

AN ABSTRACT OF THE DISSERTATION OF

Heather M. Darby for the degree of Doctor of Philosophy in Horticulture presented on March 5, 2003.

Title: Soil Organic Matter Management and Root Health.

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Annual applications of fresh or composted dairy manure were assessed for their effects on root rots of sweet corn and snap bean and damping-off of cucumber in a field soil. Soil biological and physical properties were measured as possible indicators of root rot suppressive potential. Regardless of amendment type or rate, soils amended for two seasons with either a high (average = 39.2 Mg ha⁻¹ year⁻¹) or low (average = 16.6 Mg ha⁻¹ year⁻¹) rate suppressed root rot of sweet corn, root rot of snap bean, and damping-off of cucumber by 54, 25 and 49%, respectively. Disease suppression was sustained for less than 6 mo after amendment. Severity of these three diseases was negatively ($P < 0.05$) related to soil free particulate organic matter content, fluorescein diacetate (FDA) activity, microbial biomass, and percent water stable aggregation. FDA activity was the best indicator of the soil's root rot suppressive potential. When FDA levels were $\geq 2.88 \mu\text{g min}^{-1} \text{g}^{-1}$ dry soil, disease suppression was observed.

In a container experiment, amendment with fresh (10% v/v) or composted (15% v/v) dairy manure suppressed root rot of sweet corn in soils with a high root rot

potential. Suppression was positively related to FDA activity in soil-1 ($R^2 = 0.70$) and soil-2 ($R^2 = 0.91$). Suppression was observed at FDA levels $\geq 4.00 \mu\text{g min}^{-1} \text{g}^{-1}$ dry soil.

When sudangrass and oats were grown and incorporated in a container experiment, severity of root rot of sweet corn was reduced by 22 and 18%, respectively. Annual ryegrass and cereal rye had no effect on disease severity. Disease suppression was not related to FDA activity.

Host range specificity of *P. arrhenomanes*, *Drechslera* spp. and *Phoma* spp. was determined for crops grown in rotation with sweet corn. *P. arrhenomanes* and *Drechslera* spp. were mildly pathogenic on annual ryegrass, perennial ryegrass and cereal rye. *Phoma* spp. was pathogenic only to perennial ryegrass. None of the pathogens were pathogenic on sudan grass and oats.

In conclusion, management of root rot of sweet corn through cover cropping coupled with soil amendment shows potential for disease suppression and should be investigated further.

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by
Heather M. Darby

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CONTRIBUTION OF AUTHORS

Dr. Richard Dick, assisted with laboratory procedures of Chapter 2. Dr. Mary Powelson assisted with the pathology of Chapter 3 and 4 and also contributed to editing the manuscript.

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SOIL ORGANIC MATTER MANAGEMENT AND ROOT HEALTH

CHAPTER 1 GENERAL INTRODUCTION

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Root diseases cause economic losses to farmers each year (King and Loomis, 1926; Tu, 1992; Campbell and Benson, 1994; Abawi and Widmer, 2000). The vegetable farmers of the Willamette Valley of Oregon are no exception, as root rot of snap bean and sweet corn plague the industry. Of particular concern is the recent occurrence of root rot of sweet corn in the Valley, since at this time there are no resistant cultivars or chemical pesticides available for its control (Hoinacki and Powelson, 2002). The primary methods to manage root diseases are host resistance and chemical pesticides (Agrios, 1997; Abawi and Widmer, 2000; Pscheidt and Ocanb, 2001). Soil treatment with methyl bromide can reduce severity of root rot of corn by as much as 89 %, and increase corn yields by as much as 50% (Hoinacki and Powelson, 2002), but it is not economically feasible for sweet corn growers.

Widespread adoption of more intensive row crop agriculture may partially explain the increased incidence and severity of root diseases. Intensive row crop production often involves chemical inputs (fertilizers and pesticides), short or no rotation between crops, and use of heavy machinery (Deluca, 1995). This type of agricultural system can reduce the health of the soil compared to less intensive agricultural systems (Reganold et al., 1993; Drinkwater et al., 1995). Soil health is capacity of the soil to perform functions that sustain biological productivity, promote environmental quality, and to maintain plant, animal, and human health (Herrick and Wander, 1997; Pankhurst et al., 1997). Soils of poor health have been described as those with reduced soil organic matter (SOM) contents, which in turn are associated with reduced water infiltration, porosity, and biological activity, and increased

compaction and soil erosion (Herrick and Wander, 1997). In addition, root diseases are most severe when soils are of poor quality (Tu, 1992; Abawi and Widmer, 2000). Therefore, we would propose that improving overall soil health would help alleviate root diseases in the Valley. Ecological approaches to disease control are of interest because of environmental, social and economic risks associated with pesticide use (Rechcigl and Rechcigl, 1997).

Organic amendment is considered an old practice and even at the turn of the 20th century soil scientists proclaimed, "Whatever the cause of soil unthriftiness, there is no dispute as to the remedial measures. Doctors may disagree as to what caused the disease, but agree as to the medicine. Crop rotation! Compost! The use of barnyard and green manuring! Humus maintenance! These are the fundamental needs" (Hills, Jones, and Cutler, 1908). More than 90 years later these are still the major remedies available to us.

One way to improve soil health is to enhance the level of organic matter in the soil; and this is particularly true of the SOM active pool (Herrick and Wander, 1997). In general, SOM is characterized by various pools that are compositionally and functionally heterogeneous (Herrick and Wander, 1998). Three different SOM pools are recognized: active, protected (occluded), and stable (Herrick and Wander, 1998). The stable pool is relatively resistant to decay because it is protected physically and/or chemically from rapid microbial decomposition in microaggregates and therefore is the largest and oldest pool of SOM (Carter, 1996). The protected (occluded) pool is chemically labile but relatively physically protected within macroaggregates from

microbial attack. This pool is intermediate in size and age (Carter, 1996). The active pool is composed mainly of plant residues in different stages of decomposition. This is the smallest and youngest pool of organic matter and has very short resident time in the soil (Carter, 1996). This pool is the most labile (microbially-active) organic matter pool and should therefore be the pool most involved in soil biological processes such as nitrogen mineralization and disease suppression.

Soil organic matter active and occluded pools can be estimated by physical fractionation techniques (Christensen, 1992). The free particulate organic matter (fPOM) fraction, an indirect measure of the active pool, is not associated with mineral particles and consists mostly of incompletely decomposed organic residues (Herrick and Wander, 1997). The occluded particulate organic matter (oPOM) fraction, an indirect measure of the occluded pool, is thought to include fPOM and/or low-density mineral associated organic matter most likely of microbial origin protected from microbial degradation within aggregates (Herrick and Wander, 1997).

While some aspects of organic matter loss are uncontrollable, humans can still play a large role in managing soil organic matter because it is a renewable resource. Therefore, continual additions of organic amendments to soil in various forms (plant residues, manure, composts) will increase total or active carbon fractions (e.g. POM), which regulate soil moisture, nutrient mineralization, soil physical properties and microbial community composition, and biological control activities which may lead to disease suppression (Wander, 1994; Drinkwater et al., 1995; Herrick and Wander, 1997). In a comparative tomato cropping systems project, soils farmed organically for

four or more years had higher SOM content, microbial biomass and activity, cation exchange capacity, and nitrogen mineralization potential, and lower soil bulk density. In addition, severity of corky root was reduced. All of these improvements in soil quality can be attributed to the annual return of organic matter to the system in the form of cover crops, manure, or compost (Drinkwater et al., 1995).

Organic matter inputs, from plant residues to composted organic wastes, have the potential to significantly reduce the severity of root diseases (King et al., 1934; Lyle et al., 1948; Asirifi et al., 1994; Stone et al., 2003). Dairy manure is a residue that is available to some processed vegetable growers although few use it at this time. Composting of manure can destroy weed seeds, pathogens, and odors, and reduce its volume and moisture content making it easier to handle. However, compost is more expensive than fresh manure. Therefore it is important to evaluate both products to see which one is most beneficial for improving soil health and suppressing diseases. Fresh and composted manure have both been shown to suppress disease (King and Loomis, 1926; Gorodecki and Hadar, 1990; Ringer et al., 1997; Aryantha et al., 2000). Following four years of manure amendment, the incidence of root rot of cotton was reduced 87 % compared to an unamended control (King and Loomis, 1926). Raw or composted cow manure reduced populations of *Phytophthora cinnamomi* by as much as 60 % compared to an unamended control (Aryantha et al., 2000).

Cover crops are also a source of organic matter and many processed vegetable farmers grow cover crops (Dick et al., 1997). Disease severity has been both reduced (Lyle et al., 1948; Davis et al., 1996) and increased (Koike et al., 1994) by cover

crops. Davis et al (1996) demonstrated that two or three years of annual cover cropping suppressed Verticillium wilt of potato. Some cover crops may increase disease severity by acting as alternate hosts to pathogens. Phacelia, lana wollypod vetch, and Austrian winter pea were identified as hosts for *Sclerotinia minor*, the causal agent of lettuce drop disease (Koike et al., 1996). Interestingly, Phymatotrichum root rot of cotton was controlled through rotation with sweet clover even though the clover was susceptible to Phymatotrichum root rot (Lyle et al., 1948).

Most commonly, organic matter-mediated suppression of root diseases is typically related to microbial activity (Chen et al., 1987; Boehm et al., 1992; 1993; Drinkwater et al., 1995). When organic matter is amended to soil, there is an increase in the activity of primary decomposers (mainly bacteria and fungi) that can also act as antagonists of plant pathogens through competition for nutrients, antibiosis (antibiotic production), and parasitism.

The importance of biotic factors in disease-suppressive organic substrates has been confirmed (Scher and Baker, 1982). Typically, when suppressive soils are sterilized, suppression is lost (Malajczuk, 1983; Campbell, 1989). However, the composition and activity of the soil microflora are not independent of the physicochemical soil properties (Marshall, 1975). The physical and chemical characteristics of a soil will influence the biological component (Cook and Baker, 1983). The addition of organic matter can improve a soil's physical and chemical characteristics, allowing more vigorous growth of root systems (Pallant et al., 1997). The development of a more vigorous and extensive root system might enable a plant

to better withstand or escape the attack of pathogens (King and Loomis, 1926; Garrett, 1970). In addition, better drainage can reduce the growth, movement, and plant infection of water loving pathogens such as the Oomycetes (Garrett, 1970).

The chemical properties of an amendment can also confer disease suppression. For example, decompositional nitrogen products (e.g. NH_3 and N_2O) of organic soil amendments can be toxic to pathogen propagules (Tenuta and Lazarovits, 2002). In addition, some cover crops such as oat and sudan grass can suppress pests when toxic compounds (e.g. saponins, hydrogen cyanide, glucosinolates) are released during their decomposition (Maizel et al., 1963; Patrick et al., 1965; Deacon and Mitchell, 1985; Widmer and Abawi, 2000).

Although the mechanism most often associated with OM-mediated suppression of soilborne diseases is that of competition for energy supply (Hancock, 1981; Kao and Ko, 1986; Chen et al., 1987; Boehm et al., 1993), it is essential to develop a holistic approach to suppressing diseases, knowing that no single mechanism in the soil is likely to determine the capacity of a soil-borne pathogen to establish a disease relationship.

Since poor soil health has been associated with increases in root diseases it would not be surprising if indicators of soil health also serve as indicators of disease suppression (van Bruggen and Semenov 2000). Enzyme assays, microbial biomass, total C, POM, and aggregate stability have all been used as indices soil health (Doran et al., 1994; Herrick and Wander, 1997; Pankhurst et al., 1997; Biederbeck et al., 1998). Interestingly, there is a considerable amount of evidence that enzyme assays,

[in particular hydrolysis of fluorescein diacetate (FDA)] and microbial biomass are good predictors of suppression in container and field soils (Chen et al., 1988; Boehm et al., 1993; Drinkwater et al., 1995). There is also evidence that fPOM is related to disease suppression (Stone et al., 2001).

Most lightly decomposed organic substrates colonized by a diverse array of microorganisms are suppressive to diseases caused by *Pythium* spp. (Hoitink and Boehm, 1999). The duration of suppression is related to the quality of the substrate. The sphagnum peat model best exemplifies the role of substrate quality in OM-mediated disease suppression. Only peats harvested from the top of the bog (slightly decomposed light peat) are suppressive to *Pythium* root rot (Hoitink and Boehm, 1999). As the light peat decomposes, suppression is lost. The loss of suppression is related to a decline in microbial activity (rate of hydrolysis of FDA) and carbohydrate content (Boehm et al., 1997). Interestingly, the composition of compost-derived POM suppressive to *Pythium* damping-off in a compost-amended sand was similar to that of soil fPOM as determined by ^{13}C CPMAS NMR spectroscopy (Golchin et al, 1994; Stone et al, 2001). Compost-derived POM, which had decomposed to the point where it could no longer support suppression of *Pythium* damping-off, was compositionally similar to the slightly more decomposed oPOM (Stone et al., 2001; Golchin et al, 1994). This preliminary evidence suggests that fPOM, the least decomposed and most labile soil physical fraction, may be the dominant SOM physical fraction capable of supporting suppression of *Pythium* root rot in soils.

Indirect measures of substrate quantity and quality may also be an indicator of a soil's suppressive potential. The hydrolysis of FDA appears to be a good indirect indicator of organic matter quality and has been related to organic matter-mediated suppression in container systems (Chen et al., 1988; Boehm et al., 1993; Hoitink and Boehm, 1999). Although this relationship has been demonstrated in container systems there is less evidence that microbial activity, and the quantity and quality of free particulate organic matter is related to disease suppression in field systems. In a field experiment, the severity of corky root of tomato was negatively associated with organic C in one of two years but was related to FDA activity in both years of the study (Workneh et al., 1993).

The primary objective of this study was to determine the impact of fresh and composted manure amendments and cover cropping on root diseases with a particular emphasis on the root rot of corn. The secondary objective was to identify relationships between soil biological and physical properties and disease severity, as a step towards identifying indicators of soil health that could also be used as indicators of SOM-mediated disease suppression.

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CHAPTER 2

COMPOST AND MANURE MEDIATED IMPACTS ON SOILBORNE PATHOGENS AND SOIL QUALITY IN A VEGETABLE ROTATION

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ABSTRACT

In the Willamette Valley of Oregon root rot of snap bean (*Phaseolus vulgaris* L.) and sweet corn (*Zea mays* L.) cause economic losses to farmers. This study was conducted to determine whether fresh or composted dairy manure amendments could suppress root diseases and to describe relationships between disease severity and soil characteristics. Field plots were amended with high or low rates of fresh or composted dairy manure in 2001 and 2002. Soils were collected at 2 and 12 months after the first amendment and 2 and 6 months after the second amendment. Greenhouse bioassays were conducted in treated soils to assess severity of damping-off of cucumber (*Cucumis sativus* L.) and root rots of snap bean and sweet corn. Soils were analyzed for soil free (fPOM) and occluded (oPOM) particulate organic matter content, rate of hydrolysis of fluorescein diacetate (FDA activity), arylsulfatase activity, microbial biomass-C, and percent water stable aggregates (WSA). Two months after amendment, all amendments (except the low rate of manure) reduced the severity of damping-off of cucumber 44 %, root rot of snap bean 25 %, and root rot of sweet corn 52 % compared to the non-amended control. Twelve months after amendment, amended soils no longer suppressed the diseases. All amendments were suppressive after reamendment the following year, and all were no longer suppressive 6 months later. Negative relationships were observed between severity of all three diseases and fPOM, FDA activity, microbial biomass-C, and WSA. Overall, FDA activity was the best indicator of soil organic matter (SOM)-mediated disease suppressive potential.

INTRODUCTION

Root and seedling diseases are difficult to control because few resistant varieties are available. Chemical pesticides and fumigation are the primary means of control; however, environmental, social, and economic risks associated with pesticides has increased interest in exploring approaches that suppress diseases through ecological means (Rechcigl and Rechcigl, 1997). The use of organic amendments to suppress soilborne diseases has gained recent attention by researchers (Abawi and Widmer, 2000; Aryantha et al., 2000; Bullock and Ristaino, 2002; Tenuta and Lazarovits, 2002).

Environmental concerns, including nutrient run-off into waterways, have prompted scientists and dairy farmers to seek alternative markets for dairy manure (Deluca and Deluca, 1995). Dairy manure is available to some Oregon processed vegetable growers. Composting can reduce weed seeds, pathogens, odors, volume, and moisture contents of fresh manure. However, compost is more expensive than fresh manure. Therefore it is important to evaluate both products to determine their respective impacts on soil quality and disease suppression.

Manure amendments to soil can improve soil quality by increasing soil organic matter content, biological activity, and aggregation (Williams and Cooke, 1961; Sommerfeldt et al., 1988; N'Dayegamiye and Angers, 1990; Conti et al., 1992). In addition, root and seedling diseases caused by soilborne organisms can be suppressed by the addition of fresh or composted animal manures to soils (Nesbitt et al., 1979; Chen et al., 1987; Asirifi et al., 1994). The incidence of *Sclerotinia* soft rot on lettuce

grown in soils amended with horse manure was 20 %, compared to 70 % in a non-amended control soil (Asirifi et al., 1994). Soil amended with fresh or composted chicken manure reduced populations of *Phytophthora cinnamomi* from two to zero log CFU g⁻¹ soil over a 12 wk period (Aryantha et al., 2000). In the “Ashburner System” (an organic avocado management system), several years of poultry manure and straw mulch amendments and continuous legume understory cover cropping suppressed *Phytophthora* root rot of avocado (Nesbitt et al., 1979; Malajczuk, 1983). The Chinampa agricultural system in Mexico is characterized by the extensive incorporation of plant residues, animal manure, and canal bottom sediments, resulting in suppression of indigenous and introduced species of *Pythium* that cause damping-off of radish and cucumber seedlings (Lumdsen et al., 1987).

One way to improve soil health is to enhance the level of organic matter in the soil; this is particularly true of the SOM active pool (Herrick and Wander, 1997). In general, SOM is characterized by various pools that are compositionally and functionally heterogeneous (Herrick and Wander, 1998). Three different SOM pools are recognized: active, protected (occluded), and stable SOM (Herrick and Wander, 1998). The stable pool is relatively resistant to decay because it is protected physically and/or chemically from rapid microbial decomposition in microaggregates and therefore is the largest and oldest pool of SOM (Carter, 1996). The protected (occluded) pool is chemically labile but relatively physically protected within macroaggregates from microbial attack. This pool is intermediate in size and age (Carter, 1996). The active pool is composed mainly of plant residues in different stages

of decomposition. This is the smallest and youngest pool of organic matter and has a very short resident time in the soil (Carter, 1996). This pool is the most labile (microbially-active) organic matter pool and should therefore be the pool most involved in soil microbially mediated processes such as nitrogen mineralization and disease suppression. Fractionation of soil organic matter into free and occluded POM is a gross indicator of the active and protected pools of SOM, respectively (Christensen, 1992).

Organic matter that is lightly decomposed and colonized by an array of microflora is typically suppressive to diseases caused by *Pythium* spp. (Hoitink and Boehm, 1999). The sphagnum peat model is the best-researched example of this phenomenon. Only peats harvested from the top layers of the bog (very lightly decomposed peat moss, or light peat) are suppressive to *Pythium* damping-off. The light peat is typically suppressive for up to 7 wk, but as it decomposes it loses its ability to suppress *Pythium* damping-off. This gradual loss of suppression is related to a decline in microbial activity (hydrolysis of FDA), culturable rhizosphere biocontrol agents, and carbohydrate content (Boehm et al., 1997).

As a step towards understanding these relationships in the field, the impact of POM decomposition on *Pythium* damping-off was investigated in sand amended with composted dairy manure solids (Stone et al., 2001). The composition of compost-derived POM suppressive to *Pythium* damping-off in a compost-amended sand (Stone et al, 2001) was similar to that of soil fPOM as determined by ^{13}C CPMAS NMR spectroscopy (Golchin et al, 1994). In this experiment, suppression was supported by the degradation of the compost-derived POM for approximately 1 year. Compost-

derived POM which had decomposed to the point where it could no longer support suppression of *Pythium* damping-off was compositionally similar to slightly more decomposed oPOM (Stone et al., 2001; Golchin et al., 1994). Stone et al. (2001) concluded that suppression was sustained by degradation of the less-decomposed POM or the “active” organic matter. This preliminary evidence suggests that fPOM, the least decomposed and most labile soil physical fraction, may be the dominant SOM physical fraction capable of supporting suppression of *Pythium* root rot in soils. Although the relationship between fPOM and disease suppression has been demonstrated in a container system (Stone et al., 2001), there is no evidence that the content or decomposition level of fPOM is related to disease suppression in field soil.

Indirect measures of SOM composition or decomposition level may be the best indicator of the disease suppressive potential of soil (Boehm et al., 1997; van Bruggen et al., 2000; Stone et al., 2001). For example, FDA activity is thought to be an indirect measure of organic matter quality and is also typically related to disease suppression (Hoitink and Boehm, 1999). Since the microbial biomass declines as levels of FDA activity decline, microbial biomass may also be an indirect measure of organic matter quality (Hoitink and Boehm, 1999).

Active SOM physical fractions and FDA activity have also have also been used as overall indicators of soil quality (Herrick and Wander, 1997; Bandick and Dick et al., 1999). Little information is available on whether other indicators of soil quality, such as arylsulfatase activity and percent water stable aggregation, are related to soil disease suppressive potential.

The objectives of this work were to determine the effect of fresh and composted dairy manure amendments on 1) severity of root rots of sweet corn and snap bean and damping-off of cucumber, and 2) soil biological and physical characteristics. The secondary objective was to identify relationships between the severity of these diseases and soil biological and physical characteristics, as a step towards identifying indicators of soil quality that could also be used as indicators of SOM-mediated disease suppressive potential.

MATERIALS AND METHODS

Site description and field plot management

During 2001, plots were established at the Oregon State University Vegetable Research Farm in the Willamette Valley of Oregon on a Chehalis silt loam (fine-silty, mixed, mesic Cumulic Ultic Haploxerolls). The Valley has a Mediterranean climate, with moist, cool winters and warm, dry summers. The previous crop history for this field site was snap bean in 2000 and 1999, fallow in 1998 and 1997, and sweet corn in 1996 and 1995. The plot size was 6.1 m by 9.2 m.

The experimental design was a randomized complete block (eight replications). Amendment type/rate and a non-amended control was the main effect. The treatments were separated dairy manure solids (MS) and composted dairy manure solids (MSC) applied at two rates and a control. In the spring of each year, amendments were applied on a weight basis, spread manually, and incorporated with a

rotovator to a soil depth of 15 cm. On May 15 of 2001, MS was applied at 16.8 and 33.6 dry Mg ha⁻¹ and MSC at 28 and 56 dry Mg ha⁻¹. On May 1 of 2002, all amendments were re-applied to the same field plots at 16.8 and 33.6 dry Mg ha⁻¹. The MS and MSC amendments were purchased from a local dairy. The MS was the solid fibrous fraction obtained from liquid dairy manure using a screen separator. The MSC was made from MS composted without additives in windrows for 2 months. The windrow was turned twice a week for 1 month and once a week for an additional month with a windrow turner. Materials were not applied on a mineral nutrient basis, but on a carbon basis to increase the potential for disease suppression. The chemical characteristics and nutrient content of the amendments were determined each spring prior to application (Table 2.1). Amendments were applied 4 wk prior to planting to permit sufficient residue decomposition before planting, as raw residues can increase soilborne disease severity (Lumsden et al., 1983; Grunwald et al., 2000).

Plots were planted with sweet corn (*Zea mays* L.), cv Golden Jubilee, on June 15, 2001 and snap bean (*Phaseolus vulgaris* L.), cv Oregon 91G, on June 1, 2002. At the time of corn planting 54, 130, and 45 kg ha⁻¹ N, P₂O₅, and K₂O, respectively, were row applied as starter fertilizer to all treatments. Control plots received an additional 112 kg N ha⁻¹ at the sixth leaf stage (Ritchie et al., 1995). At the time of bean planting 44, 105, and 40 kg ha⁻¹ N, P₂O₅, and K₂O, respectively, were row applied as starter fertilizer to all treatments.

Table 2.1. MS and MSC characteristics for 2001 and 2002.

Amendment	Dry matter	Soluble salts	Total P	Total K	Total N	NO ₃ -N	NH ₄ -N
				g kg ⁻¹			
				2001			
MS	216	1.6	2.16	6.41	13.5	0.42	2.18
MSC	236	1.9	3.94	8.45	18.8	0.68	0.81
				2002			
MS	199	3.5	1.77	5.82	18.8	0.15	2.81
MSC	219	1.9	3.01	7.67	20.1	0.55	0.78

Soil sampling

Soils were sampled 2 and 12 months after the first amendment and 2 and 6 months after the second amendment during the growing seasons of 2001 and 2002. Soils collected 6 months after the second amendment were only assayed for severity of root rot of sweet corn and snap bean, and damping-off of cucumber. From each plot a composite of 10 soil cores (2.5 cm dia., 15 cm depth) were sieved through a 2-mm mesh sieve and stored at 4° C, and assessed for FDA and arylsulfatase activities, and microbial biomass-C (Dick et al., 1996). A 10 g subsample was used to determine gravimetric water content. A separate set of 10 cores (5 cm dia., 15 cm depth) was composited, passed through an 8-mm mesh sieve and air-dried (48 h at 25° C) for determination of fPOM and oPOM (Wander and Yang, 2000). In addition, 10 soil wedges (approximately 13 cm x 5 cm x 15 cm) were taken with an AMS Soil Sampling Sharpshooter Shovel (AMS Inc., American Falls, ID). Soil wedges were composited; a subsample was passed through a 4.75 mm sieve and air-dried as above for WSA analyses (Buller, 1999). The remaining soil was passed through a 2.54 cm screen and used for disease assessment in the greenhouse.

Soil analyses

Microbial activity was assessed on field moist soil by measuring the rate of hydrolysis of FDA and the rate of hydrolysis of p-nitrophenyl sulfate within 48 h of soil collection. The rate of FDA hydrolysis was assessed by modification of procedures proposed by Dick et al. (1996). Briefly, 3 g of field moist soil were added

to each of four Erlenmeyer flasks. Fifty mL of 60 mM sodium phosphate buffer (pH 7.8) containing fluorescein diacetate (3', 6' diacetyl fluorescein) substrate was added to each of three flasks. The fourth flask, to which only buffer was added, served as a control. Reaction flasks were incubated for 3 h on a rotary shaker (178 rev min^{-1}) at room temperature (25°C). The reaction was then terminated by the addition of 2 mL of acetone to each flask. The extracts were centrifuged for 5 min at 15,750 rpm, filtered (Whatman #42), and the quantity of FDA hydrolyzed was determined in filtrates at 490 nm with a spectrophotometer (Beckman Model 34, Beckman Industries Inc., Irvine, CA). Activity was calculated as $\mu\text{g fluorescein hydrolyzed min}^{-1} \text{ g}^{-1}$ dry wt soil by comparing absorbance against a standard curve. Background absorbance was corrected for each treatment with the control sample.

Arylsulfatase activity was determined as described by Tabatabai (1994). In brief, 1 g of soil was placed into a 50 mL Erlenmeyer flask, and 0.25 mL of toluene, 4 mL of acetate buffer (pH 5.8), and 1 mL of *p*-nitrophenyl sulfate solution were added. Samples were incubated for 1 h at 37°C . After incubation, 1 mL of CaCl_2 and 4 mL of 0.5 M NaOH were added to each flask. Samples were filtered (Whatman #2) and absorbance was measured at 410 nm. Two analytical replicates and one control were used per sample. The results were calculated as the activity of *p*-nitrophenol (PNP) $\text{min}^{-1} \text{ g}^{-1}$ dry wt soil by comparing absorbance to a standard curve. The absorbance of the control was subtracted.

Microbial biomass-C was measured by the chloroform-fumigation incubation method (Jenkinson and Powlson, 1976). Ten grams of field moist soil was weighed

into glass scintillation vials. Vials were placed into a desiccator with a 50 mL beaker containing 40mL of ethanol-free chloroform. The desiccator was evacuated and the soil was exposed to chloroform vapor for 24 h. Soils were transferred to 125 mL Erlenmeyer flasks, stoppered, and incubated in the dark at 25° C for 10 days. The amount of CO₂ produced was measured on a Varian gas chromatograph (Varian, Palo Alto, CA).

The fPOM and oPOM were determined by densiometric separation of the light fraction by modification of the method proposed by Golchin et al. (1994) and Puget and Drinkwater (2001). Twenty grams of air-dried soil (< 8mm) were placed in a 250 mL Nalgene centrifuge bottle (Nalge Nunc International Corp., Naperville, IL) with 75 mL of sodium polytungstate solution (1.9 g cm⁻³) (Geoliquids, Chicago, IL). The solution was shaken for 1 h at 100 rpm. The soil suspension was allowed to settle for 16 h. The free POM on the top of the solution was aspirated into a 500 mL Erlenmeyer flask. Free particulate organic matter was recovered on a 0.45 µm MAGNA nylon filter (Osmonics, Inc., Minnetonka, MN). The fPOM was washed with 100 mL of dionized water (diH₂O) and then rinsed off the filter with diH₂O into aluminum pans and dried overnight at 80° C. The sodium polytungstate filtrate was returned to the 250 mL centrifuge bottle and used to obtain the oPOM, by shaking for 16 h at 150 rpm. The samples were then centrifuged for 30 min at 4000 rpm in a Beckman model TJ-6 centrifuge (Beckman Industries Inc., Irvine, CA). The supernatant was poured into the same filtration unit and rinsed with 100 mL of diH₂O and the oPOM recovered as described for fPOM.

Water stable aggregation was measured by wet sieving (Kemper and Rosenau, 1986). First the soil was sieved to remove fractions that were less than 1 mm. Four g of the remaining soil (≥ 1 mm and ≤ 4.75 mm) was placed in a screened cup (3.6 cm diameter with 0.250 mm stainless steel screen). Unstable aggregates were removed by cycling the soil through 100 mL of diH₂O for 3 min at 35 cycles min⁻¹. Stable aggregates were then recovered by cycling the remaining sample through a dispersion solution (sodium polyphosphate, 2 g L⁻¹) until only sand particles remained on the screen. Percent of WSA was calculated as follows:

$$\text{WSA (\%)} = \frac{(\text{g dry wt soil in dispersing solution} - 0.16 \text{ g}) * 100}{(\text{g dry wt soil in both dispersing and diH}_2\text{O} - 0.16 \text{ g})} \quad [1]$$

Disease bioassays

Bioassays were conducted in the greenhouse or growth chamber. Soil samples collected from the field (as described above) were placed into 550 mL conetubes (Stuewe & Sons Inc., Corvallis, OR) and assayed for their potential to suppress damping-off of cucumber and root rot of snap bean and of sweet corn. Each bioassay was replicated twice per plot (n=16).

Cucumber damping-off bioassay

Five untreated cucumber seeds (cv Straight Eight) were planted 1 cm deep in soil. Cone tubes were incubated in a growth chamber for 10 d at 20° C and 16 h illumination. Plants were watered to keep soil moisture levels near field capacity. Disease severity was rated 10 d after planting where 1 = symptomless; 2 = emerged

but wilted or with visible lesions on the hypocotyls; 3 = post-emergence damping-off; and 4 = pre-emergence damping-off. A mean disease severity rating (n=5) was determined for each container (n=16).

Root rot of bean and corn bioassay

Snap bean (cv Oregon 91G) and sweet corn (cv Golden Jubilee) seeds, treated with Captan, were surface disinfested with 10 % sodium hypochlorite for 5 min and rinsed in diH₂O before planting. Three bean or two corn seeds were planted in soil 2.5 cm deep per cone tube. After emergence, corn was thinned to one plant per cone tube. Plants were grown in a greenhouse at 21° C (day) and 15° C (night) with a 14 h photoperiod. Plants were watered daily to keep soil moisture contents near field capacity, and they were fertilized every 2 wk with a water-soluble fertilizer mixture (N-P-K/20-20-20). Snap beans were harvested and roots were evaluated for severity of root rot 4 wk after planting. Corn roots were harvested and rated at the sixth leaf stage (Ritchie et al., 1996).

Bean root rot evaluations were based on the extent of necrosis of the hypocotyl and rootball. The hypocotyl disease rating was based on a 0 to 5 scale where 0 = healthy, 1 = 1 - 10 %, 2 = 11 - 25 %, 3 = 26 - 50 %, 4 = 51 - 75 %, and 5 = 76 - 100 % of the hypocotyl is necrotic. Rootball disease rating was based on a 0 to 5 scale where, 0 = healthy, 1 = 1 - 10 %, 2 = 11 - 25 %, 3 = 26 - 50 %, 4 = 51 - 75 %, and 5 = 75 - 100 % of the rootball is necrotic. The hypocotyl and rootball ratings were combined for a total disease rating from 0 to 10. Root rot of corn was evaluated by visually assessing the proportion of the radicle that was necrotic. The radicle rating

was based on a 0 to 4 scale where 0 = healthy, 1 = lesion present, 2 = 10 - 50 %, 3 = 51 - 99 %, and 4 = 100 % of the radicle was necrotic.

Statistical analyses

Mixed-model analysis for each individual sample time was calculated using the PROC MIXED procedure of SAS (SAS Inst., 1999). Treatment means were separated by the LSD procedure when the F-test was significant ($P < 0.05$). Single degree of freedom contrasts examined the differences between predetermined comparisons of amendment types and rates. Comparisons were described when significant at $P < 0.05$. Regression analysis examined relationships between soil biological and physical characteristics and the severity of root diseases. Regression analysis was performed across sample dates 2 and 12 months after the first amendment and 2 months after the second amendment. Regression coefficients were described when significant ($P < 0.05$). Pearson correlations were performed to examine the relationship between fPOM and other measured soil biological and physical characteristics.

RESULTS

Disease severity

Two months after the first amendment all treatments, except the low rate of MS, suppressed damping-off of cucumber and root rot of snap bean and sweet corn. Damping-off was suppressed by 44 %, root rot of snap bean by 25 %, and root rot of corn by 52 %, compared to the non-amended controls (Fig. 2.1a, 2.2a, 2.3a). The high rate of MS was more suppressive than the low rate of MS to root rots of bean and corn (Table 2.2). In general, corn grown in MSC amended soil had 60 % less root rot than corn grown in MS amended soil. Twelve months after amendment, no amended treatments were suppressive to diseases (Fig. 2.1a, 2.2a, 2.3a). When the same soils were reamended the following spring, suppression was observed across all amended treatments (including the low rate of MS) for all three diseases (Fig. 2.1b, 2.2b, 2.3b). Compared to the non-amended control, two months after the soils were reamended damping off of cucumber was reduced by 55 %, root of sweet corn by 57 %, root rot of snap bean by 25 % in plants grown in amended treatments. There was no effect of type or rate of amendment on the suppression of these diseases (Table 2.2). Loss of suppressiveness to all diseases was observed 6 months after amendment in the second year (Fig. 2.1b, 2.2b, 2.3b).

Interestingly, 12 months after the first amendment, significantly higher levels of root rot of corn were observed in soils that had been amended with the high rate of MSC compared to the non-amended control (Fig. 2.3a). This trend was not observed with the other diseases, nor was it observed at 6 months after the second amendment for root rot of corn (Fig. 2.1; 2.2; 2.3b).

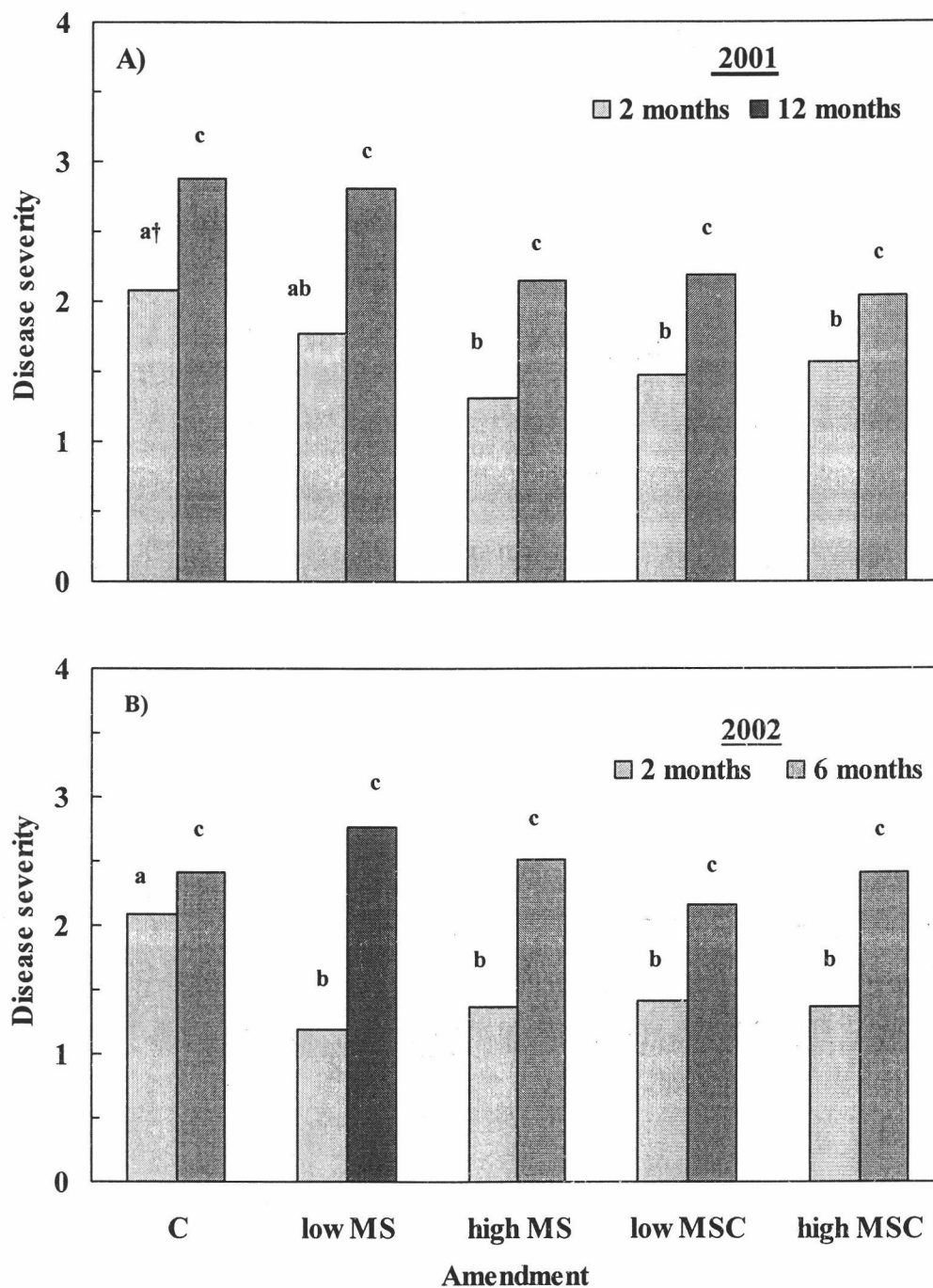


Fig. 2.1. Impact of high and low rates of MS and MSC amendment on severity of damping-off of cucumber at A) 2 and 12 months after the first amendment and B) 2 and 6 months after the second amendment. † Within each sampling date, treatment bars followed by the same letter are not significantly different ($P < 0.05$).

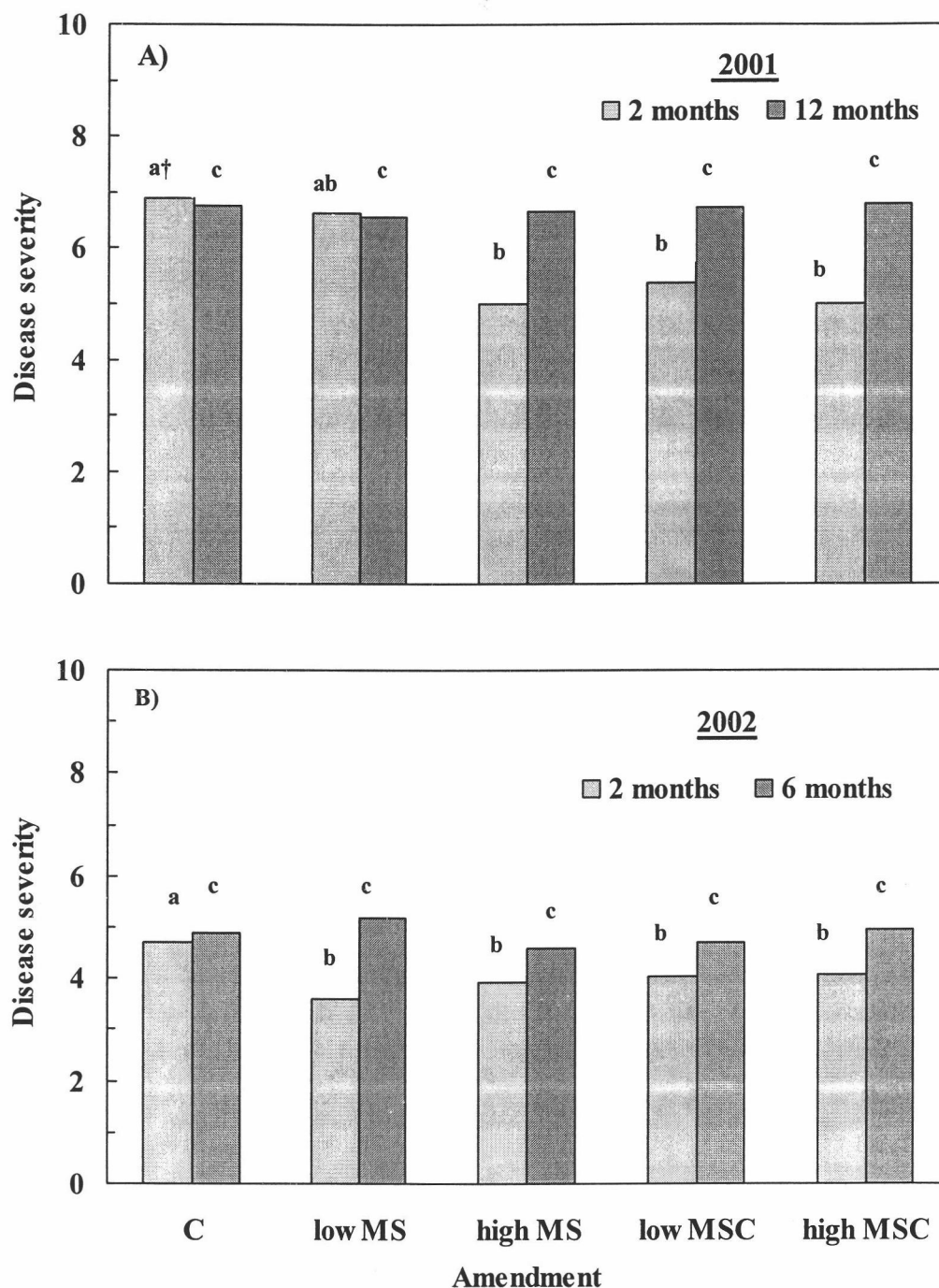


Fig. 2.2. Impact of high and low rates of MS and MSC amendment on severity of root rot of bean at A) 2 and 12 months after the first amendment and B) 2 and 6 months after the second amendment. † Within each sampling date, treatment bars followed by the same letter are not significantly different ($P < 0.05$).

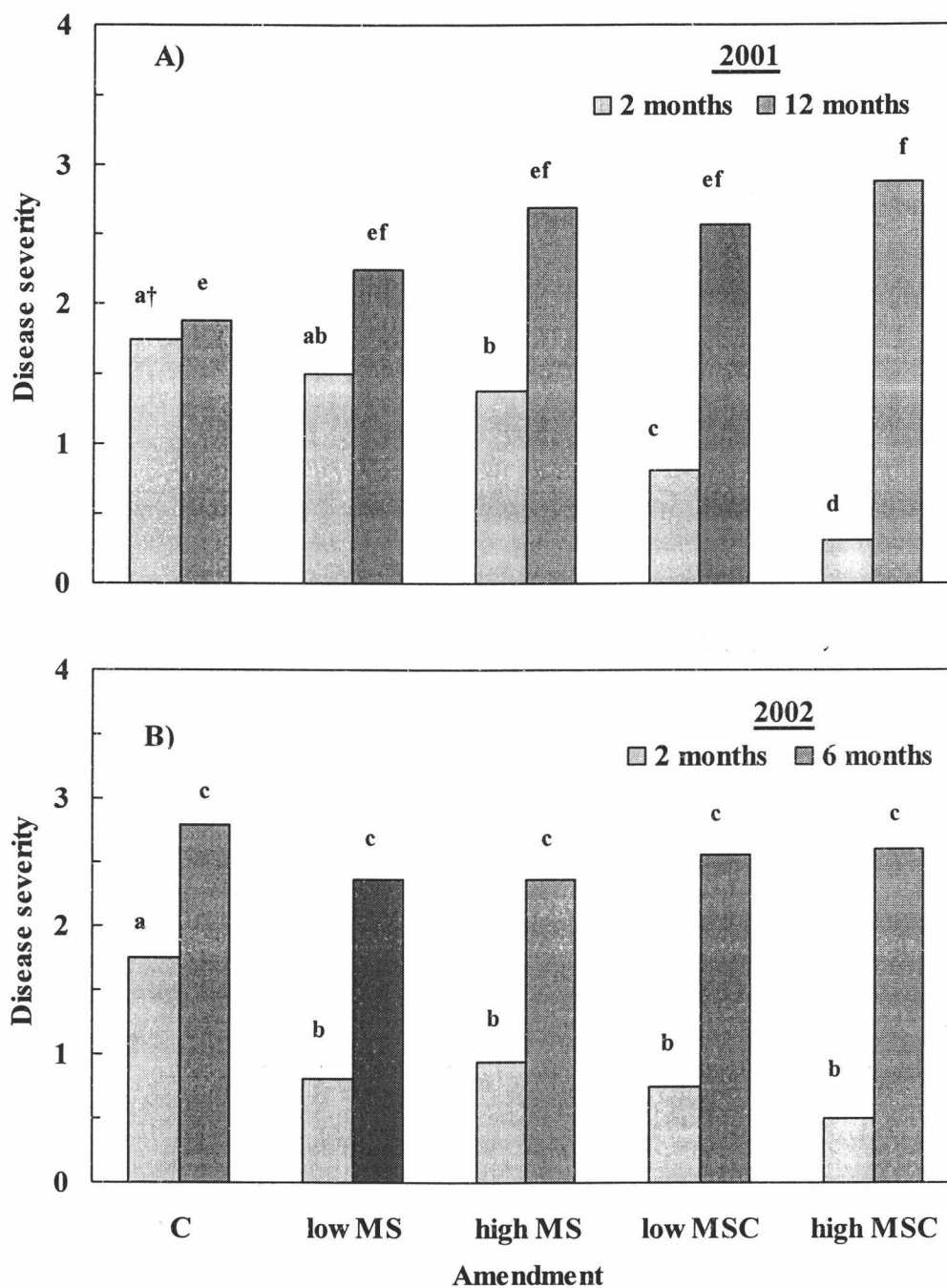


Fig. 2.3. Impact of high and low rates of MS and MSC amendment on severity of root rot of sweet corn at A) 2 and 12 months after the first amendment and B) 2 and 6 months after the second amendment.

† Within each sampling date, treatment bars followed by the same letter are not significantly different ($P < 0.05$).

Table 2.2. Single df contrasts of disease and soil characteristics at 2 and 12 months after the first amendment and 2 and 6 months after the second amendment.

Contrasts†	Disease			Soil characteristics					
	Cucumber damping-off	Root rot bean	Root rot corn	fPOM	oPOM	FDA activity	Aryl-sulfatase	Microbial biomass-C	WSA
<u>2 months after first amendment</u>									
low MS vs high MS	NS§	*‡	*	**	NS	NS	NS	NS	NS
low MSC vs highMSC	NS	NS	NS	**	NS	NS	NS	NS	NS
high vs low	NS	NS	NS	**	NS	NS	NS	NS	NS
MS vs MSC	NS	NS	***	***	NS	NS	NS	*	*
<u>12 months after first amendment</u>									
low MS vs high MS	NS	NS	NS	NS	NS	NS	NS	NS	NS
low MSC vs highMSC	NS	NS	NS	***	NS	NS	NS	NS	NS
high vs low	NS	NS	NS	**	NS	NS	*	*	*
MS vs MSC	NS	NS	NS	**	NS	NS	NS	NS	**
<u>2 months after second amendment</u>									
low MS vs high MS	NS	NS	NS	NS	NS	NS	NS	NS	NS
low MSC vs highMSC	NS	NS	NS	*	NS	NS	**	NS	NS
high vs low	NS	NS	NS	*	NS	NS	**	NS	NS
MS vs MSC	NS	NS	NS	**	**	NS	NS	NS	***
<u>6 months after second amendment¶</u>									
low MS vs high MS	NS	NS	NS						
low MSC vs highMSC	NS	NS	NS						
high vs low	NS	NS	NS						
MS vs MSC	NS	NS	NS						

† MS, fresh dairy manure solids; MSC, composted dairy manure solids; high, high rates; low, low rates.

‡ NS, no significant ($P < 0.05$) coefficients.

§ *, **, *** coefficients significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

¶ Samples taken 6 months after the second amendment were not assayed for soil characteristics.

Soil biological characteristics

Two months after the first amendment all amended soils, with the exception of the low rate of MS, had significantly higher levels of FDA activity and microbial biomass-C than the non-amended control (Fig. 2.4a and c). In soils amended with high rates of MSC, FDA activity and microbial biomass-C were 25 and 50 % greater, respectively, than the non-amended control. Microbial biomass-C was significantly greater in MSC than in MS amended soils (Table 2.2). Treatments did not differ in their level of arylsulfatase activity at 2 months after the first amendment (Fig. 2.4b).

After 12 months of decomposition, FDA activity in the amended soils was not significantly different than in the non-amended control (Fig. 2.4a). However, microbial biomass-C was still higher in all amended treatments compared to the non-amended control (Fig. 2.4c). The low MS, high MS, and low MSC treatments did not differ in their levels of microbial biomass-C. High rates of MSC had significantly higher microbial biomass-C than the low MS treatments, but did not differ from the high MS or low MSC treatments. In general, microbial biomass-C was greater in high rate treatments regardless of whether the manure was fresh or composted (Table 2.2). At 12 months after amendment, amended soils had 30 % higher arylsulfatase activities than the non-amended control (Fig 2.4b).

When soils were reamended, all amended treatments once again had higher levels of FDA activity and microbial biomass-C than the non-amended control (Fig. 2.4a and c). Arylsulfatase activity was higher than the control in all amended plots,

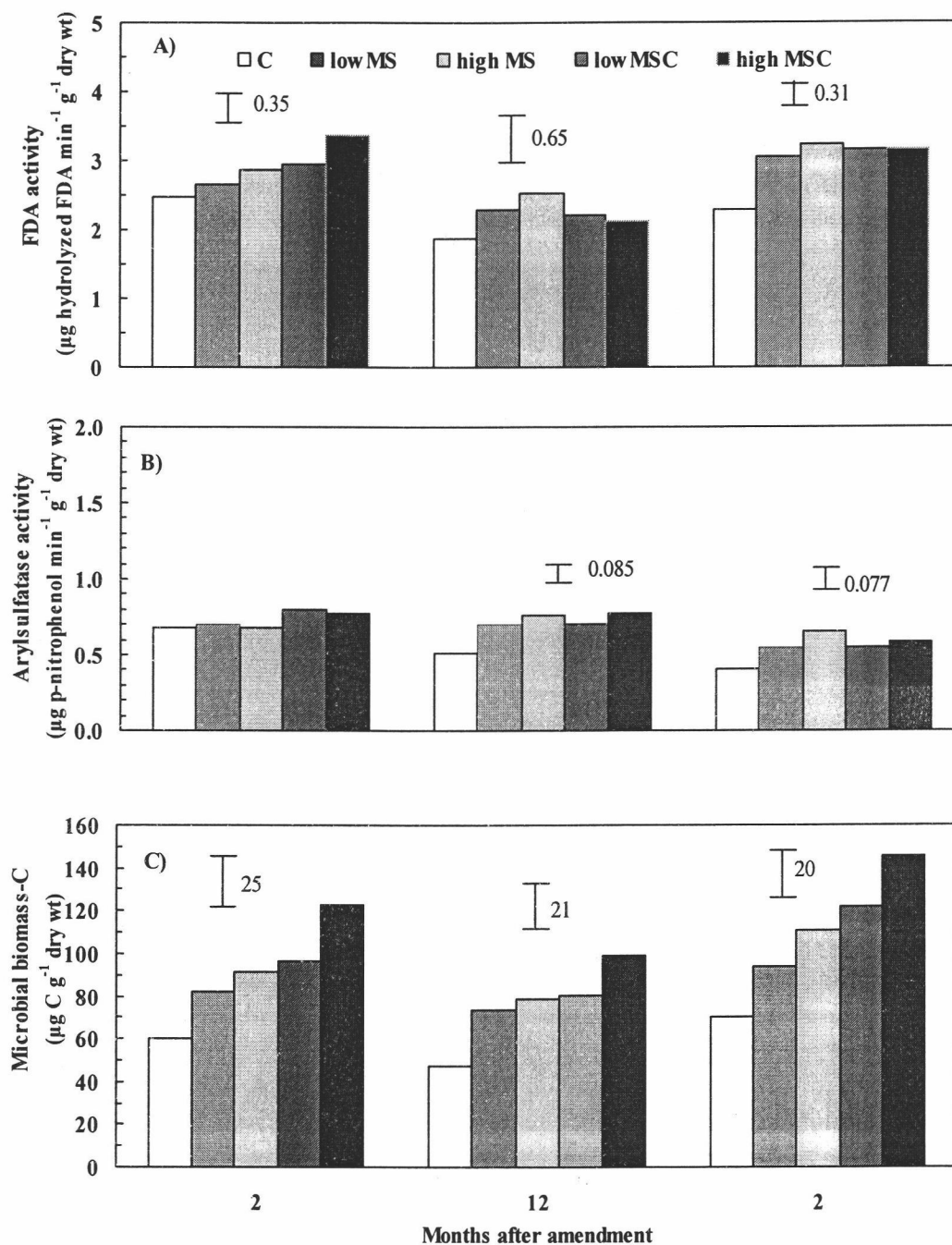


Fig. 2.4. Impact of high and low rates of MS and MSC amendment on A) FDA activity B) Arylsulfatase activity, and C) Microbial biomass-C. Vertical bars indicate LSD at $P < 0.05$.

and arylsulfatase activity was higher in the high rate than in the low rate treatments (Fig. 2.4b and Table 2.2).

Soil physical characteristics

At 2 months after the first amendment all amendments had significantly higher soil fPOM contents than the non-amended control (Fig. 2.5a). Soils amended with the high rate of MSC had 85 % more fPOM than the non-amended control. By 12 months, only soils amended with the high rate of MSC had significantly higher (83 %) fPOM contents than the control. Once the soils were reamended, all amended treatments had significantly higher soil fPOM contents than the non-amended control. The high rate amendments had significantly higher soil fPOM contents than low rate amendments (Table 2.2).

Soil oPOM contents were not significantly different among treatments at any sampling time (Fig. 2.5b). However, 2 months after the second amendment, soils amended with MS had 20 % more oPOM than MSC treatments (Table 2.2).

Amendments did not significantly impact the percent of WSA 2 months after the first amendment (Fig. 2.5c). However, after 12 months, the MS treatments and the high rate of MSC had significantly greater percents of WSA than the non-amended control. After reamendment, only the MS treatments had significantly greater percent of WSA than the non-amended control (Fig. 2.5). On average, the percent of WSA was 20 % greater in MS than in MSC treatments (Table 2.2 and Fig. 2.5c).

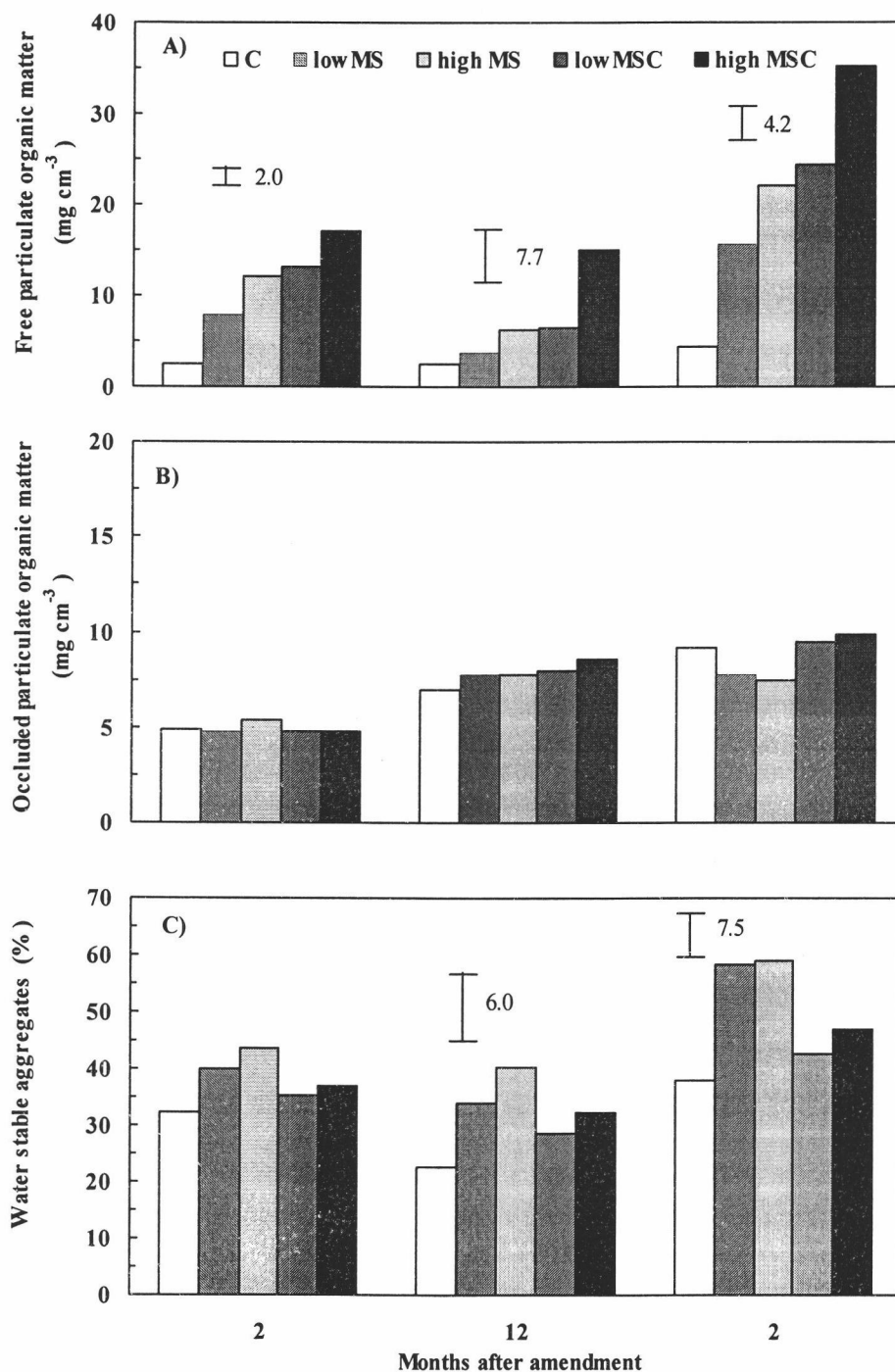


Fig. 2.5. Impact of high and low rates MS and MSC amendment on A) Free particulate organic matter B) Occluded particulate organic matter, and C) Water stable aggregates. Vertical bars indicate LSD at $P < 0.05$.

Relationships between soil properties and disease severity

Linear relationships between most soil biological and physical properties and disease severity of cucumber, snap bean, and sweet corn were negative (Fig. 2.6, 2.7, and 2.8). In general, for all diseases, as the amount of fPOM increased, disease severity decreased (Fig. 2.6a, 2.7a, and 2.8a). In this system, in the first year, disease suppression was observed when the fPOM content exceeded 12 mg cm^{-3} , and this fPOM content was designated as a putative suppressive threshold. No amended treatments were suppressive at 12 months after amendment (Fig 2.1, 2.2, and 2.3). Interestingly, one data point (high rate of MSC) fell above the proposed threshold at this sampling date, yet no suppression was observed compared to the non-amended control.

No relationship was observed between soil oPOM contents and disease severity. Disease severity was negatively related to FDA activity (Fig. 2.6b, 2.7b, and 2.8b). Treatments with FDA activity levels greater than $2.88 \text{ } \mu\text{g hydrolyzed FDA min}^{-1} \text{ g}^{-1} \text{ dry wt}$ were suppressive to all diseases. There were no relationships observed between arylsulfatase activity and disease severity for any disease. Microbial biomass-C was strongly negatively related to severity of all diseases (Fig. 2.6c, 2.7c, and 2.8c). Early in decomposition (2 months after amendment) suppression was observed in all treatments of microbial biomass-C greater than $92 \text{ } \mu\text{g C g}^{-1} \text{ dry wt}$. Later in decomposition (12 months after amendment) when suppression was no longer observed, all levels of microbial biomass were below the proposed threshold with the exception of one treatment.

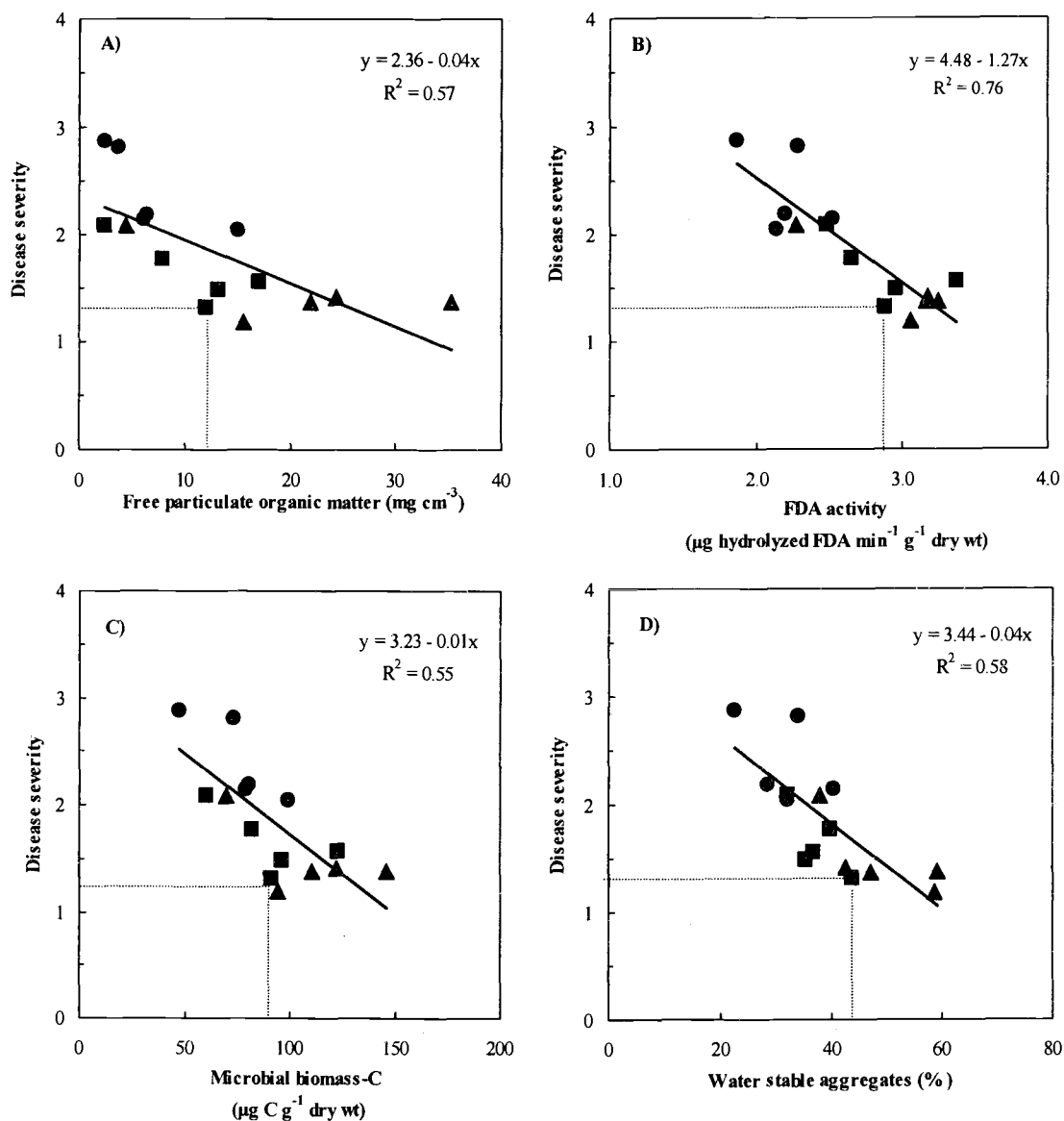


Fig. 2.6. Relationship between severity of damping-off of cucumber and A) Free particulate organic matter, B) FDA activity, C) Microbial biomass-C, and D) Water stable aggregates. Regressions are across three sampling dates, 2 months after the first amendment (\blacksquare), 12 months after the first amendment (\bullet), and 2 months after the second amendment. Each dotted line represents a putative suppressive threshold: the level of disease severity significantly different from the control ($P < 0.05$).

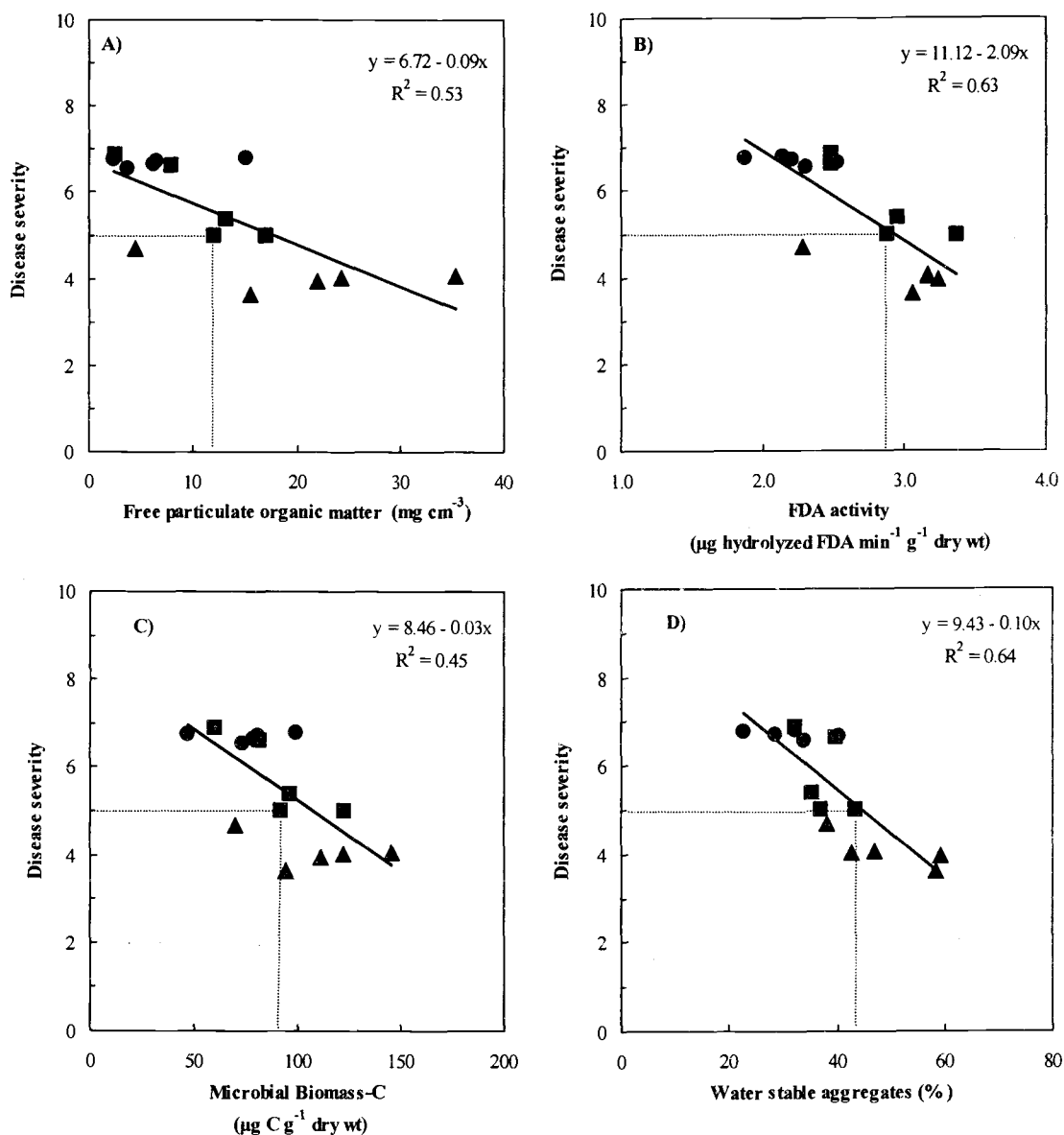


Fig. 2.7. Relationship between severity of root rot of snap bean and A) Free particulate organic matter, B) FDA activity, C) Microbial biomass-C, and D) Water stable aggregates. Regressions are across three sampling dates, 2 months after the first amendment (■), 12 months after the first amendment (●), and 2 months after the second amendment. Each dotted line represents a "suppressive threshold": the level of disease severity significantly different from the control ($P < 0.05$).

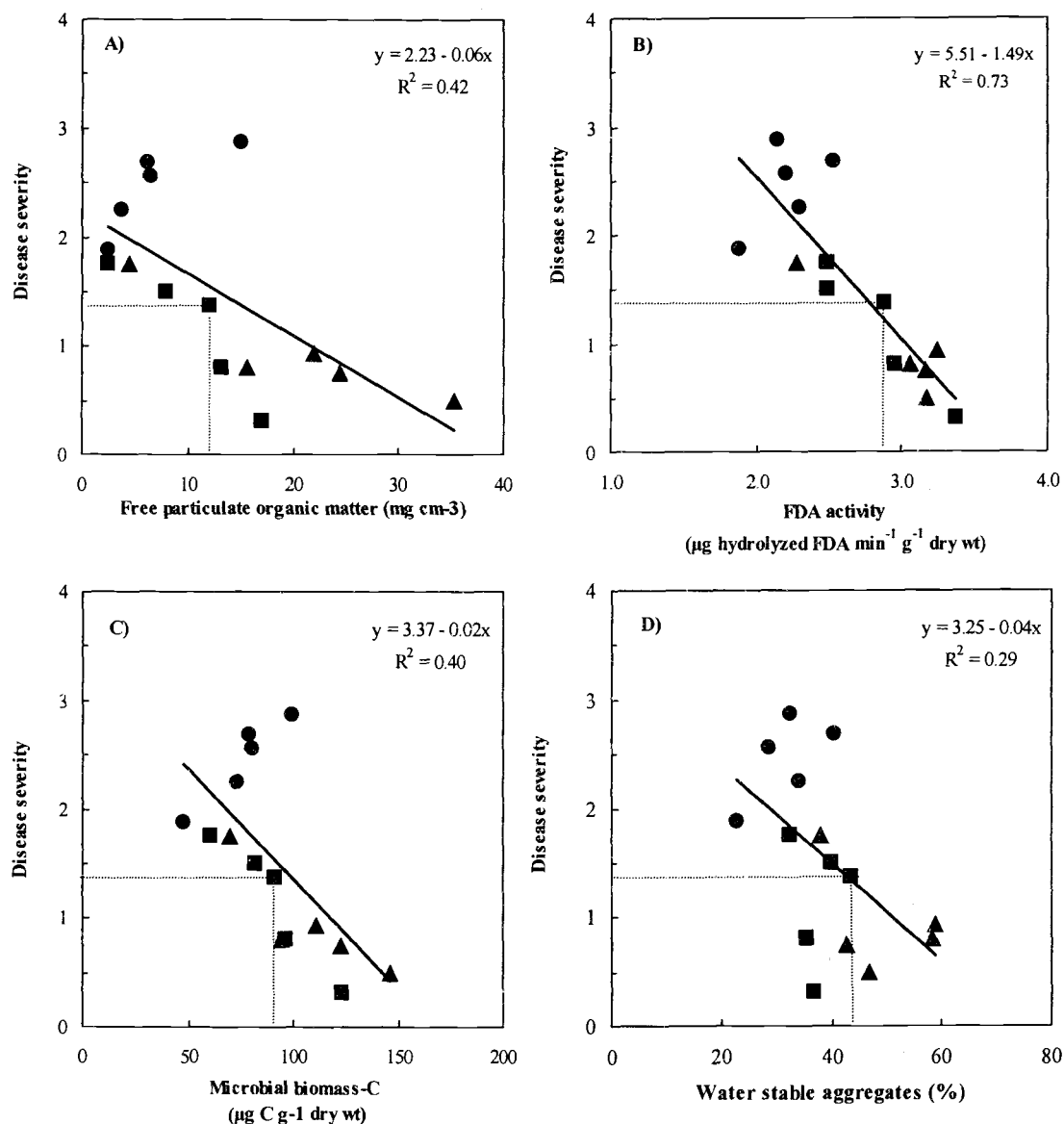


Fig. 2.8. Relationship between severity of root rot of sweet corn and A) Free particulate organic matter, B) FDA activity, C) Microbial biomass-C, and D) Water stable aggregates. Regressions are across three sampling dates, 2 months after the first amendment (\blacksquare), 12 months after the first amendment (\bullet), and 2 months after the second amendment. Each dotted line represents a "suppressive threshold": the level of disease severity significantly different from the control ($P < 0.05$).

(Fig. 2.6c, 2.7c, and 2.8c). The percent of WSA was negatively related to severity of all diseases (Fig. 2.6d, 2.7d, and 2.8d). Disease suppression was observed in all samples with 43 percent WSA or greater. At 12 months after amendment, when suppression was no longer observed, percent WSA was below this putative suppressive threshold for all treatments.

Microbial activity, microbial biomass-C, and the percent of WSA showed a positive linear response to soil fPOM contents (Fig. 2.9).

DISCUSSION

Disease severity

Soil amended with both fresh and composted dairy manure solids suppressed cucumber damping-off and root rot of snap bean and sweet corn. Suppression of diseases in soils amended with raw or composted manure has been reported previously in both container and field systems (King et al., 1934; Asirifi et al., 1994; Aryantha et al., 2000; Bulluck and Ristaino, 2001). There were few significant differences between fresh and composted treatments in terms of their effects on disease severity which follows the reports of Asirifi et al. (1994), Aryantha et al. (2000), and Stone et al. (*in press*).

Across all diseases, the low rate of MS was not suppressive until after the second year of amendment. This lack of suppression is related to low soil fPOM contents and microbial activity (as indicated by FDA activity). It took two years of

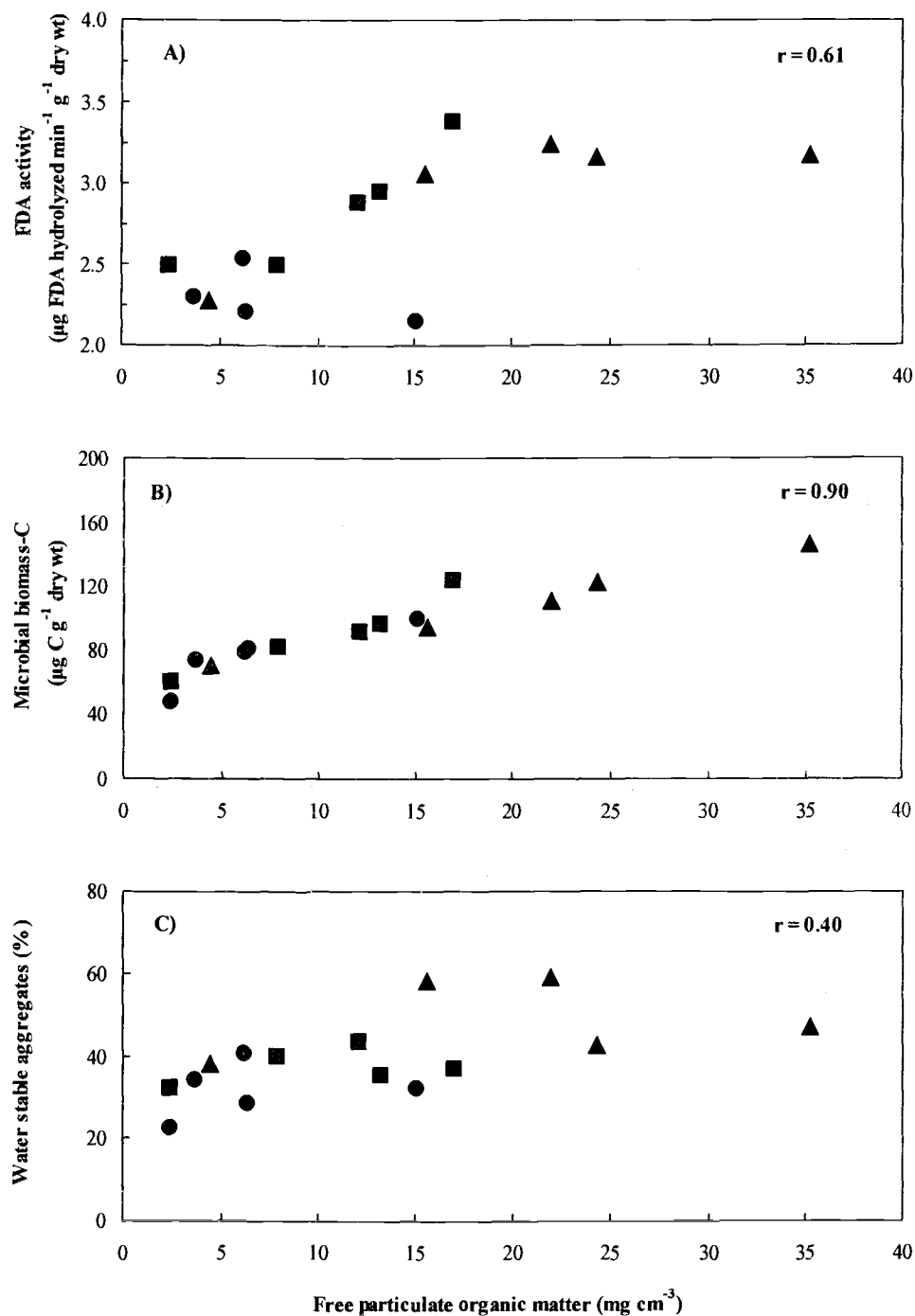


Fig. 2.9. Relationship between Free particulate organic matter and A) FDA activity, B) Microbial biomass-C, and C) Water stable aggregates. Regressions are across three sampling dates, 2 months after the first amendment (\blacksquare), 12 months after the first amendment (\bullet), and 2 months after the second amendment (\blacktriangle).

amendment at the low rate to bring fPOM content and FDA activity to levels above the putative suppressive thresholds.

Other researchers have reported variable impacts on disease incidence after only one year of amendment (Lumsden et al., 1983; Lewis et al., 1992). In contrast, studies in which soils were amended for several to many years have shown more consistent disease suppression (Asirifi et al., 1994; Workneh et al., 1993).

The relationship between repeated amendments and improvements in soil quality and function has been reported in research on transition to organic systems management (Workneh et al., 1993; Drinkwater et al., 1995). In a comparative tomato cropping systems project, soils farmed organically for four or more years had higher SOM contents, microbial biomass, FDA activity, cation exchange capacity, and nitrogen mineralization potential, and lower soil bulk density. In addition, severity of corky root was reduced. The severity of root disease was negatively related to FDA activity and soil C contents. All of these improvements in soil quality were attributed to the annual return of organic matter to the system in the form of cover crops, manure, and compost (Drinkwater et al., 1995). This suggests that long-term application and management of organic wastes and plant residues can have significant and potentially predictable impacts on disease in field soils.

Suppression in our system was lost sometime between 2 and 6 months after amendment, regardless of amendment type or rate. The loss of suppression over a 1 months to 2-year period as an organic substrate decomposes has been shown in container systems. For example, *Pythium* damping-off was suppressed in container

mixes containing peats for days to a few months, composted pine barks up to nine months, and composted hardwood bark for two years (Hoitink and Boehm, 1999). Damping-off of cucumber was suppressed for one year in a dairy manure compost-amended sand (Stone et al., 2001). In this experiment, amended field soils may have lost suppression more quickly than the amended sand (Stone et al., 2001) because of more complex soil microflora interactions, fluctuating environmental conditions, or differences in initial substrate quality. Similarly, Widmer et al. (1998) reported a loss of suppression to *Phytophthora* root rot of citrus (*P. nicotianae*) 6 months after soils were amended with municipal solid waste compost.

Soil biological characteristics

In addition to generating disease suppression, soil amendments also altered other soil biological and physical properties. Since most soils are energy limited (Lockwood and Filonow, 1981), it was not surprising that the addition of labile organic residues (i.e. fresh and composted manure) to the soil increased FDA activity (a general indicator of microbial activity) and microbial biomass. Increases in microbial biomass and/or microbial activity after soils were amended with fresh and composted animal manure has been reported previously (Fraser et al., 1988; Craft and Nelson; 1996; Albiach et al., 2000; Aryantha et al., 2000).

Arylsulfatase activity was not higher in amended treatments compared to the non-amended control 2 months after the first amendment, but was higher at all subsequent sampling dates. We may have not observed immediate changes in

arylsulfatase activity because more time was needed for a shift in biology that favors microorganisms that produce this enzyme. Longer-term soil amendment studies have reported increases in arylsulfatase activity. After four years of ovine manure amendment Albiach et al. (2000) reported a significant increase in arylsulfatase activity compared to the unamended control. Soils amended with beef manure and green manure for 65 years had arylsulfatase activity levels 60 % higher than soils that had received only chemical fertilizer (Bandick and Dick 1999). However, Ndiaye et al. (2000) found significant differences for arylsulfatase activity after 2 years of cover cropping at on-farm sites.

Soil physical characteristics

In this study, soil fPOM contents were significantly increased after amendment regardless of type or rate of amendment. Manure, historically a widely available organic amendment, consistently increases and maintains SOM and POM contents over the short and long term (Kofoed and Nemming, 1976; Wander et al., 1994; Paustian et al., 1997). Higher fPOM contents in soils amended with composts, than in those amended with manure were most likely due to the higher rate of amendment for the compost treatments in the first year.

Two months after re-amendment, fresh manure amendments significantly increased soil oPOM contents and percent of WSA relative to the composted manure treatment. Aggregation is the mechanism that generates oPOM. (Paustian et al., 1997). According to the hierarchical model of aggregate formation proposed by Oades

(1995) fPOM becomes protected inside aggregates and becomes oPOM.. This would explain the coinciding increase in both oPOM and percent WSA at 2 months after reamendment. Increases in aggregate stability have been reported after additions of manure to soils (Guttay et al., 1956). Aoyama et al. (1999) reported that an increase in OM in manure-amended soils favored the formation of macroaggregates and concluded that long-term manure amendment increased protection of C and N. Sela et al. (1998) reported that soils amended with an organic residue composted for 60 days had lower levels of aggregate stability and infiltration rates compared to soils amended with the same organic material composted for 10 days. Similarly, in this experiment, composted manure did not increase the percent of WSA as much as the fresh manure.

Relationships between soil properties and disease severity

All soil biological properties (except arylsulfatase) were correlated to disease severity. This is in agreement with other research; increased fPOM (Stone et al., 2001), FDA activity (Chen et al., 1988; Boehm et al., 1992; Workneh et al., 1993; Drinkwater et al., 1995) and microbial biomass (Chen et al., 1988) have all been positively related to suppression of soilborne diseases.

Soil fPOM contents were negatively related to the severity of all three diseases. This is in agreement with Stone et al. (2001), who concluded that suppression of damping-off of cucumber (caused by *Pythium ultimum*) was supported by coarse and mid-sized compost derived POM in a compost-amended sand. This is the first report of this phenomenon in a field soil. However, total organic-C was negatively

associated with corky root severity in one out of two years in a comparative tomato production system study (Workneh et al., 1993; Drinkwater et al., 1995). This weaker relationship may be due to the fact that total organic-C includes fractions of C that may not be biologically available and therefore do not contribute to the active C pool.

In our work, there was no relationship between soil oPOM content and disease severity. Occluded POM is considered an older pool of C that has been sequestered within aggregates. It contains more degraded C compounds than the free fraction (Golchin et al., 1994). Since this fraction is sequestered, we would not expect it to play a role in biological suppression. However, a portion of the organic matter present in the aggregates is thought to be biologically labile fPOM that is physically protected from microbial decomposition (Ladd et al., 1996). Disruption of these aggregates from such events such as tillage could release this POM, and then it could potentially play a role in disease suppression.

Boehm et al. (1992) reported that suppression of *Pythium* damping-off (causal agent *Pythium ultimum*) would be supported as long as the rate of hydrolysis of FDA was sustained above a level of $3.2 \mu\text{g min}^{-1} \text{g}^{-1}$ dry wt potting mix. In our system, suppression of all diseases was supported at a rate of $2.88 \mu\text{g min}^{-1} \text{g}^{-1}$ dry wt soil, a level slightly lower than Boehm's proposed threshold. Workneh et al. (1993) observed higher levels of FDA activity on organic farms where compost or green manures had been applied annually for four or more years. Corky root (*Pyrenochaeta lycopersici*) was on average 96% less severe on organic than on conventional farms. The levels of FDA activity were as high as $1.3\text{-}\mu\text{g min}^{-1} \text{g}^{-1}$ dry wt soil on organic

farms and $0.70 \mu\text{g min}^{-1} \text{g}^{-1}$ dry wt soil on conventional farms. Dissanayake and Hoy (1999) observed that a rate of FDA hydrolysis above $5.2\text{-}\mu\text{g min}^{-1} \text{g}^{-1}$ dry wt soil was needed to suppress root rot of sugarcane (*Pythium arrhenomanes*). Apparently no universal disease suppressive threshold exists for FDA in field soils; thresholds for this measure must be constructed within the context of each cropping and disease system.

In our work, arylsulfatase activity was not related to disease severity. Arylsulfatase plays an important role in the hydrolysis of ester sulfate. Since microbial ester sulfates are found primarily in fungi (Saggar et al., 1981), its activity is likely related to fungal biomass. The measurement of arylsulfatase activity quantifies a much more specific portion of the microbial community than the hydrolysis of FDA. Furthermore, a significant portion of its activity is derived from arylsulfatase stabilized in the soil matrix, no longer existing in viable cells. Therefore, it only partially reflects the activity of the microbial community.

Our data suggests that the decompositional level of soil fPOM content is related to disease suppression. When the fPOM was lightly decomposed (2 months after amendment), disease suppression was observed. However, after the material had become more decomposed (12 months after amendment) suppression was no longer observed. At this time, all but one fPOM data point fell below the putative threshold for suppression. Only the high rate of MSC had fPOM contents above the putative suppressive threshold. We hypothesize that although the quantity of fPOM was sufficient, it had decomposed to the point where it was probably no longer able to

support suppression. The loss of suppression as an organic material decomposes has been shown in the sphagnum peat system (Boehm and Hoitink, 1992; Boehm et al., 1997). Sphagnum peat (lightly decomposed peat moss) that is harvested from the top layers of the bog is suppressive to *Pythium* damping-off while dark peat (highly decomposed peat moss) harvested from bottom layers of the bog are not suppressive. The light peat is typically suppressive for up to 7 wk but as it decomposes it loses its ability to suppress *Pythium* damping off. This gradual loss of suppression was attributed to a decline in microbial activity (rate of hydrolysis of FDA), culturable rhizosphere biocontrol agents, and carbohydrate content. The microbial activity of the decomposed conducive peat mixes fell below $3.2 \mu\text{g min}^{-1} \text{g}^{-1}$ dry wt potting mix (Boehm and Hoitink, 1992) and the proportion of culturable bacterial species capable of inducing biocontrol of *Pythium* root rot was reduced from 10 to 1 % (Boehm et al., 1997). The major factor associated with the decline of both FDA activity and suppressiveness was a decrease in the carbohydrate concentration of the peat in the mix as determined by ^{13}C CP MAS NMR spectroscopy (Boehm et al., 1997).

The relationship between fPOM quality and *Pythium* damping off was demonstrated in sand amended with composted dairy manure solids (Stone et al., 2001). In this experiment, suppression was supported by the degradation of the coarse and mid-sized POM for approximately 1 year. During this time there was little change in the composition of total fPOM as determined by mid FT-IR and ^{13}C CP MAS NMR, but there was a considerable loss of fPOM mass. However, when suppression was lost, a change in composition was detected while there was little change in mass.

Stone et al. (2001) concluded that suppression was sustained by degradation of the less-decomposed POM.

In agreement with Hoitink and Boehm (1999), FDA hydrolytic activity is a good indicator of the level of decomposition of soil organic matter. Disease suppression (significantly different from the non-amended control) was not observed in our experiment in any treatment and at any sampling date if the rate of hydrolysis of FDA fell below $2.88 \mu\text{g min}^{-1} \text{g}^{-1}$ dry wt soil. Hoitink and Boehm (1999) stated that FDA activity is a reliable predictive measure of the suppressiveness of peat-based or compost-amended potting mixes to root diseases caused by *Pythium* and *Phytophthora* spp. Similarly, Dissanayake and Hoy (1999) reported that rate of FDA hydrolysis had potential as an indicator of soil disease suppressive potential of root rot of sugarcane. Our experiment lends further support for using FDA activity as an indicator of the OM-mediated disease suppressive potential of field soils.

Microbial biomass-C may not be a reliable measure of disease suppression or an indicator of substrate quality. At 2 months after amendment in both 2001 and 2002, disease suppression was observed in soils when levels of microbial biomass-C were above $92 \mu\text{g C g}^{-1}$ dry wt. However, as with fPOM (as described above), the HMSC treatment soils had biomass-C levels above this threshold that did not suppress disease at 12 months after amendment. In agreement, Boehm et al. (1997) reported that microbial biomass remained at high levels even after disease suppression was lost and FDA activity declined. Soil microbial mass has been related to the mass of C

available from plant residues (Fraser et al., 1988) however, it maybe too general an indicator too be related to microorganism-specific functions (Scow, 1997).

Interestingly, disease severity was linearly related to the percent WSA. This is not surprising since increased aggregation will increase aeration, water infiltration and drainage, which are all common management recommendations for control of root rots. Addition of organic matter to soil has been reported to increase soil aggregation (Aoyama et al., 1999). Enhancement of stability have been reported when high rates of manure were applied to soils with initially poor structure or high sand contents (Mbagwu, 1989; Mbagwu and Bazzoffi, 1988). When organic matter is added to the soil there is a flush in microbial biomass resulting in a rise of microbial polysaccharides, followed by an increase in the number of stable aggregates (Monnier, 1965).

It is not surprising that the amount of fPOM in the soil was related to FDA activity, microbial biomass, and percent WSA. There is considerable evidence in the literature that this labile fraction of organic matter is closely linked to soil biological characteristics (Tate, 1987; Wander et al., 1994; Scow, 1997). This evidence suggests that changes in the biology and structure of this soil leading to the suppression of disease were based on the quantity and quality of fPOM in the soil.

In conclusion, fresh or composted dairy manure amendments suppressed damping-off of cucumber and root rot of snap bean and sweet corn. Suppression was short in duration, lasting less than 6 months after amendment. Suppression was related to soil quality indicators such as fPOM, FDA activity, microbial biomass-C,

and percent WSA. However, when suppressive thresholds were tested for each of these soil factors, only the threshold for FDA activity held up over all treatments and sampling dates. Fluorescein diacetate hydrolysis was the most reliable indicator of the disease suppressive potential of the soil, as it appears to be an indirect measure of both organic matter quantity and quality relative to disease suppression.

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CHAPTER 3
COMPOST AND MANURE MEDIATED IMPACTS
ON ROOT ROT OF SWEET CORN

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Prepared for Soil Science Society of America

ABSTRACT

A complex of pathogens including *Pythium arrhenomanes*, *Drechslera* spp., and *Phoma* spp causes root rot of sweet corn. Organic amendments can induce suppression in soils. The impact of fresh (MS) and composted (MSC) dairy manure on severity of root rot caused by the pathogen complex as well as on disease caused by the individual pathogens was investigated. Two soil types (Chehalis; Clackamas) with high root rot potential were used to study repeated soil applications of MS or MSC on root rot. In either soil, there were few repeated application or repeated application x amendment type effects. Chehalis soil amended with MSC, reduced severity of root rot 20% compared to the non-amended control, while MS amendments did not suppress disease. Clackamas soil amended with MS or MSC reduced severity of root rot 38% compared to the control. Severity of root rot was negatively related to the rate of hydrolysis of fluorescein diacetate (FDA activity) in Chehalis and Clackamas soils ($R^2 = 0.70$ and 0.91 , respectively). Amendment of infested pasteurized soil with MS or MSC suppressed root rot caused by *Drechslera* spp. 48%, *Phoma* spp. 63%, and *P. arrhenomanes* 44% compared to the non-amended control. Composted manure was more suppressive to *Drechslera* spp. and *Phoma* spp. than MS. The MS was more suppressive to *P. arrhenomanes* than MSC. In general, FDA activity was negatively related to disease severity ($R^2 = 0.61$). However, the relationship did not hold true for root rot caused by *P. arrhenomanes*, suggesting that a different mechanism(s) contributed to suppression.

INTRODUCTION

Over the last 15 years there has been a gradual decline in sweet corn (*Zea mays* L.) yields in fields that have had a long history of corn production in Oregon. Yield decline has been, at least in part, attributed to an increase in root rot (Hoinacki and Powelson, *in press*).

Root rot of sweet corn is caused by a complex of pathogens including *Pythium arrhenomanes*, *Phoma* spp., and *Drechslera* spp. (Hoinacki and Powelson, *in press*). Other pathogens that are commonly associated with the disease include *Fusarium graminearum* and *F. oxysporum* (Hoinacki and Powelson, *in press*). Root rot is characterized by dark lesions on the radicle and nodal roots. The mesocotyl may or may not be necrotic. As the root ball becomes necrotic, the plant is less able to absorb water and nutrients, resulting in lowered yields.

Root rot has been reported in other sweet corn growing regions of the United States. Red root rot of corn (casual agents *Phoma terrestris*, *Pythium irregulare*, and *Fusarium acuminatum*) has caused yield reductions of 15-20 % in the Delmarva region (Deleware, Maryland, and the Virginia Peninsula) (Mao et al., 1997; Carroll, 1999). In the Georgia Coastal Plain, yield decline of sweet corn from approximately 11.3 to 7.2 t ha⁻¹ was reported in a research plot that had been double cropped continuously for 7 years (Sumner et al., 1990). The yield decline was attributed to infection by soilborne pathogens (primarily *Phoma terrestris*, *Pythium arrhenomanes*, and *Pythium* spp.).

Currently, there are no management strategies available to reduce the severity of root rot of sweet corn. Soil conditions greatly affect root growth and health (Tu and Tan, 1988; Tu, 1992; Kaspar et al., 1995; Pallant et al., 1997). Severe root rots of other crops have been partially attributed to depletion in soil organic matter and overall reduced soil quality (Tu, 1992; Abawi and Widmer, 2000). Cultural practices that improve soil quality may have the potential to reduce the severity of root rot of sweet corn.

Additions of organic matter (OM) (i.e. plant residues or organic wastes) to field soils typically improves the soil physical (Reid and Goss, 1981; Chantigny et al., 1999; Nemati et al., 2000) and biological (Pera et al., 1983; Perucci, 1990; Bandick and Dick, 1994; Albiach et al., 2000) properties and may also suppress a variety of diseases (Lumdsen et al., 1987; Asirifi, 1994; Drinkwater et al., 1995; Stone et al., *in press*). Some processed vegetable growers have dairy manure available to them, and manure could be used as an organic soil amendment. Composting can reduce some of the negative attributes of manure such as pathogens and weed seeds. In addition, composting reduces the volume and moisture content of manure making it easier to transport. However, composting incurs significant labor and financial costs that impede adoption of composting by growers.

Fresh and composted animal manure amendments can suppress a variety of diseases (King et al., 1934; Gorodecki and Hadar, 1990; Ringer et al., 1997; Aryantha et al., 2000). Aryantha et al. (2000) found that a soil based potting mix amended with fresh or composted cow manure reduced pathogen populations of *Phytophthora*

cinnamomi by as much as 60 %. Ringer et al. (1997) assessed the use of three different animal manure composts for suppression of damping-off caused by *Pythium ultimum* and *Rhizoctonia solani*. All composts suppressed damping-off caused by both pathogens relative to the non-amended control. Fresh and composted manures can suppress root rot of corn in soil with relatively low root rot potential (see Chapter 2). However, it is not clear whether these amendments can suppress root rot of sweet corn in soils of high disease potential. In addition, it is not known how these amendments impact the individual pathogens involved in this disease complex.

In general, the effect of single season soil amendments on disease incidence is highly variable (Lewis et al., 1992, Lumsden et al., 1986). In contrast, longer term (several to many years) application of organic residues can generate suppression more consistently (King et al., 1934; Lumsden et al., 1987; Asirifi et al., 1994; Drinkwater et al., 1995). Two years of low rate of manure amendment were required to suppress root rot in soils of low disease potential (see Chapter 2). Therefore, several amendments of manure or compost may be needed to generate suppressiveness to root rot of sweet corn in soils with high disease potential.

Most lightly decomposed organic substrates colonized by a diverse array of microorganisms are typically suppressive to diseases caused by *Pythium* spp. (Hoitink and Boehm, 1999). The duration of suppression is related to the quantity and quality of the substrate. Therefore, indirect measures of organic matter quantity and quality may be an indicator of a soil's suppressive potential. Fluorescein diacetate activity appears to be a good indirect indicator of organic matter quantity and quality and has

been related to OM-mediated suppression in container systems (Chen et al., 1988; Boehm et al., 1993; Hoitink and Boehm, 1999; Stone et al., 1997). In addition to FDA activity, β -glucosidase activity has been suggested as a potential indicator of soil quality because it is sensitive to organic C inputs into the soil (Bandick and Dick, 1999). β -glucosidase catalyzes the release of glucose from cellobiose providing microorganisms with an important energy source. Since β -glucosidase plays a role in the decomposition of C compounds it may be related to OM-mediated suppression of soilborne diseases.

Corn plants grown in soils amended with plant or animal residues have more dense root systems compared to those grown in non-amended soil (Pallant et al., 1997). An increase of 1 % in SOM increased root density by as much as 13 %. These denser roots would not necessarily be more resistant to infection than those growing in non-amended soils (Garrett, 1970); however, if infection resulted in 50 % of the total rootball becoming infected, a larger root system would have more functioning roots than the smaller root system.

The objective of this experiment was to determine the impact of 1) fresh and composted manure amendments on biomass and root rot of sweet corn grown in soil with high root rot potential, 2) repeated application of organic amendment on root rot of sweet corn, and 3) organic amendment on root rot severity contributed by the three primary pathogens that cause root rot of sweet corn.

MATERIALS AND METHODS

Experiment 1. Impact of fresh and composted manure on root rot complex

Soils were collected from two fields known to have high root rot potential. In April 2001, a Chehalis silt loam soil (fine-silty, mixed, mesic Cumulic Ultic Haploxerolls) (Chehalis soil) was collected from a field located near Dayton, OR. The cropping history for the last five years was sweet corn in 1999, broccoli (*Brassica oleracea*) in 1998; sweet corn in 1997; beets (*Beta vulgaris*) in 1996, and wheat (*Triticum aestivum*) in 1995. In March 2002, a Clackamas gravelly loam soil (fine-loamy, mixed, noncalcareous, mesic Typic Argiqualfs) (Clackamas soil) was collected from a field near Marion, OR. The cropping history for this field was corn in 2001, perennial ryegrass (*Lolium multiflorum* L.) in 2000, 1999, and 1998 and sweet corn in 1997. At the time of collection, soil was passed through a 2.54 cm mesh screen (to remove large pieces of undecayed plant material) before it was placed into 11 L (20 x 40 cm) plastic pots (Stuewe & Sons Inc., Corvallis, OR).

In shade houses at the Oregon State University Research Farm (Corvallis, OR) pots were arranged in a randomized complete block design with 9 factorial treatments replicated 4 times. The 9 treatments comprised a 3 x 3 factorial: 3 soil amendment types (fresh and composted dairy manure and a non-amended control) x 3 repeated applications. Treatments were initiated in May (Chehalis soil, 2001; Clackamas soil, 2002) at which time manure (10 % vol/vol) and compost (15 % vol/vol) were incorporated into the top 15 cm of the soil. The composted dairy manure solids

(MSC) were prepared by turning manure solids (MS) with a windrow turner twice a week for a month and once a week for an additional month. The chemical characteristics and nutrient content of the organic amendments are reported in Table 3.1. A non-amended (fallow) treatment served as a control. The repeated application treatments were imposed by amending pots with MS or MSC at time zero, and at two and four months after the first amendment. The pots were destructively sampled at two, four, and six months and evaluated for the effect of the treatments on severity of root rot and FDA activity. Since raw organic residues can increase disease severity (Grunwald et al., 2000), treatments were allowed to incubate for 2 months. The experimental procedure is outlined in Fig. 3.1. There were four replicates of the corn root rot bioassay per pot, resulting in 16 replicates at each sampling period.

Experiment 2: Impact of fresh and composted manure on individual pathogens

Soil (Newberg fine sandy loam: coarse-loamy, mixed mesic Fluventic Haploxerolls) was collected from the Botany and Plant Pathology Research Farm, Oregon State University. The soil was passed through a 2.54 cm mesh screen to remove large pieces of undecomposed plant debris. Soil was steam pasteurized at 99°C for 1 h on each of two consecutive days.

Pots filled with soil were arranged in a completely randomized design with 12 factorial treatments on a greenhouse bench. Treatments were 4 pathogens (*Pythium arrhenomanes*, *Phoma* spp., *Drechslera* spp., or uninfested control) x 3 amendment types (MS, MSC, and non-amended control). The treatment soils were allowed

Table 3.1. Fresh (MS) and composted dairy manure (MSC) solid amendment characteristics for 2001 and 2002 (dry weight basis).

Amendment	Dry matter	Soluble salts	Total P	Total K	Total N	NO ₃ -N	NH ₄ -N
				g kg ⁻¹			
				2001			
MS	216	1.6	2.16	6.41	13.5	0.42	2.18
MSC	236	1.9	3.94	8.45	18.8	0.68	0.81
				2002			
MS	199	3.5	1.77	5.82	18.8	0.15	2.81
MSC	219	1.9	3.01	7.67	20.1	0.55	0.78

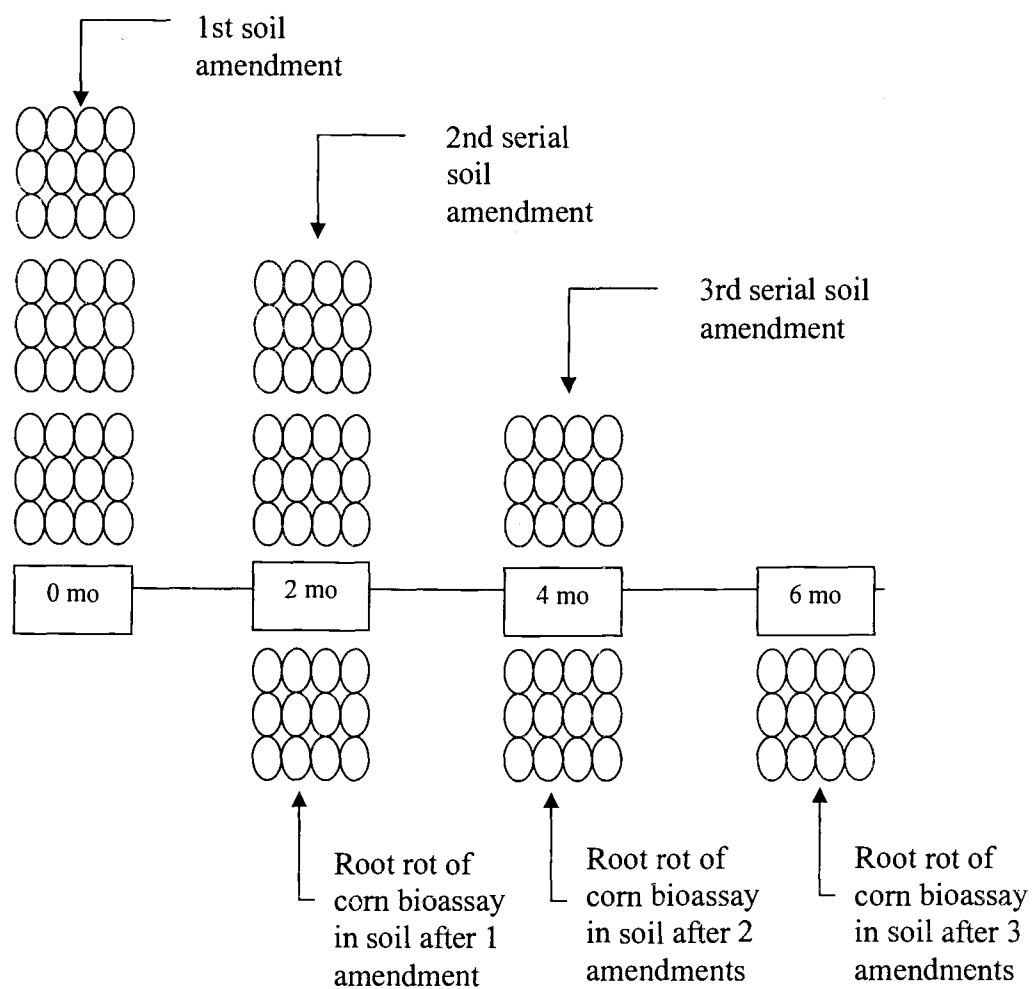


Fig. 3.1. Experiment design: Effect of serial soil amendment with fresh and composted dairy manure on the severity of root rot of corn.

to incubate for 2 months and then assayed for severity of root rot of corn and FDA activity.

Soil (32 L per soil treatment) was infested with a sand-cornmeal culture of either *Pythium arrhenomanes*, *Phoma* spp. or *Drechslera* spp. For each treatment, eight plastic pots (4 L) (OBC Northwest, Inc., Canby, OR) were filled with pathogen-infested soil. Pathogen-infested soil was amended with treatments that consisted of 10 % vol/vol MS , 15 % vol/vol MSC, and a non-amended control. For each treatment, eight plastic containers (4 L) (OBC Northwest, Inc., Canby, OR) were filled with treatment soil.

Corn bioassay

A greenhouse bioassay was used to evaluate the effect of soil amendments on severity of root rot of corn (Hoinacki and Powelson, 2002). Soil was placed into 550 mL plastic cone tubes (Stuewe & Sons Inc., Corvallis, OR). Sweet corn (cv Golden Jubilee) seeds were surface-disinfested in 10 % sodium hypochlorite for 5 min and rinsed in distilled water before planting 2.54 cm deep into the cone tubes. Plants were grown at 21° C (day) and 15° C (night) in a greenhouse with a 14 h photoperiod. After emergence, plants were watered daily to keep soil moisture levels near field capacity, and they were fertilized every other week with a water-soluble fertilizer mixture (N-P-K/20-20-20). Plants were harvested at the sixth leaf stage (Ritchie et al., 1996). Rootballs were washed and evaluated for severity of root rot (Table 3.2), and shoots

Table 3.2. Root rot severity index for root rot of sweet corn. †‡.

Rating	Components of root system		
	Mesocotyl	Radicle	Nodal root system
0	Healthy	Healthy	Healthy
1	Lesion present	Lesion present	5 – 10 % necrotic
2	100 % necrotic	10 - 50% necrotic	11 – 25 % necrotic
3		50 – 99% necrotic	26 - 50% necrotic
4		100% necrotic	> 51 % necrotic

† Total disease rating based on the sum of the 3 components of the root system, where the sum ranges from 0 to 10 (0=symptomless and 10 = > 51 % of the root ball is necrotic).

‡Hoinacki and Powelson, 2002

and roots were oven dried at 60° C and weighed. Summing the disease ratings from the mesocotyl, radicle, and nodal roots generated a total root rot severity rating.

Soil analyses

Soil was passed through a 2 mm mesh sieve and analyzed for FDA and β -glucosidase activity within 48 h of sampling (Dick et al., 1996). FDA activity was measured as modified from Dick et al. (1996). Fifty mL of 60 mM sodium phosphate buffer (pH 7.8) containing fluorescein diacetate (3', 6' diacetyl fluorescein) substrate was added to a 125 mL Erlenmeyer flask containing 3 g of field moist soil. Flasks were stoppered and incubated for 3 h on a rotary shaker (178 rev min⁻¹) at 25° C. The reaction was then terminated by the addition of 2 mL of acetone to each flask. A 30-mL aliquot was centrifuged (15,750 rpm; 5 min) and filtered (Whatman #42), and the quantity of FDA hydrolyzed was determined in filtrates at 490 nm with a spectrophotometer (Beckman Model 34, Beckman Industries Inc., Irvine, CA). The results are the average of three sample replicates, with a control (incubated without substrate) subtracted. β -glucosidase enzyme activity was measured as described by Dick et al. (1996). In brief, 1 g of soil was incubated for one hour with *p*-nitrophenyl β -D-glucose and toluene in a modified universal buffer (pH 6). After incubation, *tris*-hydroxy aminomethane (pH 12) was added to terminate the reaction. The product was measured on a spectrophotometer at 420 nm. Each sample was analyzed in duplicate and averaged following the subtraction of a control sample.

Statistical analysis

Mixed-model analysis for each soil was calculated using the PROC MIXED procedure of SAS (SAS Institute, 1999). Mean separations were determined by the LSD procedure when the F-test was significant ($P < 0.05$). Regression analysis examined the relationship between soil enzyme assays (FDA and β -glucosidase) and severity of root rot of corn. Regression coefficients were described when significant ($P < 0.05$).

RESULTS

Experiment 1. Impact of fresh and composted manure on root rot complex

There was no amendment x repeated application interactions observed for either soil (data not shown). This data suggests that amendment types varied similarly over repeated applications.

Differences due to repeated application were observed for the Chehalis soil (Table 3.3). The severity of root rot of sweet corn was 37 % higher after the first and second applications compared to three applications (Table 3.4). Sweet corn shoot and root biomass were also significantly greater after three application than one or two applications (Table 3.3 and 3.4). Severity of root rot and root and shoot biomass of sweet corn was not different between period one and two (Table 3.3).

Table 3.3. Statistical significance of treatment effects on severity of root rot and shoot and root biomass of sweet corn and FDA and β -glucosidase activity for Chehalis and Clackamas soils.

Source of variation	Corn bioassay			Soil enzyme assay	
	Root rot	Dry matter		FDA activity	β -glucosidase
		Shoot	Root		
			Chehalis		
Repeated application	***†	***	***	NS‡	NS
Amendment type	***	*	**	***	NS
Repeated application x amendment type	NS	NS	NS	NS	NS
			Clackamas		
Repeated application	NS	NS	NS	NS	NS
Amendment type	***	**	NS	**	NS
Repeated application x amendment type	NS	NS	NS	NS	NS

† *, **, *** coefficients significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

‡NS, no significant ($P < 0.05$) coefficients.

Table 3.4. Impact of repeated application of amendments on severity of root rot and shoot and root biomass of sweet corn averaged across amendment type for Chehalis soil.

Repeated application	Root rot	Dry matter	
		Shoot	Root
		-----g-----	
1	7.50a	3.59a	0.59a
2	7.71a	3.45a	0.53a
3	4.79b	4.82b	1.64b

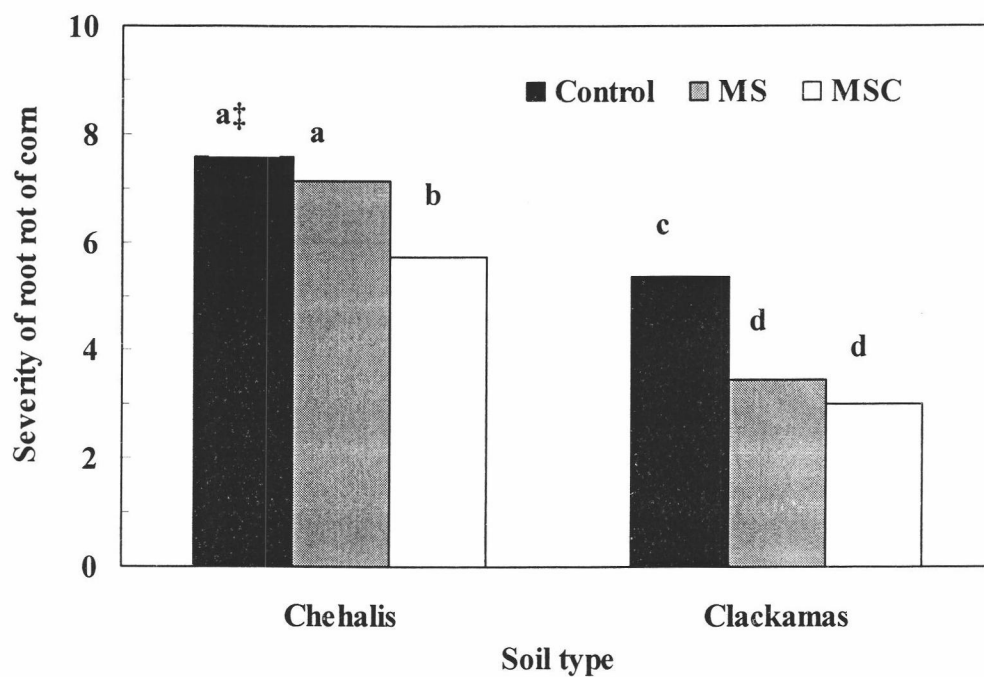


Fig. 3.2. Impact of fresh (MS) and composted (MSC) dairy manure on severity of root rot of sweet corn in two soil types averaged across repeated applications. †Within a soil type, treatment bars followed by the same letter are not significantly different ($P < 0.05$).

In both soils, the type of amendment significantly impacted severity of root rot (Table 3.3). Amendment of the Chehalis soil with MSC suppressed root rot of sweet corn by 20 % compared to the non-amended control (Fig. 3.2). Amendment with MS did not significantly reduce root rot (Fig. 3.2). Compared to the non-amended control, severity of root rot was reduced by 44 and 35 % when the Clackamas soil was amended with MSC or MS, respectively (Fig. 3.2).

Corn grown in the Chehalis soil amended with MSC had 38 % more root biomass and 19 % more shoot biomass than the corn grown in MS and the non-amended control (Table 3.5). Shoot and root biomass of corn grown in MS amended Chehalis soil did not differ from the non-amended control (Table 3.3 and 3.5). Root biomass was not significantly different among treatments in the Clackamas soil (Table 3.3 and 3.5). The shoot biomass of MSC-amended treatments was 19 % greater than in the MS- and non-amended treatments.

Fluorescein diacetate activity was highest in soils amended with MSC (Table 3.5). In the Chehalis soil, MS amendment resulted in FDA activity levels significantly lower than in MSC amended soil, but in the Clackamas soil their activities were not different (Table 3.5). β -glucosidase activity did not differ among treatments in either soil (Table 4.3).

Fluorescein diacetate activity was negatively related to disease severity in the Chehalis ($R^2 = 0.70$) and Clackamas soils ($R^2 = 0.91$) (Fig. 3.3). Treatments with FDA activities greater than $4.00 \mu\text{g fluorescein min}^{-1} \text{g}^{-1} \text{dry wt}$ were suppressive to

Table 3.5. Impact of fresh (MS) and composted (MSC) dairy manure on corn root and shoot biomass and soil enzyme assays of two soil types averaged across repeated applications.

Amendment type	Dry matter		Enzyme assay	
	Shoot	Root	FDA activity	β -glucosidase
	-----g-----		$\mu\text{g fluorescein min}^{-1}$ $\text{g}^{-1} \text{ dry wt}$	$\mu\text{g p-nitrophenol}$ $\text{min}^{-1} \text{ g}^{-1} \text{ dry wt}$
			<u>Chehalis</u>	
Control	3.57a‡	0.75a	2.17a	0.51a
MS	3.95ab	0.87ab	3.06b	0.54a
MSC	4.40b	1.20b	4.06c	0.54a
			<u>Clackamas</u>	
Control	3.41c	0.84c	3.46d	0.44b
MS	3.63c	0.89c	4.07e	0.50b
MSC	4.19d	1.01c	4.24e	0.49b

‡ Within a soil type and column, means followed by the same letter are not significantly different ($P < 0.05$).

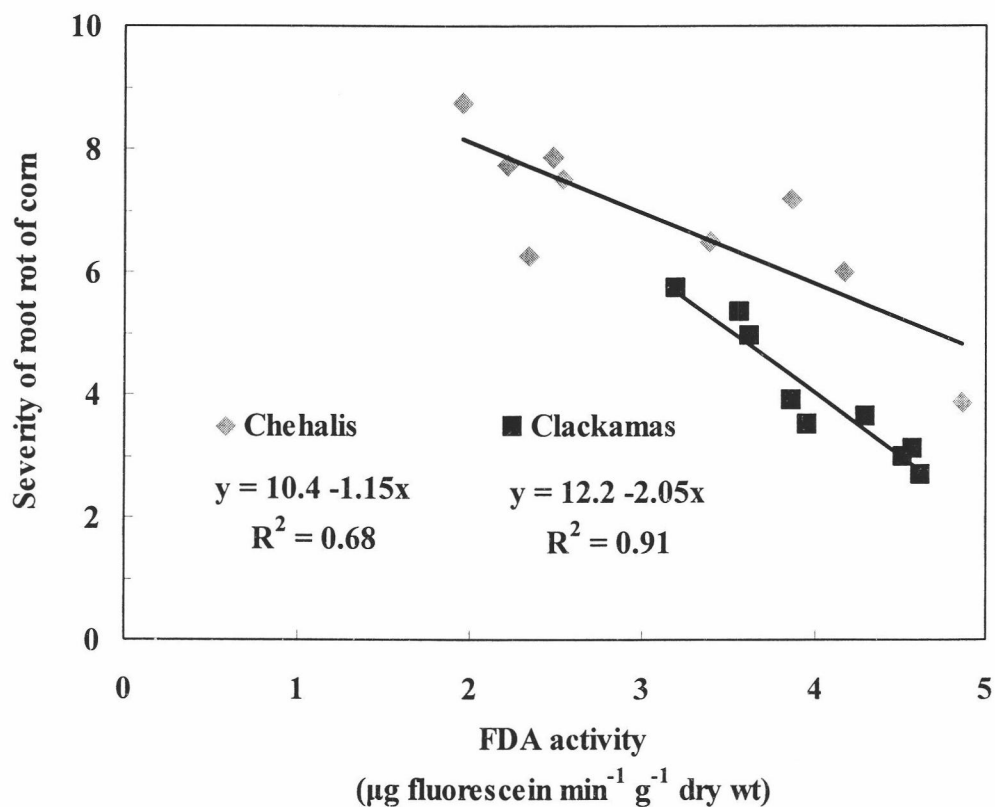


Fig. 3.3. Relationship between FDA activity and severity of root rot of sweet corn in two soil types. Each data point represents the mean across 4 blocks and 4 replicates (n=16).

root rot of sweet corn. There was no relationship between β -glucosidase activity and disease severity for the Chehalis ($P = 0.35$) or Clackamas soils ($P = 0.18$).

Experiment 2: Impact of fresh and composted manure on individual pathogens

An amendment type x individual pathogen interaction was observed for root rot severity of sweet corn (Fig. 3.4). Organic amendment reduced root rot severity in all pathogen-infested soils; however, the level of suppression varied from pathogen to pathogen. Severity of root rot caused by *Drechslera* spp and *Phoma* spp. was most reduced by the MSC amendment. However, the greatest reduction in severity of root rot caused by *P. arrhenomanes* occurred when soil was amended with MS.

The impact of pathogen infested soil on the severity of root rot and biomass of sweet corn is reported in Table 3.6. Corn grown in pathogen-infested soil had more root rot than the uninfested control. The amount of root biomass produced by corn grown in soils infested with *Drechslera* spp. and *Phoma* spp. did not differ from the uninfested control. However, corn grown in *P. arrhenomanes* infested soil had 32 % less root biomass than the noninfested control. Only corn grown in *Phoma* spp. infested soil had significantly less shoot biomass than the uninfested control.

Organic amendments reduced severity of root rot by 49 % in pathogen-infested soil (Fig. 3.6). Compared to the non-amended control, root biomass of corn was 25 % larger in amended soils (Table 3.6). Shoot biomass did not differ significantly among amendment types (Table 3.6). Across all pathogens, a negative relationship between severity of root rot of sweet corn and FDA activity was observed (Fig. 3.5).

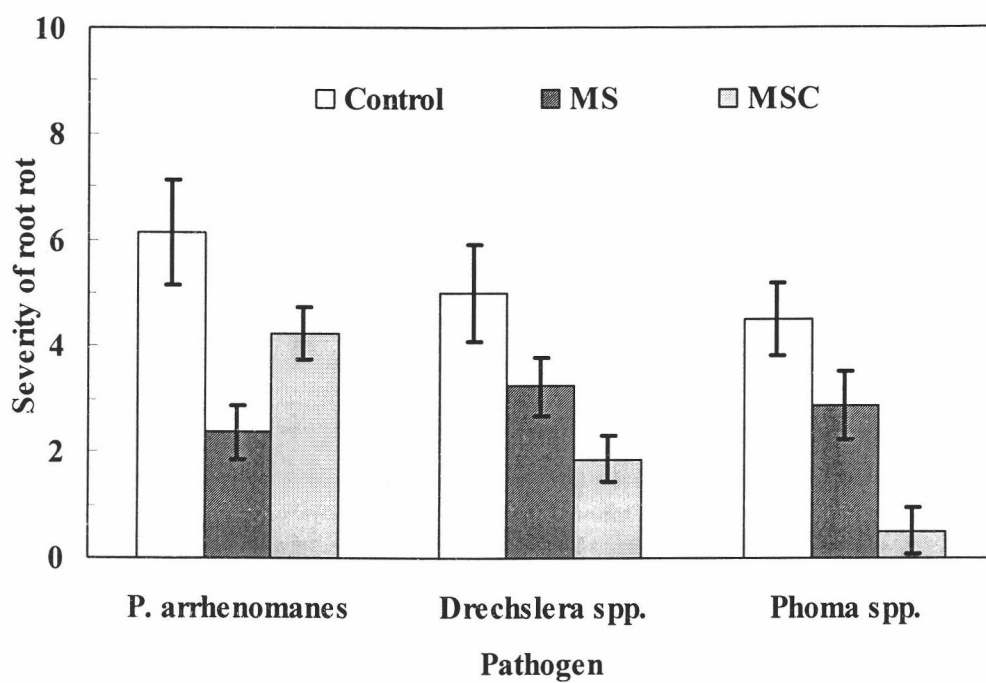


Fig. 3.4. Impact of fresh (MS) or composted (MSC) dairy manure amendment on severity of root rot of sweet corn grown in soil inoculated with either *Pythium arrhenomanes*, *Phoma* spp., or *Drechslera* spp. Vertical bars represent \pm one standard deviation.

Table 3.6. Impact of pathogens (averaged across amendments) and amendments (averaged across pathogens) on the severity of root rot and root and shoot biomass of sweet corn.

Treatments	Root rot severity	Dry matter	
		Shoot	Root
----- g -----			
Pathogen			
None	0.37a†	6.53a	2.21a
<i>P. arrhenomanes</i>	4.25c	5.26bc	1.50b
<i>Drechslera</i> spp.	3.37bc	5.86ab	1.76ab
<i>Phoma</i> spp.	2.62b	5.04c	1.82ab
Amendment§			
C	3.94y	5.43z	1.50y
MS	2.31z	5.57z	1.89z
MSC	1.72z	6.01z	2.04z
Analysis of variance			
-----Probability level -----			
Pathogen	***†	**	**
Amendment	***	NS§	**
Pathogen x amendment	***	NS	NS

† Within a column, means followed by the same letter are not significantly different ($P < 0.05$).

‡ *, **, *** coefficients significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

§ NS, no significant ($P < 0.05$) coefficients.

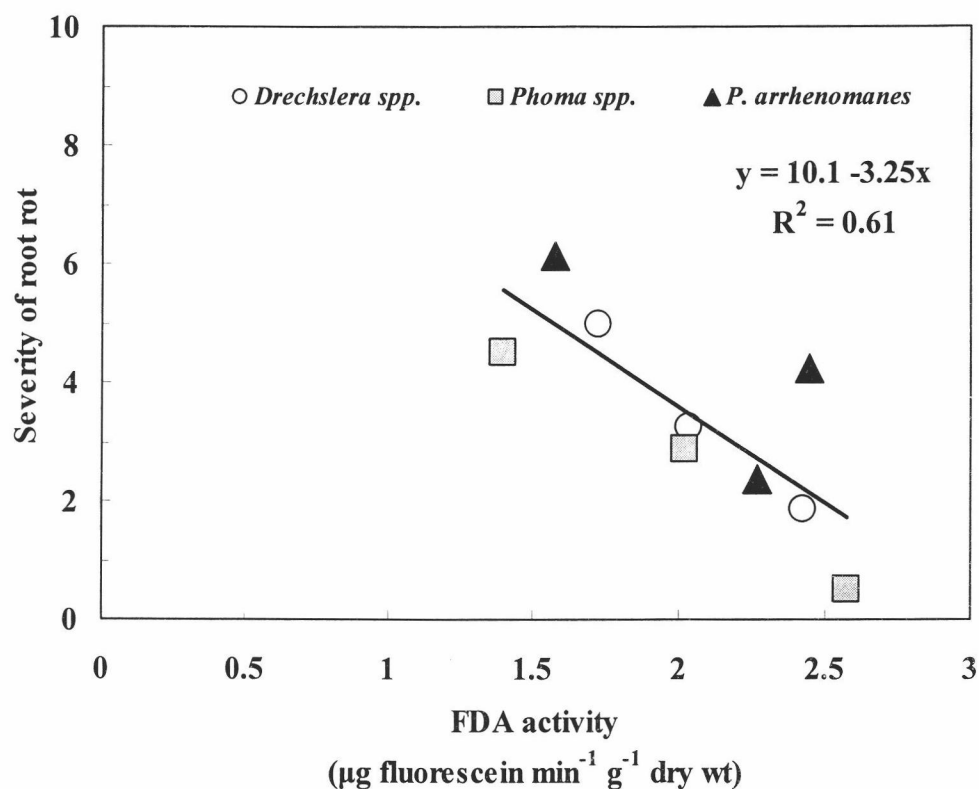


Fig. 3.5. Relationship between FDA activity and severity of root rot of sweet corn. Relationships are across 3 pathogens. Each data point represents the mean across 8 replicates.

DISCUSSION

Effects of repeated organic amendment

Repeated amendments had a significant effect on the Chehalis soil. Although there was a reduction in disease severity from the first two cycles to the last cycle, these differences were not likely due to increased number of cover crop cycles. Instead, the observed differences were probably due to the varied times of the year that the bioassays were conducted, often resulting in different environmental conditions in the greenhouse. For instance, natural sunlight and heat were present during the summer months, whereas artificial lights and supplemental heat supported plant growth during the short day, low light intensity winter rainy season.

The lack of impact of repeated amendment on the severity of disease may be due to activities generated by the amendment being of short duration. In a field of low root rot potential, disease suppression was generated at 2 months after amendment but was lost somewhere between 2 and 6 months (see Chapter 2). Preliminary evidence suggests that suppression is lost somewhere between 2 and 3 months after amendment (Darby and Stone, *unpublished*). Therefore, it is possible that continuous amendment every 2 months was needed to sustain the suppressive effect. The fact that severity of root rot did not continuously decline after each amendment also suggests that destruction of the pathogen was not a mechanism of suppression.

Effects of amendment type

Amendment of soil with manure has been a successful management strategy for the control of root rots (King, 1934; Malajczuk et al., 1983; Lumdsen et al., 1987; Volland and Epstein, 1994; Aryantha et al., 2000). In a field of low root rot potential, high (56.0 Mg ha⁻¹) or low (28 Mg ha⁻¹) rates composted manure and high (33.6 Mg ha⁻¹) rates of composted fresh manure suppressed root rot after one year of amendment and the low (16.8 Mg ha⁻¹) rate of fresh manure suppressed after 2 years (see Chapter 2). This work demonstrates that fresh and composted manure amendments can suppress root rot of sweet corn in soils of high root rot potential.

Differences in levels of suppression between MS and MSC may partially be attributed to lower rates of MS (10 % vol/vol) amendment compared to that of MSC (15 % vol/vol). In addition, the Chehalis soil MS treatments had lower FDA activities than MSC treatments; these differences may also be attributed to lower rates of MS amendment.

In a field with low root rot potential, root rot was suppressed if FDA activity was higher than 2.88 µg fluorescein min⁻¹ g⁻¹ dry wt of soil. Levels of FDA activity were higher than 2.88 µg fluorescein min⁻¹ g⁻¹ dry wt of soil when Chehalis soil was amended with MS, but severity of root rot was not reduced compared to the non-amended control. A higher level of FDA activity may be required before suppression is observed in soils of high root rot potential. This probably is the case, since suppression of root rot was observed in soils with FDA activity greater than 4.00 µg fluorescein min⁻¹ g⁻¹ dry wt. Levels of FDA activity were above 4.00 µg fluorescein

$\text{min}^{-1} \text{g}^{-1}$ dry wt when the Clackamas soil was amended with MS or MSC, and disease suppression was observed. Since FDA activity was related to disease suppression we would suggest that had MS been applied at a rate equivalent to that for MSC, the FDA activity of MS would have been similar to MSC, and root rot would have been suppressed in the Chehalis soil. Fresh and composted manure added at similar rates generated FDA activities in a soil of low root rot potential (see Chapter 2). The type of amendment appears to be less important than the amount of FDA activity generated after amendment.

This experiment suggests that amendments can suppress root rot of corn in severely infested soils, but the degree of suppression will be dependent on initial soil quality. The Chehalis soil had been in annual crop production at least the last five years with corn being grown two out of the five years. Although the Clackamas soil was also planted to corn two out of five years, there were 3 years of perennial ryegrass between them. The inclusion of perennial grass crops into a crop rotation has been recognized as a means of enhancing soil structure and soil organic matter, especially the particulate organic matter fraction (Clement and Williams, 1964; Garwood et al., 1972; Tisdall and Oades, 1982; Conti et al., 1992). When a perennial grass crop is cultivated, rapid soil organic matter decomposition by soil microorganisms occurs. An increase in microbial biomass and activity occurs because the soil has been disturbed, aggregates are broken up, and protected organic matter is made available for decomposition (Doran and Smith, 1987; Cambardella and Elliot, 1992).

A study conducted by Johnston (1986) reported that a five-year rotation that included 3 years of perennial hay crop had 25 % greater soil C than a 5-year rotation of only annual crops. A perennial grass system receiving high inputs of readily available labile C will have higher microbial biomass and activity than an annual cropping system that receives a lower input of labile C (Sparling, 1995). In general, a relatively small proportion of the soil microbial biomass is active; most of the biomass is inactive because of energy limitation (Sparling, 1995). Lockwood (1990) states that commonly there is only enough substrate in a soil to barely meet microbial biomass energy requirements for maintenance, with little to no excess available for growth. It is thought that if available organic substrate is amended to soils, then excess energy would be available for growth and the quiescent pool will begin to become active (Sparling, 1995; van Bruggen and Semenov, 2000).

We propose that the Clackamas soil (having more abundant substrate than Chehalis soil) had already enhanced its microbial biomass (active and quiescent pools) and activity. It is possible that the Clackamas soil was initially somewhat suppressive to root rot, since it had FDA activity levels higher than the threshold of $2.88 \mu\text{g}$ hydrolyzed FDA $\text{min}^{-1} \text{g}^{-1}$ dry wt proposed for a soil of low root rot potential (see Chapter 2). However, in the Chehalis soil we recognized that higher levels of FDA activity were needed to generate suppression in soil of high root rot potential. Therefore the additional energy gained from adding even more readily available substrate (MS and MSC) did not have to be used to build and maintain biomass but instead could be used to further increase its growth and activity. Under these conditions,

microbial activity increased above the putative threshold of $4.00 \mu\text{g fluorescein min}^{-1} \text{g}^{-1}$ dry wt of soil and hence disease was suppressed even at the low rate of fresh manure (MS). This is in contrast to the annually cropped soil (Chehalis soil), where soil amendment was probably first used to build biomass (active and quiescent pools) and then any additional energy was used to increase the activity of that biomass. Thus, only MSC significantly suppressed root rot of sweet corn in the Chehalis soil.

Corn root biomass was significantly impacted by amendment to the Chehalis soil but not the Clackamas soil. As mentioned previously, soil that has had several years of perennial-grass would have better soil structure than soil in an annual cropping system (Haynes et al., 1991). Although conversion of this grassland to cultivated land will result in reductions in soil structure within a few years, corn grown during this time period will still benefit from the improved structure (Angers et al., 1992). Improved soil structure will increase aeration, water infiltration, drainage, bulk density, and plant growth and biomass (Zimmerman and Kardos, 1961; Rosenberg, 1964; Allison, 1973). The Clackamas soil had a greater percent of fPOM, water stable aggregates than the Chehalis soil, at the beginning of the experiment (data not shown). Addition of MS and MSC had less of an impact on enhancing soil structure in the Clackamas soil than the Chehalis soil. Hence, roots were able to flourish in both the control and amended treatments of the Clackamas soil, resulting in no difference in root biomass among the three treatments.

Amendment of compost or manure to annually cropped soils will enhance soil structure (Williams and Cook, 1961; N'Dayegamyie and Angers, 1990). Larger corn

root systems were observed in cropping systems that included animal manure or green manure amendments compared to those with only chemical fertilizer amendments (Pallant et al., 1997). For every 1 % increase in organic matter, root length and density was increased by 9 to 13 % (Pallant et al., 1997). Therefore the addition of amendment to the Chehalis soil probably improved the soil structure compared to the control and may have developed an improved environment for root growth and hence larger biomass. The increase in the size of root biomass in the Chehalis soil could also play a role in the plants ability to escape disease (King et al., 1934; Garrett, 1970).

A recent field survey conducted in the Willamette Valley concluded that for every single unit increment increase in the root rot rating of sweet corn cv. Golden Jubilee, there was a $1.7 - 2.25 \text{ Mg ha}^{-1}$ decline in yield (A. Stone, personal communication, 2003). In this experiment, yield could potentially be increased between 2.60 and 3.40 Mg ha^{-1} if soils were annually amended with MSC (15 % v/v). In soils rotated out of perennial grass sod, MS or MSC amendment could increase yields between $3.80 - 5.00 \text{ Mg ha}^{-1}$. These yields increases are predicted from reductions in root rot severity, not from increased root biomass. This data suggests that in soils of high root rot potential fresh or composted manure amendment should suppress disease and increase yields. However, other manipulations of the cropping system (rotation with perennial grass) might lead to even greater yield increases.

Levels of FDA activity increased when amendments were added to soil and FDA activity was positively related to disease suppression. This relationship has been

observed in other systems (Chen et al., 1988; Drinkwater et al., 1995; Craft and Nelson, 1996; Dissanayake and Hoy, 1999).

Fresh and composted manure amendments did not impact levels of β -glucosidase activity. β -glucosidase is an enzyme that catalyzes the hydrolysis of cellobiose to glucose (Deng and Tabatabai, 1994). Since manure and composts are partially decomposed, cellulose and cellobiose degradation might have occurred previously to amendment. In addition, β -glucosidase activity was not measured until 2 mo after amendments; by this time, it is possible that cellobiose was already utilized. If the β -glucosidase analysis had been conducted immediately after amendment differences may have been observed among treatments. Similarly, eight mo after amendment of the soil with cow manure, Marcote et al. (2001) did not observe significant differences in β -glucosidase between cow manure amended soil and a non-amended control. In our work, β -glucosidase activity was not related to suppression of root rot of sweet corn, suggesting that β -glucosidase activity is not an indirect measure of the quantity or quality of organic matter that generates or supports suppression. Under field conditions β -glucosidase activity was sensitive to cover crops after as little as a year of cover cropping (Bandick and Dick, 1999; Ndiaye et al., 2000) and to long term manure applications (Bandick and Dick, 1999).

Effects of amendment type and individual pathogens

All pathogens caused a reduction in root biomass of the corn compared to the uninfested control. The largest reduction was observed when corn was grown in *P. arrhenomanes* infested soil. This is not surprising since *P. arrhenomanes* has been noted to cause root pruning (Deep and Lipps, 1996; Hoinacki and Powelson, 2002).

This work demonstrates that fresh and composted manure amendments suppress all of the individual pathogens that cause root rot of sweet corn. Amendment of soil with MS or MSC increased root biomass of corn compared to the non-amended control. Since severity of root rot was reduced in MS and MSC amended soils, root necrosis and death would decrease, thereby increasing root biomass. In addition, corn root biomass may have been larger in amended soils because of improved soil physical structure. As mentioned previously, increased soil structure is commonly observed after soils are amended with organic wastes (Williams and Cook, 1961; N'Dayegamyie and Angers, 1990). In support of this theory, corn that was grown in amended but non-infested soil had larger root systems compared to a non-amended and non-infested control (data not shown); therefore, not all of the increase in root biomass can be attributed to a reduction in severity of root rot. It is most likely that both of these mechanisms contributed to increased root biomass of corn grown in amended soils. This is in agreement with Abawi and Widmer (2000) who suggested that cultural practices that improve soil physical and biological characteristics would improve soil health and reduce disease incidence.

Specific pathogen interactions

Organic amendment reduced root rot severity in all pathogen-infested soils; however, the level of suppression varied from pathogen to pathogen. In general, the MSC was more suppressive to root rots caused by *Drechslera* spp. and *Phoma* spp. than the MS, but the MS was most suppressive to root rot caused by *P. arrhenomanes*.

Overall, FDA activity was negatively related to disease severity. However, MS (with FDA activity) was more suppressive to *P. arrhenomanes* than MSC (with higher FDA activity). Therefore, mechanisms other than those related to increased microbial activity (indicated by increased FDA activity) must be involved in suppression of *P. arrhenomanes* by MS. Similarly, Craft and Nelson (1996) reported a negative relationship between FDA activity and severity of root rot caused by *Pythium graminicola* for soils amended with composted brewery sludge, biosolids, leaf-chicken manure, horse manure, and leaves. However, they reported that composted turkey litter was suppressive, but this suppression was not related to high FDA activity; they suggested suppression was caused by a different mechanism.

Nitrogenous inorganic or organic soil amendments can reduce populations of soilborne pathogens (Broadbent and Baker, 1974; Chun and Lockwood, 1985; Aryantha et al., 2000; Tenuata and Lazarovits, 2002). Tenuata and Lazarovits (2002) showed that ammonia and nitrous oxide, but not ammonium, were toxic to microsclerotia of *Verticillium dahliae*. An increased concentration of ammonia in field soil, which was derived from urea, suppressed root rot caused by *Pythium ultimum*. (Chun and Lockwood, 1985). The fresh manure amendment had 71 % more

ammonium than the MSC treatment. Some animal manures produce ammonia as they decompose; therefore the generation of ammonia from MS amended soil may have also been directly toxic to propagules of *P. arrhenomanes*.

Fresh or composted manure amendments to soil suppressed root rot of sweet corn in field soils of high root rot potential. In addition, both amendment types suppressed root rot caused by the individual pathogens. Overall, suppression was most related to FDA activity. However, other mechanisms, such as improvements in soil structure and increases in soil nitrogenous compounds may also have played a role in suppression.

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CHAPTER 4

MANAGEMENT OF ROOT ROT OF SWEET CORN WITH COVER CROPS

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Prepared for Soil Science Society of America

ABSTRACT

Root rot (caused by a complex of pathogens) is one factor responsible for low yields of sweet corn in Oregon. Cover cropping can reduce the severity of soilborne diseases. The objective was to determine the impact of cover cropping on the severity of root rot caused by the pathogen complex as well as on disease caused by the individual pathogens. Two soil types (Chehalis; Clackamas) with high root rot potential were used to study repeated cover cropping on the severity of root rot caused by the complex. There were few repeated cover cropping or repeated cover cropping x cover crop species effects. Cover cropping with sudan grass and oat treatments reduced the severity of root rot 22 and 18%, respectively compared to the fallow control. Cover cropping with annual ryegrass and cereal rye did not reduce root rot compared to the control. Root rot suppression was not related to FDA activity. When pasteurized soil infested with individual pathogens was cover cropped with sudangrass, annual ryegrass, or oats, root rot severity was reduced 20, 27, and 42%, respectively. Host range specificity of *P. arrhenomanes*, *Drechslera* spp. and *Phoma* spp. was determined. *P. arrhenomanes* and *Drechslera* spp. were mildly pathogenic on annual ryegrass, perennial ryegrass and cereal rye. *Phoma* spp. was pathogenic only to perennial ryegrass. Overall, oat and sudan grass were the most promising cover crop species for the management of root rot of sweet corn.

INTRODUCTION

Root rot is one of the major factors responsible for low yields of sweet corn (*Zea mays* L.) cv. Golden Jubilee in the Willamette Valley of Oregon. A complex of soilborne organisms, including *Pythium arrhenomanes*, *Drechslera* spp., and *Phoma* spp., are the principal causal agents of root rot of sweet corn (Hoinacki and Powelson, *in press*). Corn yields can be improved by growing tolerant cultivars (J. Meyers, personal communication, 2003). The introduction of tolerant sweet corn cultivars is improving the viability of sweet corn production but relatively few tolerant cultivars are available that have acceptable processing quality. Development of disease tolerant cultivars will take time. Consequently, other management options need to be explored. Furthermore, even tolerant varieties can become susceptible so cultural management strategies must also be developed. In the future and over the long term effective integrated management systems will provide greater stability for disease suppression.

In general, root rots are more severe in soils of low organic matter content, poor physical structure, and high compaction (Burke et al., 1972; Tu, 1992; Abawi and Widmer, 2000). The introduction of cover cropping into a cropping system can improve soil conditions (Pieters, 1927; Allison, 1970; Bandick and Dick, 1999; Ndiaye et al., 2000). Growth and subsequent incorporation of a cover crop improves soil structure, soil organic matter content, microbial biomass, microbial activity, and water infiltration (Pieters, 1927; Bandick and Dick, 1999; Entry et al., 1996; Chander

et al., 1997). In addition, roots of some cover crop species penetrate deeper into the soil than many agronomic crops, breaking up compacted layers and hardpans and improving the rooting depth and plant vigor of the cash crops (Pieters, 1927; Allison, 1970).

Phymatotrichum root rot of cotton (King et al., 1934; Lyle et al., 1948), Aphanomyces root rot of pea (Tu and Findlay, 1986; Muehlchen et al., 1990; Williams-Woodward et al., 1997), root rot of bean (Manning and Crossman, 1969; Abawi and Widmer, 2000), Fusarium wilt of palm (Abadie et al., 1998), and Verticillium wilt of potato (Davis et al., 1996) have been suppressed when cover crops were incorporated as a green manure. Generally, in soils with high levels of pathogen inoculum, several years of cover cropping are required before disease is suppressed (Lyle et al., 1948; Davis et al., 1996). However, Tu and Findley (1986) reported that even one interseason green manure crop of oat or sorghum reduced severity of root rot of pea in the subsequent year in a field with high root rot potential. There is currently no information on which cover crop species or how many years of cover cropping might be required to suppress root rot of sweet corn.

Disease suppression observed after cover cropping has been correlated to increased total soil microbial activity (measured as the rate of hydrolysis of fluorescein diacetate; FDA activity) (Davis et al., 1996). Elevated FDA hydrolysis would indicate there is a more active microbial community that causes suppression of the pathogen directly or limiting its ability to infect roots. This type of suppression is

most likely generated through the actions and interactions of an enhanced (biomass and activity) population of soil microorganisms (Cook and Baker, 1983).

In addition, cover crops can be suppressive to a particular disease by other more specific mechanisms. For example, cover crops can increase populations of particular soil organisms capable of specific biocontrol activities (Abadie et al., 1998; Sturz and Christie, 1998; Davis et al., 1994). Some crops, such as sudan grass and oats release compounds (e.g. saponins and hydrogen cyanide) during decomposition that can be toxic to plant pathogenic organisms (Maizel et al., 1963; Tarr, 1967; Deacon and Mitchell, 1985; Widmer and Abawi, 2000).

Cover crops can also act as hosts for soilborne pathogens, resulting in increased pathogen populations and disease severity in subsequent agronomic host crops. Cereal rye and 'Garry' oats grown in rotation with strawberry are hosts of *Rhizoctonia fragariae* and *Pratylenchus penetrans*, the causal agents of black root rot of strawberry (LaMondia, 1994). The cover crops Phacelia, lana wollypod vetch, and Austrian winter pea were identified as hosts for *Sclerotinia minor*, the causal agent of lettuce drop disease (Koike et al., 1996).

Presently, farmers in the Willamette Valley grow a variety of annual winter cover crops to cycle nutrients, protect soil from water and wind erosion, suppress weeds, and improve soil quality. Cover cropping may have potential for managing root rot of sweet corn. Cover crops should fit into the cropping system, be non-hosts, and be effective at reducing severity of root rot of sweet corn. The objectives of this study were to determine the 1) effectiveness of cover crop species in suppression of root rot of sweet corn; 2) effect of repeated cover cropping on suppression of root rot;

3) impact of cover cropping and subsequent incorporation on the severity of root rot caused by each causal agent of root rot of corn, and 4) potential of each cover crop species as an alternate host for all three causal agents.

MATERIALS AND METHODS

Experiment 1. Impact of cover cropping on root rot complex

Soils were collected from two fields known to have high root rot potential. In April 2001 (Chehalis soil), a Chehalis silt loam soil (fine-silty, mixed, mesic Cumulic Ultic Haploxerolls) (Chehalis soil) was collected from a field located near Dayton, OR. The cropping history for the last five years was sweet corn in 1999, broccoli (*Brassica oleracea*) in 1998; sweet corn in 1997; beets (*Beta vulgaris*) in 1996 and wheat (*Triticum aestivum*) in 1995. In March 2002 (Clackamas soil), a Clackamas gravelly loam soil (fine-loamy, mixed, noncalcareous, mesic Typic Argiquolls) (Clackamas soil) was collected from a field near Marion, OR. The cropping history for this field was corn in 2001, perennial ryegrass (*Lolium perenne* L.) 2000, 1999 and 1998 and sweet corn in 1997. At the time of collection, soil was passed through a 2.54 cm mesh screen (to remove large pieces of undecayed plant material) before it was placed into 11 L (20 x 40 cm) plastic pots (Stuewe & Sons Inc., Corvallis, OR).

Pots were arranged in a randomized complete block design with 15 factorial treatments in shade houses at the Oregon State University Research Farm, Corvallis, OR. In shade houses at the Oregon State University Research Farm (Corvallis, OR) pots were arranged in a randomized complete block design with 15 factorial

treatments replicated 4 times. The 15 treatments comprised a 5 x 3 factorial: 5 cover crop species x 3 repeated periods of cover cropping.

The cover crops utilized in this experiment were annual ryegrass (*Lolium multiflorum* cv. Gulf), cereal rye (*Secale cereale* cv. Merced), oats (*Avena sativa* cv. Monida), and sudan grass (*Sorghum sudanense* cv. Piper). Sudan grass was obtained from Peaceful Valley Farm Supply (Grass Valley, CA) and all other seeds were provided by Daryl Ehrensing (Oregon State University Crop and Soil Science Dept, Corvallis, OR). In May 2001 (Chehalis soil) and 2002 (Clackamas soil), soils were planted with 50, 25, 17, or 27 seeds of annual ryegrass, cereal rye, oats, or sudan grass, respectively. Soils in unplanted pots served as the fallow control.

The repeated application treatments were imposed by planting pots with cover crops at time zero, and at 9 and 18 weeks after the first planting. The pots were destructively harvested at 5, 14, and 23 weeks and evaluated for the effect of the treatments on severity of root rot and FDA and β -glucosidase activities.. Since raw organic residues can increase disease severity (Grunwald et al., 2000), treatments were allowed to incubate for 2 months. The experimental procedure is outlined in Fig. 3.1. There were four replicates of the corn root rot bioassay per pot, resulting in 16 replicates at each sampling period.

Cover crops were grown for 5 wk in all experiments. At harvest, shoots were cut at the soil surface with pruning shears. Soil was then placed into a 40 L plastic tub (Rubbermaid Home Products, Wooster, OH), and the roots were hand-harvested. Roots of cover crops were visually assessed for disease symptoms. Disease severity

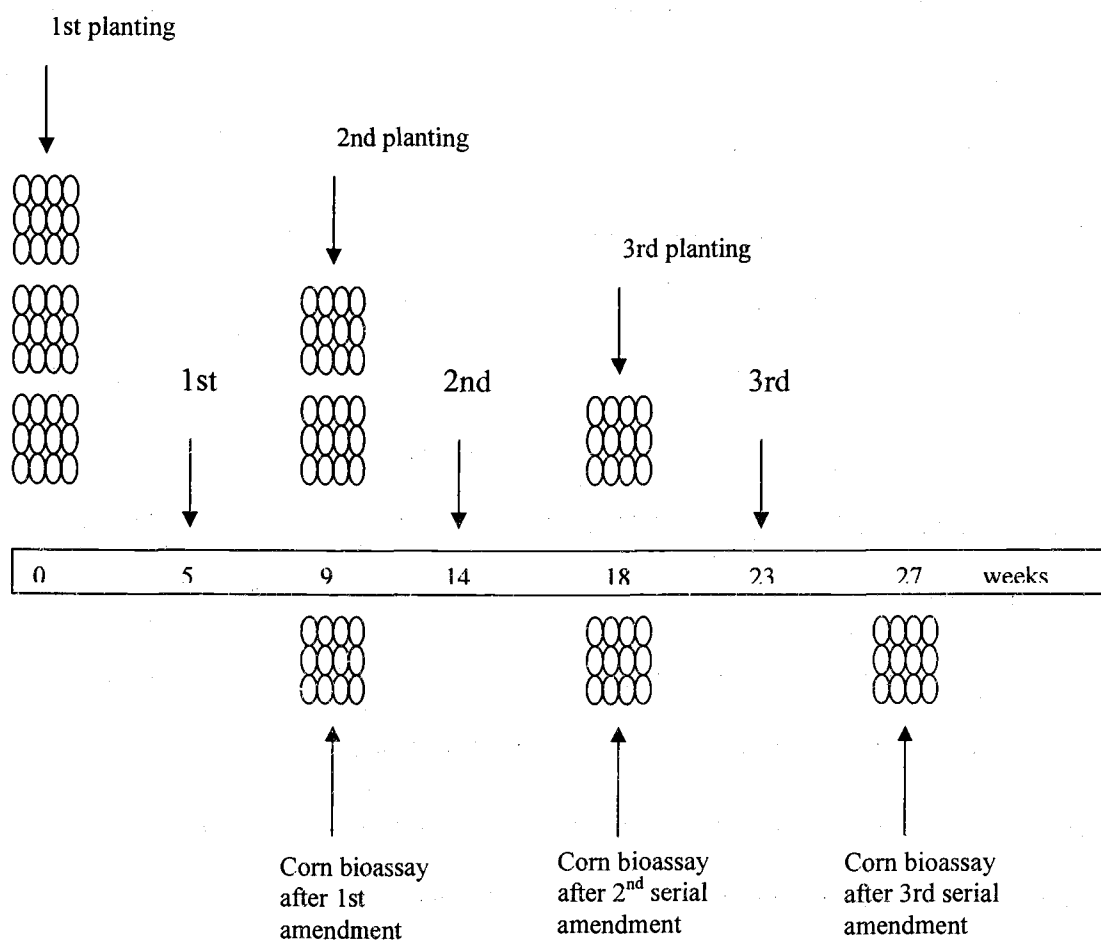


Fig. 4.1. Experimental design: effects of repeated cover cropping and cover crop incorporation on the severity of root rot of corn.

was determined based on a 0 to 4 scale, where 0 = healthy, 1 = 1- 10 %, 2 = 11 – 25 %, 3 = 26 – 50 %, 4 = > 51 % of root system was necrotic. Roots with symptomatic lesions were surface disinfested (10 % sodium hypochlorite for 30 s) and 1.0 to 1.5 cm root sections were plated on water agar amended with streptomycin sulfate (0.1 g L⁻¹) for recovery of causal pathogens. The shoots and roots were weighed and cut into approximately 2.54 cm pieces, mixed into the soil, and placed back into the container. From each treatment a subsample of shoots and roots (approximately 10 % of the total shoots and roots per treatment) was selected, weighed, oven dried (60° C), and reweighed to determine the moisture of the incorporated plant parts.

A mixed model analysis was performed separately for each soil to test the effects of cover crop species and repeated cover cropping using the PROC MIXED procedure of SAS (SAS Institute, 1999). Protected LSD were calculated when the F-test was significant ($P < 0.05$). Pearson correlations were performed to examine the relationship between cover crop biomass, corn root and shoot biomass, and soil enzyme assays (FDA and β -glucosidase) and severity of root rot of sweet corn.

Experiment 2: Impact of cover crop species on individual pathogens

Soil (Newberg fine sandy loam: coarse-loamy, mixed, mesic Fluventic Haploxerolls) was collected from Botany and Plant Pathology Research Farm, Oregon State University. The soil was passed through a 2.54 cm mesh screen to remove large pieces of undecomposed plant debris. Soil was steam pasteurized at 99° C for 1 h on each of two consecutive days. Soil (32 L per soil treatment) was infested with a sand-

cornmeal culture of either *Pythium arrhenomanes*, *Phoma* spp. or *Drechslera* spp. For each treatment, eight plastic containers (4 L) (OBC Northwest, Inc., Canby, OR) were filled with pathogen-infested soil.

Pathogen-infested soil was seeded with 25, 12, 8, or 13 seeds of annual ryegrass, cereal rye, oat, or sudan grass, respectively, and arranged in a completely randomized design on a greenhouse bench. The 20 factorial treatments were four pathogens (*P. arrhenomanes*, *Phoma* spp., *Drechslera* spp., or uninfested control) x five cover crop species (annual ryegrass, cereal rye, oat, sudan grass, or no cover crop). The cover crops were grown for 5 wk, incorporated (as described previously), and incubated for 1 month before assaying for severity of root rot of sweet corn.

Mixed models analysis was performed (SAS, Inst., 1999) with pathogen and cover crop species as the main effects. Mean separation among treatments was obtained using a LSD test when significant F-tests ($P < 0.05$) were observed. Pearson correlation coefficients (r) between disease severity and amount of cover crop biomass amended into the soils, corn root and shoot biomass, and severity of root rot of sweet corn were performed on each soil.

Experiment 3. Host specificity range

A pathogenicity test was conducted on perennial ryegrass (*Lolium perenne* L. cv. Cutter), annual ryegrass (cv. Gulf), and cereal rye (cv. Merced) to examine the inoculum dose/disease response relationship of *P. arrhenomanes*, *Drechslera* spp., and *Phoma* spp.. A cornmeal/sand inoculum mixture of each pathogen at 4 rates (1x, 2x,

10x, or 100x) was mixed with steam-pasteurized soil (as described for experiment 2) for 20 min in a twin shell dry blender (Patterson-Kelley Co., Inc., East Stroudsburg, PA) and then placed into 550 mL cone tubes. Pasteurized soil served as a control. Tubes were seeded (1.25 cm deep) with three seeds of perennial ryegrass, annual ryegrass or cereal rye. After germination, seedlings were thinned to one per cone tube. Treatments were arranged on a greenhouse bench in a complete randomized design and replicated 8 times. Crops were grown for 5 wk at which time roots were visually assessed for severity of root rot (as described previously). Roots with symptomatic lesions were surface disinfested (10 % sodium hypochlorite for 30 s) and 1.0 to 1.5 cm root sections were plated on water agar amended with streptomycin sulfate (0.1 g L^{-1}) for recovery of causal pathogens. The plants were weighed, oven dried (60° C), and reweighed to determine the dry matter biomass of the crops.

Regression analysis was used to examine the relationship between inoculum dose and disease severity for each pathogen and crop. Regression coefficients were described when significant ($P < 0.05$).

Corn bioassay

The impact of cover cropping on severity of root rot of sweet corn was assessed with a greenhouse bioassay (Hoinacki and Powelson, 2002). Treatment soils were placed in 550 ml plastic cone tubes (Stuewe & Sons Inc., Corvallis, OR) and planted with sweet corn seed (cv. Golden Jubilee) that had been surface-disinfested in 10 % sodium hypochlorite for 5 min and rinsed in distilled water. Plants were grown

at 21° C (day) and 15° C (night) in a greenhouse with a 14 h photoperiod. Plants were watered daily to keep soil moisture levels near field capacity, and they were fertilized every other week with a water-soluble fertilizer mixture (N-P-K/20-20-20). Plants were harvested at the sixth leaf stage (Ritchie et al., 1996). Rootballs were washed and evaluated for severity of root rot (Table 4.1), and shoots and roots were oven dried at 60° C and weighed. Total disease severity was calculated as the sum of disease ratings from the mesocotyl, radicle, and nodal roots (Table 4.1).

Soil analyses

Fluorescein diacetate activity was measured by determining the rate of hydrolysis of FDA (modified from Dick et al., 1996). Fifty mL of 60 mM sodium phosphate buffer (pH 7.8) containing 10 mg fluorescein diacetate (3', 6' diacetyl fluorescein) substrate was added to a 125 mL Erlenmeyer flask containing 3 g of field moist soil. Flasks were stoppered and incubated for 3 h on a rotary shaker (178 rev min⁻¹) at 25° C. The reaction was terminated by the addition of 2 mL of acetone to each flask. A 30-mL aliquot was centrifuged (15,750 rpm; 5 min), filtered (Whatman #42), and the quantity of FDA hydrolyzed was determined at 490 nm with a spectrophotometer (Beckman Model 34, Beckman Industries Inc., Irvine, CA). The results are the average of three sample replicates, with a control (incubated without substrate) subtracted. β -glucosidase enzyme activity was measured as described by Dick et al. (1996). In brief, 1 g of field moist soil was incubated for one hour with p-

Table 4.1. Root rot severity index for root rot of sweet corn. †‡

Rating	Components of root system		
	Mesocotyl	Radicle	Nodal root system
0	Healthy	Healthy	Healthy
1	Lesion present	Lesion present	5 – 10 % necrotic
2	100 % necrotic	10 - 50% necrotic	11 – 25 % necrotic
3		50 – 99% necrotic	26 - 50% necrotic
4		100% necrotic	> 51 % necrotic

† Total disease rating based on the sum of the 3 components of the root system, where the sum ranges from 0 to 10 (0=symptomless and 10 => 51 % of the root ball is necrotic).

‡ Hoinacki and Powelson, 2002

nitrophenyl β -D-glucose, and toluene, in a modified universal buffer (pH 6). After incubation, *tris*-hydroxy aminomethane (pH 12) was added to terminate the reaction. The product was measured on a spectrophotometer at 420 nm. Each sample was analyzed in duplicate and averaged following the subtraction of a control sample.

RESULTS

Experiment 1. Impact of cover cropping on root rot complex

The repeated cover cropping x cover crop species interaction was not significant in either soil (Table 4.2). Since no repeated cover cropping x cover crop species interactions for any response variable was found, these data suggest that each cover crop species responded similarly across cycles.

Repeated cover cropping differences were observed for the Chehalis soil (Table 4.2). Significantly more cover crop shoot biomass was amended to the soil after the 2nd cover cropping period than in either period 1 or 3 (Table 4.3). There was 31 % more corn biomass and 40 % less severity of root rot after the 3rd cover cropping period than periods 1 or 2 (Table 4.3).

Cover crop species

Cover crops

Differences among cover crop species were observed for the Chehalis and Clackamas soils (Table 4.2). Aboveground plant residues from the cover crop treatments ranged from 33.5 – 46.7 g for the Chehalis soil and 24.0 – 28.9 g for the

Table 4.2. Statistical significance of treatment effects on cover crop, corn, and soil enzyme assay variables for Chehalis and Clackamas soil types.

Source of variation	Cover crop			Corn bioassay			Soil enzyme assay	
	Dry matter		Root rot	Dry matter		Root rot	FDA activity	β-glucosidase
	Root	Shoot		Root	Shoot			
					Chehalis			
Repeated cover cropping	NS†	*†	NS	***	***	***	NS	NS
Cover crop species	***	***	***	*	NS	***	**	***
Repeated cover cropping x species	NS	NS	NS	NS	NS	NS	NS	NS
					Clackamas			
Repeated cover cropping	NS	NS	NS	NS	NS	NS	NS	NS
Cover crop species	***	***	NS	NS	NS	*	NS	*
Repeated cover cropping x species	NS	NS	NS	NS	NS	NS	NS	NS

† *, **, *** coefficients significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

‡NS, no significant ($P < 0.05$) coefficients.

Table 4.3. Average shoot and root biomass of cover crops and corn and severity of root rot of sweet corn averaged across cover crop species for the Chehalis soil.

Cover crop period	Cover crop		Corn bioassay		
	Dry matter		Dry matter		Root rot
	Root	Shoot	Root	Shoot	
	-----g-----		-----g-----		
1	18.3a	39.9a	0.85a	3.65a	7.87b
2	21.8a	47.9b	0.60a	3.60a	8.22b
3	16.6a	33.1a	1.44b	4.85b	4.75a

Clackamas soil (Table 4.4). In general, annual ryegrass and sudan grass generated the most root biomass (Table 4.4).

Across both soils, annual ryegrass and cereal rye had the most severe root rot, whereas oats and sudan grass had the least severe root rot (Table 4.4). Annual ryegrass exhibited 83 % higher root rot severity than oat in the Chehalis soil and 97 % more in the Clackamas soil. In both soils all pathogens (*Pythium arrhenomanes*, *Drechslera* spp., and *Phoma* spp.) were isolated from the roots of annual ryegrass and cereal rye. On the other hand, isolation of these pathogens from the sudan grass and oat was infrequent. In both soils, *P. arrhenomanes* was isolated from the roots of sudan grass. *Phoma* spp. was isolated from one symptomatic root piece of sudan grass and oats. Similarly, *Drechslera* spp. was recovered only once (Clackamas soil, period 3) from one root piece of both sudan grass and oat. In general, sudan grass and oat roots exhibited very few symptoms of root rot.

Corn

Corn grown in Chehalis soil amended with oats or sudan grass had significantly less severity of root rot of corn than the fallow control. Corn grown in Chehalis soil amended with sudan grass had 25 % less root rot than the fallow control. Corn grown in Chehalis soil amended with annual ryegrass or cereal rye, had a root rot severity equivalent to that of the fallow control. Similarly, corn grown in Clackamas soil amended with oats and sudan grass had significantly less root rot than the fallow control (Table 4.5). Root rot was suppressed by as much as 23 % in oat treatment soils compared to the fallow treatment.

Table 4.4. Average shoot and root biomass of each cover crop species and severity of root rot of cover crops.

Cover crop	Root rot severity	Dry matter	
		Root	Shoot
-----g-----			
<u>Chehalis</u>			
Annual ryegrass	2.33c†	23.2c	40.5ab
Cereal rye	1.00b	7.66a	33.5a
Oat	0.39a	12.2b	40.2ab
Sudan grass	0.71ab	23.2c	46.7b
<u>Clackamas</u>			
Annual ryegrass	1.00d	33.0d	28.9c
Cereal rye	0.31e	12.8e	24.0c
Oat	0.03e	13.1e	27.2c
Sudan grass	0.06e	22.8f	28.5c

† Within a soil and column, means followed by the same letter are not significantly different at $P < 0.05$.

Table 4.5. Impact of cover crop species on severity of root rot of corn, corn root and shoot biomass, and enzyme assays of two soils averaged across repeated cover cropping periods.

Cover crop	Root rot	Dry matter		Enzyme assay	
		Root	Shoot	FDA activity	β -glucosidase
		-----g-----		$\mu\text{g fluorescein min}^{-1}$ $\text{g}^{-1} \text{ dry wt}$	$\mu\text{g p-nitrophenol min}^{-1} \text{g}^{-1} \text{ dry wt}$
		Chehalis			
Control	7.58b†	0.75a	3.57a	2.17a	0.51a
Annual ryegrass	7.70b	0.92b	4.13a	2.89ab	0.65b
Cereal rye	7.45b	0.92b	3.72a	2.40a	0.65b
Oat	6.70a	0.96b	3.76a	3.09b	0.62b
Sudan grass	5.66a	0.92b	3.34a	2.58ab	0.63b
		Clackamas			
Control	5.34c	0.69c	3.00c	3.46c	0.43c
Annual ryegrass	4.82cd	0.75c	3.28c	3.58c	0.53d
Cereal rye	4.84cd	0.76c	3.01c	3.10c	0.48cd
Oat	4.10c	0.81c	3.46c	3.76c	0.45cd
Sudan grass	4.33xc	0.71c	3.17c	3.36c	0.47cd

† Within a soil type and column, means followed by the same letter are not significantly different ($P < 0.05$).

Corn shoot biomass was not significantly impacted by the cover crops in either soil. Corn grown in cover cropped Chehalis soil had on average 20 % more root biomass than the fallow control (Table 4.5). However, cover cropping of the Clackamas soil did not impact corn root or shoot biomass compared to the fallow control.

Fluorescein diacetate activity was greatest when the Chehalis soil was cover cropped with oats (Table 4.5). Other cover crop treatments had no effects on levels of FDA activity compared to the fallow Chehalis soil. There were no significant differences in FDA activity among cover crop treatments for the Clackamas soil. Fluorescein diacetate activity was highest (although this difference was not statistically significant) in the Clackamas soil cover cropped with oat. β -glucosidase activity was significantly higher in cover crop amended Chehalis soil relative to the fallow control. In the Clackamas soil, only the annual ryegrass treatments increased β -glucosidase activity relative to the fallow control.

Severity of root rot was not related to the amount of cover crop biomass or to FDA or β -glucosidase activity in either soil (Table 4.6). Corn root and shoot biomass were negatively related to the severity of root rot of corn in Chehalis soil but not Clackamas soil.

Experiment 2. Impact of cover crop species on individual pathogens

There was no pathogen x cover crop interactions for experiment 2 suggesting that the cover crops responded similarly to the pathogens (Table 4.7 and 4.8). Therefore only main effects of pathogen and cover crop species are reported.

Table 4.6. Pearson correlation coefficients (r) and probability levels for severity of root rot of corn and cover crop biomass, corn root and shoot biomass, and soil enzyme assays.

Measurement	Severity of root rot	
	r	Probability level
<u>Chehalis</u>		
Cover crop		
Root dry matter	0.16	0.28
Shoot dry matter	0.25	0.18
Corn		
Root dry matter	-0.68	<0.0001
Shoot dry matter	-0.53	<0.0001
Soil enzyme assays		
FDA activity	-0.47	0.20
β -glucosidase activity	0.34	0.15
<u>Clackamas</u>		
Cover crop		
Root dry matter	-0.03	0.85
Shoot dry matter	0.06	0.67
Corn		
Root dry matter	-0.14	0.29
Shoot dry matter	-0.16	0.22
Soil enzyme assays		
FDA activity	-0.13	0.32
β -glucosidase activity	0.05	0.70

Cover crops

The impact of pathogen infested soil on the severity of root rot and biomass of cover crops is reported in Table 4.7. In general, cover crops grown in pathogen-infested soil had more root rot than the uninfested control. The amount of root biomass produced by cover crops grown in soils infested with *Drechslera* spp. and *Phoma* spp. did not differ from the uninfested control. However, cover crops grown in *Pythium arrhenomanes* infested soil had 40 % less root biomass than the control. Only cover crops grown in *Phoma* spp. infested soil had significantly less shoot biomass than the uninfested control.

The severity of root rot and amount of biomass produced by cover crop species is reported in Table 4.7. Root rot severity was 44 % higher on annual ryegrass and cereal rye than on oat and sudan grass. However, the severity of root rot of the tested cover crops was low overall with less than 1 to 10 % of the root balls showing symptoms. Treatment pathogens were recovered from symptomatic roots of the cover crops. Again, the oat and sudan grass had relatively few symptomatic lesions to isolate from. In general, sudan grass produced the most biomass and cereal rye produced the least biomass.

Corn

Severity of root rot of corn did not differ among pathogens (Table 4.8). Corn root biomass was the greatest when grown in uninfested soils and lowest in soils infested with *Pythium arrhenomanes*. In noninfested soil shoot biomass averaged 5.34

Table 4.7. Impact of pathogens (averaged across cover crop species) and cover crop species (averaged across pathogens) on the severity of root rot and root and shoot biomass of cover crops.

Treatments	Root rot severity	Dry matter	
		Root	Shoot
Pathogen		-----g-----	
None	0.02a†	9.21b	16.5b
<i>P. arrhenomanes</i>	1.31b	5.39a	15.4b
<i>Drechslera</i> spp.	1.00b	8.05b	14.9ab
<i>Phoma</i> spp.	1.19b	8.13b	11.0a
Cover crop			
Annual ryegrass	1.12c	9.17d	14.0c
Cereal rye	1.12c	2.95c	11.0c
Oat	0.63d	3.79c	11.9c
Sudan grass	0.63d	14.9e	20.8d
Analysis of variance		-----Probability level -----	
Pathogen	***‡	**	***
Cover crop	***	***	***
Pathogen x cover crop	NS§	NS	NS

† Within a column, means followed by the same letter are not significantly different ($P < 0.05$).

‡ *, **, *** coefficients significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

§ NS, no significant ($P < 0.05$) coefficients.

Table 4.8. Impact of pathogen (averaged across cover crops) and cover crop species (averaged across pathogens) on the severity of root rot and root and shoot biomass of sweet corn.

Treatments	Root rot severity	Dry matter	
		Root	Shoot
Pathogen		-----g-----	
None	0.53a†	2.27d	5.34c
<i>P. arrhenomanes</i>	4.88b	1.11a	4.52b
<i>Drechslera</i> spp.	5.25b	1.36b	3.77a
<i>Phoma</i> spp.	4.90b	1.57c	4.18ab
Cover crop			
None	0.13c	1.74f	6.24f
None + pathogen	5.21z	1.46e	5.08e
Annual ryegrass	3.78e	1.71f	4.34e
Cereal rye	4.50ef	1.46e	3.72d
Oat	3.03d	1.72f	4.56ef
Sudan grass	4.18e	1.48e	4.28e
Analysis of variance			
		-----Probability level -----	

Pathogen	***‡	***	***
Cover crop	**	***	***
Pathogen x cover crop	NS§	NS	NS

† Within a column, means followed by the same letter are not significantly different ($P < 0.05$).

‡ *, **, *** coefficients significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

§ NS, no significant ($P < 0.05$) coefficients.

g. and in infested soil shoot biomass was significantly lower (between 3.77 and 4.52 g) than the noninfested control.

Cover cropping pathogen infested soil with annual ryegrass, oats, and sudan grass reduced the severity of root rot of sweet corn compared to the infested control (Table 4.8). Oats reduced the severity of root rot by 42 % compared to the infested control. Cover cropping with cereal rye had no effect on disease compared to the infested control.

Root biomass of corn grown in soil cropped with annual ryegrass or oat did not differ from the noninfested control. However, root biomass for these treatments was on average 15 % greater than the pathogen infested control. With the exception of the oat treatment, all treatments had significantly less shoot biomass than the infested control.

Corn root biomass was significantly negatively correlated with severity of root rot of corn (Table 4.9). No other correlations were significant.

Experiment 3. Host specificity range

There was a significant relationship between the rate of *Pythium arrhenomanes* and *Drechslera* spp. inoculum and severity of root rot for annual ryegrass, perennial ryegrass, and cereal rye (Fig 4.2a, b). Perennial rye was the only crop that showed a relationship between rate of *Phoma* spp. inoculum and severity of root rot (4.2c). There was no relationship between crop biomass and inoculum rate (data no shown).

Table 4.9. Pearson correlation coefficients (r) and probability levels for severity of root rot of corn and cover crop and sweet corn biomass.

Measurement	Severity of root rot	
	r	Probability level
Cover crop		
Root dry matter	-0.10	0.45
Shoot dry matter	-0.09	0.46
Corn		
Root dry matter	-0.75	<0.0001
Shoot dry matter	-0.07	0.53

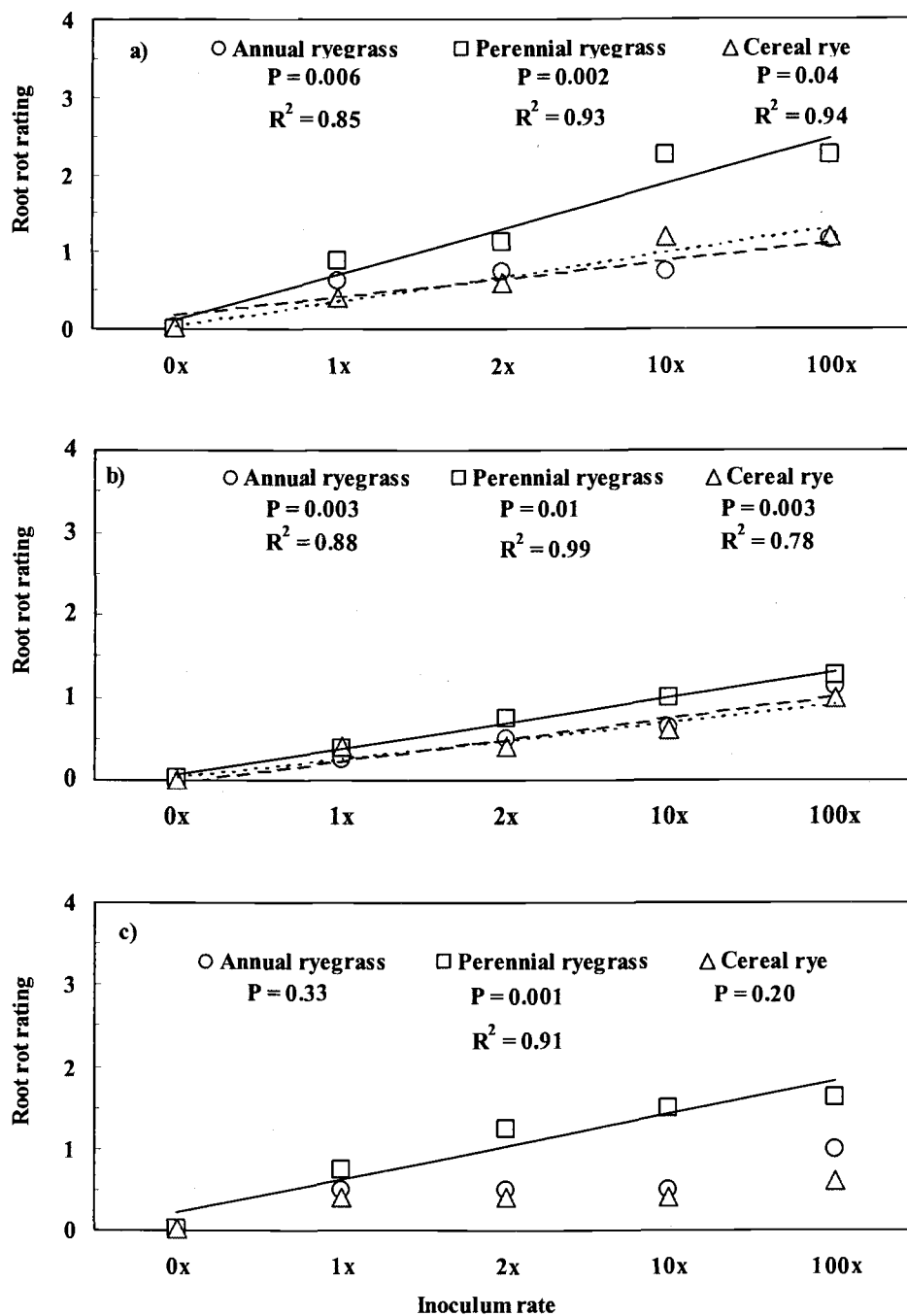


Fig. 4.2. Effect of inoculum density of a) *Pythium arrhenomanes*, b) *Drechslera* spp., and c) *Phoma* spp. on severity of root rot of annual ryegrass, perennial ryegrass and cereal rye. Each data point represents the mean across 8 replicates.

DISCUSSION

Cover crops

Repeated cover cropping main effects was only observed for the Chehalis soil. More cover crop biomass was produced during the second cover cropping period, probably because this period occurred during the month of August, while the others were grown in slightly cooler months.

Although there was a reduction in disease from the first two cover cropping periods to the last cover crop period, these differences were not likely due to repeated cover cropping. Instead, the observed differences were probably due to changes in growing conditions of the greenhouse over the course of the experiment. For instance, in the summer sunlight and temperature varied according to outside conditions whereas artificial lights and supplemental heat supported plant growth during the short day, low light intensity of the wet winter season.

Three years of sudan grass cover cropping reduced populations of *Verticillium dahliae* and reduced incidence of root infections of potato caused by this pathogen (Davis et al., 1996). Tu and Findlay (1986) reported a reduction in the severity of Aphanomyces root rot of pea after one oat or sudan grass amendment to both a moderate and heavily infested field soil. The lack of impact of repeated cover cropping on soil properties or severity of disease may be due to lower cover crop biomass generated in pots relative to that generated in the field.

Suppression of root rot of sweet corn

Sudan grass and oat were the most effective cover crops in decreasing the severity of root rot of sweet corn in all experiments. Oat and sudan grass were suppressive to the root rot complex and to the individual causal agents. Oat cover cropping has been shown to be an effective way to manage root rots (Tu and Findlay, 1986; Fritz et al., 1995; Williams-Woodward et al., 1997; Elmer and LaMondia, 1998). Oat cover crops grown in a field of high root rot of pea potential decreased disease severity by 21 % compared to a nonamended control. Davis et al. (1996) demonstrated that sudan grass cover cropping reduced populations of *Verticillium dahliae* and incidence of Verticillium wilt of the following potato crop compared to a fallow control.

Corn growth

Corn root biomass was significantly increased after the growth and amendment of cover crops to Chehalis soil. Cover cropping can improve soil structure and increase organic matter levels, all of which can promote more vigorous root growth (Pieters, 1927). Corn root biomass of corn grown in cover cropped Clackamas soil was not different from the control. This soil had a history of perennial ryegrass. Several years of perennial grass production should increase free particulate organic matter contents and microbial activity and biomass compared to annual cropped soils (Clement and Williams, 1964; Johnston, 1986; Sparling, 1985). Since physical properties of Clackamas soil

were likely better than Chehalis soil, cover cropping probably did not improve the structure of Clackamas soil compared to the control. As a result root growth was not improved.

All pathogens reduced corn root biomass compared to the uninfested control. The largest reduction was observed when corn was grown in *P. arrhenomanes* infested soil. This is not surprising, since *P. arrhenomanes* causes root pruning (Deep and Lipps, 1996; Hoinacki and Powelson, 2002).

In general, across all experiments, cover cropped soils that were more suppressive of root rot of corn also generated the largest corn root biomass. This would be expected, because reduced root disease should lead to more vigorous root systems.

Soil enzymes

Additions of cover crops into the crop rotation can improve soil biological, chemical and physical characteristics (Pieters, 1927; Allison, 1970; Bandick and Dick, 1999; Ndiaye et al., 2000). Enzyme assays have been proposed as an indicator of soil health and have been found to be sensitive to short term changes in soil management (Dick et al., 1997). In general, cover cropping increased β -glucosidase activity in Chehalis soil but not Clackamas soil. The response of this enzyme to the cover crops may be due to an increase in cellulose content which increased β -glucosidase activity or addition of β -glucosidase from the plant residue itself (Martens et al., 1992; Dick et al., 1997).

There were few significant differences among treatments for either FDA or β -glucosidase in Clackamas soil, likely due to their relatively high activity levels as a result of previous years in perennial sod.

Interestingly, neither enzyme assay was related to disease severity.

Fluorescein diacetate activity is a common indicator of the potential of a soil to suppress root diseases (Hoitink and Boehm, 1999). This type of suppression, called general suppression, is the result of the activities of many types of microorganisms (Cook and Baker, 1983). Davis et al. (1994) reported a negative relationship between incidence of Verticillium wilt of potato grown in cover cropped soils and FDA activity. In our experiment, FDA activity was not correlated with the suppression of root rot of corn.

Fluorescein diacetate activity in soils amended with annual ryegrass did not differ significantly from sudan grass, yet corn grown in sudan grass treated soils had less root rot than corn grown in annual ryegrass treated soils. Oats generally generated the highest FDA activity of all treated soils and also suppressed root rot. Therefore it is possible that oat-mediated suppression, is, at least in part, related to an increase in microbial activity. However, Chehalis soil treated with manure (see Chapter 3) or oat had virtually identical FDA activities but only the oat treatment had significantly less root rot compared to the control.

Both oat and sudan grass produce compounds that have been shown to inhibit pests (Maizel et al., 1963; Deacon and Mitchell, 1985; Abawi and Widmer, 2000).

Oat shoots and roots contain avenacin and other related saponins (Burkhardt et al., 1964). These compounds have been shown to be toxic to zoospores of various species of *Pythium* and inhibit the growth of several other fungi. Release of these compounds during the growth and decomposition of oat could have reduced the severity of root rot. A cyanoglucoside compound called dhurrin is found within the epidermal cells of sudan grass leaf tissue. When the leaf tissue is damaged or begins to decompose hydrogen cyanide is liberated as dhurrin is hydrolyzed by enzyme action (Tarr, 1962). Dhurrin content, found mostly in the leaves, is highest in young plants (Tarr, 1962). Since the sudan grass was incorporated at a young stage (5 wk old) it is possible that hydrogen cyanide may have played a role in suppression of root rot.

Cereal rye treated soils were never suppressive to root rot of corn. Compared to the other cover crops, cereal rye always generated the lowest FDA activity and smallest amount of plant biomass. Interestingly, annual ryegrass was suppressive to root rot caused by the individual pathogens but was not suppressive to root rot caused by the entire complex. It is possible that the amount of plant biomass added to the soil enhanced microbial activity to a level sufficient to suppress an individual pathogen but not sufficient to suppress a complex of pathogens. Disease may have also been easier to suppress in the infested pasteurized soil since it was biologically less complex.

It is possible that the amount of organic matter added from the cover crops grown in containers was not sufficient to generate suppression. When manures or composts are added to the soil a much greater amount of organic matter is amended than with a cover crop and hence a higher level of microbial activity can be achieved.

On average, a total of 132 g dry wt 3 kg^{-1} soil of cover crop residue was amended over 3 cover cropping periods to the soils of high root rot potential. On average, 432 g dry wt 3 kg^{-1} of manure or compost were added over 3 repeated amendments to the same soils. We have shown that severity of root rot of corn, is related to FDA activity and fPOM (see Chapter 2 and 3); and that the threshold for suppression of root rot of sweet corn in a soil of high root rot potential was $4.00 \mu\text{g fluorescein min}^{-1} \text{ g}^{-1}$ dry wt (related to 10 to 15 % v/v organic matter added). Cover crops did not reach this level of FDA activity, therefore it is very likely that suppression of root rot by oats and sudan grass was due to factor(s) other than fPOM and enhanced FDA activity.

Host specificity range

In general, all cover crops exhibited some level of root rot symptoms whether grown in naturally infested field soil or infested pasteurized soil. This was not surprising since *Pythium arrhenomanes* and species of *Drechslera* and *Phoma* have been associated with root rot of numerous grass species (Henry, 1925; Sprague, 1946; Hassan, 1956; Tarr, 1962). It should be noted that other microorganisms besides those that cause root rot of corn were recovered from symptomatic lesions of corn grown in naturally infested field soil. With the exception of the roots of annual ryegrass, most root rot ratings were below 1 (less than 10 % of the root ball had symptomatic lesions). The oats always had the lowest amount of root rot. This may partially be due to the fact that oat roots exude avenacin and other saponins, which have been shown to inhibit the growth of numerous pathogenic organisms including *Pythium*

arrhenomanes and *Drechslera* spp. (Maizel et al., 1963; Luning and Schlosser, 1976; Deacon and Mitchell, 1985).

The dose response relationships clearly show that annual ryegrass, perennial ryegrass, and cereal rye are hosts to *Pythium arrhenomanes* and *Drechslera* spp., whereas only perennial ryegrass was host to *Phoma* spp. Annual ryegrass and cereal rye are bridging hosts (they harbor the pathogen but there was no dose response) to *Phoma* spp. These pathogens appear to be much more virulent on corn than the tested rotation crops, as the biomass of alternate host crops was not reduced even at high levels of inoculum. Interestingly, Lyle et al. (1948) showed that *Phymatotrichum* root rot of cotton can be controlled by the use of a sweet clover rotation even though the clover was also susceptible to *Phymatotrichum*. This may also be a possibility for rotation with annual ryegrass, as we observed disease suppression when pasteurized soils were cover cropped with annual ryegrass. However, the role that these crops might play as bridging host should not be overlooked and future studies should be conducted to evaluate their impact on inoculum levels over time.

In conclusion, cover cropping with either sudan grass or oat may have potential as a management tool for root rot of sweet corn. However, these experiments were conducted in containers. Field trials should be conducted to determine the impact and practicality of cover cropping with these species on a field scale. Causal agents were weakly pathogenic on the roots of annual ryegrass, perennial ryegrass, and cereal rye. However, it is not known how this relates to build up of inoculum or disease potential over time.

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CHAPTER 5
GENERAL CONCLUSION

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Many different types of organic residues suppress root diseases. In a field trial, fresh and composted dairy manure solids applied at a high and low rate suppressed damping-off of cucumber and root rot of snap bean and sweet corn in a field of low disease potential. The efficacy of the fresh and composted manure was similar. However, two amendments of the low rate of fresh manure were required before disease suppression was observed. In this system, we suggest that the rate of amendment was the most important factor contributing to suppression. Disease suppression was of short duration, lasting less than 6 mo after the time amendment.

Free particulate organic matter, fluorescein diacetate (FDA) activity, microbial biomass-C, and percent of water stable aggregates (WSA) were all negatively related to severity of root rot. However, FDA activity was the best indicator of disease suppression since it captured not only the quantity (estimated by fPOM content) but also the quality of the active soil organic matter that was supporting microbial activity. Levels of FDA activity above $2.88 \mu\text{g fluorescein min}^{-1} \text{g}^{-1}$ dry wt were suppressive to root and seedling diseases.

Overall, amendment of soils with either fresh or composted dairy manure enhanced soil quality. However, fresh manure was more effective than composted manure at increasing the percent of WSA and soil oPOM content.

In container studies, fresh (10 % v/v) or composted (15 % v/v) manure amendments to soil also suppressed root rot of sweet corn in field soils of high root rot potential. In addition, both amendment types suppressed root rot caused by the individual pathogens (*Drechslera* spp., *Phoma* spp., and *Pythium arrhenomanes*).

Again, FDA activity was negatively related to severity of root rot; however, in soils with high root rot potential, higher levels of FDA activity ($4.00 \mu\text{g fluorescein min}^{-1} \text{ g}^{-1} \text{ dry wt}$) were needed to generate suppression. Other mechanisms, such as improvements in soil structure and increases in soil nitrogenous compounds may also have played a role in suppression.

In container studies, cover cropping with oat and sudan grass treatments reduced severity of root rot of sweet corn in soils of high root rot potential. Suppression was not related to FDA activity. Cover crops did not reach the FDA suppressive threshold ($4.00 \mu\text{g fluorescein min}^{-1} \text{ g}^{-1} \text{ dry wt}$), therefore it is very likely that suppression of root rot by oats and sudan grass was due to factor(s) (e.g. chemical constituents in plants) other than enhanced FDA activity. However, these experiments were conducted in containers, and field trials should be conducted to determine the impact and practicality of cover cropping with these species on a field scale.

Annual ryegrass, perennial ryegrass, and cereal rye are hosts to *Pythium arrhenomanes* and *Drechslera* spp., whereas only perennial ryegrass is a host to *Phoma* spp. Sudan grass and oats are not hosts to any of these pathogens. The impact of alternate host status on inoculum level or disease potential in a field cropping system over time must be investigated further.

In general, FDA activity was the best indicator of a soil's suppressive potential. However, there does not appear to be a universal threshold for FDA in field soils. Fluorescein diacetate disease suppressive thresholds will likely need to be established within the context of each cropping and disease system.

These data suggest that there might not be an advantage to composting for suppression of the soilborne disease investigated in this work. Composted manure is not inherently more disease suppressive than fresh manure. Differences in disease severity in amended soils were strongly related to fPOM content and FDA activity, which were more related to amendment rate than amendment type. This was observed both in chapter 2 and 3. In chapter 2, the low rate of manure was not suppressive because it did not increase fPOM contents and FDA activity to levels over the suppressive thresholds. However, higher rates of manure and both rates of compost generated suppression and generated fPOM contents and FDA activities over the thresholds. In chapter 3, MS amendment (10 % v/v) did not suppress root rot in the Chehalis soil compared the non-amended control. The MSC, applied at a higher rate (15 % v/v) suppressed root rot. In the Clackamas soil, MS and MSC both suppressed root rot compared to the non-amended control. The Clackamas soil initial FDA activities were higher than those of the Chehalis soil, and hence a lower rate of active organic matter augmentation probably increased fPOM contents and FDA activities to levels over the suppressive thresholds.

This brings to light another observation made in both Chapter 2 and 3 - 'priming effect' caused by serial amendment. In general, a relatively small proportion of the soil microbial biomass is active; most of the biomass is inactive because of energy limitation (Sparling, 1995). Lockwood (1990) states that commonly there is only enough energy in a soil to barely meet microbial biomass maintenance requirements, with little to no excess available for growth. When organic substrate is

amended to soils, excess energy becomes available for growth and the quiescent pool becomes active (Sparling, 1995; van Bruggen and Semenov, 2000). Therefore, after one amendment of fresh or composted manure the microbial biomass (active and quiescent pools) was enhanced and in some cases (low rate of compost and high rates of manure and compost) microbial activity increased over the suppressive threshold. As the organic matter decomposed, the activity of the biomass declined but the mass remained higher than in the non-amended control. The additional energy gained from adding a second amendment did not have to be used to build and maintain biomass but instead could be used to further increase its growth and activity; hence, all amendments (including the low rate of manure) suppressed diseases. These hypotheses will need to be investigated in future studies.

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