Renewable Agriculture and Food Systems: 21(4); 245–252 DOI: 10.1079/RAF2005147

Soil microbiota effects on rye growth: implications for integration of a rye cover crop into temperate cropping systems

Jason L. De Bruin[1,*], Nicholas R. Jordan[2], Paul M. Porter[2], and Sheri C. Huerd[2]

[1]Department of Agronomy, Iowa State University, 2104 Agronomy Hall, Ames, IA 50011, USA.
[2]Department of Agronomy and Plant Genetics, University of Minnesota, 411 Borlaug Hall, 1991 Buford Circle, St Paul, MN 55108, USA.
*Corresponding author: jsndbrn@iastate.edu.

Accepted 11 November 2005 **Research Paper**

Abstract

Integration of rye (*Secale cereale* L.) cover crops into the corn (*Zea mays* L.) soybean [(*Glycine max* (L.) Merr.] rotation of the upper Midwest USA can provide many agronomic and agroecological benefits. Integration is made difficult by short growing seasons, but may be facilitated by management of key agroecological interactions such as those between rye and soil microbiota. Rye growth was measured and colonization by arbuscular-mycorrhizal fungi (AMF) was determined in greenhouse experiments using soils from seven different management systems from a long-term cropping-systems experiment in southwest Minnesota. Microbial effects on rye growth were not evident before vernalization, but at final harvest (4 weeks after vernalization) soil microbial populations reduced rye shoot and root growth, relative to a pasteurized control inoculum. At final harvest, shoot biomass in 2-year rotations was 17% greater than 4-year rotations, indicating that microbial populations selected for by 4-year rotations may be more deleterious or pathogenic than those selected for by 2-year rotations. Growth of three rye cultivars was examined in all inocula; cultivars differed in their mean response to soil microbiota and their ability to host AMF. These findings suggest that management factors affect interactions between rye and soil microbiota resulting in altered rye growth.

Key words: cover crop, crop rotation, mycorrhizal fungi, organic, rye, *Secale cereale*, soil microbiota

Introduction

Cover crops provide a well-documented range of benefits including contributions to soil quality and fertility, nutrient management, erosion control, and pest management[1]. The importance of cover crops may increase as societal expectations of agriculture evolve. For example, cover crops are likely to be an important strategy for farmers engaging in carbon trading or modifying management to meet total minimum daily load (TMDL) requirements. In the upper Midwest, winter cover crops must be established during a short temporal window making this operation both difficult and risky[1–3]. Optimal agronomic functioning of winter cover crops depends on rapid early biomass accumulation the following spring season. Adoption of cover-cropping practices would likely increase if reliability of establishment and biomass production were increased. Cover-crop breeding[4] and development of technology used in cover-crop management such as planters and tillage implements may lead to such increases.

Cover crops interact with many organisms in agroecosystems, and serve as critical links in a number of agroecological processes and cycles[5]. Through these interactions, cover crops influence and are influenced by other elements of biodiversity. Interactions between plants and soil microorganisms are increasingly recognized as important factors in agroecosystems[6–8] and management of these interactions may offer additional options for improving the integration of cover crops into cropping systems.

Analysis of cover crop interactions with soil microbiota has largely emphasized effects of cover crops on microbiota. Cover crops increase total microbial biomass[9–11] and increase populations of beneficial microbiota such as arbuscular-mycorrhizal fungi (AMF). Certain cover crops can provide a live host for AMF colonization during long winter-fallow periods, thus improving AMF survival and

subsequent colonization of crops[12–15] and crop P nutrition[16,17]. Cover crops have also been shown to both increase[18] and to decrease[19] the abundance of soil-borne pathogens. These studies suggest that cover crops may be important instruments for management of soil microbiota.

Very little is known about effects of beneficial or pathogenic soil microbiota on cover crops. It is possible that interactions with soil microbiota positively affect cover-crop establishment and growth since beneficial microbiota, such as AMF and growth-promoting rhizobacteria[7,20,21], can have strong effects on plant growth, nutrition and stress resistance. Conversely, pathogenic microbiota are increasingly understood as important limiting factors even when obvious disease symptoms are not present[22,23]. It is possible that cover-crop establishment and early biomass accumulation could be improved in cropping systems managed to increase populations of beneficial microbiota, and/or to reduce abundance of pathogens that interfere with cover-crop establishment and growth. In the only relevant study known to us, large differences occurred among cropping systems on colonization of winter rye by AMF[24], supporting the hypothesis that management factors may influence cover-crop interactions with soil microbiota. Unfortunately, there appear to be no detailed experimental investigations of these possibilities in published literature.

In temperate areas rye is frequently chosen by farmers using winter cover crops, because of a range of desirable attributes such as winter hardiness, early spring growth and high biomass production[25]. However, in the upper Midwest, rye establishment following corn or soybean is complicated by a relatively late planting date. It is therefore important to identify management factors that could affect rye establishment and growth the following spring season. Accordingly, we examined how rye responded to soil microbiota from the Variable Input Crop Management Systems (VICMS) experiment located at the University of Minnesota Southwest Research and Outreach Center near Lamberton MN. The VICMS experiment was established in 1989; its treatments consist of four different management levels (minimum, low, conventional and organic input levels), each applied to one 2-year and one 4-year crop rotation. The experiment was established on a field that had a history of very few inputs and very low soil P levels. A complete description of the rotations, management treatments and associated crop yields was reported by Porter et al.[26]. These varying management systems are likely to cause differentiation among communities of AMF[27,28] and other soil microbiota[29,30] and certain soil-microbiological differences among VICMS treatments have been documented. Early in the VICMS study, AMF spore populations and colonization rates were higher in low-input than in conventional treatments[31]. Recently, others have documented that total microbial biomass was higher in organic and reduced-input treatments than in conventional ones[32]. In addition to assessing the net effect of soil microbiota from various management systems on early growth of rye, we examined two other related issues. First, we determined AMF colonization in rye grown in soils from these management systems, to assess whether positive or negative effects of soil microbiota on rye growth were associated with AMF colonization. Second, we conducted our experiments with three rye cultivars. It is plausible that effects of soil microbiota on cover-crop performance might differ among cover-crop cultivars since such effects generally occur with field crops[33]. Little effort has been made to improve germplasm for cover-crop performance in most cover-crop species. Therefore, assessment of genetic differences in relations with soil microbiota is worthwhile, since breeding to improve these relations might be a useful part of a multifaceted approach in improving the integration of cover crops into cropping systems.

Materials and Methods

Two greenhouse studies (Study I and Study II) were conducted to investigate the growth response of rye to soil microbiota and association with AMF in soils with varying management histories. In each study, the experimental design was a 3 by 8 factorial combination of three rye cultivars and eight soil inoculums with four rye harvest dates each with five replicates. Harvest 1 was approximately 14 days after planting; harvest 2, 28 days after planting; harvest 3, 14 days after a vernalization period; and harvest 4, 28 days after vernalization period. Thus, the first two harvests corresponded to post-establishment growth before winter, and the latter two corresponded to spring growth. The entire experiment was conducted twice; with Study I initiated in fall 2001 and Study II initiated in fall 2002.

The seven inoculum soils from the VICMS experiment were collected from 0 to 20 cm soil depth in the fall of 2001 and 2002. These soils are a complex of the Normania, Revere, Webster and Ves clay loams. Six of the seven inoculum soils were collected following corn production from either a 2-year or 4-year rotation, with a minimum (Min), conventional (Con) or organic (Org) management system. The seventh inoculum soil was obtained from the prairie treatment (Prairie), which was sown with a native prairie species mixture in 1989.

The 'base soil' used in both Studies I and II consisted of a 50 : 50 (by volume) mixture[34,35] of sand and a Typic Hapludoll (well-drained silt loam) soil from the Research and Outreach Center near Rosemount MN. This soil : sand mixture was steam pasteurized (twice for 60 min at 77°C) to eliminate soil biota while minimizing soil chemistry changes[36]. The base soil mixture was inoculated with 'inoculum' soil from each of the seven management systems (550 : 80, by volume; 15% inoculum) and was also used to provide a control treatment free of soil-microbiota. Plastic pots 6.4 cm in diameter and 25 cm in length were filled to 22 cm depth with the soil mix. Five rye seeds were placed in each pot, and covered with approximately 2.5 cm of soil mix. Seedlings were thinned to three per pot approximately six days after planting.

https://doi.org/10.1079/RAF2005147 Published online by Cambridge University Press

In Study I, plant shoots were clipped approximately 1 cm above the soil level at each harvest and allowed to re-grow. Whole plants (roots and shoots) were sampled 1 week after the fourth harvest, dried (55°C for 72 h) and weighed. In Study II whole plants (roots and shoots) were collected at each harvest, dried and weighed. Following the first two sample dates plants were vernalized at 4°C with a cycle of 16 h light and 8 h dark. After vernalization, plants in Study I were fertilized with approximately 12 ml pot^{-1} of 15-0-0 fertilizer. No fertilizer was added in Study II, due to lack of visual nutrient deficiencies. Nutrient levels in experimental soil mixes were assessed in soil samples collected for each soil mixture from Study II after the first and fourth harvests; soil analyses were conducted by the University of Minnesota soils testing laboratory.

Harvested roots (from final harvest only for Study I; from all harvests for Study II) were analyzed for colonization by AMF. A sub-sample of plant roots was dyed using Aniline Blue[37] and colonization ratios were determined by counting the presence or absence of AMF structures (hyphae, arbuscules and vesicles) using a light microscope at 200× from 100 views per sample. Percent colonization was calculated based on presence or absence of AMF structures in each view.

Data were analyzed using SAS (SAS Institute, Cary, NC). Analysis was done separately for each study due to heterogeneity of variance. Colonization percent was transformed using arcsine transformation (arcsine $\sqrt{y}$) to normalize data for analysis[38]. There were no significant interactions between soil type and rye cultivar. Single degree of freedom contrasts were used to determine estimated differences between management systems, rye cultivars and combinations of both factors. Contrasts consisted of the following comparisons: agricultural systems (without the prairie) versus control, 2-year versus 4-year rotations for each management system and conventional versus minimum versus organic systems averaged across rotation length.

Results

Shoot and root biomass

In both studies, soil inocula from the various management-system treatments differed in their effects on shoot biomass in seven of the eight harvests in the two studies (Table 1). Shoot biomass production before vernalization (i.e., first and second harvests), was generally greater in inocula from organic systems than in inocula from conventional and minimum-input systems (Table 1). Inocula from 2-year rotations produced greater pre-vernalization shoot biomass than 4-year rotations. These effects on early seedling growth (14 and 28 days after planting) are best explained by the high nutrient levels present in inocula from organic rotations. Soil mixes (i.e., inocula plus base soil) from 2- and 4-year organic systems had P at 22 and 15 mg kg^{-1}, respectively, compared to approximately 8 mg kg^{-1} for the other soils (Table 2) confirming field observations of high P levels in these same soils[26,32]. Field sampling also revealed a similar pattern of N levels among management systems[32] (N levels were not determined in inoculated soils used in Studies I and II). Specifically, N values were greatest in the organic management systems at approximately 16.0 and 8.0 ppm for 2- and 4-year rotations, respectively. Nitrogen values from the minimum and conventional management systems were approximately 2.5 and 8.0 ppm for both 2- and 4-year rotations, respectively[26,32]. The relatively high nutrient levels observed in organic management treatments provide a plausible explanation for the more rapid pre-vernalization shoot growth observed in response to these soil inocula. Therefore, pre-vernalization results do not particularly support the hypothesis that microbiological differences among inocula soils were affecting shoot growth during this stage. At the final harvest in both studies, inocula from all management systems reduced shoot biomass relative to the pasteurized control inoculum (Table 1). Averaged over management systems this reduction was approximately 15%. It is unlikely that this reduction resulted from nutrient differences between the pasteurized inoculum and cropping system inocula, since pasteurized inoculum soils had relatively low levels of most nutrients, despite higher biomass production (Table 2). Therefore, these results are consistent with the hypothesis that microbiological differences among inoculum soils affected post-vernalization rye growth. Shoot biomass at final harvest was different among management systems (Table 1). Inocula from 2-year rotations again produced greater shoot biomass than inocula from 4-year rotations (Table 1). For example, in Study I, inocula from the 2-year rotation treatments increased biomass by 19%, relative to 4-year treatments. The positive effect of inocula from organic systems diminished after vernalization, and had no significant effect at harvest 4 (Table 1). Again, this pattern of results is not readily explained by nutrient differences among inoculum soils (Table 2). Apparently, some non-nutrient factor differed among these inocula, and these results are consistent with the hypothesis that microbiological differences among soils from different management systems can substantially affect rye shoot growth.

Relative to the pasteurized inoculum, root biomass production was also significantly reduced by inocula from all management systems and from the prairie treatment (Table 3). However, in contrast to shoot biomass, root production was not significantly affected by inocula from management systems.

Rye cultivars differed in overall response to soil inocula from the management treatments, relative to their growth in the pasteurized control. Specifically, contrasts comparing mean shoot biomass production in management-system inocula to the pasteurized control were different among cultivars at three of four harvests in Study I and two of four harvests in Study II (Table 4). In particular, differences existed among cultivars at the fourth harvest in both studies; these were particularly pronounced in Study II.

https://doi.org/10.1079/RAF2005147 Published online by Cambridge University Press

Table 1. Shoot biomass averaged across three rye cultivars from soil mixtures inoculated with soils from seven management systems and one pasteurized control in two greenhouse studies (Studies I and II). The interval between harvest periods 2 and 3 was a vernalization period (days 30–126 for Study I and 32–83 for Study II).

	Study I				Study II			
	Harvest 1	Harvest 2	Harvest 3	Harvest 4	Harvest 1	Harvest 2	Harvest 3	Harvest 4
	Days after planting							
	14	28	145	159	16	31	100	114
Soil	mg plant^{-1}							
2-year Con	31.9	53.2	165	280	32.0	74.3	141	202
2-year Min	30.1	58.3	151	262	31.0	68.6	135	221
2-year Org	35.2	62.2	158	277	38.2	90.1	150	219
4-year Con	30.1	54.6	147	234	27.4	66.2	125	189
4-year Min	27.8	56.7	149	229	24.7	59.5	108	166
4-year Org	29.8	57.1	150	227	33.1	82.4	149	200
Prairie	30.6	57.1	171	279	33.0	76.5	132	195
Control	27.0	66.0	157	298	25.0	69.0	147	241
$P>F$	***	**	NS[1]	***	***	***	***	***
Contrasts								
Crop[2] versus Control	3.85**	−9.00***	−3.78	−46.67***	6.13***	4.56 NS	−11.56 NS	−41.91***
Con versus Min	2.08 NS	−3.59 NS	5.94	11.73 NS	2.08 NS	6.21**	11.02 NS	1.87 NS
Con versus Org	−1.52 NS	−5.69*	1.62	5.24 NS	−5.94***	−15.99***	−16.53**	−14.58 NS
Min versus Org	−3.61**	−3.61 NS	−4.32	−6.49 NS	−7.79***	−22.20***	−27.56***	−16.44 NS
2-year versus 4-year	3.15**	1.77 NS	9.55	42.97***	6.52***	8.29***	14.41**	29.07***
2-year Con versus 4-year Con	1.78 NS	−1.42 NS	18.43	45.71**	4.56**	8.07*	15.82 NS	13.36 NS
2-year Min versus 4-year Min	2.26 NS	1.62 NS	2.67	32.42 NS	6.29***	9.16**	26.27**	54.96***
2-year Org versus 4-year Org	5.41**	5.12 NS	7.55	50.78**	5.13***	7.64*	1.16 NS	18.96 NS

[1] Not significant at $P \leqslant 0.05$.
[2] Included soils from the six cropped systems [2- and 4-year conventional (Con), minimum (Min) and organic (Org) systems], but not the prairie.
* Significant at $P < 0.05$; ** significant at $P < 0.01$; *** significant at $P < 0.001$.

Table 2. Soil nutrient concentrations at the first harvest from Study II for soil mixtures inoculated with soils from seven management systems and one pasteurized control.

	Nutrient concentrations								
Soil	**P**	**K**	**Ca**	**Mg**	**Na**	**Fe**	**Cu**	**Mn**	**Zn**
	----------mg kg^{-1}----------								
2-year Con	6	44	1110	220	8	19	0.3	7	0.7
2-year Min	7	52	1333	281	6	37	0.4	14	1.3
2-year Org	22	79	1513	270	12	26	0.4	10	1.9
4-year Con	11	58	1616	281	4	38	0.6	24	2.4
4-year Min	9	42	1201	212	2	29	0.5	36	1.1
4-year Org	15	62	1260	227	6	30	0.5	19	2.2
Prairie	10	66	1546	280	5	33	0.6	22	1.6
Control	7	25	691	134	7	21	0.3	8	0.9

In the latter study, inocula from the management systems reduced shoot biomass production more sharply in the two cultivars that had greater overall biomass production (Homil21 and Rymin; results not shown) than in the less productive cultivar Dacold (Table 4). As noted above, shoot-biomass differences at the final harvest between the pasteurized control treatment and the mean of soil inocula from the management-system treatments at the final harvest were most likely due to effects of soil microbiota, supporting our inference that the rye cultivars differed in their mean response to the presence of soil microbiota. There was no difference among cultivars in their response to the inocula from the management systems at any harvest, thus the cultivars did not show any differential sensitivity to nutrient or microbiological differences among these systems.

AMF colonization

Root samples from all four harvests (from Study II) indicated that little colonization occurred prior to the third sampling date, rising to moderate levels thereafter (results from three harvests not shown). At final harvest, AMF colonization was affected by soil inoculum source (Table 5). Colonization was greater in Study I averaging 8.8%, compared with the Study II average of 5.6% (Table 5). Highest levels of colonization occurred with 2-year conventional soils, which averaged 18.7 and 7.2% colonization, and 4-year minimum soils, which averaged 12.8 and 7.5% colonization, in Studies I and II, respectively. In both studies, the lowest colonization levels were observed in inocula from organic systems, which had high P levels. Colonization levels in soils from organic systems were reduced relative to soils from conventional and minimum systems in Study I (Table 5). In Study I, 2-year rotations had higher colonization than 4-year rotations while in Study II 4-year rotations had slightly greater infection (Table 5). Colonization levels were also different among rye cultivars in Study I, where Homil21 had greater colonization levels than the other two rye cultivars (Table 6). However, no significant cultivar effects were evident in Study II where colonization rates were lower (Table 6).

Table 3. Root biomass averaged across three rye cultivars grown in soils from soil mixtures inoculated with soils from seven management systems and one pasteurized control at final harvest (159 days for Study I and 114 days for Study II).

	Study I	**Study II**
Soil	----------mg plant^{-1}----------	
2-year Con	109	158
2-year Min	116	147
2-year Org	106	150
4-year Con	104	146
4-year Min	106	149
4-year Org	93	177
Prairie	116	113
Control	223*	201*

* Significantly different from all other soils at $P \leqslant 0.05$.

Discussion

Inocula from different management-system treatments in the VICMS experiment had considerably different effects on rye shoot biomass production after vernalization. We note that our results do not definitively refute the hypothesis that differences in nutrient concentrations (or other chemical or physical factors) rather than differences in soil microbiota are the cause of the observed differences in rye growth. In fact, the different effects of inocula on pre-vernalization growth could be plausibly explained by nutrient level differences. After vernalization, however, inocula effects on growth are not well explained by nutrient differences; therefore, these effects most likely resulted from differences in some non-nutrient factor, highlighting the probable role of soil microbiological differences among inocula.

We found that soil inocula from all VICMS management systems reduced post-vernalization growth of rye. This result suggests that under field conditions, the net effect of

https://doi.org/10.1079/RAF2005147 Published online by Cambridge University Press

Table 4. Mean reduction in rye shoot biomass associated with soil inocula from management system treatments (i.e., difference from pasteurized control) for three rye cultivars.

	Study I				Study II			
	Harvest 1	Harvest 2	Harvest 3	Harvest 4	Harvest 1	Harvest 2	Harvest 3	Harvest 4
Variety	mg plant^{-1}							
Dacold	3.1	−14.8	−32.5	−55.3	3.2	3.3	−30.9	−12.1
Homil21	4.8	−4.9	1.5	−45.0	6.9	4.5	−2.3	−74.5
Rymin	3.6	−7.3	19.6	−39.7	8.3	5.9	1.5	−39.2
$P>F$	*	**	NS[1]	**	***	NS	NS	***

[1] Not significant at $P \leqslant 0.05$.
* Significant at $P < 0.05$; ** significant at $P < 0.01$; *** significant at $P < 0.001$.

soil microbiota in any of these cropping systems would be to impede rye growth, presumably due to the accumulation of some deleterious or pathogenic microbial agent. Accumulation of such sub-lethal pathogens is often suspected as a factor in yield decline in short-rotation or monoculture cropping scenarios[39]. However, previous to this study, rye had not been grown in any treatment of the VICMS experiment, and therefore it would be somewhat surprising if pathogens affecting rye occurred in all VICMS treatments. It is also possible that the observed negative effects of soil microbiota represent parasitic effects of microbes that can have important positive effects at certain growth stages. For example, AMF may be net parasites at most stages of plant growth, yet have highly beneficial effects when mycorrhizal plants encounter a variety of stress factors[40]. Likely, rye plants did not experience significant stress factors in our experiment; thus full evaluation of effects of soil microbiota will require assessment of how cover crops are affected by microbiota during periods when cover crops typically experience growth-limiting stress factors.

Our finding that soil microbiota reduce rye growth highlights the question of whether there are practical management methods that can improve soil quality for rye cover cropping by lessening negative soil microbiotic effects on rye growth. Diversification may be one such option, since there are indications that beneficial soil microbiota accumulate in more diversified cropping systems[41,42]. Our results do not support that hypothesis; we found that inocula from longer and more diversified rotations exerted more negative effects on rye than shorter rotations. These effects of rotation length on rye growth could be mediated by the size of the microbial community. A study on VICMS determined that microbial biomass was greater in the 4-year rotations compared with the 2-year rotations[32], and if rhizosphere microbial communities are correspondingly larger in longer rotations, these communities may exert a larger cost to rye plants.

Table 5. Arbuscular mycorrhizal fungi colonization averaged across three rye cultivars from soil mixtures inoculated with soils from seven management systems and one pasteurized at final harvest (159 days for Study I and 114 days for Study II).

	Study I	Study II
Soil	%	
2-year Con	18.7	7.2
2-year Min	8.5	3.4
2-year Org	6.9	2.9
4-year Con	5.8	5.8
4-year Min	12.8	7.5
4-year Org	1.9	5.0
Prairie	7.2	7.3
Control	0.5	0.2
$P>F$	***	***
Contrasts		
Con versus Min	0.02 NS[1]	0.07 NS
Con versus Org	2.00***	0.35**
Min versus Org	1.60***	0.10 NS
2-year versus 4-year	0.77**	−0.15**
2-year Con versus 4-year Con	4.10***	0.08 NS
2-year Min versus 4-year Min	−0.47 NS	−0.84***
2-year Org versus 4-year Org	1.60*	−0.30*

[1] Not significant at $P \leqslant 0.05$.
* Significant at $P < 0.05$; ** significant at $P < 0.01$; *** significant at $P < 0.001$. Analysis was conducted on arcsine $\sqrt{y}$ transformed data.

Table 6. Arbuscular mycorrhizal fungi colonization averaged across soils from soil mixtures inoculated with soils from seven management systems at final harvest (159 days for Study I and 114 days for Study II).

	Study I	Study II
Cultivar	%	
Dacold	1.5	4.5
Homil21	19.0	6.1
Rymin	8.5	5.9
$P>F$	***	NS[1]
Contrasts		
Rymin versus Dacold	7.0***	1.4
Rymin versus Homil21	−10.5***	−0.2
Homil21 versus Dacold	17.5***	1.6

[1] Not significant at $P \leqslant 0.05$.
*** Significant at $P \leqslant 0.001$. Analysis was conducted on arcsine $\sqrt{y}$ transformed data.

https://doi.org/10.1079/RAF2005147 Published online by Cambridge University Press

We also found no evidence that organic management methods increased the beneficial effects of soil microbiota on rye growth, relative to conventional or minimum-input methods. These results indicate that while diversified rotations and high-organic matter inputs may have a variety of beneficial effects on soil health and quality[43], there is no guarantee that these management approaches will beneficially affect soil microbiotic communities in all instances.

The small sample of rye germplasm that we examined responded differently to the soil microbiota populations within each management system. Therefore, our results provide some support for the hypothesis that integration of rye cover crops into cropping systems could be improved by capitalizing on favorable interactions between rye cultivars and soil biota. A more thorough test of this possibility would require a broader sample of rye germplasm and an effort to identify situations where agronomically useful interactions occur between soil microbiota and particular rye cultivars, e.g., when stress factors are operant. We also observed variation among rye cultivars in colonization by AMF. Possibly, the more heavily colonized cultivars are more effective hosts for agronomically beneficial AMF taxa, although host effectiveness cannot be inferred from colonization level alone[44]. Given that cover crops have been shown to increase the abundance of AMF and beneficial effects of AMF on crops[12–14,17], it would be prudent to screen cover crop cultivars for AMF colonization to identify and perhaps avoid cultivars that have low AMF colonization. Rye cultivars that are highly effective hosts for AMF might improve benefits provided by rye, such as N uptake[36], during the limited period available for rye cover-crop growth in the upper Midwest. Highly effective hosts might also increase the abundance of agronomically beneficial AMF during a limited growth period compared to cultivars that are less effective hosts.

In summary, inoculum soils from different VICMS management systems had different effects on rye growth and AMF colonization. In particular, inocula from 4-year rotation treatments reduced rye biomass more strongly than inocula from 2-year rotations, possibly reflecting effects of larger microbial communities in extended rotations. Rye cultivars responded consistently to management systems but differed in respect to AMF colonization, suggesting that certain cover-crop cultivars may provide more beneficial agroecological services to cropping systems. Our results suggest that soil microbiota, selected for by specific management systems, can influence cover-crop growth and AMF colonization. Our findings also suggest the importance of further work to determine how soil microbial communities could be managed to improve integration of cover crops into cropping systems in the upper Midwest.

References

1 Snapp, S.S., Swinton, S.M., Labarta, R., Mutch, D., Black, J.R., Leep, R., Nyiraneza, J., and O'Neil, K. 2005. Evaluating cover crops for benefits, costs and performance within cropping system niches. Agronomy Journal 97:322–332.

2 Brandsaeter, L.O., Smeby, T., and Tronsmo, A.M. 2000. Winter annual legumes for use as cover crops in row crops in northern regions: II. Frost resistance study. Crop Science 40:175–181.

3 Dabney, S.M., Delgado, J.A., and Reeves, D.W. 2001. Using winter cover crops to improve soil and water quality. Communications in Soil Science and Plant Analysis 32:1221–1250.

4 Teasdale, J.R., Devine, T.E., and Mosjidis, J.A. 2004. Growth and development of hairy vetch cultivars in the northeastern United States as influenced by planting and harvesting date. Agronomy Journal 96:1266–1271.

5 Altieri, M.A. 1995. Agroecology: The Science of Sustainable Agriculture. 2nd ed. Westview Press, Boulder, CO.

6 Reynolds, H.L., Packer, A., Bever, J.D., and Clay, K. 2003. Grassroots ecology: Plant–microbe–soil interactions as drivers of plant community structure and dynamics. Ecology 84:2281–2291.

7 Morrissey, J.P., Maxwell, D.J., Mark, G.L., and O'Gara, F. 2004. Are microbes at the root of a solution to world food production? European Molecular Biology Organization Journal 5:922–926.

8 Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setala, H., van der Putten, W.H., and Wall, D.H. 2004. Ecological linkages between aboveground and belowground biota. Science 304:1629–1633.

9 Schutter, M.E. and Dick, R.P. 2002. Microbial community profiles and activities among aggregates of winter fallow and cover-cropped soil. Soil Science Society of America Journal 66:142–153.

10 Reddy, K.N., Zablotowicz, R.M., and Locke, M.A. 2003. Cover crop, tillage, and herbicide effects on weeds, soil properties, microbial populations, and soybean yield. Weed Science 51:987–994.

11 Jackson, L.E., Ramirez, I., and Yokota, R. 2004. On-farm assessment of organic matter and tillage management on vegetable yield, soil, weeds, pests, and economics in California. Agriculture, Ecosystems and Environment 103: 443–463.

12 Galvez, L., Douds, D.D., Wagoner, P., Longnecker, L.R., Drinkwater, L.E., and Janke, R.R. 1995. An overwintering cover crop increases inoculum of VAM fungi in agricultural soil. American Journal of Alternative Agriculture 10:152–156.

13 Kabir, Z., O'Halloran, I.P., and Hamel, C. 1997. Overwinter survival of arbuscular mycorrhizal hyphae is favored by attachment to roots but diminished by disturbance. Mycorrhiza 7:197–200.

14 Boswell, E.P., Koide, R.T., Shumway, D.L., and Addy, H.D. 1998. Winter wheat cover cropping, VA mycorrhizal fungi and maize growth and yield. Agriculture, Ecosystems and Environment 67:55–65.

15 Troeh, Z.I. and Loynachan, T.E. 2003. Endomycorrhizal fungal survival in continuous corn, soybean, and fallow. Agronomy Journal 95:224–230.

16 Kabir, Z. and Koide, R.T. 2000. The effect of dandelion or a cover crop on mycorrhiza inoculum potential, soil aggregation and yield of maize. Agriculture, Ecosystems and Environment 78:167–174.

17 Kabir, Z. and Koide, R.T. 2002. Effect of autumn and winter mycorrhizal cover crops on soil properties, nutrient uptake,

https://doi.org/10.1079/RAF2005147 Published online by Cambridge University Press

and yield of sweet corn in Pennsylvania, USA. Plant and Soil 238:205–215.
18 Manici, L.M., Caputo, F., and Babini, V. 2004. Effect of green manure of *Pythium* spp. population and microbial communities in intensive cropping systems. Plant and Soil 263:133–142.
19 Abawi, G.S. and Widmer, T.L. 2000. Impact of soil health management practices on soilborne pathogens, nematodes and root diseases of vegetable crops. Applied Soil Ecology 15:37–47.
20 Leake, J.R., Johnson, D., and Donnelly, D.P. 2004. Networks of power and influence: the role of mycorrhizal mycelium in controlling plant communities and agroecosystem functioning. Canadian Journal of Botany 82:1016–1045.
21 Selosse, M.A., Baudoin, E., and Vandenkoornhuyse, P. 2004. Symbiotic microorganisms, a key for ecological success and protection of plants. Comptes Rendus Biologies 327:639–648.
22 Johnson, N.C. 1993. Can fertilization of soil select less mutualistic mycorrhizae. Ecological Applications 3:749–757.
23 Kremer, R.J. and Li, J.M. 2003. Developing weed-suppressive soils through improved soil quality management. Soil and Tillage Research 72:193–202.
24 Sattelmacher, B., Reinhard, S., and Pomikalko, A. 1991. Differences in mycorrhizal colonization of rye (*Secale cereale* L.) grown in conventional or organic (biological–dynamic) farming systems. Journal of Agronomy and Crop Science 167:350–355.
25 Stoskopf, N.C. (ed.) 1985. Rye. In Cereal Grain Crops. Reston Publishing Co., Reston, VA. p. 403–414.
26 Porter, P.M., Huggins, D.R., Perillo, C.A., Quiring, S.R., and Crookston, K.R. 2003. Organic and other management strategies with two- and four-year crop rotations in Minnesota. Agronomy Journal 95:1–11.
27 Douds, D.D. Jr and Millner, P.D. 1999. Biodiversity of arbuscular mycorrhizal fungi in agroecosystems. Agriculture, Ecosystems and Environment 74:77–93.
28 Oehl, F., Sieverding, E., and Mader, P. 2004. Impact of long-term conventional and organic farming on the diversity of arbuscular mycorrhizal fungi. Oecologia 138:574–583.
29 Shannon, D., Sen, A.M., and Johnson, D.B. 2002. A comparative study of the microbiology of soils managed under organic and conventional regimes. Soil Use and Management 18:274–283.
30 Lupwayi, N.Z., Rice, W.A., and Clayton, G.W. 1998. Soil microbial diversity and community structure under wheat as influenced by tillage and crop rotation. Soil Biology and Biochemistry 30:1733–1741.
31 Kurle, J.E. and Pfleger, F.L. 1994. Arbuscular mycorrhizal fungus spore populations respond to conversions between low-input and conventional management practices in a corn–soybean rotation. Agronomy Journal 86:467–475.
32 Kuratomi, M. 2003. A soil assessment of alternative crop management practices. M.S. thesis, Department of Soils, Water, and Climate, University of Minnesota, St. Paul, MN.
33 Hetrick, B.A.D., Wilson, G.W.T., and Cox, T.S. 1993. Mycorrhizal dependence of modern wheat cultivars and ancestors: a synthesis. Canadian Journal of Botany 71:512–518.
34 Al-Karaki, G.N. and Clark, R.B. 1999. Varied rates of mycorrhizal inoculum on growth and nutrient acquisition on barley grown with drought stress. Journal of Plant Nutrition 22:1775–1784.
35 Kilironomos, J.N. 2003. Variation in plant response to native and exotic arbuscular mycorrhizal fungi. Ecology 84:2292–2301.
36 Hawkins, H.J., Johansen, A., and George, E. 2000. Uptake and transport of organic and inorganic nitrogen by arbuscular-mycorrhizal fungi. Plant and Soil 226:275–285.
37 Grace, C. and Stribley, D.P. 1991. A safer procedure for routine staining of vesicular-arbuscular mycorrhizal fungi. Mycological Research 95:1160–1162.
38 Oehlert, G.W. 2000. A First Course in Design and Analysis of Experiments. W.H. Freeman and Company, New York, NY.
39 Marschner, H. 1995. Mineral Nutrition of Higher Plants. Academic Press, San Diego, CA.
40 Johnson, N.C., Graham, J.H., and Smith, F.A. 1997. Functioning of mycorrhizal associations along the mutualism-parasitism continuum. New Phytologist 135:575–585.
41 Eason, W.R., Scullion, J.R., and Scott, E.P. 1999. Soil parameters and plant responses associated with arbuscular mycorrhizas from contrasting grassland management regimes. Agriculture, Ecosystems and Environment 73: 245–255.
42 Feldmann, F. and Boyle, C. 1999. Weed-mediated stability of arbuscular mycorrhizal effectiveness in maize monoculture. Journal of Applied Botany 73:1–5.
43 Martini, E.A., Buyer, J.S., Bryant, D.C., Hartz, T.K., and Denison, R.F. 2004. Yield increases during the organic transition: improving soil quality or increasing experience? Field Crops Research 86:255–266.
44 Bever, J.D. 2002. Negative feedback within a mutualism: host-specific growth of mycorrhizal fungi reduces plant benefit. Proceedings of the Royal Society of London 269:2595–2601.