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Arable weeds, cover crops, and tillage drive soil microbial community composition in organic cropping systems

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ABSTRACT

Cover crops have traditionally been used to reduce soil erosion and build soil quality, but more recently cover crops are being used as an effective tool in organic weed management. Many studies have demonstrated microbial community response to individual cover crop species, but the effects of mixed species cover crop communities have received less attention. Moreover, the relationship between arable weeds and soil microbial communities is not well understood. The objective of this study was to determine the relative influence of cover crop diversity, early-season weed communities, and tillage on soil microbial community structure in an organic cropping system through the extraction of fatty acid methyl esters (FAMEs). A field experiment was conducted between 2009 and 2011 near Mead, NE where spring-sown mixtures of zero (control), two, and eight cover crop species were included in a sunflower–soybean–corn crop rotation. A mixture of four weed species was planted in all experimental units (excluding the no-cover control), and also included as an individual treatment. Cover crops and weeds were planted in late-March, then terminated in late-May using a field disk or sweep plow undercutter, and main crops were planted within one week of termination. Three (2009) or four (2010–11) soil cores were taken to a depth of 20 cm in all experimental units at 45, 32, and 25 days following cover crop termination in 2009, 2010, and 2011, respectively. Total FAMEs pooled across 2009 and 2010 were greatest in the two species mixture–undercutter treatment combination (140.8 ± 3.9 nmol g^{-1}) followed by the eight species mixture–undercutter treatment combination (132.4 ± 3.9 nmol g^{-1}). Abundance of five (2009 and 2010) and seventeen (2011) FAME biomarkers was reduced in the weedy treatment relative to both cover-cropped treatments and the no-cover control. In 2009 and 2010, termination with the undercutter reduced abundance of most actinomycete biomarkers while termination with the field disk reduced abundance of C18:1(*cis*11) and iC16:0. Canonical discriminant analysis of the microbial community successfully segregated most cover crop mixture by termination method treatment combinations in 2009 and 2010. Microbial communities were most strongly influenced by the presence and type of early-spring plant communities, as weeds exerted a strong negative influence on abundance of many key microbial biomarkers, including the AMF markers C16:1(*cis*11) and C18:1(*cis*11). Weeds may alter soil microbial community structure as a means of increasing competitive success in arable soils, but this relationship requires further investigation.

1. Introduction

Soil microbial community composition responds to a broad range of ecosystem and management factors. Knowledge of microbial community composition and diversity can provide valuable insight into soil functions such as soil organic carbon and nitrogen retention, nutrient cycling and overall soil stability and health (Jackson et al., 2003; van Bruggen and Semenov, 2000). Several specific factors that may influence soil microbial community structure include soil type and texture, pH, plant community composition, climatic conditions, soil water availability, and soil management (Cookson et al., 2008; Drenovsky et al., 2004; Waldrop et al., 2000). In agricultural management systems both tillage and cover cropping are thought to influence microbial community structure, though these changes to the community are likely the result of complex interactions (Buckley and Schmidt, 2001; Carrera et al.,

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2007; Drijber et al., 2000). For example, one management decision (e.g., cover cropping) can substantially alter the subsequent weed community, labile soil carbon, and soil moisture, all of which may have unique impacts on microbial community structure (Buyer et al., 2010).

One management factor that consistently alters microbial community composition is the addition of organic carbon substrates, typical of organic cropping systems (Bossio et al., 1998). Microbial communities are often limited by organic carbon availability; thus, it is not surprising that the addition of labile organic matter (e.g., compost, manure, and plant residue) will result in changes to community structure (Drenovsky et al., 2004). In the short-term, organic management (e.g., cropping systems dependent on organic carbon substrates for soil fertility) selects for microbial species that have the highest growth rate and ability to scavenge nutrients (Alden et al., 2001). Previous studies have reported, among other changes, increased abundance and diversity of bacteria and arbuscular mycorrhizal fungi (AMF), as well as greater physiological diversity of microbes in organically managed soils (Oehl et al., 2003; Shannon et al., 2002; van Diepeningen et al., 2006). Cover crops are a common source of labile organic carbon in organic cropping systems and have been shown to increase abundance or diversity of gram-negative bacteria, fungi and AMF, actinomycetes, and protozoa for several months following cover crop termination (Buyer et al., 2010; Carrera et al., 2007; Ramos-Zapata et al., 2012; Schutter et al., 2001). Moreover, the presence of cover crops has been identified as the primary factor affecting microbial community composition, despite differences in soil moisture and temperature (Buyer et al., 2010). However, the species of cover crop (rye vs. vetch) had little effect on community composition (Buyer et al., 2010); rather, the addition of any labile organic matter (e.g., cover crops or compost) may result in similar community changes (Drenovsky et al., 2004). It has been hypothesized that differences in the biochemical composition of plant species and the subsequent organic compounds available to microbes may alter the composition of microbial communities (Zak et al., 2003). Indeed, Ramos-Zapata et al. (2012) found that cover crop mulches from different species had variable effects on AMF species richness.

Several recent studies have reported plant species-dependent changes in microbial communities of either the root rhizosphere or bulk soil (Germida et al., 1998; Kowalchuk et al., 2002; van Diepeningen et al., 2006; Zak et al., 2003). Individual plant species and communities have been shown to foster different levels of bacterivorous nematode species (van Diepeningen et al., 2006), bacterial diversity (Germida et al., 1998), microbial group abundance, and overall community composition (Zak et al., 2003). Zak et al. (2003) found that increasing plant community diversity reduced the abundance of soil bacteria and actinomycetes, but increased the abundance of soil fungi, though the effects were confounded by differences in plant primary productivity (productivity increased with diversity). Nonetheless, these studies suggest that a diverse plant community and the individual species therein have the capacity to influence the composition of the soil microbial community.

Weed communities may also exert species-specific impacts on soil microbial community composition. Indeed, previous studies have demonstrated substantial effects of weed species (e.g., *Centaurea maculosa*) on soil microbial functional group abundance and community composition (Batten et al., 2006; Lutgen and Rillig, 2004; Marler et al., 1999). These changes in microbial community composition are often viewed as a novel competitive strategy and defense mechanism adapted by certain weedy and invasive species (Callaway and Ridenour, 2004; Marler et al., 1999). However, many of these observations have been limited to invasive weeds of unmanaged ecosystems, and studies on the effects of agricultural weeds on soil microbial community composition are less common. Just as crops are influenced by specific microbial species or functional groups, weeds are also subject to these effects. For example, AMF (*Glomus intraradices*) has been shown to reduce the growth and competitiveness of weeds relative to crop species (Veiga et al., 2011). Weeds, which often succeed under stressful environmental conditions, may be at a competitive disadvantage in a fertile and biologically "healthy" soil (Tollenaar et al., 1994). Thus, as an adaptation to high quality agricultural soils, some weed species may exhibit a deleterious effect on microbial abundance or activity.

Soil tillage is another agricultural management factor that results in immediate and long-term changes to microbial community structure (Drijber et al., 2000; Jackson et al., 2003). In general, tillage shifts soil microbial communities toward aerobic species with high metabolic rates typical of bacterial species (Roper and Gupta, 1995). Several studies have shown that switching from a no-tillage system to a disk or plow management system reduces the ratio of fungi to bacteria (Frey et al., 1999; Pankhurst et al., 2002). Soil tillage has also been shown to reduce diversity of soil bacteria and abundance of microeukaryotes (Jackson et al., 2003; Lupwayi et al., 1998). While general soil disturbance often results in predictable changes to the microbial community, there is some evidence that different tillage practices (e.g., disk, moldboard plow, chisel plow) will have variable effects on community structure, as one study demonstrated unique community differences between a moldboard plow and a sub plow undercutter tillage system (Drijber et al., 2000). With regard to cover crops, soil tillage associated with different plant termination methods may influence microbial community structure.

Typically, cover crops are used as green manures for increasing soil nitrogen, especially in organic cropping systems. To this end, soil incorporation of the cover crop with a field disk or moldboard plow is usually most effective. This management practice has been shown to increase abundance of total bacteria and gram-negative bacteria, while the abundance of actinomycetes and fungi either decreases or remains stable (Drenovsky et al., 2004; Elfstrand et al., 2007; Lundquist et al., 1999; Zelles et al., 1992). In contrast, utilizing cover crops for weed control may require that residue be mulched and left on the soil surface (Teasdale and Mohler, 1993). In general, residue placement on the soil surface leads to greater abundance of fungi and AMF compared to soil incorporation of residue (Doran, 1980; Elfstrand et al., 2007; Holland and Coleman, 1987; Ramos-Zapata et al., 2012; Roper and Gupta, 1995). In addition to weed suppressive benefits, maintenance of cover crop residue on the soil surface appears to create a favorable habitat for fungal growth characterized by greater soil moisture and limited soil disturbance (Elfstrand et al., 2007). Fungal species generally have greater C:N ratios in their biomass (relative to bacteria); thus, increasing the abundance of fungi may increase soil carbon storage in agricultural systems (Holland and Coleman, 1987).

The objectives of this study were to quantify changes in total microbial community structure and individual functional group abundance in response to increasing cover crop diversity, early-season weed communities, and tillage (e.g., cover crop termination methods). To accomplish these objectives, we used soil extractions of fatty acid methyl esters (FAMEs) to quantify the abundance of soil microbial functional groups and changes in total community structure. We hypothesized that the combined effects of increasing cover crop diversity and the management of residue on the soil surface (via tillage with a sweep plow undercutter) will result in a unique microbial community structure characterized by an increased abundance of fungal biomarkers. Moreover, we hypothesized that total FAMEs, a proxy for microbial biomass, would increase as the total biomass of plant residues (e.g., cover crops and weeds) included in the cropping system increased.

Table 1
Cover crop species and seeding rates (kg ha^{-1}) used in individual cover crop mixtures between 2009 and 2011 (2CC, two species mixture; 8CC, eight species mixture).

Common name	Scientific name	Seeding rate	
		2CC (kg ha^{-1})	8CC (kg ha^{-1})
Hairy vetch	*Vicia villosa* Roth	22.4	5.6
Buckwheat (2009)	*Fagopyrum sagittatum* Moench	28.0	7.0
Idagold mustard (2010)	*Sinapus alba* L.	6.7	1.7
Field pea	*Pisum sativum* L.		14.0
Pacific gold mustard	*Brassica juncea* (L.) Czern.		1.1
Oilseed radish	*Raphanus sativus* L.		2.1
Crimson clover	*Trifolium incarnatum* L.		3.5
Dwarf essex rape	*Brassica napus* L.		1.7
Chickling vetch	*Lathyrus sativus* L.		8.4

2. Materials and methods

2.1. Experimental site and design

A field experiment was conducted between 2009 and 2011 at the University of Nebraska-Lincoln Agricultural Research and Development Center (ARDC) near Mead, Nebraska. Dominant soil type at the site is a Sharpsburg silty clay loam (fine, smectitic, mesic typic Argiudoll) with 0–5% slopes. The experiment was conducted in a 2.8 ha field that is certified for organic production (OCIA International, Lincoln, NE), and is managed without irrigation. This field was in organic alfalfa hay production from 2004 through the 2008 cropping seasons. In the fall of 2008 the experimental area was amended with 50 Mg ha^{-1} of liquid beef feedlot manure that was incorporated with a field disk.

The experiment was designed as a split-plot randomized complete block design within a 3-year crop rotation with 4 replications. The rotation sequence consisted of confectionery sunflower (*Helianthus annuus*)–soybean (*Glycine max*)–corn (*Zea mays*). Within each crop species, whole-plots (9.1 × 21.3 m; 12 crop rows spaced 0.76 m apart) were defined by cover crop treatment, while split-plots (4.5 × 21.3 m; 6 crop rows spaced 0.76 m apart) were defined by plant termination method. Each "crop × cover crop mixture × termination method" treatment combination was replicated within each block so that each phase of the 3-year crop sequence was present each year within each block. There were four whole-plot cover crop treatments: (1) two-species cover crop mixture (2CC), (2) eight-species cover crop mixture (8CC), (3) weedy but no cover crop prior to main crop planting (WD), and (4) no cover crop and weed-free prior to main crop planting (NC control). The NC whole-plots were field disked and hand-hoed twice prior to main crop planting to remove emerged weed seedlings, while weeds in the WD whole-plots were left unmanaged until cover crop termination (e.g., a "natural" cover crop). Details on the individual species and seeding rates included in each cover crop treatment whole-plot are included in Table 1. On March 15, 2009, the 2CC, 8CC, and WD treatments were seeded with 8.1 kg ha^{-1} of velvetleaf (*Abutilon theophrasti*) seed, 2.6 kg ha^{-1} of common lambsquarters (*Chenopodium album*) seed, 1.2 kg ha^{-1} of redroot pigweed (*Amaranthus retroflexus*) seed, and 3.7 kg ha^{-1} of green foxtail (*Setaria viridis*) seed to establish a common weed seedbank for weed suppression data collection (Wortman et al., 2013).

Split-plot cover crop residue management methods included either disking or undercutting. Disking was conducted with a 4.6 m wide Sunflower 3300 (Sunflower Mfg., Beloit, KS, USA) disk to an approximate depth of 15 cm. Undercutting was conducted with either a Buffalo 6000 (Buffalo Equipment, Columbus, NE, USA) cultivator (modified for undercutting) with seven overlapping 0.75 m wide sweep blades (2009) or a Miller Flex-Blade sweep plow undercutter (2010 and 2011) with three overlapping 1.5 m sweep blades. The undercutter sweeps are designed to cut a level plane through the soil at an approximate depth of 10 cm, severing plant roots and minimizing soil inversion, resulting in a layer of intact surface residue. Details on the design of the undercutter can be found in Creamer et al. (1995).

Cover crop mixtures were planted via hand-crank broadcast seeding followed by light incorporation (to a depth less than 3 cm) with a John Deere 950 cultipacker (Deere and Company, Moline, IL, USA). Generally, cover crops were planted in late-March, terminated in late-May, and main crops were planted within one week of cover crop termination. Specific dates for field operations across three years are detailed in Table 2. Seeding rates for confectionery sunflower, soybean, and corn were 62,000, 556,000, and 86,000 seeds ha^{-1}, respectively. All main crops were inter-row cultivated once (2009) or twice (2010 and 2011) approximately 30 days after planting. Seeds of all legume cover crop and crop species were inoculated with appropriate rhizobia bacterial species prior to planting in 2009 and 2010.

2.2. Soil sampling

Soil samples were taken for fatty acid methylated esters (FAME) soil microbial analysis from 84 experimental units at 45, 32, and 25 days after cover crop termination (DAT) in 2009, 2010, and 2011, respectively (Table 2). These samples represented four whole-plot treatments, two split-plot treatments, three main crops, and four replications in each of three years. The NC control treatment did not include split-plots, as there were no plants to terminate and compare methods. This resulted in 252 composite samples for extraction and analysis.

Soil sampling was conducted in an aseptic manner whenever possible. To this end, nitrile gloves were worn during sampling and all supplies (soil probe, buckets, and gloves) were sprayed with 91% isopropyl alcohol and allowed to air-dry before sampling each experimental unit. Three (2009) or four (2010 and 2011) soil cores (3.2 cm diameter by 20 cm depth) were taken within crop rows in each experimental unit. Cores were sampled from undisturbed soil within crop rows to avoid the effects of inter-row cultivation that occurred prior to sampling. Cores from each experimental unit were pooled in a plastic bucket and mixed by hand to break up large aggregates and create a homogenous mixture of soil profiles. A subsample of approximately 300 grams was placed in a plastic

Table 2
Timing of field operations and data collection for each year of the study.

Operation	Year		
	2009	2010	2011
Cover crop planting	20 March	30 March	21 March
Cover crop termination	22 May	28 May	3 June
Main crop planting	28 May	1–3 June	6 June
1st interrow cultivation	1 July	28 June	30 June
2nd interrow cultivation		1 July	8 July
Soil sampling	6–7 July	29–30 June	28 June

freezer bag, sealed and placed in an iced cooler for no more than 2 h. When soil sampling was complete, subsamples were stored in a refrigerator at 2 °C for less than 24 h until processing.

Soil samples were sieved with a 0.47 cm sieve to remove large organic residues. Similar to the sampling process, sieving was conducted aseptically by wearing nitrile gloves, and spraying all equipment (gloves and sieves) with 91% isopropyl alcohol (allowed to air-dry) between samples. Prior to spraying with isopropyl alcohol, all soil was physically removed from the sieves between samples via brush and paper towel. After sieving, 100 g of soil was weighed and placed back into each plastic freezer bag. Sieved samples were then stored at −20 °C in 2009 and 2010 or 2 °C in 2011 until the time of FAME extraction (3–6 months after sampling). The change in storage temperature between 2010 and 2011 was a mistake, but previous studies have demonstrated successful FAME extraction and analysis from samples stored for prolonged periods at 2–4 °C (Lee et al., 2007; Schutter and Dick, 2000). Moreover, observed differences in FAME profiles due to variable storage conditions were modest compared to the effects of soil type or extraction method (Schutter and Dick, 2000). Nonetheless, samples from 2011 were analyzed separately to avoid any confounding effects of storage conditions.

2.3. FAME extraction

Microbial community composition was determined from fatty acid methyl esters (FAMEs). The method, adapted from White et al. (1979), is fully described in Grigera et al. (2007), and results in a direct hydrolysis, derivatization, and extraction of FAMEs from soil microorganisms in situ. FAMEs extracted from 10 g frozen soil were stored in 1.0 ml hexane at −20 °C until preparation for gas chromatography (GC) analysis. In preparation for GC analysis, hexane was evaporated under N_2 gas until completely dry and then 500 μl of hexane with C19:0 (0.05 mg/ml; as an internal standard) was added to each vial. A 50 μl aliquot of each sample was transferred to the GC vial and capped for analysis.

Individual FAMEs were separated by capillary gas chromatography on a Hewlett Packard 5890 Series II gas chromatograph (Hewlett-Packard Company, Palo Alto, CA) with helium as the carrier gas. The instrument contained an Ultra 2 HP capillary column (50 m, 0.2 mm I.D., 0.33 μm film thickness). Oven temperature in the GC was held at 50 °C for 2 min and then increased by 40 °C min^{-1} to 160 °C and held for 2 min. Temperature was then increased by 3 °C min^{-1} to a final temperature of 300 °C and held for 30 min. Injector and flame ionization detector temperatures were 280 °C and 300 °C, respectively. Determination of FAME identity was accomplished through a comparison of retention times and equivalent chain lengths with known standards (Bacterial Acid Methyl Esters CP Mix, Supelco USA). FAME identities were confirmed by gas chromatography mass spectrometry (GC–MS). FAMEs were represented and written as the total number of carbon atoms followed by a colon, the number of double bonds followed by the position of those double bonds from the carboxyl end of the molecule, and its *cis* or *trans* configuration in brackets (e.g., C16:1(*cis*11)).

2.4. Data analysis

Consistent with previous studies, total and individual FAME abundance was reported and analyzed as nmol g^{-1} for univariate analyses and converted to nmol% for multivariate analysis (Petersen et al., 1997; Reichardt et al., 1997). FAMEs with retention times less than C14:0 and greater than C20:0 were deleted from the data matrix, which resulted in a total of 39 FAME biomarkers for analysis across years. FAMEs were first analyzed by analysis of variance (Proc MIXED; SAS 9.2, SAS Institute Inc., Cary, NC, USA) to determine differences in abundance of total FAMEs and individual biomarkers (nmol g^{-1}) among cover crop mixture, termination, and main crop treatments. FAME data were log-transformed prior to analysis of variance to improve normality and homogeneity of variances for total FAMEs in 2011. Fixed effects in the analysis of variance model included main crop, cover crop mixture, termination method, and all possible interactions of these effects. Random effects included block and the interaction of block by main crop by cover crop mixture. Least square (LS) means and standard errors were calculated for all significant fixed effects at an alpha level of 0.05. Significant differences among LS means are indicated by different letters among treatment levels in all tables and figures.

Stepwise discriminant analysis and canonical discriminant analysis (Proc STEPDISC and Proc CANDISC; SAS 9.2) were then performed on nmol% FAMEs to characterize changes in overall soil microbial community structure in response to cover crop mixture and termination method treatment combinations. Stepwise discriminant analysis was used to identify individual FAMEs contributing most to treatment segregation. The resulting discriminant model was subjected to a canonical discriminant analysis. Mahalanobis distances and the associated probabilities of significance (p-values) were used to detect differences among treatment combinations. The number of significant ($p < 0.05$) canonical discriminant functions (linear combinations of important FAME markers – those identified in stepwise discriminant analysis) determined the number of dimensions used to segregate among treatment groups. The first canonical discriminant function always explains the most variation among treatment groups, followed by the second function, and so on. Total canonical structure was used to determine the relative magnitude and directional relationship of FAME variables contributing to the canonical discriminant functions. Discriminant scores were then calculated for each experimental unit within each significant discriminant function. Class means for all discriminant scores within treatment combinations were plotted along with the correlation coefficients for FAMEs in the significant discriminant functions. Data for 2009 and 2010 were pooled for statistical analyses where possible (e.g., where there was no interaction effect for year), whereas the 2011 data were always analyzed individually due to variable cold storage conditions.

3. Results

3.1. Total FAMEs

While total extracted FAMEs is not a direct measure of microbial biomass, this method has been well correlated with more traditional measures of biomass (Zelles et al., 1992). Total FAMEs were greatest in the 2CC – undercutter treatment combination (140.8 ± 3.9 nmol g^{-1}) followed by the 8CC – undercutter treatment combination when pooled across years 2009 and 2010 (132.4 ± 3.9 nmol g^{-1}; Fig. 1). Differences among cover crop treatments in 2011 were only approaching significance ($F = 2.68$, $df_n = 2$, $df_d = 19.8$, $p = 0.093$), but total FAMES were generally lowest lowest in the WD treatment (118.2 nmol g^{-1}) and greatest in the NC control and 2CC treatments (139.3 and 137.3 nmol g^{-1}; Fig. 1).

3.2. Individual FAME abundance

Five FAME biomarkers (iC16:0, i10MeC17:0, i10MeC18:0, C16:1(*cis*11), C18:1(*cis*11)) were influenced by cover crop treatment in 2009 and 2010. More specifically, abundance of these biomarkers was reduced in response to the WD treatment (unmanaged early-season weed communities; Table 3). Results in 2011 were consistent with those in 2009 and 2010 although the effect was more pronounced. Seventeen individual FAME biomarkers were influenced by cover crop treatment in 2011,

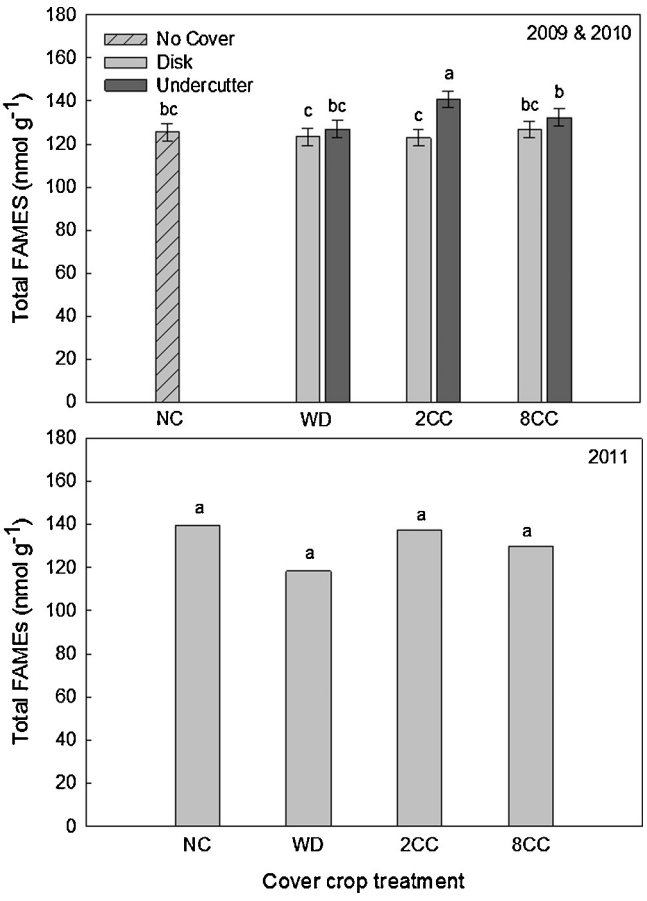

Fig. 1. Effects of cover crop mixture and termination method on total FAMEs (nmol g^{-1}) at 45 and 32 days after cover crop termination (DAT) in 2009 and 2010, respectively (top), and effects of cover crop mixture (no significant interaction with termination method) at 25 DAT in 2011 (bottom). Error bars for 2009 and 2010 data represent the standard error of the LS means. Data shown for 2011 are back-transformed least square (LS) means. Differences among treatments are indicated by different letters above bars. Cover crop treatments include: NC, no cover control; WD, weedy mixture; 2- and 8CC, two and eight cover crop species mixtures, respectively (Table 1).

including ten biomarkers associated with bacterial functional groups, five associated with actinomycetes, and two associated with AMF groups (Table 4 and Fig. 2). For each of these seventeen FAME biomarkers, abundance was consistently reduced or lowest in the WD treatment relative to the other three cover crop treatments (NC, 2CC, or 8CC). For example, pooled abundance of the ten bacterial markers was 22.67 ± 0.89 nmol g^{-1} in the WD treatment compared to 26.07 ± 1.27 nmol g^{-1} in the NC treatment and 26.54 ± 0.89 nmol g^{-1} in the 2CC treatment. The trend for actinomycetes was similar where pooled abundance was 10.02 ± 0.47 nmol g^{-1} in the WD treatment and 12.22 ± 0.47 nmol g^{-1} in the 2CC treatment (Table 4). Plant termination with the undercutter reduced abundance of four actinomycete biomarkers (8MeC16:0, i10MeC17:0, i10MeC18:0, a10MeC18:0), but increased abundance of the actinomycete marker, 10MeC18:0, relative to termination with the field disk in 2009 and 2010. In addition, termination with the field disk resulted in a reduced abundance of the AMF/bacteria biomarker C18:1(*cis*11) and the bacterial marker iC16:0 relative to termination with the undercutter (Table 5). Influence of termination method on individual FAMEs in 2011 was quite different. Only bacterial functional groups were influenced, and the effect was an interaction of crop by termination method (Table 6). In soybean and sunflower, disk termination reduced abundance of bacterial functional groups relative to termination with the undercutter or the NC control. In contrast, termination with the undercutter reduced abundance of bacterial markers in corn (Table 6).

Only three individual FAMEs were influenced by the main crop in 2009 and 2010. Sunflower reduced the abundance of bacterial biomarkers iC15:0 and aC15:0 relative to soil sampled

Table 3
LS means and standard errors of individual FAME abundance (nmol g^{-1}) as influenced by cover crop treatment in 2009 and 2010. Differences among treatments are indicated by different letters within a biomarker row.

	Cover crop treatment			
	NC	WD	2CC	8CC
Bacteria				
iC16:0	4.53 (0.08) a	4.38 (0.06) b	4.56 (0.06) a	4.55 (0.06) a
Actinomycetes				
i10MeC17:0	1.31 (0.08) a	1.15 (0.06) b	1.36 (0.06) a	1.28 (0.06) a
i10MeC18:0	3.65 (0.28) a	3.13 (0.20) b	3.79 (0.20) a	3.60 (0.20) a
AMF/Bacteria				
C16:1(*cis*11)	2.59 (0.13) b	2.41 (0.10) b	2.85 (0.10) a	2.69 (0.10) ab
C18:1(*cis*11)	4.70 (0.10) a	4.42 (0.07) b	4.74 (0.07) a	4.77 (0.07) a

Table 4
LS means and standard errors of individual FAME abundance (nmol g^{-1}) as influenced by cover crop treatment in 2011. Differences among treatments are indicated by different letters within a biomarker row.

	Cover crop treatment			
	NC	WD	2CC	8CC
Bacteria				
iC16:0	5.91 (0.33) a	5.13 (0.23) b	6.12 (0.23) a	5.71 (0.23) a
iC15:1(*cis*4)	0.82 (0.06) a	0.70 (0.05) b	0.85 (0.05) a	0.77 (0.05) ab
iC15:0	8.01 (0.47) a	7.12 (0.33) b	8.23 (0.33) a	7.73 (0.33) ab
C15:0	1.28 (0.07) a	1.06 (0.05) b	1.25 (0.05) a	1.17 (0.05) a
iC16:1(*cis*9)	1.71 (0.11) a	1.52 (0.08) b	1.79 (0.08) a	1.70 (0.08) a
iC17:0	3.21 (0.14) ab	2.83 (0.10) c	3.30 (0.10) a	3.09 (0.10) b
aC17:0	3.76 (0.24) a	3.16 (0.17) b	3.75 (0.17) a	3.60 (0.17) a
cyC17(9,10)	2.84 (0.17) a	2.22 (0.12) c	2.61 (0.12) ab	2.50 (0.12) b
cyC19(9,10)	0.85 (0.06) a	0.73 (0.05) b	0.89 (0.05) a	0.81 (0.05) ab
cyC19(11,12)	5.67 (0.24) ab	5.33 (0.17) b	5.99 (0.17) a	5.65 (0.17) b
Bacteria pooled	26.07 (1.27) a	22.67 (0.89) b	26.54 (0.89) a	25.00 (0.89) a
Actinomycetes				
i10MeC17:0	1.51 (0.12) b	1.38 (0.09) b	1.73 (0.09) a	1.53 (0.09) b
i10MeC18:0	4.05 (0.40) ab	3.60 (0.28) b	4.56 (0.28) a	4.12 (0.28) ab
a10MeC18:0	0.61 (0.06) ab	0.53 (0.04) b	0.63 (0.04) a	0.57 (0.04) ab
10MeC18:0	2.06 (0.10) a	1.74 (0.07) b	2.07 (0.07) a	1.95 (0.07) a
10MeC19:0	3.30 (0.18) a	2.76 (0.13) b	3.23 (0.13) a	3.12 (0.13) a
Actino. pooled	11.53 (0.67) a	10.02 (0.47) b	12.22 (0.47) a	11.29 (0.47) a
AMF/Bacteria				
C18:1(*cis*11)	7.74 (0.63) a	6.06 (0.45) b	7.76 (0.45) a	7.11 (0.45) a

Table 5
LS means and standard errors of individual FAME abundance (nmol g^{-1}) as influenced by cover crop termination method in 2009 and 2010. Differences among treatments are indicated by different letters within a biomarker row.

	Cover crop termination method		
	No cover	Disk	Undercutter
Bacteria			
C17:0	0.736 (0.011) a	0.718 (0.006) b	0.739 (0.006) a
Actinomycetes			
8MeC16:0	1.85 (0.08) a	1.88 (0.04) a	1.71 (0.04) b
i10MeC17:0	1.31 (0.08) ab	1.33 (0.05) a	1.20 (0.05) b
i10MeC18:0	3.65 (0.28) ab	3.71 (0.16) a	3.30 (0.16) b
a10MeC18:0	0.453 (0.020) ab	0.467 (0.012) a	0.441 (0.012) b
10MeC18:0	1.438 (0.028) ab	1.430 (0.016) b	1.468 (0.016) a
AMF/Bacteria			
C18:1(*cis*11)	4.70 (0.10) ab	4.56 (0.06) b	4.72 (0.06) a

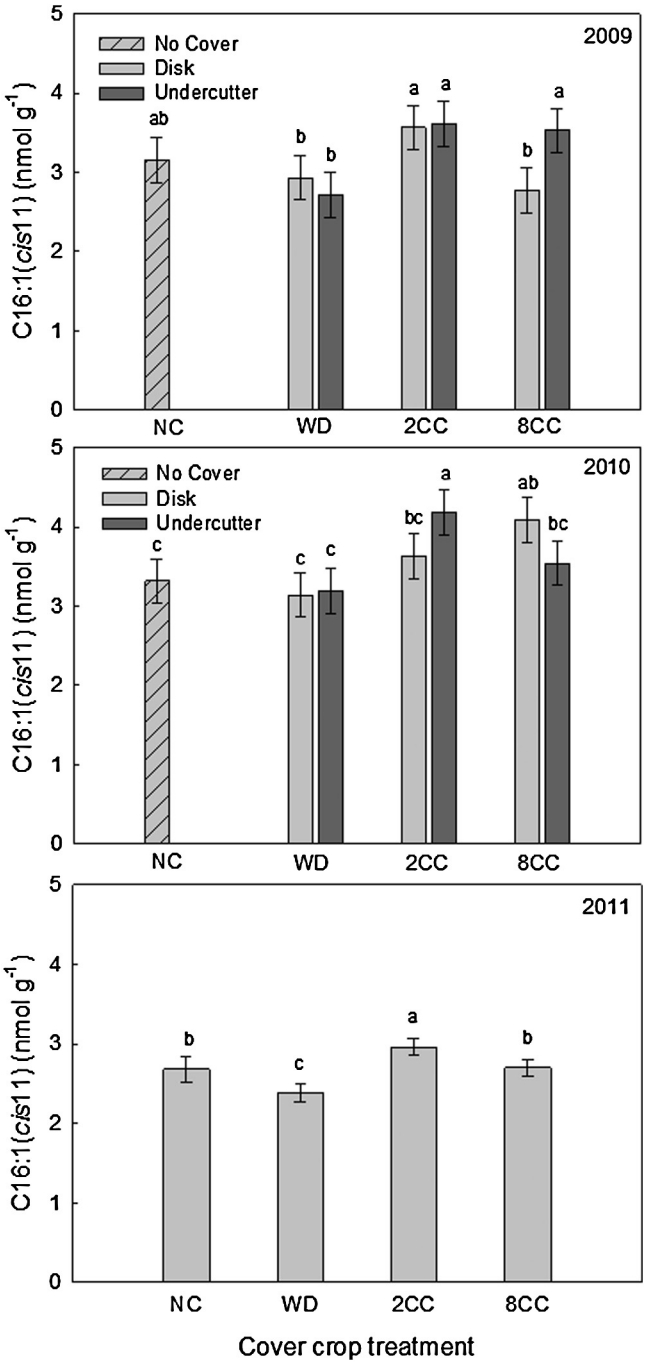

Fig. 2. Effects of both cover crop treatment and termination method (2009 and 2010) or only cover crop treatment (2011) on abundance of the AMF biomarker C16:1(*cis*11) (nmol g^{-1}) at 45, 32, and 25 days after cover crop termination in 2009, 2010, and 2011, respectively. Error bars represent the standard error of the LS means. Differences among treatments are indicated by different letters above bars. Cover crop treatments include: NC, no cover control; WD, weedy mixture; 2- and 8CC, two and eight cover crop species mixtures, respectively (Table 1).

in the corn crop (Table 6). In contrast, sunflower promoted the abundance of the C18:2 (*cis*9, 12) saprophytic fungi biomarker (6.32 ± 0.18 nmol g^{-1}) relative to soil sampled in the corn (5.74 ± 0.18 nmol g^{-1}) or soybean (5.77 ± 0.18 nmol g^{-1}) crops (Table 6). In 2011 there was a crop by termination method interaction for several bacterial biomarkers, and as previously discussed, this interaction seems to be driven by the relative abundance of bacterial groups among termination methods in each crop.

Table 6
LS means and standard errors of individual FAME abundance (nmol g^{-1}) as influenced by current crop in 2009 and 2010. Differences among treatments are indicated by different letters within a biomarker row.

	Current crop		
	Corn	Soybean	Sunflower
Bacteria			
iC15:0	5.46 (0.06) a	5.37 (0.06) ab	5.30 (0.06) b
aC15:0	3.71 (0.06) a	3.69 (0.06) ab	3.58 (0.06) b
Fungi			
C18:2(*cis*9,12)	5.74 (0.18) b	5.77 (0.18) b	6.32 (0.18) a

3.3. Abundance of AMF biomarker C16:1(cis11)

The FAME C16:1(*cis*11) is commonly cited as a biomarker for AMF (Olsson et al., 1995; Drijber et al., 2000), and was influenced by the three way interaction of cover crop treatment, termination method, and year ($F = 13.11$, $df_n = 2$, $df_d = 122$, $p < 0.0001$) for the pooled 2009 and 2010 data. Abundance of C16:1(*cis*11) in the 8CC – undercutter treatment combination (3.53 ± 0.28 nmol g^{-1}) was greater than the 8CC – disk treatment (2.77 ± 0.28 nmol g^{-1}) and both the WD – disk and WD – undercutter treatment combinations (2.93 ± 0.28 nmol g^{-1} and 2.71 ± 0.28 nmol g^{-1}, respectively) in 2009 (Fig. 2). C16:1(*cis*11) abundance was also elevated in the 2CC – disk and 2CC – undercutter treatment combinations (3.56 ± 0.28 nmol g^{-1} and 3.61 ± 0.28 nmol g^{-1}, respectively), but none of the treatment combinations in 2009 were different from the NC control (3.15 ± 0.28 nmol g^{-1}). In 2010, C16:1(*cis*11) abundance was generally greater in cover-cropped treatments compared to both WD treatments and the NC control (Fig. 2). The response to termination method was inconsistent across cover crop treatments as the undercutter increased C16:1(*cis*11) abundance in the 2CC cover crop mixture (4.18 ± 0.28 nmol g^{-1}) but reduced abundance in the 8CC cover crop mixture (3.54 ± 0.28 nmol g^{-1}) relative to termination with the disk. In 2011, C16:1(*cis*11) was only influenced by cover crop treatment ($F = 4.54$, $df_n = 2$, $df_d = 60$, $p = 0.015$). Consistent with the trends in 2009 and 2010, AMF abundance was lowest in the WD treatment, followed by the NC and 8CC treatments, and greatest in the 2CC treatment (Fig. 2).

3.4. Microbial community composition

Of the 39 FAMEs identified among all soil samples, 9 were included in the discriminant function after stepwise discriminant analysis for the pooled 2009 and 2010 dataset. Canonical discriminant analysis then identified two significant discriminant functions (DA1 and DA2), which explained 65.2 and 14.3% of the variance, respectively, for a total explained variance of 79.5%. Significance of pairwise squared Mahalanobis distances indicated that a majority of cover crop by termination method treatment groups segregate from one another (Table 7). However, the most obvious segregation occurred between the WD treatments (both disk and undercutter termination methods) and all other treatment groups. This finding is consistent with univariate analyses in all years indicating that the WD treatments reduced abundance of numerous bacterial, actinomycete, and fungal biomarkers relative to both cover-cropped treatments and the NC control (Tables 3 and 4). Termination method was effective in treatment segregation within the 2CC mixture, but not within the 8CC or WD treatments. Cover-cropped treatments only segregated from the NC control when combined with the undercutter for termination. In contrast to our hypothesis, there were relatively minor differences in microbial community composition among the 2CC and 8CC treatments. Instead, early-season weed communities were driving the most

Table 7
Pairwise squared mahalanobis distance for FAMEs between cover crop mixture by termination method treatment groups pooled across main crops and two years (2009 and 2010). An (*) indicates the distance is significant at a rejection level of $\alpha = 0.05$.

Treatment	2CC/D	2CC/U	8CC/D	8CC/U	WD/D	WD/U	NC
	Squared mahalanobis distance						
2CC/D[a]	0.00	2.19*	1.49	1.94*	1.77*	2.33*	1.39
2CC/U	2.19*	0.00	1.53*	0.70	4.27*	5.14*	2.62*
8CC/D	1.49	1.53*	0.00	0.48	3.17*	4.26*	1.38
8CC/U	1.94*	0.70	0.48	0.00	3.70*	4.92*	2.27*
WD/D	1.77*	4.27*	3.17*	3.70*	0.00	0.41	1.90*
WD/U	2.33*	5.14*	4.26*	4.92*	0.41	0.00	2.48*
NC	1.39	2.62*	1.38	2.27*	1.90*	2.48*	0.00

[a] 2CC/D, two species mix + disk; 2CC/U, two species mix + undercutter; 8CC/D, eight species mix + disk; 8CC/U, eight species mix + undercutter; WD/D, weedy control + disk; WD/U, weedy control + undercutter; NC, no cover crop (or weeds) control.

substantial changes in microbial community composition (Table 7; Fig. 3).

FAMEs positively correlated to DA1 included C18:1(*cis*11) (AMF/bacteria), C20:n, C16:1(*cis*5), C17:1(*cis*9) (bacteria; Wortmann et al., 2008), cyC19(9,10) (bacteria), and i10MeC18:0 (actinomycete; Wortmann et al., 2008) (in order of strongest to weakest correlations; Fig. 3b). Abundance of these FAMEs was generally greatest in cover-cropped treatment groups and lowest in the WD treatments. In contrast, there was a negative correlation between DA1 and FAMEs for C18:0, C18:1(*cis*13), and a10MeC18:0 (in order of strongest to weakest correlations; Fig. 3b). DA2 was positively correlated with FAMEs for C17:1(*cis*9), C18:1(*cis*13), C20:n, C16:1(*cis*5), C18:0, and C18:1(*cis*11), and negatively correlated with FAMEs for i10MeC18:0, cyC19(9,10), and a10MeC18:0 (in order of strongest to weakest correlations; Fig. 3b). The largest segregation among treatment groups by DA2 was between the NC control treatment and the undercutter treatments (Fig. 3a). This segregation suggests that C17:1(*cis*9) (a bacterial biomarker), C18:1(*cis*13), C20:n, C16:1(*cis*5), C18:0, and C18:1(*cis*11) (a fungal and bacterial marker), were greater in treatments with plant residue managed on the soil surface (cover crops or weeds), whereas i10MeC18:0, a10MeC18:0 (both actinomycete markers), and cyC19(9,10) were greater in the NC treatment without any plant growth or subsequent residue cover.

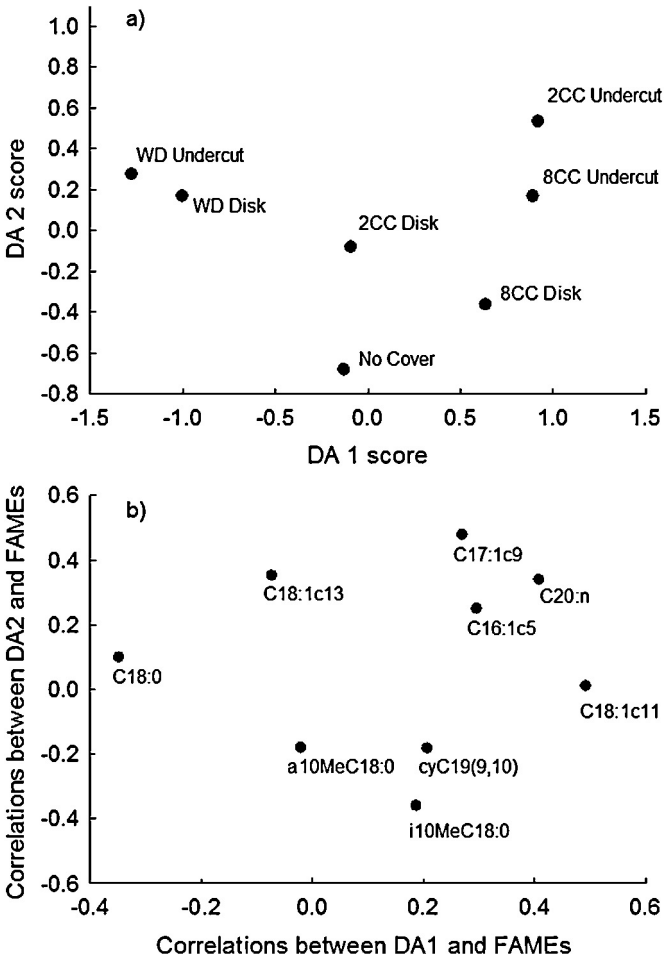

Fig. 3. Discriminant score means for all cover crop mixture by termination method treatment groups (a), and standardized canonical coefficients for FAMEs (b) contributing to the two significant discriminant functions DA1 and DA2 in 2009 and 2010.

Canonical discriminant analysis of 2011 data yielded only one significant discriminant function that explained 62.7% of the total variance. Segregation of treatments with this function was limited as only the NC treatment was consistently different from all other treatment combinations, excluding the 8CC – disk treatment combination (data not shown). In this case, univariate analyses were more useful in understanding microbial community response.

4. Discussion

4.1. Conservation tillage increased total FAMEs

In contrast to our hypothesis, increasing carbon inputs (in the form of cover crop and weed residue) did not consistently increase short-term total FAMEs. However, cover crop termination with the undercutter generally increased total FAMEs in 2009 and 2010 (Fig. 1). This suggests that termination with the undercutter resulted in a more favorable microbial habitat early in the growing season. In previous studies, incorporation of plant residue via disking or plowing typically increased bacterial abundance and reduced the ratio of fungi to bacteria (Drenovsky et al., 2004; Elfstrand et al., 2007; Lundquist et al., 1999; Pankhurst et al., 2002; Zelles et al., 1992). However, the results of this study suggest that disk incorporation may reduce total FAMEs regardless of functional group, relative to cover crop termination and surface residue management with a conservation tillage implement like the undercutter. These results may indicate a general reduction in microbial abundance and biomass as tillage intensity increases. This is consistent with previous studies where microbial biomass was greater in surface soils of no-till treatments relative to plowed treatments in a long-term wheat-fallow cropping system (Doran, 1987; Drijber et al., 2000).

4.2. Actinomycetes and C18:1(cis11) sensitive to termination method

Despite an increase in total FAMEs, abundance of actinomycete FAME biomarkers (e.g., i10MeC18:0) was generally reduced in response to cover crop termination with the undercutter in 2009 and 2010 (Table 5). This result was surprising as previous studies have shown that actinomycete abundance is either unaffected or reduced following cover crop termination with more intensive tillage implements like a field disk or plow (Drenovsky et al., 2004; Elfstrand et al., 2007; Lundquist et al., 1999; Zelles et al., 1992). The sweepplow undercutter is a conservation tillage implement that limits soil disturbance, and we hypothesized that microbial community response would more closely mimic other conservation tillage strategies (e.g., no-till systems). Canonical discriminant analysis of microbial community composition also demonstrated a negative correlation between the cover crop – undercutter

treatment combinations and the actinomycete markers (i10MeC18:0 and a10MeC18:0), providing further evidence that the soil environment following an undercutting operation is not conducive to actinomycete growth (Fig. 3). To our knowledge, this is the first evidence that the sweep plow undercutter for cover crop termination negatively affects actinomycete growth and abundance.

The effects of termination with a field disk were more consistent with our hypotheses, as disking reduced abundance of the FAME biomarker C18:1(*cis*11) relative to termination with the undercutter in 2009 and 2010 (Table 5). Reduced abundance of the C18:1(*cis*11) marker highlights the potentially negative effects of inversion tillage (e.g., field disking) on soil fungi. While C18:1(*cis*11) has been cited as a bacterial FAME marker (Zelles, 1999), it is also found in arbuscular mycorrhizal fungi (AMF), particularly in the neutral lipid fraction essential to AMF metabolism (Olsson, 1999). The reduction in C18:1(*cis*11) following disk incorporation (relative to undercutting and the NC control) observed in 2009 and 2010 is congruent with many previous studies demonstrating that residue placement on the soil surface leads to greater abundance of fungi and AMF compared to full soil incorporation of residue (Doran, 1980; Elfstrand et al., 2007; Holland and Coleman, 1987; Roper and Gupta, 1995). Reduced fungal abundance in the disk treatment may be due to the complex interaction of factors associated with the soil habitat, including reduced soil moisture and increased soil disturbance (Elfstrand et al., 2007). Despite the effects on the C18:1(*cis*11) marker, it was surprising that termination method did not yield predictable changes in abundance of the more common C16:1(*cis*11) AMF biomarker (Fig. 2). We hypothesized that cover crop termination with the disk would reduce AMF abundance as intensive tillage has been shown to reduce ratios of fungi to bacteria and AMF hyphal length and abundance (Drijber et al., 2000; Frey et al., 1999; Pankhurst et al., 2002).

4.3. Influence of cover crop diversity is subtle

While arable weeds influenced soil microbial communities in this study, there was no consistent difference in individual FAME abundance between the 2CC and 8CC treatments in 2009 and 2010 (Table 3). Moreover, cover crop composition and diversity had only a minor influence on overall microbial community structure in 2009 and 2010 (Table 7; Fig. 3). The effects of individual plant species and increasing aboveground plant diversity on soil microbial diversity and community composition are often subtle and only detected within the root rhizosphere (Buyer et al., 1999; Kowalchuk et al., 2002; Waldrop et al., 2006; Kielak et al., 2008). Thus, the sampling approach used in this study (i.e., bulk soil samples to a depth of 20 cm) may have been too crude to detect subtle changes in microbial communities driven by plant species composition. Moreover, individual FAME abundance was typically not different between cover-cropped treatments (2CC and 8CC) and the NC control (Tables 3 and 4). It is worth noting that many previous studies regarding the effects of cover crops on microbial community structure have focused on fall-sown winter annual species (e.g., rye and hairy vetch; Buyer et al., 2010), not spring-sown annual species as was studied here. Differences in cover crop species and planting date may partially explain results that are inconsistent with previous studies.

While not typically different between the 2CC and 8CC treatments, the general presence of cover crops often led to increased abundance of FAME markers or positive correlations with (in the case of canonical discriminant analysis) i10MeC18:0, C17:1(*cis*9), C18:1(*cis*11), and C16:1(*cis*11) (Table 3; Figs. 2 and 3). The i10MeC18:0 marker has been cited as a FAME biomarker for actinomycetes, while C17:1(*cis*9) has been cited as a biomarker for bacteria (Wortmann et al., 2008). Increased ratios of actinomycetes and fungi in the cover-cropped soils are congruent with previous studies (Buyer et al., 2010; Carrera et al., 2007; Schutter et al., 2001). Similarly, increased abundance of the AMF marker C16:1(*cis*11) is consistent with Drijber et al. (2000) who found that abundance of C16:1(*cis*11) decreased in the absence of carbon substrates (fallow period). However, it is unique that the type of plant residue (weeds vs. cover crops) affected the abundance of C16:1(*cis*11) in this study. Despite the addition of fresh carbon substrates (e.g., early-season weeds) in the WD treatment, C16:1(*cis*11) was often lower (though not always significantly so) than levels in the cover-cropped treatments (Table 3; Fig. 2). This reduction in AMF abundance following growth of weedy species is congruent with previous studies (Lutgen and Rillig, 2004; Mummey and Rillig, 2006), and is also consistent with the directional response of many other FAMEs in this study.

4.4. Arable weeds consistently reduced abundance of key FAMEs

The arable weed communities in the WD treatments seemed to be the single largest driver of individual FAME abundance and microbial community composition in this study (Tables 3, 4 and 7; Figs. 2 and 3). More specifically, results suggest that early-season arable weed communities (primarily *Chenopodium album*, *Abutilon theophrasti*, *Amaranthus retroflexus*, *Thlaspi arvense*, and *Setaria viridis* in this study) were altering microbial communities by reducing abundance of many key microbial functional groups relative to soil with and without cover crop growth. The unique influence of weedy and invasive plant species on soil microbial community composition and specific functional groups has been observed previously (Batten et al., 2006). However, the effect of weeds on soil microbial communities is not always consistent.

Previous studies have found that weedy species (i.e., *Centaurea maculosa*, *Centaurea solstitialis*, and *Aegilops triuncialis*) can alter microbial community composition and increase the abundance of beneficial microbial groups (i.e., AMF species; Batten et al., 2006; Marler et al., 1999). In addition, these changes in microbial community structure have been shown to increase the competitive advantage of the weedy species relative to native competitors (Marler et al., 1999). In contrast, others have reported that *C. maculosa* reduces the abundance and diversity of AMF (Lutgen and Rillig, 2004; Mummey and Rillig, 2006), which is more consistent with the results of this study. The reduction of C16:1(*cis*11) and C18:1(*cis*11) following early-season weed growth in this study (Tables 3 and 4; Fig. 2) is especially relevant, as these have been cited as biomarkers for AMF (Olsson et al., 1995, 1999; van Aarle and Olsson, 2003). Mycorrhizal fungi can form mutualistic relationships with many crop species, improving nutrient uptake and subsequent crop yield (Mosse, 1973); thus, it would seem reduction of AMF abundance could be an effective competitive strategy for weeds.

Veiga et al. (2011) reported reduced growth and competitive ability of weeds in the presence of AMF (*Glomus intraradices*). Given the potentially negative effects of AMF on arable weeds, the reduction in AMF abundance observed here suggests that one or more of the weeds present in this study (e.g., *Chenopodium album*, *Thlaspi arvense*, *Abutilon theophrasti*, *Setaria faberi*, and *Amaranthus retroflexus*) may have expressed a negative soil feedback mechanism to limit the growth of AMF. Possible negative feedback mechanisms include the production of fungicidal root exudates or simply a reduction in the quantity and quality of root exudates from these species (Bais et al., 2006). Because weeds are adapted to stressful growing conditions (Tollenaar et al., 1994), the hypothesized negative feedback mechanism could increase the competitive advantage of weedy species in higher quality agricultural soils typical of organic cropping systems (Pimentel et al., 2005).

While invasive plant species (primarily *C. maculosa*) have been extensively studied for effects on soil microbial communities, there have been relatively few studies examining the role of arable system weeds on soil microbial community structure in

agroecosystems. Soil microbes have been viewed as a potential weed management tool (e.g., seedbank depletion and plant pathogenic fungi; Okalebo et al., 2011; Schafer and Kotanen, 2003), but the influence of unmanaged weed communities on soil microbial community dynamics represents a new frontier in weed and soil ecology. Indeed, changes in the soil microbial community may influence competitive outcomes between weed and crop species (Marler et al., 1999); thus, these interactions warrant further investigation.

5. Conclusions

Although the results for individual FAMEs and overall community composition were sometimes inconsistent with previous studies, it is clear from this work that the type of residue (e.g., cover crops vs. weeds) and the method of plant termination and residue management result in unique changes to microbial community structure. However, it is important to note that these changes were likely transient (e.g., limited to the early summer following cover crop and weed growth) as previous studies have shown strong seasonal changes in microbial communities of arable soils (Bossio et al., 1998). It is likely that as the cropping season progressed beyond our sampling interval (25–45 DAT) the microbial community structure would have become more strongly influenced by the growing crop (Drijber et al., 2000).

Tillage is often a strong driver of soil microbial community structure in managed ecosystems (Drijber et al., 2000), but the results of this study highlight the strong negative impact of arable weed communities on specific soil microbial functional groups and community structure as a whole. Previous studies have found that plant species, community composition, and diversity are relatively weak drivers of microbial community composition (Kielak et al., 2008), but these results demonstrate the potential influence of the plant rhizosphere when comparing different plants classifications (e.g., weedy and invasive species vs. cultivated crops). Future studies should be directed toward understanding the prominent role of arable weed communities in driving microbial community composition and also toward determining the functions of these unique communities and functional groups (Torsvik and Øvreaas, 2002).

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