (reduced-till organic, hereafter). Each management system followed the same 5-year crop rotation, with each crop present every year. Year 1: safflower (*Carthamus tinctorius* L.), with yellow sweet clover [*Melilotus officinalis* L. (Pall.)] under sown, Year 2: yellow sweet clover, Year 3: winter wheat (*Triticum aestivum* L.), Year 4: lentil (*Lens culinaris* L.) and year 5: winter wheat.

Chemical inputs in the conventional no-till system mimicked standard practices in the Northern Great Plains and included 2,4-D, bromoxynil, dicamba, fluroxypyr, glyphosate, MCPA, pinoxaden and urea to manage weeds and nutrient availability. Both organic systems began the organic transition in July 2012 and were USDA-certified organic in 2015. In the tilled organic

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system, a chisel plow, tandem disk, rotary harrow or field cultivator was used, as necessary, for weed control, seedbed preparation and cover crop incorporation. The reduced-till organic system used sheep grazing to terminate cover crops and manage weeds with an average of 50 sheep/per ha for 30 days. Further details of the management practices used within each system can be found in Johnson (2015). Between 1994 and 2004, the entire site was used for pasture and consisted of a mixture of perennial grasses. Between 2004 and 2010, plots at the site were assigned to a cropping sequence of continuous spring wheat, spring wheat-fallow and winter wheat-fallow. To homogenize potential legacy effects, the entire site was seeded to canola in 2011 before starting the field experiment in 2012. For more information on the previous management of the field see Sainju *et al.* (2011) and Barroso *et al.* (2015).

Soil characterization

Ishaq *et al.* (2020) assessed soil physical and chemical characteristics, and microbial communities from the wheat phase of the field experiment five times during the 2016 field season: April 21, May 12, June 1, June 22 and July 25. Briefly, DNA was extracted from all samples using a Power Soil isolation kit. The V3–V4 region of the 16S rRNA was amplified and used to elucidate OTUs at a 0.03 nearest neighbor cutoff. Microbial communities were evaluated by comparing Shannon diversity values through Conover tests and PERMANOVAs on Jaccard and Brey–Curtis dissimilarity matrices. Soil from the July 25th sampling event was sent to Agvise Laboratories (Northwood, North Dakota, US) for the quantification of soil organic matter, nitrate, phosphorous, potassium and pH. We fit linear models to the reported soil data [Table S2 in Ishaq *et al.* (2020)] with the farm system as a fixed effect to analyze the data. After confirming normality and equal variance, we conducted type III ANOVAs on the linear models. For more information on soil properties see Ishaq *et al.* (2020).

Plant–soil feedback experiment soil sampling

Soil from each safflower, yellow sweet clover and year-5 winter wheat split-plot was collected on August 8th and 9th, 2017. Soil was sampled at least 3 m from any edge by dividing each split-plot into quadrants and collecting ~500 g of soil in each quartile. Samples were taken to a depth of 15 cm using a 2-cm diameter soil corer and soil from each split-plot was homogenized. To minimize cross-contamination, all sampling equipment was washed in 70% ethanol and air dried between split-plots. After extraction, all soil samples were immediately placed on ice and upon return to the lab, they were kept at −20°C.

Plant–soil feedback experiment design

Following Brinkman *et al.* (2010) and Kulmatiski *et al.* (2008), we assessed the PSFs of different crop sequence pairs and farm systems in a greenhouse experiment. The experiment used the soil collected in the field experiment as inoculum mixed with a sterilized soil mix. The soil mix contained equal parts loam, washed concrete sand and Canadian Sphagnum peat moss, with AquaGro 2000 G wetting agent incorporated at 0.5 kg m^{-3} used for the greenhouse study. We replicated the experiment three times. Prior to each of the three experimental trials, the soil mix was sterilized with autoclavation at 134°C for 90 min.

Square pots (10 × 9 × 9 cm) were washed and sterilized in a 10% bleach solution and air dried before being filled with the sterile soil mix. We established a biologically active treatment (BA+) by inoculating every-other pot with 4%, by volume of soil collected from each split-plot. While this inoculation technique may weaken soil microbe effects (Brinkman *et al.*, 2010), various studies report measurable PSFs using this method (Hol *et al.*, 2013; Miller and Menalled, 2015; Johnson *et al.*, 2017). The biologically inactive (BA−) treatment was the remaining un-inoculum pots, these pots were filled with 100% sterile soil mix. Each BA+ treatment was paired with a BA− pot (Fig. 2). Treatment pairs were subjected to the same seeding rates and placed next to each other throughout the greenhouse experiment. Either 14 yellow sweet clover, ten safflower or seven winter wheat seeds were sown 2 cm deep in each pot. For the conditioning phases, we seeded the crop that was growing when the BA+ soil was sampled in summer 2017. For the response phase, we seeded the subsequent crop. PSF calculations compared BA+ and BA− pairs utilizing response phase data.

Prior to seeding, all seeds were soaked in bleach for 1 min, rinsed with 70% ethanol and air dried for sterilization. Intraspecific competition was minimized by thinning to one seedling per pot immediately after seedling emergence. Each treatment pair was replicated three times for a total of 54 pots per trial [3 systems × 3 crops × 2 sterilization levels (BA+ and BA−) × 3 replications]. The entire experiment was replicated in three trials (start dates: October 14th, October 28th and February 24th, 2018). In every trial, BA + and BA− pairs were randomly assigned to one of four blocks, ensuring to not replicate a unique treatment pair in any block.

Plants grew for two 5-week periods (conditioning phases 1 and 2) and were harvested and reseeded after each growing period (Fig. 2). Conditioning phases were intended to allow for sufficient growth and differentiation of soil microbe communities found in the field system before the response phase. This approach has successfully been used in similar PSF experiments (Miller and Menalled, 2015; Johnson *et al.*, 2017). Following the two conditioning phases, we seeded the subsequent crop species that would had been planted in the field rotation (response phase): yellow sweet clover was planted in pots conditioned with safflower; winter wheat in pots conditioned with yellow sweet clover and safflower in pots conditioned with winter wheat. Plants were grown during the response phase for 7 weeks and harvested at the soil level. After each response phase harvest, all samples were individually dried at 40°C before biomass was weighed. Crop emergence in the BA+ treatment was recorded during the first two trials of the conditioning phase; response phase crop emergence in the BA+ treatment was recorded for all trials.

During planting, thinning and harvesting, all materials were sterilized with 70% ethanol to prevent sample contamination. Plants were maintained under a 16-h photoperiod of natural sunlight supplemented with mercury vapor lamps (165 uE m^{-2} s^{-1}) at 22°C/18°C day per night. To account for greenhouse temperature and light variation, pots were rotated weekly. To prevent cross-contamination, pots were situated 10 cm apart and were watered at low pressure to minimize splashing. Throughout the length of the study, the soil was maintained moist and all weeds pulled as they emerged.

Emergence analysis

Emergence of plants in the BA+ treatment was recorded for trials one and two of the conditioning phase and all trials of the

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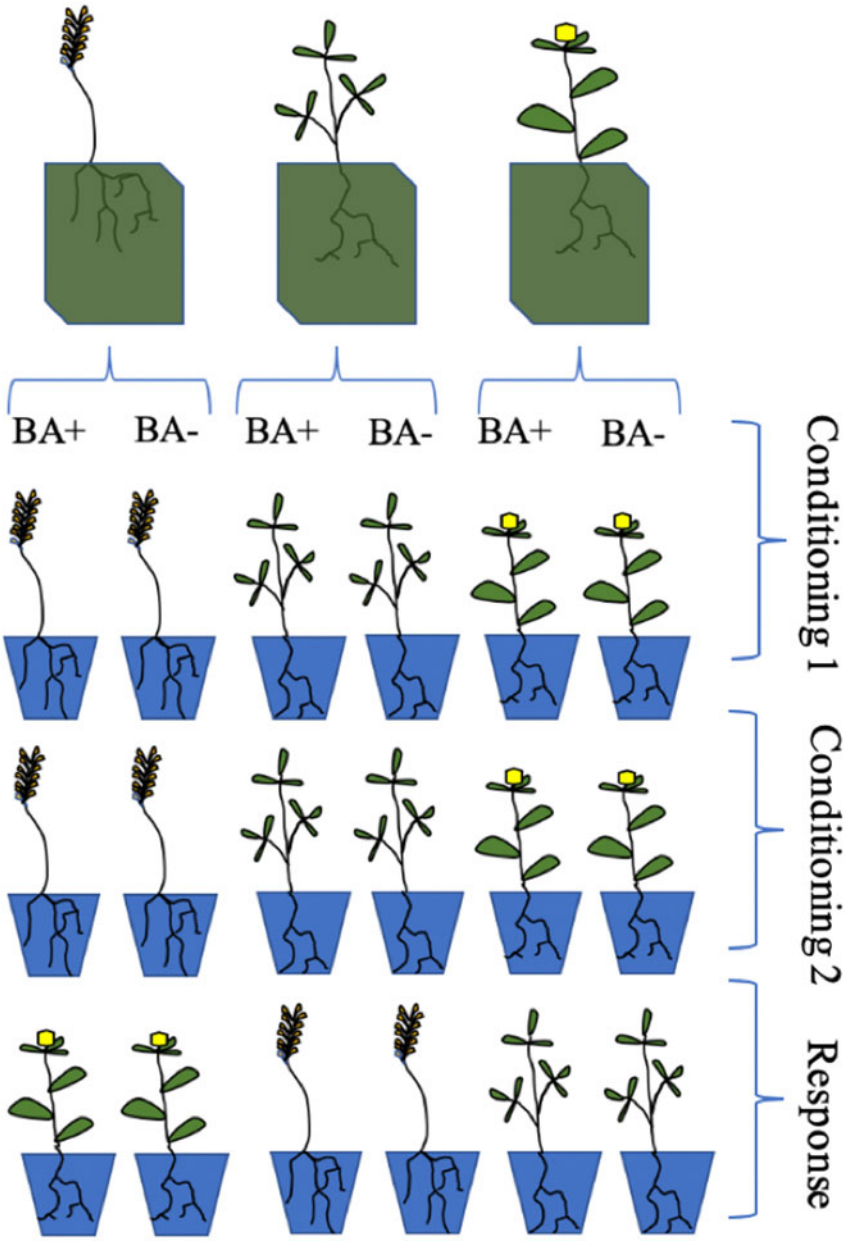


Fig. 2. Greenhouse experiment design. Both conditioning phases lasted 5-weeks; the response phase was 7 weeks. All biologically-active (BA+) and biologically-inactive (BA−) pairs were replicated three times in each unique farm system species treatment for a total of 54 pots per trial [3 systems × 3 crops × 2 sterilization levels (BA+ and BA−) × 3 replications].

response phase. We fit the emergence data to a hierarchical Bayesian generalized linear mixed effects models to address convergence failure due to singularity with the 'blme' R package (Chung *et al.*, 2013). Emergence was fit in response to preceding crop, farm system and the interaction of both fixed effects; greenhouse trial was included as a random effect. The Bayesian models fully converged and provided confident posterior probability distributions. The effect of predictor variables on emergence was assessed using type III chi-squared ANOVA and *post-hoc* estimated marginal means pair-wise comparisons (Lenth *et al.*, 2019).

Plant–soil feedback analysis

Following previous studies (Kulmatiski *et al.*, 2008; Brinkman *et al.*, 2010; Miller and Menalled, 2015; Johnson *et al.*, 2017), PSFs were calculated by comparing the biomass harvested in the response phase of each unique BA+ and BA− pair as:

$$\frac{\mathrm{PSF}_{ijk} = \ln(\mathrm{biomass}_{ijk}(\mathrm{BA+}))}{\mathrm{biomass}_{ijk}(\mathrm{BA-})},$$

where $\mathrm{biomass}_{ijk}$ (BA+) denotes the biomass of species *i* grown in a soil that received a biologically active inoculum from management system *j* and conditioned by species *k*, and $\mathrm{biomass}_{ijk}$ (BA−) denotes the biomass of species *i* grown in an un-inoculated soil from management system *j* and conditioned by species *k*. If ratios were positive or negative, then results indicated that PSFs either enhanced or suppressed plant growth, respectively.

PSF calculations were fit to linear mixed effect models (Kuznetsova *et al.*, 2017) where greenhouse trial was a random effect. Before modeling, assumptions of normality were checked

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Table 1. Seedling emergence and PSF test statistics. Superscript letters denote crop and farm system pairwise comparisons at a 95% confidence level. The first superscript in the emergence data describes differences within conditioning or response phases; the second letter denotes differences between conditioning and response phases.

Emergence					PSF	
Conditioning phases			Response phase		Response phase	
	Percent emergence	SD	Percent emergence	SD	Mean	SD
Crop						
Yellow sweet clover	$92^{a,a}$	0.28	$93^{a,a}$	0.267	0.28^{a}	0.79
Safflower	$52^{b,a}$	0.511	$100_{a,b}$	0	-0.12^{a}	1.87
Winter wheat	$75^{ab,a}$	0.439	$22^{b,b}$	0.424	-0.05^{a}	0.15
Farm system						
No-till chemical	$69^{a,a}$	0.471	$63^{a,a}$	0.495	0.11^{AB}	1.32
Organic till	$78^{a,a}$	0.422	$78^{a,a}$	0.482	-0.51^{A}	1.33
Organic reduced till	$80^{a,a}$	0.407	$67^{a,a}$	0.424	0.89^{B}	1.06

with qqPlots and equal variance was confirmed with Levene tests. The models were interpreted through type III ANOVA tests, which assessed whether PSFs differed by crop sequence, farm system or a crop sequence by farm system interaction. Post-hoc estimated marginal means tests elucidated pair-wise relationships between variables. All analyses were done in R (R Core Team 2018) and plotted in ggplot2 (Wickham, 2016).

Results and discussion

During the conditioning phases of trials one and two, safflower emergence (52%) was lower than yellow sweet clover (92%) and marginally lower than winter wheat (75%) ($P < 0.01$ and $P < 0.10$, respectively; Table 1). During the response phase, winter wheat had the lowest emergence (22%) and differed from safflower and yellow sweet clover (100 and 93% emergence; $P < 0.01$ and 0.001, respectively). Throughout all conditioning and response phases, the farm system did not affect crop emergence ($P = 0.73$ and 0. 48, respectively). Likewise, there was no crop identity by the farm system interaction in conditioning and response phase emergence patterns ($P = 0.90$ and 0. 99, respectively). However, the crop-specific emergence patterns in conditioning and response phases ($P < 0.05$ and $P < 0.001$, respectively) suggest that crop sequence may have greater effects on emergence than the farm management system.

Our experiment did not seek to assess the mechanisms responsible for species-specific effects on crop emergence. However, reduction in winter wheat emergence between conditioning (75%) and response phases (22%; $P < 0.001$; Table 1) suggests a repressive effect of yellow sweet clover on winter wheat. Previous studies report that yellow sweet clover has allelopathic effects on Poaceae weeds including wild oat (*Avena fatua* L.) (Moyer *et al.*, 2007), downy brome (*Bromus tectorum* L.) (Blackshaw *et al.*, 2001), barnyard grass [*Echinochloa crusgalli* (L.) Beauv.] (Wu *et al.*, 2010) and annual bluegrass (*Poa annua* L.). Considering the phylogenetic closeness of these Poaceae species with winter wheat, yellow sweet clover could have repressed winter wheat emergence through similar allelopathic mechanisms. Correspondingly, Moyer *et al.* (2007) found that wheat yields were reduced when intercropped with yellow sweet clover. However, given a fallow period, yellow sweet clover is recommended as a cover crop before winter wheat because of its weed suppression capabilities (Blackshaw *et al.*, 2001; Moyer *et al.*, 2007). Thus, a study that varies the maturity of yellow sweet clover at termination and the length of the fallow period before winter wheat could elucidate the tradeoffs between yellow sweet clover allelopathy, weed suppression and potential impacts on winter wheat yield.

When assessing the impact of the three studied cropping systems on soil physical–chemical and microbiological characteristics, Ishaq *et al.* (2020) observed that soil organic matter, nitrate, phosphorous, potassium and pH did not differ as a function of the farm system. However, the farm system and soil sampling date affected soil microbe OTU community composition with a greater abundance of putative nitrogen-fixing bacteria in the reduced-till organic system (Brey–Curtis and Jaccarad's PERMNAOVA: $P < 0.01$). While we did not compare soil microbial communities across the three studied crops, our results in combination with Ishaq *et al.* (2020) underscores the potential impact that changes in microbial communities could have on plant growth and PSFs.

Farming systems affected the magnitude and direction of PSFs, ($P < 0.01$) with the most negative PSFs observed in the tilled organic soils. The PSF of the tilled organic system was lower than that of the reduced-till organic system ($P < 0.01$, Table 1), which harbored the highest mean PSF. Differences between PSFs of the two organic systems suggest that microbially-mediated plant performance cannot be broadly described as a function of organic management, as Johnson *et al.* (2017) suggests. Furthermore the difference between organic systems ($P < 0.01$) infers that tillage intensity is negatively correlated to PSF. Tillage reduction has been associated with increased microbial abundance (Johnson and Hoyt, 1999; Martens, 2001), enzyme activity (Gianfreda and Ruggiero, 2006; van Capelle *et al.*, 2012; Zuber and Villamil, 2016), soil microaggregate stability and organic matter stabilization (Six *et al.*, 2002). In our study, the incorporation of livestock may have influenced PSFs through its effects on soil health. Well managed mixed livestock-crop farming systems can improve soil physical, chemical and biological properties through increased nutrient inputs (Malhi *et al.*, 2013).

Crop sequence did not affect PSF ($P = 0.82$) but there was an interaction between the identity of the preceding crop and farm

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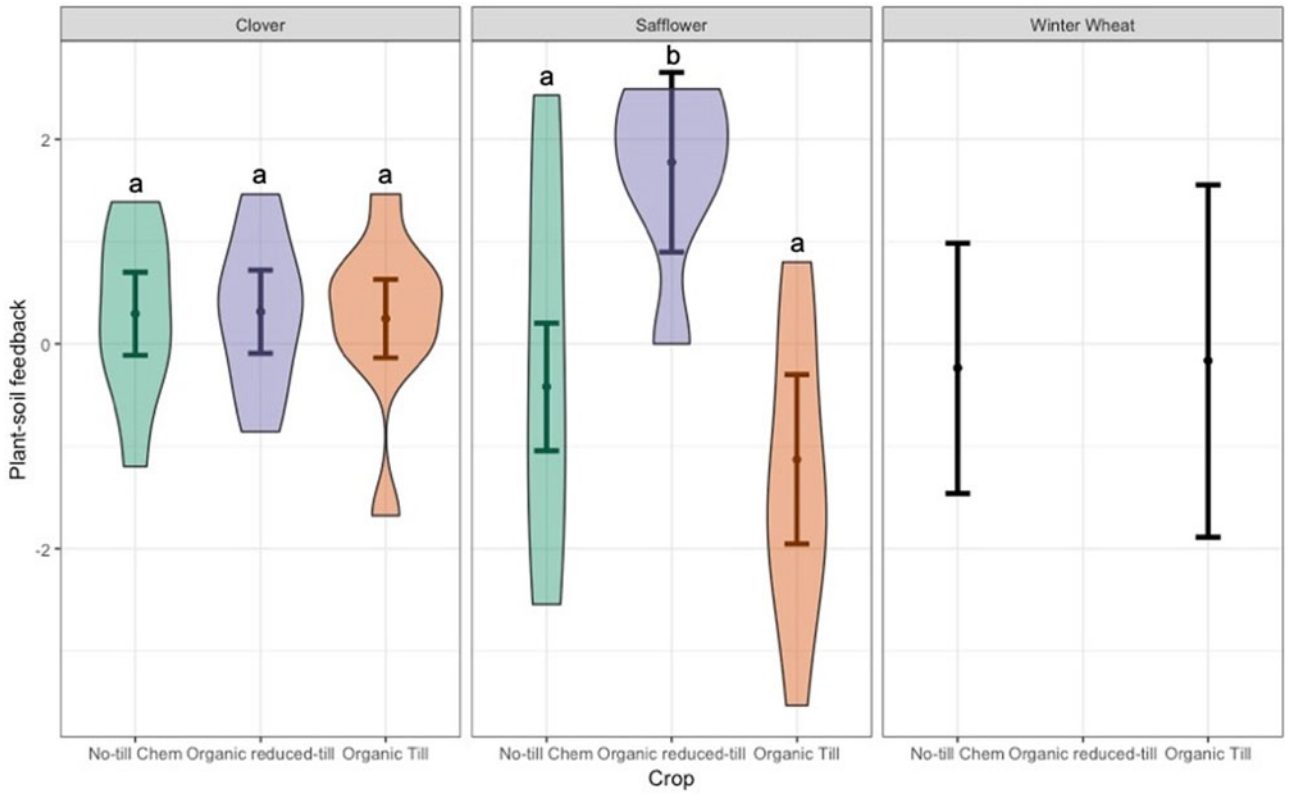


Fig. 3. Plant soil feedback values as a function of crop sequence and farm system interactions. Pairwise-comparisons denote $p < 0.05$ and the error bars are centered upon the fitted PSF means of the linear mixed effects model used to analyze PSFs. Winter wheat pairwise analysis is omitted due to low emergence. All PSFs in each facet of the figure had the same crop sequence but differed in the farm system. Thus, differences in PSF within the safflower facet suggest that the observed farm system effects on PSFs were driven by the interaction between the clover (conditioning crop) to safflower (response crop) cropping sequence and farm system.

system ($P < 0.05$). Safflower's response to farm management (Fig. 3) drove this interaction. Seeding safflower after winter wheat in the reduced-till organic system fostered positive PSFs (Mean = 1.67; SD = 0.929). In contrast, in the organic till system, this crop sequence lead to negative PSFs (Mean = −1.30; SD = 1.37), which differed from the organic reduced till system ($P < 0.001$). The conventional no-till safflower PSF was intermediate (Mean = −0.13; SD = 1.94) and differed from the reduced till organic system ($P < 0.05$). The other two crop sequences had different interactions with our farm system treatments. The PSF of the safflower to yellow sweet clover rotation sequence did not differ as a function of the farming system. Furthermore, low response phase winter wheat emergence in soils from the organic reduced till system prevented analysis of an interaction between the farm system and winter wheat PSF because no biologically active and inactive sample pair emerged. The differential response of crop sequence PSFs to farm management illustrates the importance of crop identity in the establishment of PSFs. In accordance, Miller and Menalled (2015) determined that the crop rotation sequence was responsible for over 80% of variation in PSFs.

In Johnson *et al.*'s (2017), all chemical conventional systems sampled were no-till whereas all organic systems used intensive tillage and tended to have higher rotational diversity. Our research suggests that tillage intensity has a negative effect on PSFs. Therefore, the higher mean PSFs that Johnson *et al.* (2017) found in organic systems may have been driven by rotational diversity, which could have masked the negative effect of increased tillage in the organic system. Increased crop rotation diversity could influence PSFs through more diverse soil nutrient inputs (Karlen *et al.*, 1994; McDaniel *et al.*, 2014) and resulting increases in soil microbe diversity (Lupwayi *et al.*, 1998).

Overall, this study suggests that differences between the PSFs of the organic till and reduced till systems cannot be accurately described as only a function of organic or chemical farm management. However, our work infers that the effects of the farming system on PSFs are best illustrated when taken into account with cropping sequence. As such, the combined effects of the farm management system and crop sequence on PSFs are a relevant avenue through which farmers can influence ecologically-mediated crop performance.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S1742170519000528.

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