Environmental Entomology, 47(2), 2018, 292–299
doi: 10.1093/ee/nvy004
Advance Access Publication Date: 9 February 2018
Research

Community and Ecosystem Ecology

Influence of Winter Cover Crop Mulch on Arthropods in a Reduced Tillage Cucurbit System

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Subject Editor: Deborah Finke

Received 21 September 2017; Editorial decision 4 January 2018

Abstract

Winter cover crop mulches can diversify agricultural habitats and provide a range of benefits for crop production and pest management. Here we report the influence of strip tilled winter cover crop mulches on arthropod abundance in organic vegetable plots. Crookneck squash (*Cucurbita pepo* L.; Cucurbitales: Cucurbitaceae) was direct seeded into mowed and strip tilled barley (*Hordeum vulgare* L.; Poales: Poaceae), crimson clover (*Trifolium incarnatum* L.; Fabales: Fabaceae), a barley + crimson clover mixture, or a no-cover crop control. Arthropods on squash plants were assessed weekly using visual counts. Seed predation was assessed using weed seed arenas. In 2013, mixed species cover crops produced the most ground cover, fewest weeds, and largest squash plants, but herbivore and predator abundance were not correlated with any of those factors. In 2014, mixed species cover crops again produced the most ground cover and fewest weeds, but the largest squash plants were found in no-cover crop control plots, which also had the highest herbivore abundance per plant. Predator and herbivore abundance were positively correlated with squash plant size in 2014. There were no differences in seed predation across treatments. Differences in ground cover biomass and weed presence between the 2 yr may have contributed to differences in squash plant quality and subsequent herbivore abundance between seasons. Results suggest that arthropods on plants responded largely indirectly to cover crops through host plant quality. Results are interpreted in light of overall costs and benefits of cover cropping.

Key words: pest management, strip tillage, reduced tillage, barley, crimson clover

Since roughly the middle of the last century, western agriculture has consisted predominantly of monoculture planting, which requires high pesticide input to manage insect damage relative to polyculture planting (Horwith 1985, Altieri 1991, Malezieux et al. 2009). Practices to diversify agricultural fields, such as intercropping or planting buffer strips, can increase natural enemy abundance and diversity (Altieri and Letourneau 1982, Landis et al. 2000, Langellotto and Denno 2004, Snyder et al. 2006, Letourneau et al. 2010) and reduce insect pest abundance (Tonhasca and Byrne 1994, Ponti et al. 2007, Malezieux et al. 2009, Kremen and Miles 2012), relative to monoculture plantings. However, these effects do not always improve crop yield (Poveda et al. 2008, Kremen and Miles 2012). While direct effects of agricultural diversification on pest suppression have been suggested, for example, by interfering with host plant detection (Finch and Collier 2000, Morley et al. 2005, Manandhar et al. 2017), indirect effects via natural enemy attraction are more commonly studied.

Methods to attract natural enemies of insect pests and weed seeds are particularly needed for organic vegetable production, a growing industry for which insect damage and weed pressure present major constraints (Oerke 2006, Zehnder et al. 2007, USDA ERS 2016). Living, dying, or dead cover crops or other vegetation such as weedy or natural areas can provide habitat for arthropod predators of pests and weed seeds, subsequently increasing their abundance and activity (Bugg et al. 1991, Carmona and Landis 1999, Lundgren and Fergen 2010, Diehl et al. 2011, Lundgren and Fergen 2011, Sereda et al. 2015). The effects of cover crop residue have been well-studied in terms of weed suppression, where ground cover biomass is key for weed suppression, particularly early in the growing season (Teasdale 1996, Mirsky et al. 2013). Weed seed predators are often a focus of cover crop residues studies, with somewhat inconsistent results: cover crop residue has been found to decrease (Quinn et al. 2016) or increase weed seed predator activity density (Ward et al. 2011, Blubaugh and Kaplan 2015), responses potentially dependent on the frequency or timing of disturbance within systems. In addition, weed seed predators have been found to respond to weed biomass within cover cropped systems (Blubaugh and Kaplan 2015), suggesting that weed presence in response to cover cropping is an important consideration. Despite recent attention given to cover crops for ecosystem services, there are still uncertainties about the influence of cover crops for pest suppression. Predictions based on cover crops in field crop rotations suggest that while cover crops are expected to increase services from beneficial arthropods, they may not provide pest suppression (Schipanski et al. 2014). These models, however, did not include the influence of cover crop species mixtures, which the authors suggest may be relevant to understanding the benefits of cover crops.

Spring-killed cover crops, particularly when suppressed by mowing (Laub and Luna 1992), can increase predation and reduce damage in maize (Lundgren and Fergen 2010). However, the influence of single and mixed species spring-killed cover crop mulches on foliar pest and predator arthropod abundance in organic vegetable systems in particular is not well understood. The current study was part of a larger study designed to investigate the effects of mowed and strip-tilled winter cover crops on nematodes, weeds, and arthropods in organic vegetable plantings in the mid-Atlantic region. Maryland organic vegetable growers frequently plant cereals such as barley (*Hordeum vulgare* L.) or mixtures of cereals and legumes such as crimson clover (*Trifolium incarnatum* L.), which are well-suited for the temperature and precipitation conditions of the mid-Atlantic (Clark 2007), and moreover are eligible for the state's cover crop cost-share program (Maryland Department of Agriculture 2015). Cover crop species mixtures are popular among many growers because they provide a desired combination of characteristics, such as plant architecture, biomass accumulation, or nitrogen fixation (Snapp et al. 2005), and can increase structural diversity and encourage predator populations (Woodcock et al. 2007). Previously reported results from this study showed that mowed crimson clover, barley, or a barley + crimson clover mixture were similarly effective at weed suppression, and that cover crop biomass was a key factor in weed suppression and crop yield in organic crookneck squash (*Cucurbita pepo* L.) (Buchanan et al. 2016). Here we ask whether crimson clover and barley cover crops grown alone and in mixture influenced pest and natural enemy arthropod populations in organic crookneck squash. We also ask whether pest and natural enemy abundance are correlated with vegetative factors associated with cover crop treatments: ground cover biomass, weed density, and squash plant quality.

Agricultural diversification has been shown to reduce pest abundance in cucurbit crops (Hooks et al. 1998, HansPetersen et al. 2010, Hinds and Hooks 2013). Cucurbits are an important commodity in the United States, comprising roughly 5% of the production value of all commercial vegetables (National Agricultural Statistics Service 2016). Cucurbits, including squash, cucumber, and pumpkin, experience a range of specialist and generalist insect pests which can damage fruit or foliage, reduce yield, and vector disease (Hladun and Adler 2009, Shapiro et al. 2014). Squash bugs (*Anasa tristis* (De Geer) and *Anasa armigera* (Say), Hemiptera: Coreidae) are important specialist pests of cucurbit crops. Squash bugs overwinter as adults, emerging in the spring to feed and lay eggs on cucurbit plants. The piercing-sucking feeding habit of juveniles and adults causes leaf wilt, and prolonged feeding can lead to leaf or plant death (Doughty et al. 2016). Chemical control is commonly used for squash bugs, but organic tactics are less effective (Doughty et al. 2016). Management techniques such as trap cropping and companion planting give inconsistent results for squash bug control (Dogramaci et al. 2004, Grasswitz 2013, Fair and Braman 2017, Kahn et al. 2017), but straw and plastic mulches have been shown to increase squash bug numbers, potentially via direct effects such as microclimate effects and physical protection (Cartwright et al. 1990, Cranshaw et al. 2001).

Specialist striped cucumber beetles (*Acalymma vittatum* (F.), Coleoptera: Chrysomelidae) and generalist spotted cucumber beetles (*Diabrotica undecimpunctata* Mannerheim, Coleoptera: Chrysomelidae) are also important cucurbit pests. Both species overwinter as adults, emerging in the spring to feed on cucurbit leaves and flowers, and cause severe damage through girdling. Striped cucumber beetles lay eggs at the base of cucurbit plants, and larvae feed on cucurbit roots. Cucumber beetles are direct and indirect pests of cucurbits, and can vector bacterial wilt (Leach 1964, Snyder 2015). In organic systems, predators may provide a measure of management for cucumber beetles. Gut content analysis has shown that generalist predators feed on cucumber beetles (Lundgren et al. 2009) and that increasing the abundance of generalist predators can help suppress pests and subsequently reduce damage in cucurbits (Brust 1997, Sasu et al. 2010).

Here, we report how cover crop mulches of barley, crimson clover, and a barley + crimson clover mixture influenced arthropod pest and predator abundance in organic crookneck squash, in comparison to a no-cover crop control. During two growing seasons, abundance of foliar arthropods, aboveground vegetative biomass, weed density, and squash plant quality were measured to test three hypotheses: 1) winter cover crop mulch decreases pest abundance, 2) winter cover crop mulch increases predator abundance, and 3) mixed species winter cover crops support more predators and lead to greater pest suppression than single species winter cover crops.

Materials and Methods

Experimental Design

This experiment was conducted at the Central Maryland Research and Education Center in Upper Marlboro, MD in 2013 and 2014 in a field under organic transition since 2010. The entire field area was 66 × 71 m and was divided into sixteen 17 × 17 m plots. The experiment consisted of four replicates of four treatments in a Latin square design: barley (160 kg/ha seeding rate), crimson clover (33 kg/ha), barley + crimson clover mixture (84 and 15 kg/ha, respectively), and a no-cover crop control. Plots were separated by at least 7 m wide fescue (*Festuca* sp. L., Poales: Poaceae) alleyways maintained with regular mowing. Plots were seeded on 30 September 2012 and 20 September 2013, and treatments were consistently applied to the same plots across years.

Approximately 1 mo before main crop seeding (see Supplementary Table S1 for experimental timeline), cover crops and weeds were mowed (flail mower, John Deere 360, Moline, IL) and rows to be planted with the crop were tilled in strips (two-row strip tiller, Ferguson Manufacturing, Sulfolk, VA) in 12 rows per plot. Mowing during flowering killed the cover crops, although a small amount of reemergence occurred later in the season. Rows were 0.3 m wide with 1 m inter-row spacing. Prior to crop seeding in 2013, germinated weeds in tilled strips were sprayed with organic herbicide (Avenger Weed Killer, Cutting Edge Formulations, Inc., Buford, GA); however, rainfall shortly after application may have partially compromised herbicide effectiveness. In 2014, weed pressure across all plots necessitated re-tilling in strips of cover crop plots (Craftsman 4-cycle Mini Tiller, KCD IP, LCC, Hoffman Estates, IL), and control plots received light cultivation (Craftsman 190CC rear tine tiller, KCD IP, LCC) across the entire plot prior to planting.

Crookneck squash ('Yellow Organic' Johnny's Selected Seeds, Winslow, ME) were direct seeded within the tilled strips at 1.2 m intra-row plant spacing, 10 plants per row. After seeding, plots were fertilized at 78–90 kg N/ha with pelletized 3-2-3 N-K-P organic chicken manure (MicroSTART60, Perdue AgriRecycle, Sussex Co., DE). Throughout the 2013 season, all plots were hand weeded as needed by hand-pulling or hoeing throughout the plot. Due to heavy weed pressure in 2014, a 0.5-m-diameter circle around each squash plant was hand weeded, and the remainder of each plot was mowed twice during the season. Mowing events took place 8 to 11 d prior to any subsequent arthropod survey, and so while mowing likely disturbed arthropods within plots, arthropods would have had time to recolonize squash plants before surveys. Squash plants were drip irrigated as needed to mitigate periods of low rainfall.

Data Collection

Plant Characteristics

Although the objectives of this study focus on arthropods, factors such as host plant size or quality and neighboring plant density or diversity can be affected by cover crops, and can in turn influence arthropods (Mattson 1980, Price 1991, Knops et al. 1999, Haddad et al. 2001, Altieri and Nicholls 2004). A detailed analysis of characteristics of the main crop, the cover crop, and weeds across all 4 yr of this study can be found in a previous publication (Buchanan et al. 2016); here we focus on the relationships between arthropods and ground cover biomass, early season weed density, squash plant size, squash leaf nutrients, and squash yield. Biomass of aboveground plant material (cover crops and weeds) prior to mowing (6 May 2013 and 8 May 2014) was measured in four 0.3 × 0.3 m quadrats per plot, dried, and weighed. After squash planting (29 June 2013 and 18 June 2014), weeds in eight 0.3 × 0.3 m quadrats between (n = 4) or within (n = 4) planted rows were counted and identified to species using a reference guide (Uva et al. 1997). Squash plant size was measured by maximum height and width at the beginning of harvest (26 July 2013 and 28 July 2014). Squash plant leaf nutrients were measured within 3 d of first harvest each year: one newly expanded leaf was excised from eight plants chosen at random per plot, combined into a single sample per plot, dried, and sent to A&L Laboratories (Memphis, TN) for assessment of nitrogen, potassium, and phosphorus. Squash plants were harvested every 3 d between 26 July 2013 and 16 August 2013, and between 28 July 2014 and 26 August 2014. Fruits assessed as marketable were weighed in the field.

Arthropods

Weekly foliar arthropod surveys began when squash plants had four fully expanded true leaves, corresponding to 19 days after planting (DAP) in 2013 and 30 DAP in 2014. Each week, one plant was selected at random from each of the 10 inner plot rows and visually examined for arthropods and egg masses. Squash plants were examined on the top and bottom of leaf surfaces, stems, and the ground surface immediately around the plant where squash bug adults are often found (Palumbo et al. 1991). Squash bug egg masses, newly hatched squash bug nymph clusters, and stink bug (various spp.) egg masses were each counted as a single unit, representing a conservative estimate of abundance. All other arthropods were counted as individuals and identified to species or genus for cucurbit specialists, or to order (Table 1) using reference guides (White 1998, Eaton and Kaufman 2007, Evans 2007).

Two surveys of seed predation were conducted each year in the early and late growing season. In each plot, two seed arenas consisting of bottom-perforated Petri dishes were filled with soil and sunk flush with the ground. One seed arena in each replicate was covered with a mesh screen mounted 1.5 cm off the ground surface to prevent bird and mammal predation, the other arena in each replicate was left uncovered. Ten seeds each of common lambsquarters (*Chenopodium album* L.; Caryophyllales: Amaranthaceae) and redroot pigweed (*Amaranthus retroflexus* L.; Caryophyllales: Amaranthaceae) were placed on the soil surface of each seed arena. After 24 h in the field, remaining seeds were counted.

Statistical Analyses

Plant Characteristics

Pre-mowing aboveground plant biomass (g/m^2), weed density, squash plant size (m^2), squash leaf nitrogen, potassium, and phosphorus (% of dry weight), and squash yield (kg/ha) from 2013 and 214 were each analyzed separately using generalized linear models (function = glm, package = MASS) in response to treatment and spatial blocks as fixed factors. All data followed Gaussian distributions except weed density and yield in 2014, which followed a Poisson distribution. Pairwise correlations among biomass, weed density, squash plant size, and squash yield were analyzed with Spearman rank correlation test (function = cor.test, package = stats).

Arthropods

Pest arthropods that specialize on non-cucurbit plants and any arthropod taxa making up <1% of the remaining individuals were excluded from analysis. Remaining arthropod taxa included specialist and generalist cucurbit pests and potential predators of those pests (Table 1). Due to inter-annual variability, arthropods were analyzed separately for 2013 and 2014. All data were analyzed in R version 3.2.2 (R Core Team 2015). Abundance of foliar arthropod groups was summed across each season and analyzed with generalized linear models using either Gaussian or Poisson distributions according to each population's distribution; striped cucumber beetle data in 2013 did not fit a known distribution and so was log-transformed to meet Gaussian distribution assumptions (function = glm; package = MASS, family = Gaussian or Poisson) (Venables and Ripley 2002). Models included treatment and row-wise and column-wise Latin square blocks as fixed factors (Quinn and Keough 2002). Means separations were performed using Tukey's Honestly Significant Difference (HSD) test. Herbivorous and predacious

Table 1. Arthropod taxa abundance on squash plants in 2013 and 2014

Common name	Taxa	2013	2014
Squash bug egg mass	*Anasa* spp.	1,681	759
Squash bug nymph	*Anasa* spp.	357	542
Squash bug adult	*Anasa* spp.	234	86
Striped cucumber beetle	*Acalymma vittatum*	619	8
Spotted cucumber beetle	*Diabrotica undecimpunctata*	77	89
Flea beetle	Alticini	27	851
Leafhopper	Membracidae	73	762
Caterpillar	Lepidoptera	149	48
Scale insect	Coccoidea	26	113
Grasshopper	Acrididae	67	40
Pest stink bug egg mass	Pentatomidae	27	41
Spider	Araneae	262	183
Lady beetle larva & adult	Coccinellidae	33	28
Cricket	Gryllidae	27	24

Plants were surveyed weekly for 6 wk in each year. Non-cucurbit pests, pollinators, and arthropods comprising <1% of the remaining total were excluded from analysis. Arthropods were identified to the taxonomic level listed in the table.

species were each combined to analyze pairwise relationships between herbivore and predator abundance and ground cover biomass, weed density, and squash plant size, and between abundance of herbivores and predators. Correlations were performed with Spearman rank correlation test (function = cor.test, package = stats).

Preliminary analysis showed no difference in seed removal between seed species, so proportion seed removal was combined across seed species. Proportion of seeds removed for covered and uncovered arenas was averaged across the two trials per date in each plot, and analyzed with repeated measures mixed models (function = lmer; package = lme4) (Bates et al. 2015). Original model included treatment and spatial blocks as fixed factors, and plot number as a random factor.

Results

Plant Characteristics

Weed species encountered in each year are listed in Supplementary Table S2, and a thorough description of weed community characteristics is provided in a previously published paper (Buchanan et al. 2016). Ground cover biomass, weed density, and squash plant size were significantly influenced by cover crop treatments in 2013 and 2014 (Table 2). In 2013, cover crop treatments provided nearly three times or more the ground cover biomass as the control treatment, and had at up to three times fewer weeds. Only plants in the mixed species treatment had larger squash plants. In 2014, ground cover biomass was overall lower than in 2013, and was twice as high in treatments with crimson clover relative to those without. Weeds were twice as dense but squash plants were bigger in control plots compared to cover crop plots in 2014. Squash yield patterns were similar to plant size in both years (Supplementary Table S3). Squash leaf nutrients were significantly influenced by cover crop treatment in 2014 but not in 2013 (Supplementary Table S3).

Ground cover biomass and weed density were significantly negatively correlated in both years (Fig. 1A and 1D); ground cover biomass and squash plant size were positively correlated in 2013 (Table 3). Weed density and squash plant size were negatively correlated in 2013 and positively correlated in 2014 (Fig. 1B and 1E). Squash yield and plant size were positively correlated in both years, and squash yield and ground cover biomass were positively correlated in 2013 (Table 3).

Arthropods

Arthropod abundance by taxa and year are provided in Supplementary Materials (Supplementary Figs. S1 and S2). In 2013, abundance of herbivorous arthropods was influenced by treatment (χ^2 = 26.8, df = 3, P < 0.0001) but predatory arthropods were not (χ2= 0.6, df = 3, P = 0.9, Supplementary Table S4), and herbivore and predator abundance were not significantly correlated (Spearman's ρ = 0.04, P = 0.9, Table 3). Pairwise comparisons were not significantly different, but crimson clover plots had over twice as many herbivorous species than control plots. Of the individual taxa analyzed, striped cucumber beetles were the only group to be influenced by treatment (χ^2 = 41.8, df = 3, P < 0.0001, Supplementary Table S4). Again pairwise comparisons were not significantly different, but crimson clover and mixed species plots had 40% more striped cucumber beetles than control or barley plots (Supplementary Tables S4 and S5). Neither predator nor herbivore abundance were correlated with ground cover biomass, weed density, squash plant size, or yield in 2013 (all P > 0.09, Table 3, Fig. 1C).

In 2014, herbivorous species were again influenced by treatment (χ^2 = 15.3, df = 3, P < 0.01) while predatory species were not (χ^2 = 1.6, df = 3, P = 0.7, Supplementary Table S4), however in this year control plots contained over twice as many herbivores as plots with cover crop mulches (Table 2) and predator and herbivore abundance were positively correlated (Spearman's ρ = 0.9, P < 0.0001, Table 3). Squash bug egg masses were influenced by treatment (χ^2 = 9.2, df = 3, P = 0.03), with more egg masses in control plots relative to barley plots (Tukey's HSD P = 0.02, Supplementary Table S4 and S5). Aphid abundance was also influenced by treatment (χ^2 = 1.6, df = 3, P = 0.7), with a nonsignificant increase in abundance in mixed species cover crop plots relative to barley plots (Supplementary Table S4 and S5). In 2014, predator and herbivore abundance were positively correlated with squash plant size and yield (Table 3, Fig. 1F). There was no effect of cover crop or survey date on proportion of seeds removed in either study year for either covered or uncovered seed arenas (Supplementary Table S4). Average seed removal rate after 24 h was 52% in 2013 and 24% in 2014.

Discussion

We found mixed support for our original hypotheses. We predicted 1) that winter cover crop mulch treatments would decrease pest abundance, and found that true in 1 yr. In 2013, squash plants in crimson clover plots had 30% more herbivores per plant than those in control plots. In 2014, in contrast, squash plants in control plots had twice as many herbivores as those in cover crop plots. We next predicted that 2) winter cover crop mulch would increase predator abundance, and that 3) mixed species cover crops would have the most predators and fewest pests of all the cover crop treatments.

Table 2. Mean ± SEM average ground cover dry biomass, weed density, squash plant size, and herbivore abundance averaged across plots for 2013 and 2014

Year	Treatment	Ground cover biomass (g/m^2)	Weed density (/m^2)	Squash plant size (m^2)	Herbivore no. (/plant)
2013	Control	194.8 ± 13.3$_a$	421.6 ± 55$_a$	0.6 ± 0.1$_a$	17.9 ± 3.9$_a$
	Barley	546.3 ± 76.6$_b$	238.3 ± 36.4$_{ab}$	0.5 ± 0.1$_a$	19.2 ± 2.2$_a$
	Crimson clover	603.6 ± 16.1$_b$	303.3 ± 61$_{ab}$	0.6 ± 0.04$_{ab}$	25.1 ± 3.4$_a$
	Mixed	797.4 ± 24.6$_c$	115.5 ± 28.7$_b$	0.8 ± 0.01$_b$	20.4 ± 1.4$_a$
2014	Control	111.3 ± 5.5$_a$	601.9 ± 37.5$_a$	0.3 ± 0.03$_a$	13.3 ± 5.8$_a$
	Barley	128.2 ± 24.7$_a$	273.9 ± 38.4$_b$	0.1 ± 0.03$_b$	5.5 ± 1.6$_a$
	Crimson clover	223.1 ± 2.8$_b$	260.9 ± 65$_b$	0.2 ± 0.01$_b$	5.8 ± 1.3$_a$
	Mixed	244.5 ± 12.5$_b$	250.6 ± 37.5$_b$	0.2 ± 0.01$_b$	6.5 ± 1.2$_a$

Ground cover biomass was measured prior to mowing in four 0.3 × 0.3 m quadrats per plot. Weed density was measured in eight 0.3 × 0.3 m quadrats per plot. Plant size was measured as maximum height by width of each squash plant. Herbivore abundance was visually assessed weekly. Subscript letters indicate differences at α = 0.05 using Tukey's HSD.

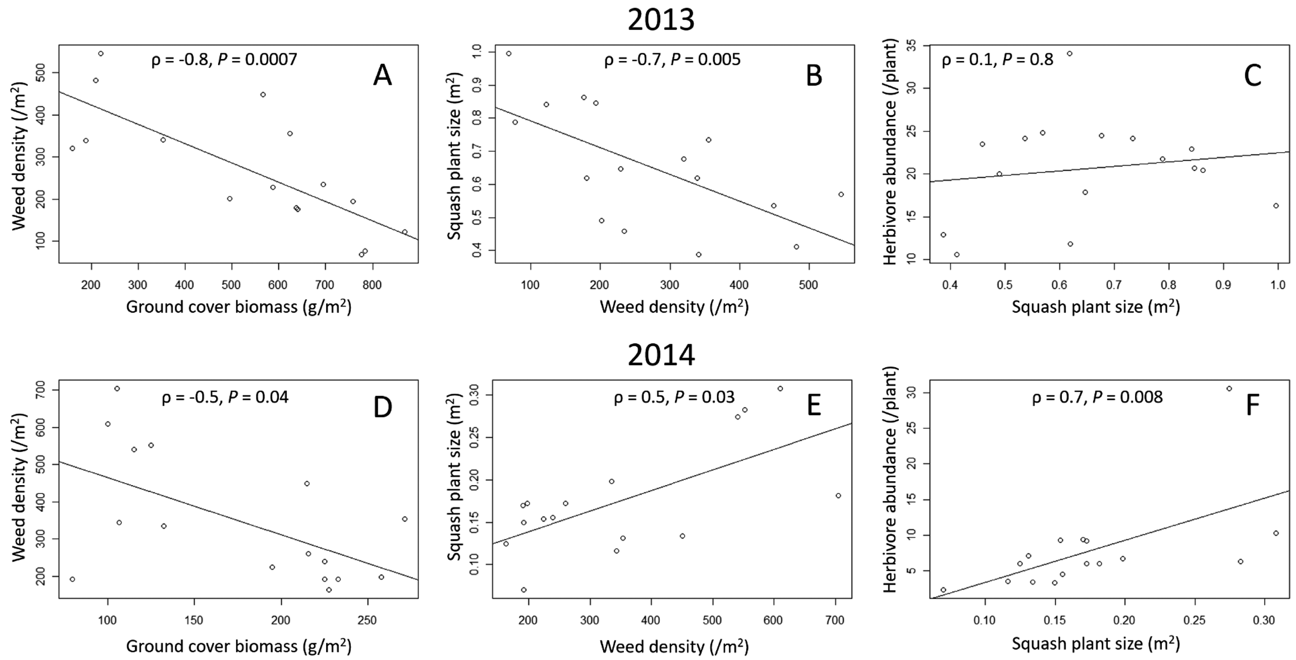

Fig. 1. Correlations between ground cover biomass and weed density in 2013 (A) and 2014 (D), between weed density and squash plant size in 2013 (B) and 2014 (E), and between squash plant size and herbivore abundance in 2013 (C) and 2014 (F). Rho (ρ) and *P* values are from Spearman rank correlation tests. Ground cover biomass was measured prior to mowing in four 0.3 × 0.3 m quadrats per plot. Weed density was measured in eight 0.3 × 0.3 m quadrats per plot. Plant size was measured as maximum height by width of each squash plant. Herbivore abundance was visually assessed weekly.

Table 3. Spearman rank correlation results for pairwise comparisons among plant characteristics and arthropod abundance for 2013 and 2014

2013	Biomass (g/m^2)	Weed density (/m^2)	Squash size (m^2)	Yield (kg/ha)	Herbivores (/plant)
Weed density (/m^2)	**ρ = −0.8** ***P* = 0.0007**				
Squash size (m^2)	**ρ = 0.6** ***P* = 0.02**	**ρ = −0.7** ***P* = 0.005**			
Yield (kg/ha)	**ρ = 0.5** ***P* = 0.05**	ρ = −0.4 *P* = 0.08	**ρ = 0.7** ***P* = 0.007**		
Herbivores (/plant)	ρ = 0.1 *P* = 0.7	ρ = 0.1 *P* = 0.8	ρ = 0.1 *P* =0.8	ρ = 0.3 *P* = 0.2	
Predators (/plant)	ρ = 0.2 *P* = 0.5	ρ = −0.3 *P* = 0.3	ρ = 0.4 *P* = 0.1	ρ = 0.3 *P* = 0.2	ρ = 0.04 *P* = 0.9

2014	Biomass (g/m^2)	Weed density (/m^2)	Squash size (m^2)	Yield (kg/ha)	Herbivores (/plant)
Weed density (/m^2)	**ρ = −0.5** ***P* = 0.04**				
Squash size (m^2)	ρ = 0.2 *P* = 0.4	**ρ = 0.5** ***P* = 0.03**			
Yield (kg/ha)	ρ = 0.08 *P* = 0.7	**ρ = 0.4** ***P* = 0.09**	**ρ = 0.7** ***P* = 0.002**		
Herbivores (/plant)	ρ = −0.1 *P* = 0.8	ρ = 0.3 *P* = 0.2	**ρ = 0.7** ***P* = 0.008**	**ρ = 0.7** ***P* = 0.01**	
Predators (/plant)	ρ = 0.05 *P* = 0.9	ρ = 0.3 *P* = 0.3	**ρ = 0.6** ***P* = 0.02**	**ρ = 0.6** ***P* = 0.01**	**ρ = 0.9** ***P* < 0.0001**

Results in bold indicate a significant (α = 0.05) correlation. Ground cover biomass was measured prior to mowing in four 0.3 × 0.3 m quadrats per plot. Weed density was measured in eight 0.3 × 0.3 m quadrats per plot. Plant size was measured as maximum height by width of each squash plant. Herbivore and predator abundance was visually assessed weekly.

However, we found no predator response to treatments in either year and no significant benefits to the mixed species cover crop over single species.

Patterns of ground cover biomass, weed density, and squash plant quality in response to treatment and across years may provide some insight to why herbivore abundance changed in response to treatment across years. While ground cover biomass and weed density responded similarly to treatment in 2013 and 2014—with the lowest biomass and most weeds in control plots—squash plant size did not respond predictably across years. We would expect the largest crop plants where there are the fewest weeds, as has been found in previous studies (Einhellig 1996, Evans et al. 2003), but in 2014 squash plants were largest and had the highest yield in control plots, the plots with the most weeds. That we found the most herbivores on the largest plants in that year suggests that herbivores responded to host plant quality reflected in plant size more than cover crop treatment. Evidence for herbivore attraction to larger plants or plant parts has been shown in a number of systems (Price 1991). Indirect effects of cover crops and other management tactics on arthropods are important (Bugg et al. 1991), and are predicted to increase under agricultural diversification (Mediene et al. 2011). Although plant size may lead to higher arthropod numbers simply due to an increase in leaf area, from a pest management standpoint where control tactics are implemented based on pest thresholds, numbers of pests per plant is the measurement of interest. That we see strong correlations between squash plant size and arthropod abundance in 2014 but not in 2013 when squash plant quality overall was higher, suggests that when plant quality reaches a lower threshold, arthropods may begin to more strongly differentiate among host quality.

The heterogeneous environment provided by cover crop mulches or weeds, in contrast to a monoculture crop on bare ground, may be expected to be less attractive to specialist crop pests like squash bugs and cucumber beetles (Agrawal et al. 2006), since they must search through non-host materials to find suitable hosts. Squash bugs depend on contact with plants to determine suitability (Cook and Neal 1999), making heterogeneous environments potentially time consuming. However, we found that squash bugs laid more eggs in control plots in 2014, which had the highest density of mowed weeds and therefore potentially the most heterogeneous environment. Previous research found more squash bugs in mulched relative to bare ground plots, suggesting that factors such as temperature, moisture, or protection may be more important than host apparency to squash bugs (Cartwright et al. 1990, Cranshaw et al. 2001).

Striped cucumber beetles were most abundant in crimson clover plots in 2013. Previous research found cucumber beetles to be less abundant in cucurbits when intercropped with sun hemp (Hinds and Hooks 2013), and abundance of some cucurbit pests has been reduced when living mulch or border crops were implemented (Hooks et al. 1998, HansPetersen et al. 2010). The presence of living secondary crops may have contributed to cucumber beetle suppression in the previous study, where an increase in spider abundance was also detected. While the current study contained living vegetation in the form of weeds, particularly in 2014, weedy vegetation may provide less predictable natural enemy resources when compared to phenologically similar living secondary crops of one or two species.

Some results in 2014 were unexpected: the largest squash plants were in the plots with highest weed density, and weed density correlated positively with squash plant size. This may indicate the influence of other unmeasured environmental variables in this study. Across all treatment plots from 2013 to 2014, ground cover biomass dropped by 67%, squash plant size dropped by 68%, and herbivore abundance dropped by 64%, while weed density increased by 29%. The overall increase in weed density necessitated a change in weed management practices, where weeds in all plots were mowed rather than manually removed. Mowing for weed management differed from mowing to suppress the cover crops, in that mowing a flowering cover crop prevents regrowth and results in a nonliving surface mulch, while mowing a diverse weed community results in a short stand of living vegetation capable of competing with or allelopathically affecting crop plants. Because this tactic was applied equally to all plots on the same dates, treatment effects can still be determined, but it is possible that weed competition or allelopathy is responsible for the observed reductions in squash plant size and leaf nutrient content from 2013 to 2014, particularly when combined with cover crops. Cereal cover crops such as barley, for example, are strong competitors (Akemo et al. 2000, Snapp et al. 2005, Flower et al. 2012, Hayden et al. 2012), and may deplete water or nutrient resources prior to main crop planting. Because plant size and nutrient content can influence arthropod behavior (Price 1991, Awmack and Leather 2002), changes in weed density and management across years may also explain the reduction in arthropod abundance in 2014.

Our second hypothesis, that natural enemies would be enhanced by cover crop mulch, was not supported by our results. Habitat complexity is expected to increase natural enemy abundance (Landis et al. 2000, Letourneau et al. 2010), particularly when provided by ground surface residue (Langellotto and Denno 2004). Previous studies have found cover crops increase foliar (Bryant et al. 2013, 2014) as well as ground-dwelling or subterranean (Shearin et al. 2008; Lundgren and Fergen 2010, 2011) natural enemies. Ground-dwelling arthropods respond positively to structural complexity provided by cover crops and weeds (Altieri et al. 1985, Carmona and Landis 1999, Rypstra et al. 1999, Woodcock et al. 2007, Jackson and Harrison 2008, Shearin et al. 2008, Diehl et al. 2011, Sereda et al. 2015). Because the structural complexity that these previous studies found contributing to natural enemy activity is a direct effect of cover crops, and our study found no responses by natural enemies, this may indicate further support for the importance of indirect effects relative to direct effects in this study. Many previous natural enemy studies focused on ground-dwelling arthropods, however, a group not sufficiently investigated in our study. Although there were no treatment effects on seed predation, lack of differences in seed removal between covered and uncovered seed arenas suggests that vertebrate seed predators, which were excluded by covered arenas, were not important agents of weed seed predation in this study. A previous study using six weed seed species, including common lambsquarters used in our study, in cover crops also found most weed seed predation done by invertebrates (Gallandt et al. 2005).

Contrary to the prediction of our final hypothesis, mixed species cover crops were not better at attracting predators or suppressing pests relative to single species cover crops. Generally, we found the effects of the mixed species treatment similar to that of the crimson clover treatment. Although habitat diversification is expected to increase arthropod diversity and pest suppression (Letourneau et al. 2010), in practice single species cover crops can provide equivalent or better pest suppression or support for predators relative to more diverse plant communities (Altieri et al. 1985, Creamer et al. 1997). This suggests that the identity of cover crop species, whether used singly or in mixture, remains an important consideration for pest suppression, as has been suggested in previous studies (Landis et al. 2000, Bryant et al. 2014). Cover crop composition is particularly important considering that cover crops may influence not only arthropod populations, but also soil conditions, weed presence, and crop performance (Teasdale and Mohler 1993, Creamer et al. 1997, Dabney et al. 2001, Nascente et al. 2015). In our study, the presence of cover crops resulted in smaller plants and lower yield in one study year. Cover crop selection must balance providing habitat diversity to support arthropod populations and community stability, as well as provide appropriate growing conditions for crop performance. Therefore, careful consideration of cover crop species within mixtures and tactics to reduce cover crop-main crop competition, such as proper timing of cover crop suppression to prevent cover crop re-emergence, are essential. Our results emphasize the need for longer studies and meta-analyses of shorter studies (e.g., Tonhasca and Byrne 1994) to understand the overall direct and indirect effects of cover crops in agro-ecosystems.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

Acknowledgments

We thank L. N. Kolb, G. Chen, L. G. Hunt, P. L. Coffey, and many field technicians for field assistance, and the facilities crew at the Central Maryland Research and Education Center in Upper Marlboro, MD. Many helpful comments were provided by the Szendrei lab group at Michigan State University and the Hooks and Hamby lab groups at the University of Maryland. This project was funded by USDA-NIFA-OREI 2010-51300-21412.

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