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Short-term cover crop decomposition in organic and conventional soils: Characterization of soil C, N, microbial and plant pathogen dynamics

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Abstract

Stages of oat–vetch cover crop decomposition were characterized over time in terms of carbon and nitrogen cycling, microbial activity and damping-off pathogen dynamics in organically and conventionally managed soils in a field and a controlled incubation experiment. A measurement of relative growth consisting of radial growth of a fungal colony over non-sterilized soil divided by that over sterilized soil was used as an assay of suppressiveness. No differences in relative growth of *Pythium aphanidermatum* and *Rhizoctonia solani* were detected between organic and conventionally managed soils amended with cover crop residue. Significant effects of cover crop decomposition stage on the relative growth of both pathogens were obtained. Relative growth of *P. aphanidermatum* was highest just after incorporation and decreased 3 weeks after incorporation. Relative growth of *R. solani* was highest about 20 days after incorporation, and decreased 2 weeks later in the organic system, but continued to increase in the conventional system. In both experiments, the N or C content, C : N ratio or dry weight of retrieved debris were significantly correlated with relative growth of *P. aphanidermatum*. Relative growth of *R. solani* was significantly correlated with the C : N ratio of soil or the C or N content of debris. Microbial activity was not consistently associated with relative growth of either pathogen.

Introduction

Numerous studies have compared soil structure, microbiology and chemistry in conventional and organic or reduced-input farming systems. Soil organic matter, polysaccharide content, and microbial biomass have been shown to be generally higher in organic or reduced-input farms compared to conventional farms (Doran et al.,1988; Lockeretz et al., 1981; Reganold et al., 1987). Differences in microbial activity assessed either by soil respiration or N mineralization were even greater than differences in microbial biomass between a reduced-input field and a conventional field (Hassink et al., 1991). Contrary to the large number of studies on soil physical, chemical, and microbiological characteristics, very few studies have compared disease incidence and severity in conventional and organic or reduced-input farms. In Europe, several root and stem diseases of wheat and damping-off of sugar beet were shown to be less severe in organic or reduced-input farms than in conventional farms (El Titi and Richter, 1987; Piorr and Hindorf, 1986). However, relationships between reductions in disease and soil microbial dynamics or soil nutrient status were not investigated.

A recent on-farm comparative study of tomatoes grown in California showed that Phytophthora root rot (*Phytophthora parasitica*) and corky root (*Pyrenochaeta lycopersici*) were less severe in organic

farms that used cover crops and/or compost compared to conventional farms where no organic matter other than cash crop residue was added to the soil (Workneh et al., 1993). The reduction in corky root was related to higher microbial activity and nitrogen mineralization rates in soil and lower nitrogen concentrations in tomato tissue on organic farms, while reduction in Phytophthora root rot was related to physical properties of the soil (Workneh et al., 1993). Subsequent greenhouse studies confirmed that corky root was suppressed by biological factors in organically managed soil (Workneh and van Bruggen, 1994). Winter cover crops used on organic farms may have played an important role in corky root suppression by soil microbial communities.

Many studies in which conventionally managed soils were used in the greenhouse or field showed that incorporation of organic amendments could suppress growth of soilborne plant pathogens (Huber and Watson, 1970; Lewis and Papavizas, 1975; 1977; Lumsden et al., 1983). Several mechanisms have been put forward to explain this kind of suppressiveness. In the absence of a susceptible host, organic amendments could stimulate germination of propagules of many fungi, followed by lysis of the hyphae (Huber and Watson, 1970). An increase in available organic C may also stimulate antagonistic microorganisms (Gilpatrick, 1969; Lewis and Papavizas, 1975; Malajczuk, 1996; Papavizas et al., 1968; Zentmyer, 1963). The effectiveness of these amendments depends on the C : N ratio, the specific material used, the time elapsed since incorporation, and the pathogen under study (Lewis and Papavizas, 1975; 1977; Papavizas et al., 1968; Snyder et al., 1959). Sometimes, organic debris increased plant disease by enhancing survival of broad host-range pathogens or by providing a food base for facultatively saprophytic pathogens (Lewis and Papavizas, 1975; 1977; Lumsden et al., 1983). The ultimate effects of incorporation of organic debris on diseases in a subsequent crop depend very much on the stage of decomposition of the debris (Patrick et al., 1963; Phillips et al., 1971).

Stages of decomposition of compost and peat have been related to disease suppressiveness under controlled environmental conditions (Boehm and Hoitink, 1992; Hoitink et al., 1991). Thus, immature composts have been shown to cause nutritional and disease problems (for example *Pythium* and *Rhizoctonia* damping-off) in plants grown in these media, whereas more mature composts can be suppressive, particularly to nutrient dependent fungi like *Pythium* spp. (Chung et al., 1988). However, a sufficient food base needs to be present to support antagonists as exemplified by the decrease in suppressiveness to *Pythium* damping-off as peat becomes highly oxidized (Boehm and Hoitink, 1992). Stages of decomposition were monitored by various techniques and related to disease suppressiveness (Inbar et al., 1990). Microbial activity, as measured by fluorescein diacetate hydrolysis, was identified as a potential indicator for disease suppressiveness in container media (Chen et al., 1988).

While the effect of peat or compost decomposition on nursery plants in containers is fairly well understood (Hoitink et al., 1991; Hoitink and Fahy, 1986; Inbar et al., 1990), indicators for decomposition stages of organic debris in field soil associated with disease suppressiveness have not been characterized. Both the farming system and the decomposition stage of cover crop debris may play a role in determining suppressiveness to soil-borne plant pathogens. The goal of the research presented here was to describe soil carbon, nitrogen, and microbial dynamics associated with damping-off pathogen dynamics in two farming systems at different stages of cover crop decomposition and thus contribute to an understanding of the mechanisms underlying the natural controls observed after cover crop incorporation.

Materials and methods

Soils and cover crops

Our research was conducted with soils from two different comparative farming systems projects: Experiment 1 was conducted in the field, while Experiment 2 was conducted in the laboratory using air-dried and rewetted field soil, to which dried cover crop residue was added.

Experiment 1

The soils used for Experiment 1 came from a farming systems project started in 1986 to study the long-term effects of winter green manure/cover crops in a semi-arid irrigated system on N availability for subsequent crops and soil structural and biological properties (Stivers and Shennan, 1991; Shennan 1992). The soil is a coarse-loamy, mixed, Thermic Mollic Xerofluvent soil with a pH of 7.7, CEC of 25.4 meq $100\,g^{-1}$ soil, and 33 ppm $NaHCO_3^-$ extractable P. The design of the experiment was a split-plot with four replicate

blocks, in which the main plot treatments were either different kinds of winter green manuring (organic system) or winter fallow and use of different levels of ammonium sulphate fertilizer (conventional system). The sub-plot treatments were different nitrogen levels, added as ammonium-sulphate in conventional plots and as different kinds of cover crops in the organic plots. We chose the winter-fallow plots that received 168 kg N ha^{-1} in the form of ammonium-sulphate and the green manured plots that were seeded with an oat–vetch mixture, supplying a similar amount of nitrogen. In the autumn of 1992, the experiment was terminated by planting a cover crop mixture consisting of oats (*Avena sativa* L.) and lana wooly pod vetch (*Vicia dasycarpa* cv. lana) in all plots, including the previously not cover-cropped plots. The oat–vetch cover crop was mowed and incorporated with a disk on April 14, 1993. Soil samples (> 30, 20 cm deep cores per plot, for a total of 90 kg soil $plot^{-1}$) were taken with a Dutch auger (6 cm diam) 3 days before incorporation, and 7, 20, and 35 days after incorporation of the cover crop and stored in plastic buckets with a lid at 5 °C until processed. The field was irrigated 8–9 days after cover crop incorporation for a subsequent corn crop which was planted 2 weeks after incorporation. In Experiment 1, soil moisture and temperature were determined at two locations per plot for a conventionally and an organically managed plot using cylindrical gypsum block sensors (Campbell Scientific Inc., Logan, UT, USA) and water-resistant thermistor probes at 10–15 cm depth, respectively. All sensor signals were sampled at 5 min intervals with a 21X datalogger (Campbell Scientific Inc.) and averaged to hourly values. Daily average soil water potential values during cover crop decomposition remained between −0.2 and −0.6 bars, although a drop in water potential around day 35 after cover crop incorporation can be attributed to growth of corn (Figure 1). Soil temperatures fluctuated considerably and could potentially have an impact on most of the soil C, N and microbial variables measured in Experiment 1 (Figure 1).

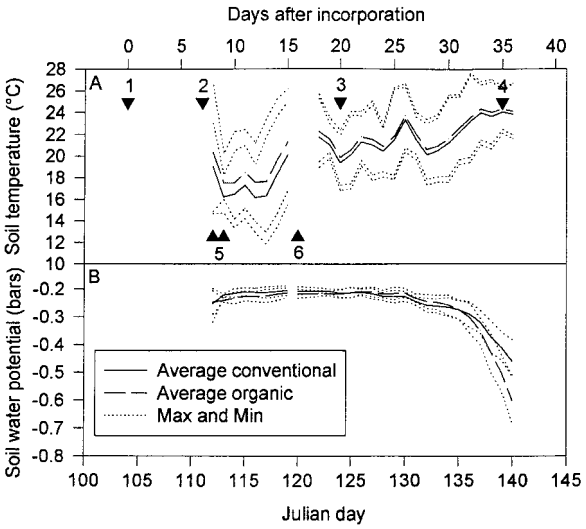

Figure 1. (A) Average, maximum and minimum soil temperature (°C) and (B) average, maximum, and minimum soil water potential (bars) during cover crop decomposition in Experiment 1 (field decomposition) at the Student Experimental Farm at UC Davis. Numbers in graph (A) refer to (1) date of cover crop incorporation, and sampling after (2) 7, (3) 20, and (4) 35 days of decomposition respectively. Plots were (5) furrow irrigated on April 22–23 and (6) corn was planted on April 30. Soil temperature was measured with a Campbell XR-21 datalogger equipped with 4 soil moisture and temperature probes, of which two of each were placed in an organic and conventional plot, respectively, and averaged by plot. Maxima and minima of temperature and soil water potential are shown.

Experiment 2

For Experiment 2, soil was available from the Sustainable Agriculture Farming Systems project, which was started in 1989 at UC Davis, where a conventional system with a 2-year rotation, and conventional, low input and organically managed systems with 4-year rotations were compared (Temple et al., 1995). The soil is a Reiff sandy-loam with a texture consisting of 39.1% sand, 44.1% silt, and 16.8% clay. More information on the 4-year rotations, consisting of processing tomatoes (*Lycopersicon esculentum* Mill.), safflower (*Carthamus tinctorius* L.), corn (*Zea mays* L.), wheat (*Triticum aestivum* L.), and dry beans (*Phaseolus vulgaris* L.) planted in the same season as wheat, was reported by Temple et al. (1995). In November 1993, following the bean crop and preceding tomatoes, we sampled a total of 90 kg of soil (in dry weight equivalents) per plot using a Dutch auger (6 cm diam). Three replicate plots were sampled and each replicate was treated and kept separately. Soils were air-dried on greenhouse benches and kept in buckets at air-temperature until used. Cover crops used for incorporation consisted of field grown oats (*Avena sativa* L.) and lana wooly pod vetch (*Vicia dasycarpa* Ten.) harvested from plots adjacent to Experiment 1 in April 1993 with as much root material as possible, at early flowering of vetch and before flowering of oat. The cover crop material was then separated into oat and vetch and

air-dried in an air-flow oven at 40 °C. The C : N ratio of this cover crop material was 33.6 for oats and 13.3 for vetch. Dry cover crop material was shredded twice and mixed in plastic bags to attain a uniform mixture. Before incorporation of oat–vetch debris, 16.5 kg dry weight soil were gently brought to 10% moisture using spray-bottles. Soils were subsequently incubated in 20 l buckets with lids for 48 h in the dark at room temperature. At this point we either added a cover crop mixture consisting of 76.0 g air-dried oats and 38.0 g air-dried vetch and another 3% distilled water, or just 3% water for the treatment where no cover crop was incorporated. The soil was divided into two plastic buckets (8.0 kg each) for incubation in the dark at 22 ± 2 °C. After each incubation period, soils were harvested and two plastic buckets were combined by field replicate. Soil NO_3-N, NH_4-N and hot-water soluble carbohydrates were analyzed immediately and the rest of the soils were kept in a cold room at 3–5 °C for further chemical and microbial analyses. All analyses using fresh soil samples were completed within 6 days after soil harvest. More details on composition of cover crop inputs were described by Hu et al. (1997).

Effect of soil on pathogen growth

Radial growth and relative growth of *Pythium aphanidermatum* (Edson) Fitzp. and *Rhizoctonia solani* Kühn AG-4 [teleomorph *Thanatephorus cucumeris* (Frank) Donk] over autoclaved and natural soil were determined using an *in vitro* method (Grünwald et al., 1997). Radial growth of fungi was measured on a cellophane membrane laid over natural or autoclaved soil, inoculated with 48-h-old potato dextrose agar plug cultures of *P. aphanidermatum* or *R. solani*. Relative growth was subsequently estimated as

$$\text{Relative growth} = \frac{\text{Radial growth (cm) on unsterilized soil}}{\text{Radial growth (cm) on sterilized soil}}.$$

Soil nutrient cycling

Soil C : N ratios were determined using a random sub-sample sieved through a 4 mm mesh Hu et al. (1997). Organic debris larger than 4 mm was cut and passed through the mesh. Finely ground, air-dried soil samples were used for measuring C and N contents by combustion using a Carlo-Erba C/N analyzer (Carlo Erba, Milano, Italy) at the DANR Analytical Laboratory of the University of California. Plant debris was extracted from ca. 2000–3000 g soil using a wet-sieving method (Weinhold, 1977). Floating materials were composited per plot, dried in an oven at 60 °C, and ground for analysis of fiber and total C and N content of debris. More details on NH_4-N, NO_3-N, as well as total N and C of soil and debris are described by Hu et al. (1997) in relation to the process of cover crop decomposition.

Soil microbial biomass and activity

Fluorescein diacetate (FDA) hydrolytic activity, considered to be a measurement of general soil microbial activity, was determined on 5 g sub-samples in three pseudoreplications per plot and three or four replications for each treatment (Workneh et al., 1993). Active bacterial colony numbers, as well as actinomycete and fungal hyphal length, were estimated by direct observation after staining with fluorescein diacetate (FDA) (Ingham and Klein, 1984). Total hyphal length of fungi and actinomycetes as well as hyphal diameters were estimated using differential interference microscopy (Colinas et al.,1994). Hyphae which were smaller than 1 μm in diameter were considered to be actinomycetes. Biomass was calculated by multiplying bacterial and fungal biovolume by an average bacterial density of $0.33\,\mathrm{g\,cm^{-3}}$ and an average hyphal density of $0.41\,\mathrm{g\,cm^{-3}}$, respectively (Ingham et al.,1991). All direct counts were conducted by the Soil Microbial Biomass Service at Oregon State University (Corvallis, OR, USA).

Stastistical analysis

Initial analyses consisted of descriptive statistics for each variable by experiment, farming system and decomposition stage of the cover crop. Analyses of variance conducted on Experiment 1 used a randomized complete block design with farming system (organic vs. conventional) in the main plot and decomposition stage in the sub-plot. Analyses of variance for Experiment 2 were conducted using a factorial design with factorial farming-system/decomposition-stage treatment combinations. All soil nutrient cycling, microbial community, and disease variables were tested for normality by univariate analysis. Decomposition rate constants k ($\mathrm{day^{-1}}$) were estimated with an exponential decay model of the form

$$y = a\mathrm{e}^{-kt}$$

Table 1. Definitions of abbreviations used for soil C and N cycling and microbial variables used in Experiments 1 and 2

Variable	Abbreviation	Units
Soil nutrient cycling		
C : N ratio of soil	C : N soil	—
Dry weight of debris	DW debris	mg g^{-1} soil
C : N of debris	C : N debris	—
Soil microbial dynamics		
FDA-hydrolytic activity	FDA	μg g^{-1} soil min^{-1}
Potentially mineral izable N	PMN	μg N g^{-1} soil
Active biomass of bacteria	AB	μg biomass g^{-1} soil
Active biomass of fungi	AF	μg biomass g^{-1} soil
Active biomass of actinomycetes	AA	μg biomass g^{-1} soil

fit to dry weight debris data from Experiments 1 and 2, where y corresponds to dry weight of debris (g kg^{-1} soil), the intercept a corresponds to initial level of substrate (kg^{-1} soil) at time 0 and t is time (days). Half-life was calculated as $t_{1/2} = \ln(2) \times k^{-1}$. Initial inputs of cover crop biomass as dry weight of debris in Experiment 1 were calculated from estimates of above ground stand in kg ha^{-1} for each replicate (Hu et al., 1997). A soil bulk density of 1.5 cm^3 g^{-1} soil was assumed and the depth of incorporation was 15 cm. Initial cover crop input in Experiment 2, being the same for all replicates, was 7.1 g kg^{-1} soil. These initial inputs were added to the dry weight (DW) of the debris extracted from soil before incorporation in order to obtain estimates at time 0. All statistics were performed using the procedures within the Statistical Analysis System library (1988). Abbreviations used for soil microbial, C and N variables throughout this manuscript are presented in Table 1 with the corresponding units.

Results

Soil and debris variables

Dry weight of extracted debris was generally higher in the organic system (Figure 2A, F), although the difference was significant only in Experiment 2 (Table 2). In both Experiments, the decomposition stage had a significant effect on DW debris (Table 2). Rate constants obtained from fitting an exponential decay model to the DW debris data were higher in conventional as compared to organically treated soils, which was reflected

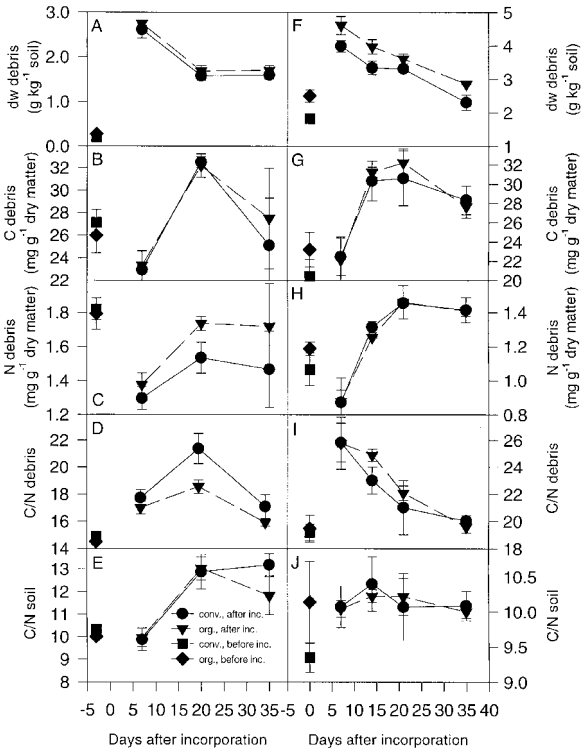

Figure 2. (A) Dry weight of extracted, coarse debris, (B) carbon content of debris, (C) total nitrogen content of debris, (D) C : N ratio of debris, and (E) C : N ratio of soil for Experiment 1 (field experiment) and (F) dry weight of extracted, coarse debris, (G) carbon content of debris, (H) total nitrogen content of debris, (I) C : N ratio of debris, and (J) C : N ratio of soil for Experiment 2 (controlled incubation). Coarse debris was extracted from soil by wet-sieving and flotation. Abbreviations in legend: conv. = conventionally managed; org. = organically managed; after inc. = after incorporation of debris; before inc. = before incorporation of debris. Values are mean ± SE.

in the fact that the half-life of incorporated debris is higher in conventional soils (Table 3). The half-life of decomposing cover crop debris ranged from 13 to 38 days for short-term decomposition of an incorporated oat–vetch cover crop. Overlap of the asymptotic confidence intervals for rate constants in Experiments 1 and 2 indicates that the rates were not different between organic and conventional soils. Half-lives of DW debris decomposition were considerably higher in Experiment 1 than in Experiment 2 (Table 3).

The C content of extracted debris behaved similarly in both experiments, being lowest at about 7 days after incorporation and then increasing and being highest about 20–21 days after incorporation (Figure 2B, G). In both experiments a significant effect

Table 2. Analyses of variance results for variables from Figure 2 for Experiments 1 (field experiment) and 2 (controlled incubation) showing F values and levels of significance for each source of variation and each dependent variable, respectively. Experiment 1 was analyzed as a randomized complete block design with system in the main plot and decomposition stage in the subplot. Experiment 2 was analyzed as a factorial combination of farming system and decomposition stage. All F values in bold typeface are significant at $P \leq 0.05$

Source of variation	Dependent variable									
	DW debris		C debris		N debris		C : N debris		C : N soil	
	F values	Pr > F	F values	Pr > F	F values	Pr > F	F values	Pr > F	F values	Pr > F
Experiment 1										
System	0.19	0.6901	3.03	0.1801	**11.26**	0.0439	**10.30**	0.0490	1.38	0.3246
Decomposition stage	**55.15**	0.0001	**6.08**	0.0048	**5.21**	0.0091	**28.89**	0.0001	**10.86**	0.0010
System × Decomposition stage	0.07	0.9723	0.23	0.8736	0.54	0.6618	1.75	0.1927	0.85	0.4931
Experiment 2										
System	**23.16**	0.0001	0.52	0.4786	0.08	0.7769	0.59	0.4519	0.42	0.5231
Decomposition stage	**44.26**	0.0001	**12.15**	0.0001	**20.94**	0.0001	**11.71**	0.0001	0.86	0.5062
System × Decomposition stage	0.34	0.8470	0.29	0.8794	0.4	0.8058	0.34	0.8499	0.77	0.5551

Table 3. Parameter estimates of an exponential decay model fit to dry weight of debris data in Experiments 1 and 2, respectively

Experiment	System	a (g kg^{-1} soil)	k (day^{-1})	Asymptotic CI[1] lower 95%	Asymptotic CI[1] upper 95%	$t_{1/2}$ (days)
Field experiment	Conventional	3.13	0.0248	0.034	0.016	27.95
	Organic	2.90	0.0183	0.024	0.013	37.88
Controlled incubation	Conventional	8.06	0.0535	0.071	0.036	12.96
	Organic	8.64	0.0474	0.063	0.032	14.62

The model used was $y = ae^{(-kt)}$, where y is dry weight debris (g kg^{-1} soil), a is the intercept (g kg^{-1} soil), k is the decomposition rate constant (day^{-1}) and t is time (days). Initial input of cover crop debris as dry weight in Experiments 1 (field experiment) were calculated for estimates of above ground stand for each replicate (means were 6175 kg ha^{-1} in organic and 7098 kg ha^{-1} in conventional, respectively) assuming a soil bulk density of 1.5 cm^3 g^{-1} soil and a depth of incorporation of 15 cm. Initial cover crop input in Experiment 2 (controlled incubation) was 7.1 g kg^{-1} soil and was the same for all replicates. These initial inputs were added to DW debris before incorporation to obtain time 0 estimates. Half-life is calculated as $t_{1/2} = \ln(2) \times k^{-1}$.

[1]'Asymptotic CI' = Asymptotic confidence interval for estimates of rate constant k.

of decomposition stage (Table 2) was obtained. The N content of extracted debris declined in both experiments right after cover crop incorporation (Figure 2C, H). Subsequently, N debris increased and was highest 20–21 days after incorporation (Figure 2C, H). In both experiments a significant effect of decomposition stage was obtained (Table 2). A significant effect of farming system on N debris was found in Experiment 1 (Table 2).

C : N ratios of extracted debris showed a significant effect of decomposition stage in both experiments (Table 2), although C : N debris was highest after 20 days in Experiment 1 and right after incorporation in Experiment 2 (Figure 2D, I). Although the dynamics of the C (Figure 2B, G) and N contents of debris (Figure 2B, C, G, H) were very similar in Experiments 1 and 2, the C : N debris seemingly behaved differently (Figure 2D, I). The oat debris had a higher C : N ratio (33.6) than the vetch debris (13.3) (Hu et al., 1997), resulting in a C : N ratio of debris of about 14.5 for the initial cover crop mixture in the organic plots and a C : N ratio of debris of about 20.6 in the conventional plots in Experiment 1. In Experiment 2, the C : N ratio of added cover crop debris was 23.45 (Hu et al., 1997). The C : N ratio of soil increased from about 10, before and right after incorporation of the cover crop debris, to

12–13 at 20–35 days after incorporation in Experiment 1 (Figure 2E). This resulted in a significant effect of decomposition stage on C : N soil, while no differences could be detected between farming systems (Table 2). In Experiment 2, C : N soil did not change significantly before or after incorporation and remained around 10 (Table 2, Figure 2J). No significant interaction of farming system and decomposition stage could be detected for C : N debris, CN soil or DW debris (Table 2). The C : N ratios for debris and soil were positively correlated, although the relationship was significant only in Experiment 1 (Table 5). The C and N content of debris were significantly positively correlated in both Experiments (Table 5).

Soil microbial variables

Incorporation of a cover crop in Experiments 1 and 2 led to a significant increase in microbial activity (Table 4). Microbial activity was generally highest 1 week after incorporation and then declined (Figure 3D, J). Even after 5 weeks of decomposition, FDA hydrolytic activity remained significantly higher than before incorporation (LSD = 0.40 and 0.39 for Experiments 1 and 2, respectively). Although the FDA-hydrolytic rate was generally higher in the organic farming system, only Experiment 2 showed significant differences between the two farming systems (Table 4). Generally, the rate of hydrolysis of FDA was higher in Experiment 2, ranging from about 4 to 6 $\mu g\, g^{-1}$soil min^{-1}, compared to 2–4 $\mu g\, g^{-1}$ soil min^{-1} in Experiment 1 (Figure 3D, J).

Active biomass of bacteria, fungi and actinomycetes, determined by FDA-staining, generally increased after incorporation of cover crop debris in Experiments 1 (Figure 3A, B, C). In Experiment 2, active biomass of bacteria increased immediately after incorporation and then declined to pre-incorporation levels (Figure 3G), while active biomass of fungi only increased 3 and 5 weeks after incorporation in the organic and conventional soil, respectively (Figure 3H). Active biomass of actinomycetes continually increased after debris incorporation in organic soil and increased after 3 weeks in the conventional soil (Figure 3I). Generally, active biomass of bacteria was highest right after incorporation (Figure 3A, G), whereas active biomass of fungi was highest about 20–21 days after incorporation (Figure 3B, H). As was the case with FDA-hydrolytic activity measurements (Figure 3D, J), active biomass of bacteria, fungi and actinomycetes was higher in Experiment 2 after incorporation of the cover crop (Figure 3). In Experiment 1, active biomass was always higher in the organic farming system (Figure 3A–C), although significant differences were only established for active biomass of bacteria and fungi (Table 4). In Experiment 2, only active biomass of fungi was significantly higher in the organic as compared to the conventional farming system (Figure 3H, Table 4). No significant effects of decomposition stage could be detected for Experiment 1, while in Experiment 2 active biomass of bacteria, fungi and actinomycetes was significantly affected by decomposition stage (Table 4). No significant interactions between farming system and decomposition stages were detected for any of the microbial variables (Table 4).

The rate of FDA hydrolysis was best correlated with active biomass of bacteria among the three active biomass variables with significant positive correlations between FDA and active biomass of bacteria (Table 5). FDA hydrolytic rate was significantly positively correlated to DW debris in both Experiments 1 and 2 and C : N debris in Experiment 2 (Table 5).

Plant pathogen variables

Relative growth (RG) of *P. aphanidermatum* and *R. solani* were significantly affected by decomposition stage and not affected by farming system (Table 4), although RG in organic soils was commonly lower for both pathogens (Figure 3E, F, K, L). Relative growth of *P. aphanidermatum* was highest 1 week after incorporation and then declined, slowly in Experiment 1 (Figure 3E) and in a more pronounced fashion in Experiment 2 (Figure 3K). In Experiment 2, RG of *P. aphanidermatum* started to increase again after 21 days of incubation (Figure 3K). Levels of RG of *P. aphanidermatum* remained around 0.6–0.7 after cover crop incorporation in Experiment 1 (Figure 3E). In Experiment 2, the RG dropped to 0.6–0.7, after an initial increase right after incorporation, 14–21 days after incorporation and then increased slightly to 0.7–0.8 35 days after incorporation (Figure 3K). After cover crop incorporation, RG of *R. solani* increased quickly to 0.8 and thereafter increased only slightly in Experiment 1 (Figure 3F) and gradually increased to 0.8 by 14–21 days after incorporation in Experiment 2 (Figure 3L). In both Experiments, RG of *R. solani* peaked at 20 days after incorporation and then decreased in the organic soils, while at that time RG in the conventional soils was still increasing (Figure 3F, L). No significant interactions between

Table 4. Analyses of variance results for variables from Figure 3 for Experiments 1 (field experiment) and 2 (controlled incubation) showing F values and levels of significance for each source of variation and each dependent variable, respectively. Experiment 1 was analyzed as a randomized complete block design with system in the main plot and decomposition stage in the sub-plot. Experiment 2 was analyzed as a factorial combination of farming system and decomposition stage. All F values in bold typeface are significant at $P \leq 0.05$

Source of variation	Dependent variable											
	FDA		AB		AF		AA		RG *P. aphanid*		RG *R. solani*	
	F values	Pr $> F$	F values	Pr $> F$	F values	Pr $> F$	F values	Pr $> F$	F values	Pr $> F$	F values	Pr $> F$
Experiment 1												
System	1.29	0.3384	**56.33**	0.0049	**21.15**	0.0193	5.93	0.0929	0.71	0.4600	0.27	0.6406
Decomposition stage	**29.45**	0.0001	2.55	0.0880	1.50	0.2487	0.64	0.5983	**26.13**	0.0001	**9.81**	0.0015
System × decomposition stage	1.44	0.2628	0.08	0.9703	0.27	0.8463	0.19	0.9029	0.82	0.5016	0.36	0.7815
Experiment 2												
System	**22.28**	0.0001	0.19	0.6661	**9.58**	0.0057	0.03	0.8559	0.37	0.5491	1.35	0.2585
Decomposition stage	**111.98**	0.0001	**5.42**	0.0040	**4.42**	0.0101	**4.42**	0.0101	**15.84**	0.0001	**6.79**	0.0013
System × decomposition stage	2.61	0.0666	1.34	0.2896	2.02	0.1299	2.13	0.1143	0.09	0.9833	0.20	0.9330

Table 5. Simple correlations among variables from Experiment 1 below the diagonal (field experiment) ($n = 26$ for C : N soil, DW debris and RG *R. solani* and $n = 36$ for all other variables) and from Experiment 2 above the diagonal (controlled incubation) ($n = 30$). Numbers in bold typeface are significant at $P \leq 0.05$

	DW debris	C debris	N debris	C : N debris	C : N soil	FDA	AB	AF	AA	RG Pyth.	RG Rhiz.
DW debris	*1.00*	0.12	−0.29	**0.67**	0.29	**0.84**	**0.48**	−0.07	0.05	0.15	−0.04
	0.0000	0.5182	0.1235	**0.0001**	0.1179	**0.0001**	**0.0073**	0.6976	0.7709	0.4459	0.8284
C debris	**−0.43**	*1.00*	**0.80**	0.11	0.35	0.16	−0.17	0.13	0.34	**−0.68**	**0.53**
	0.0284	*0.0000*	**0.0001**	0.5712	0.0617	0.3877	0.3574	0.5070	0.0654	**0.0001**	**0.0026**
N debris	**−0.46**	**0.77**	*1.00*	**−0.50**	0.08	−0.26	−0.36	0.27	**0.40**	**−0.74**	**0.53**
	0.0174	**0.0001**	*0.0000*	**0.0055**	0.6864	0.1659	0.0521	0.1526	**0.0308**	**0.0001**	**0.0028**
C : N debris	−0.03	**0.42**	−0.24	*1.00*	0.33	**0.74**	**0.38**	−0.25	−0.12	0.29	−0.11
	0.8843	**0.0167**	0.1784	*0.0000*	0.0750	**0.0001**	**0.0394**	0.1920	0.5461	0.1152	0.5549
C : N soil	**−0.50**	0.34	0.05	**0.51**	*1.00*	0.24	0.11	0.09	−0.07	−0.13	0.22
	0.0089	0.0940	0.8191	**0.0080**	*0.0000*	0.2030	0.5515	0.6413	0.7264	0.5086	0.2489
FDA	**0.75**	−0.27	**−0.43**	0.15	−0.34	*1.00*	**0.53**	0.0004	0.21	0.24	0.10
	0.0001	0.1296	**0.0146**	0.4223	0.0897	*0.0000*	**0.0029**	0.9982	0.2641	0.2050	0.6113
AB	0.11	0.17	0.22	−0.09	−0.27	**0.41**	*1.00*	0.22	0.05	0.33	0.03
	0.5930	0.3593	0.2240	0.6283	0.1855	**0.0185**	*0.0000*	0.2499	0.8045	0.0733	0.8875
AF	0.10	0.34	0.33	0.02	−0.16	**0.40**	**0.66**	*1.00*	0.36	−0.17	0.23
	0.6144	0.0536	0.0612	0.9311	0.4361	**0.0243**	**0.0001**	*0.0000*	0.0542	0.3603	0.2234
AA	0.21	0.12	0.174	−0.09	−0.20	0.14	**0.43**	**0.50**	*1.00*	−0.25	0.31
	0.3149	0.5150	0.3588	0.6074	0.3178	0.4460	**0.0151**	**0.0038**	*0.0000*	0.1799	0.0916
RG Pyth.	**0.54**	−0.09	**−0.55**	**0.59**	0.16	**0.43**	−0.07	0.15	0.10	*1.00*	**−0.58**
	0.0046	0.6290	**0.0012**	**0.0004**	0.4294	**0.0137**	0.6968	0.4161	0.5834	*0.0000*	**0.0009**
RG Rhiz.	−0.11	0.06	−0.18	0.35	**0.42**	−0.23	−0.35	−0.10	−0.04	**0.61**	*1.00*
	0.6024	0.7540	0.3861	0.0843	**0.0332**	0.2580	0.0763	0.6315	0.8468	**0.0009**	*0.0000*

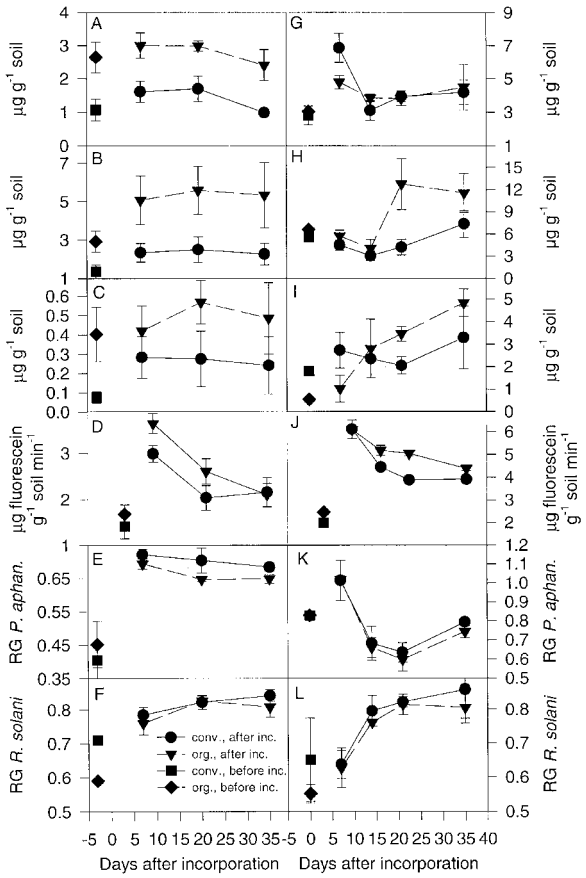

Figure 3. Active biomass of (A) bacteria, (B) fungi and (C) actinomycetes for Experiment 1 (field experiment) and active biomass of (G) bacteria, (H) fungi and (I) actinomycetes for Experiment 2 (controlled incubation). Active biomass was measured using an epi-fluorescence microscope following FDA-staining. General microbial activity for soils from (D) Experiment 1 (field experiment) and (J) Experiment 2 (controlled incubation) assessed by measuring the rate of hydrolysis of fluorescein diacetate (FDA) to fluorescein in 30 min batch incubations (see legend in Figure 2 for meaning of symbols). Relative growth of (E) *Pythium aphanidermatum* and (F) *Rhizoctonia solani* for Experiment 1 (field Experiment) and relative growth of (K) *P. aphanidermatum* and (L) *R. solani* for Experiment 2 (controlled incubation). Relative growth is calculated by taking the ratio of mean radial growth of a fungal colony growing over non-sterilized soil over mean radial growth over sterilized soil. A reduction in growth is attributed to the effects of competition and antibiosis by the soil microbial community to the fungus. Abbreviations in legend: conv. = conventionally managed; org. = organically managed; after inc. = after incorporation of debris; before inc. = before incorporation of debris. Values are mean ± SE.

farming system and decomposition stage of cover crop debris were detected for any measurements of RG (Table 4).

Relative growth of *P. aphanidermatum* and *R. solani* were positively correlated in Experiment 1 and negatively correlated in Experiment 2, although the positive correlation in Experiment 1 depended on the observations before incorporation only (Table 5). By removing those observations before incorporation a positive, non-significant correlation ($r = 0.08$; $P = 0.7097$) was obtained. In Experiment 1, RG of *P. aphanidermatum* was positively correlated with the variables, the C : N debris, DW of debris and FDA activity, and significantly negatively correlated with N debris (Table 5). In Experiment 2, RG of *P. aphanidermatum* was significantly negatively correlated with C debris and N debris (Table 5). RG of *R. solani* was significantly positively correlated to the C : N soil in Experiment 1 and significantly negatively correlated to the C and N contents of debris in Experiment 2 (Table 5).

Discussion

In a previous paper, we showed that an *in vitro* bioassay measuring RG was directly correlated to disease severity/incidence and inversely correlated to suppressiveness of the soil (Grünwald et al.,1997). Suppressiveness of *P. aphanidermatum*, as measured with the *in vitro* bioassay, was generally lowest just after cover crop incorporation and then increased, i.e. RG decreased (Figure 3E, K). In the case of *R. solani*, suppressiveness was lowest about 20 days after incorporation, and then increased in the organic system but continued to decrease in the conventional soils (Figure 3F, L). It is apparent that cover crop incorporation affects *P. ultimum* and *R. solani* differently, and that suppression of soil to *P. aphanidermatum* sets in earlier as compared to *R. solani*.

Suppression of *Pythium* species is thought to be rather general in nature (Lumsden et al., 1990) and was found to be well correlated with general microbial activity (Chung and Hoitink, 1990). However, in the first experiment, there was a positive correlation between RG of *P. aphanidermatum* and FDA hydrolytic activity, while there was no correlation in the second experiment. The initial flush in nutrient availability may have outweighed the increase in microbial activity so that the RG of *Pythium* increased simultaneously with the increase in microbial activity.

Bouhot (1981) found that suppression of Pythium damping-off, induced by the addition of composted organic wastes, was due to saprophytic competition for substrate and not the elimination of *Pythium* spp. Similarly, Boehm et al. (1993) found that none of several bacterial biocontrol agents applied as single treatments induced a level of disease suppression equal to that of the non-autoclaved control treatments infested with *Pythium* spp. They subsequently reasoned that general suppression best described suppression to Pythium damping-off in suppressive bark/hardwood potting mixes. The positive correlation between DW debris and RG of *P. aphanidermatum* in both experiments (although only significant in Experiment 1) lends support to this hypothesis.

Suppression of *Rhizoctonia* species, on the other hand, is considered to be of a more specific nature. Chung (1988) suggested that a lack of correlation between disease severity, and total microbial activity and biomass, indicated a more specific kind of suppression of soil to *R. solani*. In our experiments, RG of *R. solani* and FDA hydrolytic activity were not significantly correlated, although microbial activity initially increased and then decreased, while RG of *R. solani* was low at first and then increased. This hypothesis could explain why suppression of *R. solani* sets in later than that of *P. aphanidermatum*, in that the antagonists need to grow to establish themselves before soils become suppressive. Another possible explanation for the dynamics of *R. solani* obtained here might be associated with cellulose availability. According to Rouse and Baker (1978), cellulose added to soil resulted in a significant reduction in slope values of the log–log relationship between inoculum density of *R. solani* and disease incidence, indicating that the same log of inoculum density leads to less log of infections under cellulose amendment. More recently, Chung and Hoitink (1990) reported that cellulose availability in bark compost medium limited population development of *R. solani* (itself being cellulolytic) and that disease severity was lower in compost amended with low levels of cellulose, while high levels of cellulose amendment increased both populations of *R. solani* and disease severity. We observed negative correlations between cellulose content of wet-sieved/extracted debris and RG of *R. solani* and a positive correlation with RG of *P. aphanidermatum* in both Experiments 1 and 2 for treatments that received a cover crop (data points before incorporation were excluded), although a significant relationship was only established for Experiment 2 [unpublished results]. Lumsden et al. (1983) have attempted to link the idea that antagonism to *Rhizoctonia* is specific, whilst there is enhancement of suppression by cellulose availability.

It is now thought that microbial biomass and activity are almost always significantly higher in organically than in conventionally farmed soils (Gunapala and Scow, 1998). Similarly, agricultural soils receiving cover crops or other organic inputs generally have higher microbial biomass than those receiving synthetic fertilizers as a nitrogen source (Anderson and Domsch, 1989; Powlson et al., 1987; Gunapala and Scow, 1998). Significantly higher microbial activity was found in organically farmed soil in Experiment 2, and, although not significant, activity in Experiment 1 was generally higher (Figure 3D, J; Table 4). The rate of hydrolysis of FDA seems to reflect active biomass of bacteria most strongly (Table 5). Several studies have shown that FDA can be hydrolyzed by most bacteria (Schnürer and Rosswall, 1982; Lundgren, 1981; Medzon and Brady, 1969), fungi (Schnürer and Rosswall, 1982; Medzon and Brady, 1969; Söderström, 1977) and other organisms (Medzon and Brady, 1969). However, FDA has been shown to be inefficient in direct staining of gram-negative bacteria, since it is not efficiently taken up into the cell (Bloem et al., 1995). FDA hydrolytic activity was generally higher in Experiment 2. This coincided with higher active biomass of fungi, bacteria and actinomycetes in the microscopic counts (Figure 3). The higher activity of microorganisms might reflect the more controlled nature of the Experiment with a higher mean temperature and less fluctuations in temperature (Figure 1), as well as higher dry weights of debris during the course of that Experiment (Figure 2A, F).

Rates of decomposition were expected to be higher in the organic soils (Table 2) (Hu et al., 1997; Gunapala, 1994), but higher rates were found in the conventional soils. The rate k was estimated on debris extracted from soil by wet-sieving and flotation, and since the organically managed systems always have higher levels of coarse organic debris from previous cover crops and cash crops, it is to be expected that the rate k would be lower. In essence, the residual organic matter from the previous year would constitute a second pool of organic matter with a considerably lower k value and fitting a double exponential model and thus comparing k values for the rapidly decomposing pool would have been more appropriate. Due to the small number of observations and over-parameterization of

a two compartment model for our data, this model could not be used. Estimated *k* values in a litterbag experiment with oat–vetch debris, that excludes debris from previous years, conducted in plots of the Sustainable Agriculture Farming Systems project in 1995 under varying soil moisture and temperature conditions, were 0.031 for the organic plots and 0.025 for the conventional soils (Hu et al., 1997) . These values are similar to those obtained for Experiment 1 under fluctuating soil moisture and temperature conditions.

The initial increase in C content of extracted debris observed between 7 and 14 days after cover crop incorporation is contrary to a steady decrease in the content of debris generally observed in litterbag studies (Beare et al., 1992; Koenig and Cochran, 1994). This can be explained by an increased loss of small molecular weight carbon sources with a relatively low C : N ratio during the wet sieving procedure. The half-life of decomposing cover crop debris estimated from debris extracted by wet-sieving and flotation (Table 3) was always close to the number of days elapsed since incorporation to the lowest RG of *P. aphanidermatum* value obtained after incorporation (Figure 3E, K). The half-life of decomposing debris indicates how fast decomposition proceeds, integrates the effects of soil moisture and temperature fluctuations and thus could well be suitable as an indicator for damping-off disease due to *P. aphanidermatum*, provided that a similar technique is used to separate the organic debris from soil.

The present results indicate that a different kind of suppressiveness might be in evidence for *P. aphanidermatum* and *R. solani* during short-term cover crop decomposition. *P. aphanidermatum* appears to be generally suppressed by microbial competition for nutrients and strongly dependent on nutrient availability. We hypothesize that *R. solani* suppressiveness, on the other hand, seems to set in much later, and could depend on the establishment of cellulolytic antagonists that do not become abundant until the 3rd to 5th week of cover crop decomposition.

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References

Anderson T-H and Domsch KH (1989) Ratios of microbial carbon to total organic carbon in arable soils. Soil Biology and Biochemistry 21: 471–479

Beare MH, Parmelee RW, Hendrix PF and Cheng W (1992) Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems. Ecological Monographs 62: 569–591

Bloem J, Bolhuis PR, Veninga MR and Wieringa J (1995) Microscopic methods for counting bacteria and fungi in soil. In: Alef K and Nannipieri P (eds) Methods in Applied Soil Microbiology and Biochemistry. Academic Press, New York

Boehm MJ and Hoitink HAJ (1992) Sustenance of microbial activity in potting mixes and its impact on severity of Pythium root rot of poinsettia. Phytopathology 82: 259–264

Boehm MJ, Madden LV and Hoitink HAJ (1993) Effect of organic matter decomposition level on bacterial species diversity and composition in relationship to Pythium damping-off severity. Applied and Environmental Microbiology 59: 4171–4179

Bouhot D (1981) Induction d′une resistance biologique aux *Pythium* dans les sols par l′apport d′une matière organique. Soil Biology and Biochemistry 13: 269–274

Chen W, Hoitink HAJ, Schmitthenner AF and Tuovinen OH (1988) The role of microbial activity in suppression of damping-off caused by *Pythium ultimum*. Phytopathology 78: 314–322

Chung YR (1988) Suppression of *Rhizoctonia solani* and its interaction with *Trichoderma hamatum* in bark compost media. Ph.D. Dissertation, Ohio State University, USA

Chung YR and Hoitink HAJ (1990) Interactions between thermophilic fungi and *Trichoderma hamatum* in suppression of rhizoctonia damping-off in a bark compost-amended container media. Phytopathology 80: 73–77

Chung YR, Hoitink HAJ and Lipps PE (1988) Interactions between organic-matter decomposition level and soilborne disease severity. Agriculture, Ecosystems and Environment 24: 183–193

Colinas C, Ingham E and Molina R (1994) Population responses of target and non-target forest soil organisms to selected biocides. Soil Biology and Biochemistry 26: 41–47

Doran JW, Fraser DG, Culik MN and Liebhardt WC (1988) Influence of alternative and conventional agricultural management on soil microbial processes and nitrogen availability. J Alternative Agriculture 2: 99–106

El Titi A and Richter J (1987) Integrierter Pflanzenschutz im Ackerbau: Das Lautenbach Projekt. III. Schädlinge und Krankheiten 1979–1983. Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz 94: 1–13

Gilpatrick JD (1969) Effect of soil amendments upon inoculum survival and function in *Phytophthora* root rot of avocado. Phytopathology 59: 979–985

Grünwald NJ, Workneh F, Hu S and van Bruggen AHC (1997) Comparison of an *in vitro* and a damping-off assay to test soils for suppressiveness to *Pythium aphanidermatum*. European Journal of Plant Pathology 103: 55–63

Gunapala N (1994) Soil microbial dynamics and nitrogen availability in organic, low input and conventional cropping systems. Ph.D. Dissertation, University of California at Davis, USA

Gunapala N and Scow KM (1998) Dynamics of soil microbial biomass and activity in conventional and organic farming systems. Soil Biology and Biochemistry 30: 805–816

Hassink J, Lebbink G and van Veen JA (1991) Microbial biomass and activity of a reclaimed-polder soil under a conventional or a reduced-input farming system. Soil Biology and Biochemistry 23: 507–513

Hoitink HAJ and Fahy PC (1986) Basis for the control of soilborne plant pathogens with composts. Annual Review of Phytopathology 24: 93–114

Hoitink HAJ, Inbar Y and Boehm MJ (1991) Status of compost-amended potting mixes naturally suppressive to soilborne diseases of floricultural crops. Plant Disease 75: 869–873

Hu S, Grünwald NJ, van Bruggen AHC, Gamble GR, Drinkwater LE, Shennan C, Demment MW (1997) Short-term effects of cover crop incorporation on soil carbon pools and nitrogen dynamics. Soil Science Society of America Journal 61: 901–911

Huber DM and Watson RD (1970) Effects of organic amendments on soil-borne plant pathogens. Phytopathology 60: 22–26

Inbar Y, Chen Y, Hadar Y and Hoitink HAJ (1990) New approaches to compost maturity. Biocycle 31: 64–69

Ingham ER, Griffiths RP, Cromack K and Entry JA (1991) Comparison of direct vs fumigation incubation microbial biomass estimates from ectomycorrhizal mat and non-mat soils. Soil Biology and Biochemistry 23: 465–471

Ingham ER and Klein DA (1984) Soil fungi: relationship between hyphal activity and staining with fluorescein diacetate. Soil Biology and Biochemistry 16: 273–278

Koenig RT and Cochran VL (1994) Decomposition and nitrogen mineralization from legume and non-legume crop residues in a subartic agricultural soil. Biology and Fertility of Soils 17: 269–275

Lewis JA and Papavizas GC (1975) Survival and multiplication of soil-borne plant pathogens as affected by plant tissue amendments. In: Bruehl GW (ed) Biology and Control of Soil-borne Plant Pathogens (pp 84-99) American Phytopathological Society, St. Paul, MN

Lewis JA and Papavizas GC (1977) Effect of plant residue on chlamydospore germination of *Fusarium solani* f. sp. *phaseoli* on Fusarium root rot of beans. Phytopathology 67: 925–929

Lockeretz W, Shearer G and Kohl DH (1981) Organic farming in the corn belt. Science 211: 540–546

Lumsden RD, García-ER, Lewis JA, and Frías-TGA (1990) Reduction of damping-off disease in soils from indigenous mexican agroecosystems. In: Gliessman SR (ed) Agroecology. Researching the Ecological Basis for Sustainable Agriculture (pp 83–103) Springer-Verlag, New York, USA

Lumsden RD, Lewis JA and Papavizas GC (1983) Effect of organic amendments on soilborne plant diseases and pathogen antagonists. In: Lockeretz W (ed) Environmentally Sound Agriculture (pp 51–70) Praeger Scientific, New York

Lundgren B (1981) Fluorescein diacetate as a stain of metabolically active bacteria in soil. Oikos 36: 17–22

Malajczuk N (1996) Microbial antagonism to *Phytophthora*. In: Erwin DC, Bartnicki-Garcia S, and Tsao PH (eds) *Phytophthora*: Its Biology, Taxonomy, Ecology, and Pathology (pp 197–218) American Phytopathological Society, St. Paul, MN

Medzon EL and Brady ML (1969) Direct measurement of acetylesterase in living protist cells. Journal of Bacteriology 97: 402–415

Papavizas GC, Lewis JA and Adams PB (1968) Survival of root-infecting fungi in soil. II. Influence of amendment and soil carbon-to-nitrogen balance on Fusarium root rot of beans. Phytopathology 58: 365–372

Patrick ZA, Tousson TA and Snyder WC (1963) Phytotoxic substances in arable soils associated with decomposition of plant residues. Phytopathology 53: 152–161

Phillips DJ, Watson AG, Weinhold AR and Snyder WC (1971) Damage of lettuce seedlings related to crop residue decomposition. Plant Disease Reporter 55: 837–841

Piorr H-P and Hindorf H (1986) The implication for plant diseases and pests during the conversion from conventional to biological agriculture. In: Vogtman H, Boehncke E and Fricke I (eds) The importance of biological agriculture in a world of diminishing resources (pp 421–435) Verlagsgruppe Witzenhausen, Witzenhausen

Powlson DS, Brookes PC and Christensen BT (1987) Measurement of soil microbial biomass provides an early indication of changes in total soil organic matter due to straw incorporation. Soil Biology and Biochemistry 19: 159–164

Reganold JP, Elliot LF and Unger YL (1987) Long-term effects of organic and conventional farming on soil erosion. Nature 330: 370–372

Rouse DI and Baker R (1978) Modeling and quantitative analysis of biological control mechanisms. Phytopathology 68: 1297–1302

SAS Institute (1988) SAS/STAT User's Guide. Release 6.03 edition. Sas Institute Inc. Cary, NC

Schnürer J and Rosswall T (1982) Fluorescein diacetate hydrolysis as a measure of total microbial activity in soil and litter. Applied and Environmental Microbiology 43: 1256–1261

Shennan C (1992) Cover crops, nitrogen cycling, and soil properties in semi-irrigated vegetable production systems. Horticultural Science 27: 749–754

Snyder WC, Schroth MN and Christou T (1959) Effect of plant residues on root rot of bean. Phytopathology 49: 755–756

Söderström BE (1977) Vital staining of fungi in pure cultures and in soil with fluorescein diacetate. Soil Biology and Biochemistry 9: 59–63

Stivers LJ and Shennan C (1991) Meeting the nitrogen needs of processing tomatoes through winter cover cropping. Journal of Production Agriculture 4: 330–335

Sugimoto EE, Hoitink HAJ and Tuovinen OH (1990) Oligotrophic pseudomonads in the rhizosphere: suppressiveness to Pythium damping-off of cucumber seedlings (*Cucumis sativus* L.). Biology and Fertility of Soils 9: 231–234

Temple SR, Somasco OA, Kirk M and Friedman D (1995) Conventional, low-input and organic farming systems compared. California Agriculture 48: 14–19

Weinhold AR (1977) Population of *Rhizoctonia solani* in agricultural soils determined by a screening procedure. Phytopathology 67: 566–569

Workneh F and van Bruggen AHC (1994) Suppression of corky root of tomatoes in organically managed soil associated with soil microbial activity and nitrogen status of soil and tomato tissue. Phytopathology 84: 688–694

Workneh F, van Bruggen AHC, Drinkwater LE and Shennan C (1993) Variables associated with corky root and Phytophthora root rot of tomatoes in organic and conventional farms. Phytopathology 83: 581–589

Zentmyer GA (1963) Biological control of *Phytophthora* root rot of avocado with alfalfa meal. Phytopathology 53: 1383–1387