

ORIGINAL CONTRIBUTION

Preceding crop affects soybean aphid abundance and predator–prey dynamics in soybean

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Keywords

Aphis glycines, cover crops, crop rotation, integrated pest management, predator, rotation effect

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Abstract

Crop rotations alter the soil environment and physiology of the subsequent crop in ways that may affect the abundance of herbivores and their natural enemies. Soybean aphids are a consistent pest of soybean throughout North America, but little work has focused on how preceding crops may affect pest–predator dynamics. In a replicated experiment over three years, we examined how two preceding crops (spring wheat or an oat/pea mixture) affected seasonal soybean aphid pressure and the ratio of aphids to their predator community. Peak aphid populations were reduced by 40% and 75% in years 1 and 2 by planting spring wheat before soybeans (relative to the oat–pea mixture). Aphid densities were unaffected by preceding crop in the third year of study (aphids were at threshold in this year). Predators responded positively to aphid population increases and were unaffected by preceding crops. Additional research on how crop rotations can be used as a tool to manage soybean aphids warrants further attention.

Introduction

Crop rotation has multifaceted benefits to crop production, including pest management (Bullock 1992). Each crop uniquely alters soil biology, chemistry and structure in ways that can be harnessed to synergize with subsequently planted crops and promote farm profitability (Crookston 1995; Anderson 2011). The simplest of these rotations (soybean–corn) can help reduce fertilizer costs and improve yields (Pederson and Lauer 2004; Wilhelm and Wortmann 2004). Long-term agronomic benefits accrue as the rotation is lengthened (Brust and King 1994; Pikul et al. 2005; Anderson 2008; Stanger and Lauer 2008). These rotations can be an important tool for managing insects, weeds and diseases. A primary focus has been on the ability of crop rotations to break pest and disease cycles for species whose colonization of a crop is strongly or solely coupled with the crop; for example insect pests and diseases that overwinter with a crop's residue (wheat stem sawfly, corn rootworm), and weeds whose life cycle mimics that of the cash crop (Criddle 1922; Liebman and Dyck 1993; Brust and

King 1994; Kiss et al. 2005; Anderson 2008). However, it is also feasible that preceding crops could alter the soil environment or subsequent crop's physiology and morphology (Williams and Weil 2004; Westgate et al. 2005) in ways that may reduce pest abundance and impact for species that are polyphagous or whose colonization is not broken by the rotation. This synergistic aspect of crop rotation on insect pests merits further attention from researchers.

Soybean aphids (*Aphis glycines* Matsumura) are the dominant pest of soybean in North America and represent a major economic input for farmers (Ragsdale et al. 2011). Soybean aphids are consistently present in soybean fields, and if left unchecked, the aphids can alter the soybean plant's physiology (Riedell et al. 2009) and reduce yields (Ragsdale et al. 2007). The primary management response to soybean aphids is insecticide applications. Prophylactic, neonicotinoid seed treatments are pervasive throughout much of the soybean crop, but can leave economically threatening numbers of aphids that require additional foliar applications of insecticides (McCornack and Ragsdale 2006; Johnson et al. 2009; Seagraves and Lundgren

2012). Natural enemy communities reduce soybean aphid numbers and thus provide a valuable ecological service for farmers (Landis et al. 2008; Hallett et al. 2014), but these beneficial arthropods are negatively affected by insecticide applications targeting soybean aphids (Ohnesorg et al. 2009; Lundgren et al. 2013). Host plant resistance is also an important non-chemical management tool for soybean aphids (Wiarda et al. 2012; Hesler et al. 2013). Nevertheless, soybean aphids remain a threat and additional tools that work within current agronomic frameworks may help improve the profitability of soybean production.

Diversified crop rotations are under development for the Northern Great Plains that can simultaneously improve soybean profitability and reduce weed pressure over repetitive planting of single crops, or commonly planted soybean–corn rotations, are in development (Anderson 2011). Although soybean aphid management has received substantial expenditure by researchers, little attention if any has been given to how diversifying rotations might be used to lower soybean aphid management costs and how rotation sequence affects insect community dynamics in general. Here, we explored two rotations that vary in the crop that precedes soybean (either an oat–pea mixture or spring wheat). Specifically, we tested the hypothesis that soybean aphid seasonal populations are not affected equally by two preceding crops. Furthermore, we examine how aphid predator communities respond to these preceding crops and the resultant aphid populations.

Materials and Methods

Experimental design

This research was conducted during the summers of 2011–2013 on the Eastern South Dakota Soil and Water Research Farm (44.3535 and –96.8059; latitude and longitude). Treatments were established in the year preceding the experiment. At this point, plots were selected to receive either spring wheat (Briggs, Milborn Seeds, Brookings, SD, USA, 2.9 million plants per ha) or a 1 : 2 (by weight) mixture of oat/pea forage (oat: var. Jerry; pea: var 4010; 3.2 million plants per ha, Milborn Seeds). These cool season crops were planted at 20-cm row spacing on 16 April 2010, 29 April 2011 and 2 April 2012. Following harvest of these cool season crops, an oat/radish cover crop was planted (9 August 2010, 11 August 2011 and 6 August 2012) and allowed to persist through the following spring. Radishes (var. Daikon, Milborn Seeds, Brookings, SD) were planted at 370 000 seeds per ha, and oat

(var. Stallion, Milborn Seeds, Brookings, SD) were planted at 585 000 seeds per ha. All crops and covers were planted with a no-till drill with single disc openers. The cover crops put on fall growth, and winter killed so no further management was necessary. Soybeans (Pioneer 91B56 RR, Pioneer Hibred International, Johnston, IA) were planted 11 May 2011, 17 May 2012 and 26 May 2013 at a rate of 395 000 seeds per ha and 0.5-m row spacing. No fertilizer, fungicide or insecticides were applied to these plots at any point in the experimental rotation. Weeds were managed with a single application of glyphosate at a rate of 840 g/ha pre-planting. These treatments were replicated three times each per year in a randomized complete block design. Plots were 7 × 10 m in size, and plots occasionally abutted one another. Yields were collected from each plot (data pooled from two 3 × 10 m areas per plot) using a small-plot combine.

Insect sampling

Soybean aphid populations per plant per plot were evaluated approximately weekly throughout the growing season. Aphid sampling commenced formally when aphid populations were first detected and continued until the soybeans began to yellow. In 2011, aphids were sampled on 6, 13, 22, 29 July, 8, 19 August. In 2012, aphids were sampled on 9, 18, 25, 31 July, 9, 17, 28 August. In 2013, aphids were sampled on 5, 11, 19, 25 July, 7, 14, 21, 29 August, 5 September. All aphids were counted on 20 plants per plot (15 plants in 2011) until aphid populations reached approximately 250 per plant; 10 plants per plot were sampled for the remainder of the season. The mean number of aphids per plant per plot per date was used for subsequent analyses.

Sweep nets were used to estimate predator populations. Sweep samples invariably occurred on the same day as the soybean aphid counts. A 38-cm diameter net was swept 50 times per plot. All arthropods exiting the net were identified by sight to the lowest taxonomic level possible. The number of each taxon per sweep per plot per date was calculated.

Data analysis

We compared the mean numbers of aphids per plant between treatments over the season using independent linear mixed models for each year; treatment was a fixed effect in the model, and block and date were random effects (SYSTAT 13; Systat Software Inc, San Jose, CA). A second set of linear mixed models (one for each year), with treatment, date and their

interaction as fixed factors were also evaluated to determine whether the trends in aphid numbers per treatment were similar throughout the season. Cumulative aphid days in each treatment and year were calculated using the formula of Hodgson et al. (2004).

$$(x_{i-1} + x_i)/2 \times t,$$

where x_i is the number of aphids on a given sample date, x_{i-1} is the aphid number on the previous sample date and t is the number of days between the two sample dates. Two-way ANOVAs of predator abundance per sweep per date, predator species richness per sweep per date, predator species diversity (Shannon H), predator community evenness (J) and seasonal aphids per predator per plot were used to examine the effects of year and treatment on predator-prey dynamics. Correlations between seasonal aphid abundance and the aforementioned predator community characteristics per field were evaluated using linear regression models. Seasonal abundances of individual predator taxa were similarly regressed against aphid populations per field. To determine whether the community responded similarly to small and large aphid outbreaks, the season was divided into two periods: pre- and post-aphid population outbreaks. The outbreak was distinguished when mean aphid abundance per plant exceeded the traditional economic injury level (EIL; 792 aphids per plant before soybean growth stage R4; Ragsdale et al. 2007). Yield per plot was compared between the plots using a linear mixed model, with treatment as a fixed effect, and year and block as random effects. All statistics were run using SYSTAT 13 (Systat Software, Inc.).

Results

Preceding crop had a significant and substantial effect on soybean aphid densities in two of the three sample years (fig. 1). This was true in 2011 ($F_{1,326} = 5.43$, $P = 0.02$) and 2012 (treatment: $F_{1,705} = 14.94$, $P < 0.001$), but treatments had similar aphid numbers in 2013 (treatment: $F_{1,818} = 0.03$, $P = 0.86$). In all years, date had a significant effect on aphid populations ($P < 0.001$), and there were no significant interactions between date and treatment.

In 2011, maximum aphid number was reduced by 40% by including spring wheat in the rotation before soybeans and by 75% in 2012 (relative to oat-pea). Soybean aphids only consistently exceeded the traditional economic injury level in one of the three years of study (2011). Aphid densities in 2012 never exceeded 140 aphids per plant, which was below the

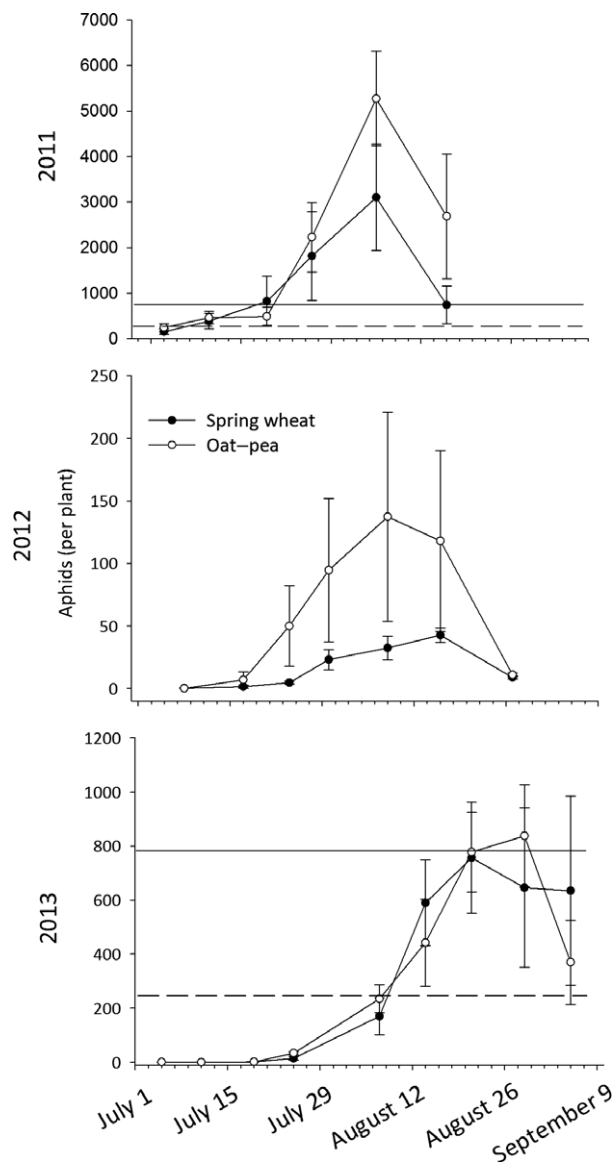


Fig. 1 Mean (SEM) soybean aphid abundance in soybeans preceded by spring wheat or an oat-pea mixture ($n = 3$). Seasonal mean aphid abundance in the two treatments varied significantly among sample dates in 2011 and 2012, and additional tests were performed to determine which dates had significantly different means ($\alpha = 0.05$). Dashed lines refer to the economic threshold (ET; 250 aphids per plant), and solid horizontal lines refer to the economic injury level for soybean aphids (792 aphids per plant); aphid populations in 2012 did not reach the ET. Asterisk (*) denotes significance of $P < 0.05$.

economic threshold for this pest. In 2011, mean (SEM) cumulative aphid days were $108\,561 \pm 25\,077$ and $59\,275 \pm 17\,112$ in the oat-pea and spring wheat treatments, respectively. In 2012, mean cumulative aphid days were 3510 ± 2090 and 1005 ± 145 in the oat-pea and spring wheat treatments, respectively. In 2013, mean cumulative aphid days were $21\,166 \pm$

5521 and $22\,522 \pm 8342$ in the oat-pea and spring wheat treatments, respectively. There were no effects of treatment on yields ($F_{1,10} < 0.01$; $P = 0.99$). Mean (SEM) yields were 1680 ± 380 and 1318 ± 53 (2011), 803 ± 178 and 983 ± 180 (2012), and 1820 ± 205 and 1880 ± 49 (2013) kg/ha in soybeans preceded by spring wheat and oat-pea, respectively.

Our sweep samples collected 17 539 predators representing 41 predator OTUs (operational taxonomic units, or morphotaxa). Although sample year significantly affected predator community structure, preceding crop did not have a significant effect on predator abundance (year: $F_{2,12} = 41.96$, $P < 0.001$; treatment: $F_{1,12} = 2.67$, $P = 0.13$; interaction: $F_{2,12} = 0.92$, $P = 0.43$), predator species richness (year: $F_{2,12} = 102.83$, $P < 0.001$; treatment: $F_{1,12} = 0.20$, $P = 0.66$; interaction: $F_{2,12} = 0.38$, $P = 0.69$), predator diversity (H) (year: $F_{2,12} = 21.15$, $P < 0.001$; treatment: $F_{1,12} = 0.42$, $P = 0.53$; interaction: $F_{2,12} = 0.18$, $P = 0.84$) or predator community evenness (year: $F_{2,12} = 15.45$, $P < 0.001$; treatment: $F_{1,12} = 1.24$, $P = 0.29$; interaction: $F_{2,12} = 0.46$, $P = 0.64$). Because the aphids were fewer in the fields preceded by spring wheat and predators remained comparable regardless of treatment, the ratios of aphids per predator were significantly lower for soybeans preceded by spring wheat (year: $F_{2,12} = 55.20$, $P < 0.001$; treatment: $F_{1,12} = 4.74$, $P = 0.05$; interaction: $F_{2,12} = 0.83$, $P = 0.46$) (fig. 2). There was a positive correlation between seasonal aphid density per plant per date and predator abundance ($F_{1,16} = 50.83$, $P < 0.001$), predator species richness ($F_{1,16} = 43.34$, $P < 0.001$) and predator species diversity ($F_{1,16} = 5.54$, $P = 0.03$), but predator community evenness was unaffected by aphid infestation levels ($F_{1,16} = 0.57$, $P = 0.46$; fig. 3).

Certain predators were clearly well adapted to responding to soybean aphid outbreaks. The most abundant predators (>2% of all specimens) in the system were consistently ants (Hymenoptera: Formicidae), spiders (Araneae), lacewing adults and larvae (Neuroptera: Chrysopidae), lady beetle larvae (Coleoptera: Coccinellidae), *Harmonia axyridis* adults (Coccinellidae), *Hippodamia convergens* adults (Coccinellidae), *Nabis americoferus* (Hemiptera: Nabidae), *Orius insidiosus* (Hemiptera: Anthracoridae) and hoverfly adults (Diptera: Syrphidae). Based on their population responses to soybean aphid densities, these predators could be easily grouped into aphidophilous (taxa whose abundances were positively correlated with seasonal aphid abundance per field) and non-aphidophilous guilds. In this community, seasonal abundances of spiders ($r^2 = 0.25$; $F_{1,16} = 5.39$, $P = 0.03$), lacewing adults ($r^2 = 0.40$; $F_{1,16} = 10.82$,

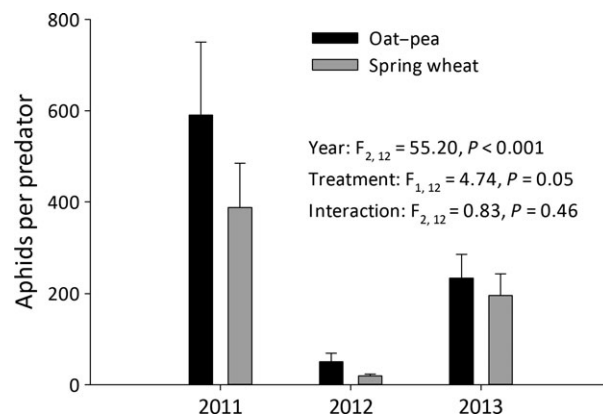


Fig. 2 Seasonal mean (SEM) aphids per predator in soybean preceded by spring wheat or an oat-pea mixture ($n = 3$ fields per year). Predators that are presented per sweep were collected with a sweep net, and aphids were visually sampled per plant. A two-way ANOVA revealed significant effects of both year and preceding crop on aphid to predator ratios ($\alpha = 0.05$).

$P = 0.005$), coccinellid larvae ($r^2 = 0.80$; $F_{1,16} = 62.63$, $P < 0.001$), *Ha. axyridis* ($r^2 = 0.68$; $F_{1,16} = 33.25$, $P < 0.001$) and syrphid adults ($r^2 = 0.55$; $F_{1,16} = 19.71$, $P < 0.001$) were positively correlated with aphid abundance per fields. In contrast, ants ($r^2 = 0.001$; $F_{1,16} = 0.02$, $P = 0.88$), lacewing larvae ($r^2 = 0.14$; $F_{1,16} = 2.54$, $P = 0.13$), *Hi. convergens* ($r^2 = 0.05$; $F_{1,16} = 0.75$, $P = 0.40$), *N. americoferus* ($r^2 = 0.04$; $F_{1,16} = 0.64$, $P = 0.44$) and *O. insidiosus* ($r^2 = 0.07$; $F_{1,16} = 1.26$, $P = 0.28$) seasonal populations were not correlated with aphid abundance per plot, and thus, these taxa are considered non-aphidophilous. There were no significant differences in the abundances of predators per treatment before aphids reached the EIL (year: $F_{2,12} = 12.61$, $P < 0.001$; treatment: $F_{1,12} = 4.39$, $P = 0.06$; interaction: $F_{2,12} = 1.09$, $P = 0.37$).

Discussion

Preceding crop had a strong and consistent effect on soybean aphid densities in 2 of 3 study years. Specifically, spring wheat reduced aphids significantly relative to oat-pea when these crops preceded soybeans. Crop rotation had no effect on aphid populations during the third study year; this year had intermediate aphid densities. If the complex interactions that produce these aphid populations can be understood, crop rotation could be a valuable tool for farmers that wish to reduce soybean aphid pressure and associated pesticide use. This initial comparison of two potential preceding crops illustrates that crop rotations may be a valuable tool, but these specific crops may or may not represent optimal rotation sequences for reducing

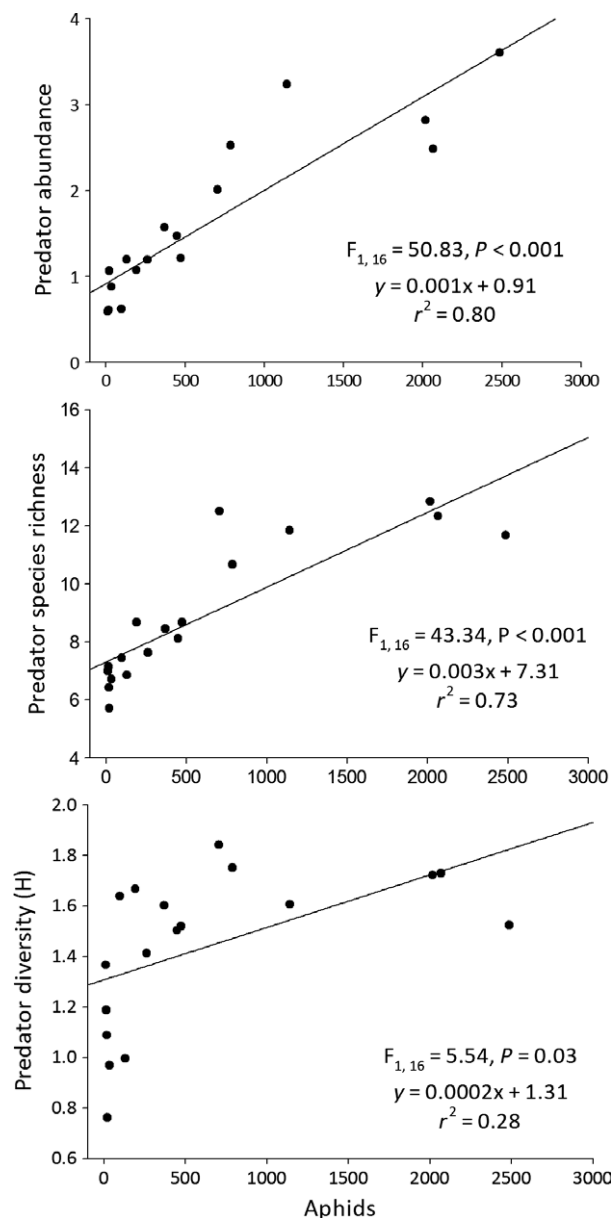


Fig. 3 Correlations between predator community structure and seasonal aphid abundance in soybean. Data points on the figure are soybean fields, units represent seasonal predator communities per sweep and aphids are per plant. All data are pooled across sample years and treatments. Linear regressions were fitted with each comparison ($\alpha = 0.05$).

aphid pests in soybeans. Other research has shown that non-crop plants (i.e. cover crops) preceding soybeans can affect soybean aphid abundance (Koch et al. 2012, 2015; Lundgren et al. 2013). It is not clear how corn, the typical crop preceding soybeans, affects aphid abundance relative to other crop species. Replicated soybean plots were fairly small and near one

another, and thus, we suspect that alates were unable to control their dispersion enough to selectively colonize one treatment vs. another at the scale of our experiment (fig. 1). This means that the strong reductions in aphid abundance were likely largely due to suppression of aphid population growth rates. Ultimately, the mechanisms that underlie the observed effects of crop rotation on soybean aphid should receive additional attention, but could be related to the effects of rotations on the abiotic or biotic components of the soil.

Preceding crop had no detectable direct effects on the predator community, members of which responded to soybean aphid increases. The small plots and close proximity of plots did not prohibit predators from moving among replicates, and this may be one reason why predator communities were similar in the two treatments. Given this caveat, it is noteworthy that the predators did not display a clear preference for soybeans (or soybean aphids) that were preceded by different crops. All of this said, biological control tentatively appears to be compatible with crop rotations within the constraints of our experimental design. Indeed, biological control may even add or synergize with the factors that spring wheat contributes to reducing soybean aphid pressure (Bottrell et al. 1998; Barbosa et al. 2009). Certain aphidophilous predators had a strong, positive numerical response to aphid populations. Some of these taxa are well known aphidophagous species, such as *Harmonia axyridis* (Costamagna and Landis 2006; Bannerman et al. 2015). Others are more glucophagous (e.g. lacewing and syrphid adults; Schneider 1969; Haslett 1989; Canard 2001) and may have responded to the aphid honeydew as a nutritional resource, or they may have been foraging for oviposition sites with high prey densities. A surprising result is that *O. insidiosus* and *Hippodamia convergens* were uncorrelated with aphid abundance as has been previously documented (Desneux and O'Neil 2008; Harwood et al. 2009; Lundgren et al. 2013; Bannerman et al. 2015), questioning the biological control potential of these predators within this study system. It may also be that the rising abundance of certain aphidophilous taxa may limit the aphid-driven population responses of these less specialized predators through competition or intraguild predation (Gardiner and Landis 2007; Gardiner et al. 2011). The positive relationship between aphid abundance and predator diversity and species richness suggests that high aphid abundance did not restrict predator diversity towards only aphidophilous taxa, although other prey populations or habitat characteristics may also have driven these community

patterns. The fact that the community continued to gain species richness as aphids became more abundant suggests that this community is unsaturated. This predator species saturation is regarded as important in reducing pest pressure in at least one other agroecosystem: corn (Lundgren and Fergen 2014; Lundgren and Fausti 2015).

Preceding crops affect the structure and chemistry of soils in ways that can affect insect–plant interactions within a given crop. Water infiltration and holding capacity, soil organic matter, soil aggregate size and bulk density are just some of the physical characteristics of soil that are influenced by crop rotation (Bullock 1992), and these soil characteristics can directly affect plants. Herbivorous insects, especially phloem feeding insects like aphids, are commonly nitrogen limited, and thus, crop rotations that affect N concentrations of the soybeans could affect soybean aphid populations. Indeed, N content of soybeans is positively associated with soybean aphid and potassium is negatively associated with aphid abundance (Noma et al. 2010). In a study investigating the effects of leguminous living mulches on soybean aphid populations, Schmidt et al. (2007) found that N concentration of the soybean plants was affected by the living mulch and this nutrient difference could at least partially explain soybean aphid abundance in plots with and without mulches. Many other nutrients are also affected by rotations (Ferreira et al. 2000; Pederson and Lauer 2004; Anderson 2012). In addition to affecting soil nutrients and physical structure, crops also produce chemistries that can be allelopathic to subsequent crops (Batish et al. 2001). The role of allelopathic rotation sequences on insect populations has not been directly investigated.

Crop rotation can also affect the biology associated with the soil, which in turn affects insect communities and pest populations in a focal phase of the rotation. Soil microbial communities strongly influence the physiology of crop plants, and these communities are often affected by crop rotation or sequence of crops within a rotation (Hungria et al. 2009; Yin et al. 2010; Lupwayi and Blackshaw 2013). A good example is how crop sequences alter the microbial symbioses associated with the roots of soybeans (Ferreira et al. 2000) and maize (Arihara and Karasawa 2000) and the microbe-associated physiology of these crops. Soil entomopathogens are also affected by crop rotations (Susurluk and Ehlers 2008; Jabbour and Barbercheck 2009), and the relative abundances of specific pathogens influence pest populations (Vega and Kaya 2012). Finally, more complex rotations

have been associated with greater predator diversity, which could affect the relative abundance of pests in these systems (Brust and King 1994; O'Rourke et al. 2008). We monitored predator populations in the current system, and this will be a focus of a more in-depth investigation into how aphids and weed communities interact with predator communities in soybean.

It is unlikely that many farmers will change their crop rotation practices solely because of potential pest management benefits pointed out in our study when alternative management strategies (e.g. host plant resistance, biological control and insecticides) remain economically viable. Producers will gain an array of benefits when diversifying the rotations, including reducing the need for pesticides (Deytieux et al. 2012, Colbach et al. 2014). Wexel et al. (2014), reviewing agroecological practices related to sustainable agriculture, noted that diverse crop rotations are poorly integrated with agriculture. As food production systems are altered to increase farm resilience, it gives opportunities to producers to optimize multifunctional rotations, and pest management is a key consideration for these rotations.

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