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FULL RESEARCH PAPER

Effect of prior tillage and soil fertility amendments on dispersal of *Phytophthora capsici* and infection of pepper

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Abstract Organic soil amendments including composted cotton gin trash, composted poultry manure, an incorporated rye-vetch green manure, or synthetic fertilizer were applied to subplots, and main plots were either tilled frequently or surface-mulched in experimental field plots between 1997 and 2004. Soil from each replication of the tillage and fertility treatments was sampled in August of 2001, 2002, and 2003, brought to the greenhouse, and infested with *Phytophthora capsici* to study the effect of previous soil treatments on disease incidence and dispersal of the pathogen. Both the previous tillage and fertility amendments affected the incidence of disease and dispersal of the pathogen. Final disease incidence, AUDPC and the distance of pathogen spread were significantly greater in soils with previous surface mulch applications than in frequently tilled soils. Final disease incidence, AUDPC and the distance of pathogen spread were also significantly higher in soils amended with cotton gin trash, than rye-vetch green manure, poultry manure, or synthetic fertilizer. Soils amended with cotton gin trash had higher soil water content, lower bulk density, higher humic matter content, higher porosity and higher levels of mineralizable N, than soils with other fertility amendments. Soil water content, soil porosity, humic matter content, and net mineralizable levels nitrogen were positively correlated and bulk density was negatively correlated with final incidence of disease.

Keywords *Phytophthora capsici* · Epidemiology · Organic amendment · Physical · Chemical and biological parameters · Disease spread

Introduction

Disease caused by the Oomycete pathogen *Phytophthora capsici* is responsible for significant economic losses on a wide range of agronomic plants including bell pepper (*Capsicum annum*; Hausbeck and Lamour 2004; Ristaino and Johnston 1999). Disease is a major source of disturbance in agroecosystems and is partially responsible for the extensive use of pesticides applied annually on crop plants. Species of *Phytophthora* produce sporangia and motile zoospores that can be dispersed either in soil, via surface water movement down rows, from rain splash dispersal or by movement of humans or invertebrate activity (Ristaino et al. 1994; Ristaino and Johnston

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1999). Motile zoospores of the pathogen move in water-filled pores during saturation periods (Duniway 1983). During conditions of heavy wind and rain, *P. capsici* can be distributed over entire fields and can cause extensive losses within a few days (Ristaino 1991). The pathogen is heterothallic and can produce oospores readily that survive in soil between crops (Ristaino and Johnston 1999).

Management of Phytophthora blight has become increasingly difficult in recent years. Resistance in *P. capsici* to the commonly used fungicide mefenoxam has limited the efficacy of this group of phenylamide fungicides for disease control and other classes of chemicals are currently in use in many areas of the US (Brent and Hollomon 1998; Cohen and Coffey 1986; Hausbeck and Lamour 2004; Parra and Ristaino 2001). A variety of cultural practices are recommended to reduce the incidence of disease (Hausbeck and Lamour 2004; Ristaino and Johnston 1999). Disease spread within a cropping season can be greatly reduced by planting into stubble from a no-till wheat or rye-vetch cover crop (Ristaino et al. 1997; Ristaino and Gumpertz 2000). However, yield is often compromised in the no-till planting of pepper (Ristaino et al. 1997). Surface mulch reduced the spread of *Phytophthora cactorum* in strawberry fields by reducing rain splash dispersal of propagules of the pathogen (Madden and Ellis 1990). However, little is known about the impact of long-term applications of organic matter in the field on soil physical factors and disease development. Surface-applied straw mulches are often incorporated at the end of the season into soils and yearly applications can change the physical, chemical, and biological characteristics of soils.

There has been limited research on the impact of soil-incorporated organic amendments on the incidence of Phytophthora blight of pepper. Organic growers use composted plant residues or animal manures and their impact on Phytophthora blight and disease suppression are unknown. Incorporation of soil amendments such as chitosan or crab shell waste were suppressive in some years to Phytophthora blight on pepper but results were variable in other years in studies in Florida (Kim et al. 1997). Composted plant residues such as cotton gin trash are suppressive to southern blight (Bulluck and Ristaino 2002). Composted swine manure has been demonstrated to suppress *P. parasitica* and composted poultry manure suppressed *P. cinnamomi* in potting mixes (Aryantha et al. 2000; Fitchner et al. 2004). Both biotic and abiotic factors including reductions in soil pH and aluminum play a role in disease suppressiveness in potting mixes (Fitchner et al. 2004; Hoitink and Boehm 1999; Muchovej et al. 1980).

Soils in organic production systems have shown increased suppressiveness to some plant pathogens (Bulluck and Ristaino 2002; Elliott and Lynch 1994; Workneh and van Bruggen 1994). Organic soil amendments increase water holding capacity and cation exchange capacity of soils, lower bulk density, and foster beneficial microorganisms (Atlas et al. 1991; Doran 1995; Drinkwater et al. 1995). Benefits of composted amendments to soil also include pH stabilization and improved water infiltration rates. Soils in organic production systems released less nitrogen into nearby water systems than did soils from conventional production systems (Drinkwater et al. 1995; Liebhardt et al. 1989). The mineralization of soil nitrogen in fields under conventional production systems was negatively correlated with soil microbial activity, whereas mineralization of soil nitrogen in fields under organic production was positively correlated with soil microbial activity (Gunapala and Scow 1998).

Organic growers in the southeast utilize a variety of soil fertility amendments including animal manures, cover crops and composted plant debris to improve soil quality. Organic agriculture offers positive ecological gains including increased soil biodiversity, reduced pesticide use, improved nutrient cycling, and energy conservation, but there is still much to be learned about the impact of these soil fertility amendments on Phytophthora diseases (Aryantha et al. 2000; Atlas et al. 1991; Drinkwater et al. 1995; Van Bruggen and Semeov 1999).

The objective of these experiments was to determine the impact of long-term soil fertility amendments and tillage or surface mulch applications on the incidence of disease and dispersal of *P. capsici* through soils. We used greenhouse flat and pot assays to test the suppressiveness of soils removed from previously amended field plots to disease. Soil physical, chemical and biological factors were also assessed to determine their relationship to development of disease. A preliminary report of some of the research has been presented (Liu and Ristaino 2003).

Materials and methods

Experimental design

Soil was collected from a field experiment that was underway for another soil fertility experiment, at the Horticultural Crops Research Experiment Station (HCRS) in Clinton, North Carolina (Bulluck and Ristaino 2002). Studies were done in greenhouse bioassays because we did not want to infest the experimental field plots with the pathogen. The soil in the field was an Orangeburg Loamy sand and contained 87% sand, 8% clay, and 5% silt. The field did not have a history of Phytophthora blight and the pathogen was not detected by soil dilution plating or PCR prior to the experiments (Ristaino et al. 1998).

Soil was amended each spring between 1997 and 2004 in a series of experimental plots to develop contrasting organic and conventional soil fertility treatments (Bulluck and Ristaino 2002). No synthetic or non-organic pesticides were used in any of the plots. The field plots were initially established in 1996 by planting a fall cover crop. The initial soil pH was 5.6 and organic C levels were 5.0 g kg^{-1}. Tomatoes were grown in the field each year with the exception of 2001 when bell pepper was grown. The experimental design was a randomized split plot. The frequency of tillage during the growing season differed between the main plot treatments (two levels) and included either tillage on bare soil or surface mulch application with wheat straw after a single initial tillage. Main plots that received tillage were tilled weekly (4–5 times per season) until plants were too large for a tractor to clear. In the surface mulch plots, wheat straw was applied to the soil surface 2 weeks after transplanting. The surface mulch was incorporated into plots each fall after harvest.

The plots were arranged in four blocks. Soil fertility amendments were applied in the subplots (four levels) and included either a conventional synthetic fertilizer (10-10-10 applied at 67 kg N ha^{-1}, and 45 kg N ha^{-1} at first flower cluster), or organic amendments including a composted cotton gin trash (applied at 62,250 kg DW ha^{-1}), composted poultry manure (28,000 kg DW ha^{-1}), or an incorporated rye-vetch green manure. Winter rye was broadcast seeded at a rate of 56 kg ha^{-1} and hairy vetch at a rate of 28 kg ha^{-1} every fall and mowed and incorporated to a depth of 30 cm each spring. Rates of each soil amendment were standardized to obtain approximately 112 kg plant-available nitrogen per hectare. The inputs of extractable nutrients varied in the plots. Properties of the organic substrates that were used have been published (Tu et al. 2005). Treatments were applied each year except in 2000 when a sudan grass cover crop was planted in all plots. Between 1997 and 1999, swine manure waste was used in the animal manure plots. Between 2001 and 2003, composted poultry manure was used in the animal manure plots.

Soil sampling

Soil samples were collected in late August of 2001, 2002, and 2003 from each of the 32 plots. Soil cores were collected (15 cm depth × 5.5 cm wide) from each of the centre four rows of the plots, bulked, placed into plastic bags, held at 25°C, and assayed within 1 week of sampling for physical, chemical and biological factors (see below). Surface mulch was removed before sampling to avoid collecting surface organic matter. Larger bulk soil samples were composited for the greenhouse assays. Soil was sampled with a shovel to depths of 15 cm from the centre four rows of each experimental unit, mixed in plastic bags, and placed in the greenhouse for immediate use.

Inoculum production

Inoculum of the pathogen was prepared by culturing *P. capsici* on V-8 vermiculite media. Mason jars containing the V-8 vermiculite medium were autoclaved for 1 h at 120°C on two consecutive days before the inoculation of *P. capsici*. Isolate R-16 was grown at 25°C for 4 weeks on V-8 vermiculite media [500 cm^3 vermiculite, 250 ml of V-8 broth (800 ml of water, 200 ml of V-8 juice, and 2 g of $CaCO_3$ in 1-l jars)] (Sujkowski et al. 2000).

Disease incidence in greenhouse pot assay

Soil from each of the main plots (tillage or surface mulch) and subplots (soil fertility amendment treatments including either synthetic fertilizer, cotton gin trash, animal manure, or rye-vetch green manure) was amended with *P. capsici* at a rate of 1% (v/v contained 600 cfu g^{-1} of vermiculite). Soil infested with the pathogen was incubated for 2 weeks in the greenhouse at 25°C (day) and 23°C (night). Soil was distributed into two 15 cm diam plastic pots and planted with four pepper seedlings (4 week-old, cv. Camelot). Plants were watered from below with a saucer after planting and every 4 days thereafter. Disease incidence was evaluated three times weekly for 4 weeks. Disease incidence and the area under the disease progress curve (AUDPC) were calculated as proportion of disease day^{-1}.

Dispersal of introduced inoculum of *P. capsici* through soils

Bulked, non-sieved soil from each replicate of each treatment (32 samples) was placed in separate plastic flats (70×55×15 cm, and 0.5 cm diam drainage holes). Paper was placed inside each flat prior to filling to avoid soil and inoculum leakage out of the flats. Bell pepper seedlings (4 week-old, cv. Camelot) were planted in 10 rows of 9 plants each in a uniform grid of 90 plants per flat. Plant spacing within rows was 6 cm (<0.3 m field spacing). V-8 vermiculite medium (50 cm^3) containing sporangia and mycelia of the pathogen was placed in the transplant hole of one plant in the centre row at one end of each flat (Ristaino et al. 1997; Sujkowski et al. 2000) to simulate a point source of inoculum.

Plants were irrigated by sub-surface methods. Flats containing pepper plants were placed into a flat with no drainage holes, containing water to 10 cm depth, and saturated from below for 2 h every 3 days for the duration of the experiment. Water did not pool on the soil surface during saturation events. Sub-surface irrigation was used rather than overhead irrigation to promote pathogen movement within the soil and to avoid splash dispersal of inoculum on the soil surface that would have killed the plants too quickly (Ristaino et al. 1993; Ristaino et al. 1994). Greenhouse temperatures were approximately 25°C.

Disease incidence was recorded three times per week by evaluating disease on each plant. Disease incidence data was recorded by spatial location (row and plant number) within each flat. Disease incidence and AUDPC were calculated using disease data from the entire flat of 90 plants. AUDPC was calculated as $[(Y_{i+1}+Y_i)]/[X_{i+1}-X_i]$, where Y_i=disease incidence at the ith observation, X_i=time (weeks) at the ith observation.

The log of disease incidence at each sampling time, the log of AUDPC, and the dispersal distance at each sampling time were analyzed using a split-plot model with the tillage treatment as the whole plot factor and the soil amendment as the subplot factor:

$$y_{ijkl} = \mu + B_i + T_j + \delta_{ij} + A_k + \gamma_{ik} + (TA)_{ik} + \varepsilon_{ijk}. \tag{1}$$

where B_i is a random block effect, δ_{ij} a random whole plot error, γ_{ik} a random block by amendment interaction, ε_{ijk} is a random subplot error, and the remaining terms in the model are defined as in Eq. 2.

Repeated measures analysis of variance was used to quantify disease progress and pathogen dispersal over time, using the following model:

$$\begin{aligned} y_{ijkl} &= \mu + B_i + T_j + \delta_{ij} + A_k + (TA)_{ik} + S_l \\ &\quad + (TS)_{jl} + (AS)_{kl} + (TAS)_{jkl} + \eta_{ijkl}, \end{aligned} \tag{2}$$

where the response variable y_{ijkl} is either ln (% diseased+1) or distance of disease spread for the ith block, the jth tillage treatment, the kth soil amendment, and the lth sampling time. In this model B_i is a random block effect, T_j the tillage effect, δ_{ij} is a random whole-plot error, A_k is an amendment effect, S_l is the treatment sampling time effect, ε_{ijkl} stands for random error among sampling times within a subplot, and the remaining terms are interactions. The errors ε_{ijkl} are assumed to be independent between subplots and follow an AR correlation structure over time within sub-plots. Tests of the effect of tillage and fertility amendment interactions with sampling time were performed using Wald-type F tests with the Kenward-Roger approximation for the denominator degrees of freedom (SAS Proc Mixed, SAS Institute, Cary NC).

The distance of pathogen spread was calculated using the middle row of plants within each flat. The distance of pathogen spread was analyzed using repeated measures analysis of variance. The rate of spread was calculated as distance divided by time. The EPIMODEL (Campbell and Madden 1990; Nutter and Parker 1997) statistical software programme was used for fitting the data. The EPIMODEL computer programme fits temporal disease progress to five population growth models commonly used in the analysis of plant disease epidemics, including the monomolecular, exponential, logistic, Gompertz and linear models (Campbell and Madden 1990; Nutter and Parker 1997).

The experiments were done twice with soil sampled from all 32 plots in 2002. Data were analyzed separately. Means from combined experiments are shown for the distance of spread data.

Soil physical parameters

Undisturbed soil cores of known volume were collected from the field at the same time as bulk soil samples in 2001–2003, dried in an oven, and bulk density, soil porosity, and soil water content calculated (Mehlich 1973). Soil from each treatment replicate combination was sieved (10-mm mesh) and repacked to the average bulk density. A soil moisture release curve was determined for reconstituted soil at Ψ_m values between 0 and −100.0 millibars (mb) using Buchner tension funnels (Duniway 1983; Klute 1986).

Soil chemical and parameters

Soils were tested by the Soil Testing Laboratory of the North Carolina Department of Agriculture (Raleigh, NC, USA). Soil tests included: extractable acidity (EA), cation exchange capacity (CEC), base saturation (BS), soil pH, humic matter (HM), macro- and micronutrients including potassium (P), calcium (Ca), magnesium (Mg), sodium (Na), manganese (Mn), zinc (Zn), and copper (Cu). Soil testing protocols developed by Mehlich (1972); Mehlich (1973); Mehlich et al. (1976) and Mehlich (1984) . Soil extractable organic C and N were estimated by the methods of Hu et al. (1997), and net N mineralization was calculated by the methods of Hart et al. (1994) on soils sampled in June and August of each year. Microbial biomass carbon (MBC) and microbial biomass nitrogen (MCN) were determined using the chloroform fumigation extraction method of Ross (1992) and Vance et al. (1987). Soil microbial respiration was measured using an incubation-alkaline absorption method (Coleman et al. 1978).

Numbers of culturable bacteria, fluorescent pseudomonad bacteria, enteric bacteria, total fungi, thermophilic microorganisms, *Trichoderma*, and Oomycete species were quantified by dilution plating using previously described methods (Alexander 1977; Bulluck et al. 2002). Soil samples were analyzed for selected soil microorganisms using 10-fold serial dilutions of soil on different selective media. Data were expressed as cfu g^{-1} dry soil.

Data from the physical, biological and chemical properties of the soils were analyzed using analysis of variance and a randomized split-plot model. Correlation analyses were performed to relate the final incidence of disease to soil physical, chemical and biological parameters.

Results

Disease progress in time

Disease was evaluated over time in the greenhouse assays. The tillage effect was significant in each year in all the greenhouse assays (Table 1). Disease onset occurred earlier in soils previously surface-mulched than in tilled soils (Fig. 1a, c, e, g). Disease progressed more rapidly and incidence over time was significantly higher in previously surface-mulched than tilled soil (Fig. 1a, c, e, g). Final disease incidence ranged from 23 to 36% in surface-mulched soils and 55–58% in tilled soils (Table 1). AUDPCs were also significantly higher in soils from previously surface-mulched than tilled soils in both the pot and flat assays.

Disease onset occurred earlier and final disease incidence in each year was highest in soils amended with cotton gin trash (Fig. 1b, d, f, h). Disease increase over time was significantly higher ($P=0.0001$) in soils amended with cotton gin trash than the other soil amendments in both the pot assays (Fig. 1b, d; Table 1) and the flat (Fig. 1f, h) assays. Final disease incidence ranged from 60 to 64% in soil amended with cotton gin trash and 53–54, 47–49, and 20–21% in soils amended with poultry manure, synthetic fertilizer or rye-vetch green manure in the pot assay (Table 1). Final disease incidence was significantly lower in soils amended with the rye-vetch green manure than the other amendments in the pot assay (Fig. 1b, d; Table 1). In the flat assay, where experiments ran for 15 weeks, there were no significant differences in the final incidence of Phytophthora blight among soils amended with synthetic fertilizer, poultry manure or the rye-vetch green manure (Table 1, Fig. 1f, h).

Table 1 Final incidence of Phytophthora blight as affected by previous tillage, surface mulch or soil fertility amendments

Main plot	Pot assay 1		Pot assay 2		Flat assay 1		Flat assay 2	
	Final Disease Incidence (%)	AUDPC	Final Disease Incidence (%)	AUDPC	Final Disease Incidence (%)	AUDPC	Final Disease Incidence (%)	AUDPC
Tillage	34	5.3	36	5.3	23	11	23	11
Surface mulch	56	8.1	58	8.4	55	31	57	32
Subplots								
Fertility amendment								
Synthetic fertilizer	47	6.3	49	6.4	31	15	35	17
Cotton gin trash	60	10	64	10.2	70	40	71	40
Poultry manure	53	7.8	54	8.1	31	17	31	17
Green manure	21	2.6	20	2.7	24	12	23	12
P>F								
Tillage	0.0001	0.0001	0.0001	0.0001	0.0002	0.0001	0.0001	0.0001
Amendment	0.0001	0.0001	0.0001	0.0001	0.0005	0.0002	0.0004	0.0001
Tillage×amendment	0.0004	0.0003	0.001	0.0001	0.409	0.1455	0.5731	0.1262

Data transformed using ln (%) based on model [1]. Non-transformed means shown. Mean data from two experiments shown.

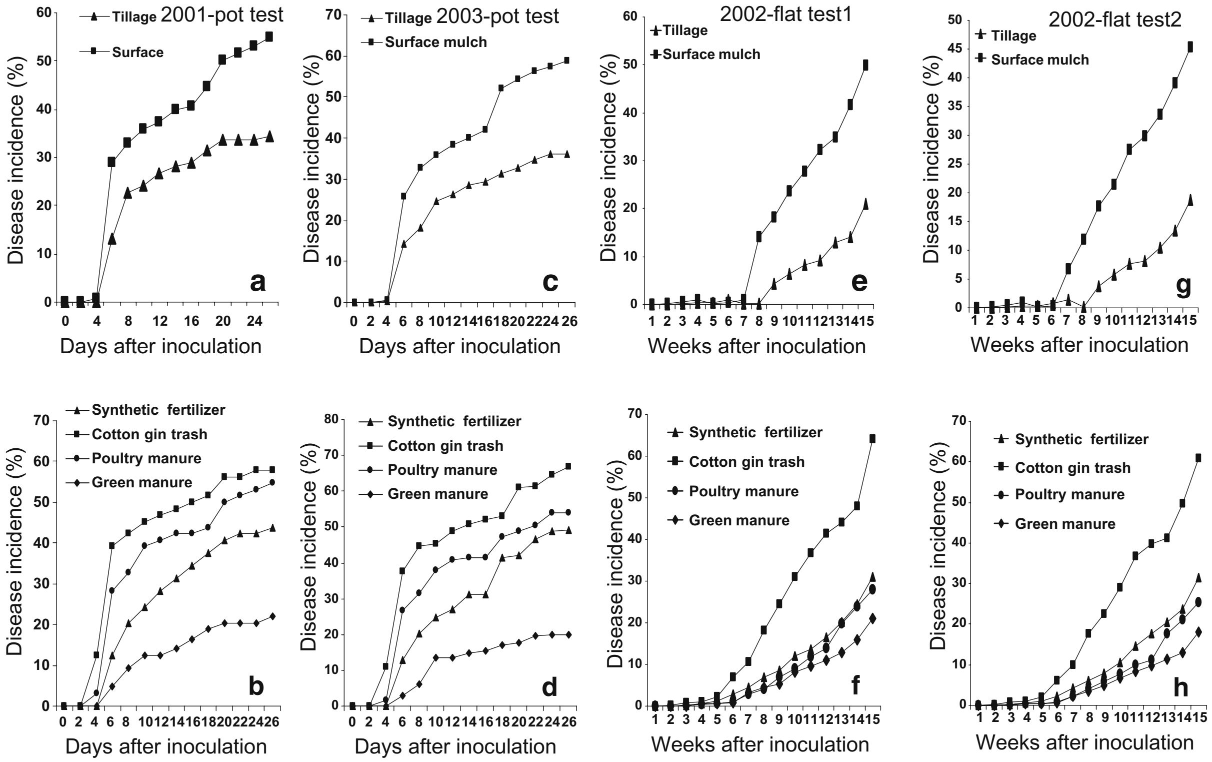

Fig. 1 Disease progress of Phytophthora blight caused by *Phytophthora capsici* in greenhouse pot and flat assays in soils: **a**, **c**, **e**, **g** previously tilled or surface-mulched with straw; **b**, **d**, **f**, **g** amended with synthetic fertilizer (conventional) or organic (cotton gin trash, poultry manure, rye-vetch green manure) soil fertility amendments

Spatial pattern of disease

Both tillage and soil fertility amendments impacted the spread of *P. capsici* in the flats. Disease symptoms on the source plant appeared 5 days after inoculation in soils amended with cotton gin trash and 7 days after inoculation in soils amended with animal manure, a rye-vetch green manure or synthetic fertilizer (data not shown). The plant adjacent to the source plant in the same row became diseased first, and then disease spread down rows.

Disease was observed only around the source plant in the same row 5 weeks after inoculation (Figs. 2 and 3). After 10 weeks, disease was observed down only four rows in soils previously tilled, whereas disease occurred down all 9 rows to the other end of the flat in soils previously surface-mulched (Fig. 2). Disease was not observed after 15 wks at the other end of the flats in previously tilled soils.

Disease was observed after 10 weeks down only 3 rows in soils amended with rye-vetch green manure (Fig. 3). In contrast, disease was observed after 10 weeks down 9 rows to the other end of the flats in soils amended with cotton gin trash (Fig. 3). In soils amended with either the rye-vetch green manure or composted poultry manure, disease did not occur in plants at the ends of the flats after 15 wks (Fig. 3).

Distance and rate of pathogen spread in soils with conventional or organic fertility amendments under tillage or surface mulch

The distance of pathogen spread down the centre row of plants in each flat was calculated. Spread down the centre row was significantly affected by time, tillage and amendment ($P=0.0233$). Spread over time was greater in soils that were previously surface-mulched than tilled ($P=0.0025$; Fig. 4). Distance of pathogen spread was also affected by soil fertility amendments ($P=0.0027$; Fig. 4). The final distance of spread down the centre row of plants was significantly higher in soils amended with cotton gin trash than other fertility amendments (Fig. 4).

The exponential model of spread provided the best fit for the rate of disease spread in soils tilled or previously surface-mulched, as well as in soils amended with synthetic fertilizer or poultry manure (Table 2). The linear model provided the best fit for the rate of spread in soil amended with cotton gin trash or green manure (Table 2). The average rate of disease spread was less in previously tilled than surface-mulched soils (2.0 cm week^{-1} versus 2.96 cm week^{-1}). The average rate of disease spread was significantly higher in soils amended with cotton gin trash (3.75 cm week^{-1}), then rye-vetch green manure (1.87 cm week^{-1}), synthetic fertilizer (2.13 cm week^{-1}) or poultry manure (2.4 cm week^{-1}; Table 2).

	Five-week										Ten-week										Fifteen-week									
Tillage	0	0	0	0	0	0	0	0	0	0	4	2	2	1	0	0	0	0	0	0	9	9	8	4	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	5	5	3	1	0	0	0	0	0	0	9	10	6	4	2	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	6	6	3	3	1	0	0	0	0	0	10	10	8	5	3	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	14	8	5	3	1	0	0	0	0	0	12	10	8	6	4	0	0	0	0	0
	16	0	0	0	0	0	0	0	0	0	16	16	10	5	4	0	0	0	0	0	16	15	12	9	7	2	1	0	0	0
	1	0	0	0	0	0	0	0	0	0	14	10	8	3	2	0	0	0	0	0	13	12	8	7	3	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	8	7	7	3	2	0	0	0	0	0	12	11	8	5	3	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	6	5	4	2	1	0	0	0	0	0	12	10	7	4	2	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	6	5	3	0	0	0	0	0	0	0	12	10	5	3	2	0	0	0	0	0
Straw mulch	0	0	0	0	0	0	0	0	0	0	13	11	10	7	6	4	4	1	1	0	16	16	16	13	10	5	5	4	3	1
	0	0	0	0	0	0	0	0	0	0	14	13	12	8	6	5	4	1	1	0	16	16	16	13	11	6	5	4	3	1
	0	0	0	0	0	0	0	0	0	0	14	14	12	8	6	5	4	1	1	0	16	16	16	14	11	6	5	4	3	1
	1	0	0	0	0	0	0	0	0	0	14	14	12	9	6	5	4	1	1	1	16	16	16	15	12	8	5	5	3	1
	16	0	0	0	0	0	0	0	0	0	16	16	15	13	7	5	5	5	2	1	16	16	16	16	11	11	6	5	5	3
	2	0	0	0	0	0	0	0	0	0	16	15	15	11	10	5	5	2	2	1	16	16	16	15	11	8	5	5	3	1
	0	0	0	0	0	0	0	0	0	0	16	15	13	8	7	5	5	2	1	1	16	16	16	15	11	8	5	4	3	1
	0	0	0	0	0	0	0	0	0	0	16	15	11	7	7	5	5	2	1	0	16	16	16	15	9	7	5	4	3	1
	0	0	0	0	0	0	0	0	0	0	12	12	9	9	7	5	5	2	2	0	16	16	16	13	9	6	5	4	3	1

Fig. 2 Spatial pattern map of disease after 5, 10, and 15 weeks caused by *Phytophthora capsici* in bell pepper in soil previously tilled or surface-mulched with straw. *Numbers* indicate the frequency of infected plants in that location from 16 flats

	Five-week									
Synthetic fertilizer	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
Cotton gin trash	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0	0	0
	1	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
Poultry manure	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	1	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0	0	0
	1	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
Green manure	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0

	Ten-week									
Synthetic fertilizer	3	3	3	2	0	0	0	0	0	0
	4	4	3	3	0	0	0	0	0	0
	4	5	3	3	1	1	0	0	0	0
	4	5	3	3	1	1	0	0	0	0
	8	8	8	6	3	2	0	0	0	0
	6	6	6	4	2	2	0	0	0	0
	6	6	4	4	2	2	0	0	0	0
	6	6	3	2	1	2	0	0	0	0
	5	3	2	3	0	0	0	0	0	0
Cotton gin trash	6	5	5	4	4	4	4	1	1	0
	6	6	6	4	4	4	4	1	1	0
	6	6	6	5	4	4	4	1	1	0
	8	8	6	5	4	4	4	1	1	1
	8	8	8	5	5	4	4	4	2	1
	8	8	8	5	4	4	4	2	2	1
	8	8	7	5	4	4	4	2	1	1
	6	6	6	5	4	4	4	2	1	0
	6	6	6	4	4	4	4	2	2	0
Poultry manure	4	4	4	2	2	0	0	0	0	0
	4	4	4	2	2	1	0	0	0	0
	5	5	5	3	2	1	0	0	0	0
	8	5	5	3	2	1	0	0	0	0
	8	5	5	3	3	1	1	1	1	0
	8	5	5	3	3	1	1	1	1	0
	5	5	5	2	3	1	1	0	0	0
	5	5	4	2	3	1	1	0	0	0
	5	5	4	2	2	1	1	0	0	0
Green manure	4	1	0	0	0	0	0	0	0	0
	5	4	2	0	0	0	0	0	0	0
	5	4	2	0	0	0	0	0	0	0
	8	4	3	1	0	0	0	0	0	0
	8	8	4	4	0	0	0	0	0	0
	8	4	4	3	0	0	0	0	0	0
	5	3	4	0	0	0	0	0	0	0
	5	3	2	0	0	0	0	0	0	0
	3	3	0	0	0	0	0	0	0	0

	Fifteen-week									
Synthetic fertilizer	8	8	8	6	2	0	0	0	0	0
	8	8	6	5	4	2	0	0	0	0
	8	8	6	5	4	2	0	0	0	0
	8	8	6	6	5	2	0	0	0	0
	8	8	8	7	5	3	2	0	0	0
	8	8	6	7	3	2	2	0	0	0
	8	8	6	6	3	2	2	0	0	0
	8	8	6	6	3	2	2	0	0	0
	8	8	5	5	3	2	0	0	0	0
Cotton gin trash	8	8	8	6	6	4	4	4	3	1
	8	8	8	6	6	5	4	4	3	1
	8	8	8	6	6	5	4	4	3	1
	8	8	8	7	6	5	4	4	3	1
	8	8	8	8	8	7	5	4	5	3
	8	8	8	7	6	5	4	4	3	1
	8	8	8	7	6	5	4	4	3	1
	8	8	8	7	6	5	4	4	3	1
	8	8	8	6	6	5	4	4	3	1
Poultry manure	4	4	4	4	4	1	1	0	0	0
	4	5	5	4	4	1	1	0	0	0
	5	5	5	5	4	1	1	0	0	0
	7	5	5	5	4	2	1	1	0	0
	8	8	7	5	5	3	1	1	1	0
	7	7	5	5	4	2	1	1	0	0
	6	6	5	5	4	2	1	0	0	0
	6	6	5	4	4	2	1	0	0	0
	6	5	4	4	4	1	1	0	0	0
Green manure	5	5	4	1	0	0	0	0	0	0
	5	5	4	1	1	0	0	0	0	0
	5	5	5	3	2	0	0	0	0	0
	5	5	5	4	4	1	0	0	0	0
	8	7	5	5	2	3	1	0	0	0
	6	5	5	4	2	1	0	0	0	0
	6	5	5	3	1	1	0	0	0	0
	6	5	4	3	0	0	0	0	0	0
	6	5	4	1	0	0	0	0	0	0

Fig. 3 Spatial pattern map of disease after 5, 10, and 15 weeks caused by *Phytophthora capsici* in bell pepper in soil amended with synthetic fertilizer or cotton gin trash, poultry manure, or rye-vetch green manure. *Numbers* indicate the frequency of infected plants in that location from 8 flats

Soil physical parameters

Soil physical factors were affected by tillage and amendment. Soil porosity and water content were higher and bulk density was lower in soils previously surface-mulched than tilled (Table 3). Soil bulk density was significantly lower in soils amended with cotton gin trash than in soils amended with synthetic fertilizer, poultry manure or rye-vetch green manure in 2 of 3 years (Table 3). In contrast, soil porosity and soil water content were significantly higher in soils amended with cotton gin trash than in soils with the other fertility amendments in two of 3 years (Table 3).

Soil moisture (r=0.614, 0.672, and 0.607; P<0.05) and soil porosity (r=0.511, 0.393, and 0.354; P<0.05, respectively) were correlated with the final incidence of Phytophthora blight in each year, whereas soil bulk density was negatively correlated (r=−0.587, −0.412, and −0.353; P<0.05) with the incidence of disease (Table 4).

Soil chemical parameters

Levels of Ca, Mg, and CEC were significantly higher in previously surface-mulched than tilled soils. None of the other chemical factors were affected by tillage or surface mulch (data not shown).

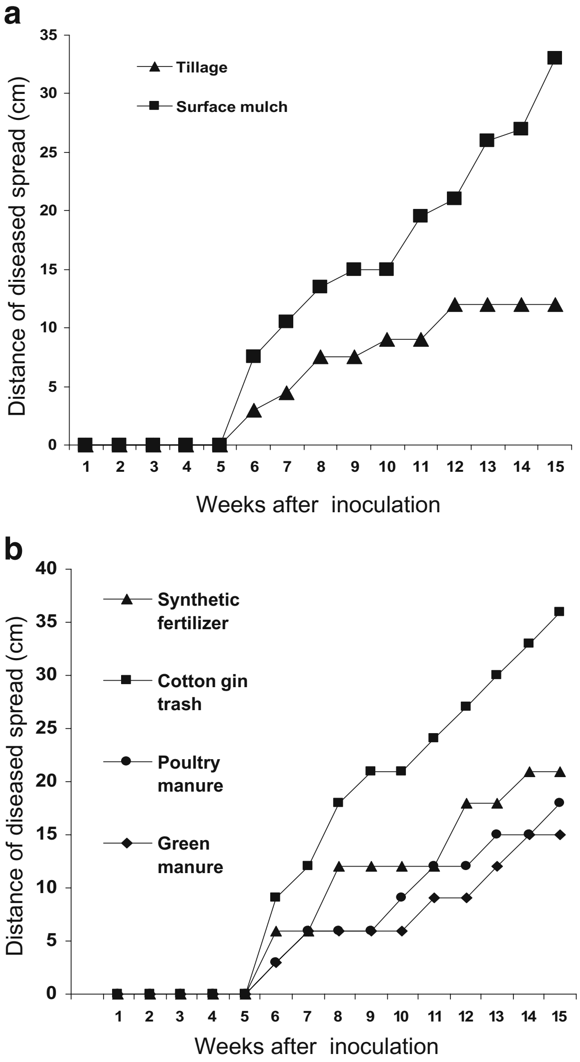

Fig. 4 Distance of spread (cm) of *Phytophthora capsici* down the centre row of plants in a greenhouse flat assay in soils **a** previously tilled or surface-mulched with straw; or **b** amended with synthetic fertilizer or cotton gin trash, poultry manure, rye-vetch green manure

Soil pH was significantly higher in soils with organic amendments than synthetic fertilizer (data not shown). Phosphorous, Zn, and Mn levels were higher in soils amended with poultry manure than the other amendments. Extractable acidity, sum of cations, CEC, and K, Ca, Mg and humic matter levels were all significantly higher in soils amended with cotton gin trash than synthetic fertilizer, poultry manure, or rye-vetch green manure. Cu levels were lower in soils amended with cotton gin trash (P=0.032) than those with synthetic fertilizer, poultry manure or the rye-vetch green manure. Soil amendments did not influence the Na levels.

Soil microbial respiration, MBC, MBN, net mineralizable N, and extractable C were higher in soils surface-mulched than tilled (Table 5). Soil microbial respiration, MBC, MBN, extractable N, net mineralizable N and extractable C were also significantly higher in soils amended with cotton gin trash than the other soil amendments. Final disease incidence was positively correlated with net mineralized nitrogen (r=0.32, 0.67, 0.54; $P<0.05$) in each year (Table 4). None of the other soil chemical factors were positively correlated with final disease incidence (Table 4).

Soil biological parameters

Population densities of total soil bacteria, fungi, *Trichoderma*, enteric bacteria and *Pseudomonas* spp. were not significantly different in soils with previous tillage or surface mulch, or in the soils with different fertility amendments (data not shown). Although there were significantly higher levels of thermophilic organisms in soils amended with cotton gin trash each year, there was no correlation between the population levels of thermophiles or the other soil microbes and final disease incidence (data not shown).

Discussion

We examined the effect of previous tillage and soil fertility amendments on the conduciveness of soils to Phytophthora blight. We addressed three questions. First, is pathogen spread through soils more rapid in soils that have been disturbed more frequently via tillage than soils that have been surface mulched? Secondly, are soils that contain organic amendments more suppressive to dispersal and disease than soils amended with synthetic fertilizer? Thirdly, soil physical, chemical and biological factors were also assessed to determine their relationship to development of disease.

Our data demonstrated that disease incidence in soils in pot and flat assays conducted in the greenhouse was affected by previous tillage and surface-mulch applications. Disease was not greater in soils that were tilled more frequently. In contrast, disease incidence and spread was more rapid in soils from the field that had multiple applications of

Table 2 Best model fit, slope, and average rate of spread of *P. capsici* down the centre row of plants after 15 weeks in greenhouse assays of field soils previously tilled or surface-mulched, or amended with soil fertility amendments

	Model [a]	Intercept	Slope	R^2	Root MSE	Average rate (cm week^{-1})	Distance of pathogen spread [b] (cm)
Main plot tillage							
Tillage	Exponential	−0.449	0.036	0.372	0.177	2.0	30
Surface mulch	Exponential	−0.644	0.050	0.872	0.073	2.96	44.5
Subplot – amendment							
Synthetic fertilizer	Exponential	−0.350	0.025	0.261	0.160	2.13	32
Cotton gin trash	Linear	0.729	0.023	0.547	0.081	3.75	56
Poultry manure	Exponential	−1.278	0.096	0.840	0.159	2.40	36
Green manure	Linear	0.351	0.046	0.744	0.102	1.87	28

[a] Model fitting done using EPIMODEL.

[b] LSD=1.127 for the main plot means and 1.159 for the subplot means. Means with the same letter are not significantly different. Alpha= 0.05, error degrees of freedom=18, error mean square=2.39.

surface-mulch over a 6-year period. The rate of disease increase, final disease incidence and dispersal down the centre row of plants in the flats was significantly higher in previously surface-mulched than tilled soils in the greenhouse flat assay. Similar results on final disease incidence were also observed in the pot assay. In soils where surface mulch was previously incorporated in the field soil, soil amendments such as poultry manure, synthetic fertilizer or a rye-vetch green manure were not suppressive to disease. Surface mulch was removed from soil samples before they were brought to the greenhouse for assay. However, the previously incorporated mulch significantly affected disease progress in the greenhouse assays. Surface mulch was incorporated into the field plots for six previous seasons. Field measurements of soil physical factors including soil porosity and soil water content were higher in previously surface-mulched than tilled soils. Zoospores of *Phytophthora* species move in water-filled pores, and this may in part, explain the conduciveness of these soils to disease in our greenhouse assays (Duniway 1983).

In our previous field research, stubble left on the surface from a wheat cover crop was suppressive to pathogen spread (Ristaino et al. 1997). In studies conducted in 1995, we used a rye-vetch no-till cover crop in the study of the spread of Phytophthora blight

Table 3 Soil physical factors as affected by soil tillage and fertility amendments

	Bulk density (g cm^{-3})			Soil porosity (%)			Soil water content (g water g^{-1} dry soil)		
Mainplot – Tillage	2001	2002	2003	2001	2002	2003	2001	2002	2003
Tillage	1.2	1.3	1.4	54.9	51.6	45.7	0.10	0.017	0.09
Surface mulch	1.1	1.2	1.3	58.1	54.8	50.7	0.13	0.002	0.12
Subplot – amendment									
Synthetic fertilizer	1.2	1.26	1.37	54.9	52.5	48.2	0.11	0.014	0.08
Cotton gin trash	1.0	1.11	1.35	62.4	58.1	49.0	0.13	0.026	0.11
Poultry manure	1.2	1.29	1.36	54.5	51.3	48.5	0.11	0.018	0.11
Green manure	1.2	1.31	1.39	53.8	50.8	47.4	0.11	0.015	0.11
P>F									
Source									
Tillage	0.0338	0.1486	0.0237	0.0338	0.0001	0.0003	0.0275	0.1080	0.0033
Amendment	0.0018	0.0117	0.0799	0.0018	0.0001	0.7958	0.8219	0.0006	0.0834
Till x amendment	0.8652	0.7019	0.6002	0.8652	0.8213	0.593	0.9967	0.7603	0.2755

2002 was a dry year and samples were taken prior to irrigation

Table 4 Correlation coefficients between soil physical, chemical, and biological parameters and the final incidence of Phytophthora blight

Soil property	Correlation coefficients (*r*)		
	2001	2002	2003
Bulk density (g ml^{-1})	−0.587*	−0.412*	−0.353*
Porosity (%)	0.511*	0.393*	0.354*
Soil water content	0.614*	0.672*	0.607*
P (mg dm^{-3})	−0.086	0.018	−0.167
K (meq 100 cm^{-3})	0.393*	0.015	0.404*
Ca (meq 100 cm^{-3})	−0.081	0.170	0.167
Mg (meq 100 cm^{-3})	0.223	0.267	0.359*
Na (meq 100 cm^{-3})	ND	−0.102	−0.051
PH	−0.064	−0.205	−0.187
EA (meq 100 cm^{-3})	−0.16	0.337*	0.158
CEC (meq 100 cm^{-3})	0.119	0.194	0.252
BS (%)	0.27	−0.220	−0.012
Humic matter (g 100 cm^{-3})	−0.435*	0.134	−0.247
Mn (mg dm^{-3})	0.395*	0.439*	0.252
Zn (mg dm^{-3})	−0.058	0.106	−0.024
Cu (mg dm^{-3})	−0.241	−0.137	−0.206
Soil respiration (CO_2 mg kg^{-1})	−0.093	−0.244	−0.13
Microbial biomass C (mg kg^{-1})	0.130	−0.189	0.011
Microbial biomass N (mg kg^{-1})	0.011	−0.291	−0.143
Extractable N (mg kg^{-1})	0.121	0.001	−0.124
Net N mineralized (mg kg^{-1})	0.315*	0.676*	0.542*
Extractable C (mg kg^{-1})	0.096	−0.194	0.038

ND Not determined

*Indicates significantly different at $P=0.05$.

in a field experiment, and obtained significant disease suppression and yield improvement (Ristaino and Gumpertz 2000). However, the stubble was not repeatedly tilled into the soil as mulch over six seasons, as was done in the field experiments described here, but was treated with a herbicide. Others have demonstrated that surface mulch can reduce splash dispersal of *P. cactorum* in strawberry (Madden and Ellis 1990). Further experiments would be needed to determine the effect of tillage versus surface-applied straw mulch on the spread of disease in field plots.

The second question addressed in this research was whether soils that contain organic amendments are more suppressive to dispersal and disease than soils amended with synthetic fertilizer. The type of organic soil amendment had a large impact on disease. The rate of disease increase, final incidence of disease and dispersal down the centre row of plants

Table 5 Soil respiration, and chemical analysis in field plots that amended with either synthetic or organic fertility amendments and tilled or straw-mulched in 2001, 2002 and 2003

	Soil respiration (CO_2 mg kg^{-1})			MBC (mg kg^{-1})			MBN (mg kg^{-1})			Extractable N (mg kg^{-1})			Net N Mineralized (mg kg^{-1})			Extractable C (mg kg^{-1})		
Year	2001	2002	2003	2001	2002	2003	2001	2002	2003	2001	2002	2003	2001	2002	2003	2001	2002	2003
Tillage	29.7	24.3	14.9	168.4	156.5	190	19.12	15.1	22.3	2.35	1.9	2.6	7.53	8.6	3.4	44.02	43.8	39.9
Surface mulch	38.37	43.1	20.1	235.48	247.4	253.6	21.55	25.6	34.3	3.89	4.3	4.8	13.54	12.5	7.3	55.63	55.8	47.1
Synthetic fertilizer	30.81	21.7	13.85	172	141.5	160.45	18.31	15.95	19.65	1.99	1.55	2.65	9.91	6.7	5.15	46.98	34.6	36.1
Cotton gin trash	37.95	50.5	22.1	195.9	317.15	297.6	19.03	29.05	36.35	3.57	6.4	5.25	10.26	20.15	6.9	47.6	74.9	54.1
Poultry manure	35.82	36.45	19.2	225.03	195.35	247.05	22.52	22.25	31.45	3.83	3.15	3.7	11.29	8.35	3.95	53.81	53.4	48.95
Green manure	32.41	26.25	14.8	214.92	153.8	182.2	21.48	14.0	25.7	3.09	1.35	3.1	10.68	6.9	5.25	50.91	36.35	38.45
P>F																		
Tillage	0.9289	0.0001*	0.0005*	0.0240	0.0001*	0.0001*	0.4608	0.0001*	0.0001*	0.3734	0.0001*	0.0001*	0.1071	0.0001*	0.0001*	0.2023	0.0003*	0.0010*
Amendment	0.0001*	<.0001*	0.0004*	0.0001*	<.0001*	<.0001*	0.0001*	<.0001*	<.0001*	0.0001*	<.0001*	<.0001*	0.0001*	<.0001*	<.0001*	0.001*	<.0001*	<.0001*
Till*amendment	0.0111	.0497*	0.204	0.0001	0.4387	0.6761	0.3723	0.5880	0.2837	0.8140	0.1879	0.2907	0.2493	0.3489	0.2563	0.4438	0.1731	0.1536

MBC Microbial biomasse carbon, *MBN* microbial biomass nitrogen.

*Indicates significantly different at $P=0.05$.

in the flats was significantly higher in soils amended with cotton gin trash than poultry manure or a rye-vetch green manure. In contrast, soils amended with rye-vetch green manure were suppressive to disease when compared to soils amended with synthetic fertilizer in the pot assays. However, poultry manure amendment was not suppressive to disease when compared to synthetic fertilizer in any year. These data were surprising since other workers have documented that composted animal or municipal wastes were suppressive to Phytophthora diseases (Aryantha et al. 2000; Fitchner et al. 2004; Hoitink and Boehm 1999; Widmer et al. 1998).

Most studies have focused on the effect of physical factors, particularly soil water on Phytophthora blight (Bowers and Mitchell 1990; Duniway 1983; Gumpertz and Ristaino 1997; Larkin et al. 1995). Soil amended with cotton gin trash retained higher levels of soil water at saturation and had higher soil water content than soils with the other three amendments and disease spread much more rapidly in these soils than soils with synthetic fertilizer, poultry manure, or a rye-vetch green manure. Our data also indicated that soils amended with cotton gin trash had lower bulk densities and higher levels of soil porosity and humic matter than soils with the other fertility amendments. The final incidence of Phytophthora blight was positively correlated with the soil water content and soil porosity (Table 4). Incidence of Phytophthora blight was negatively correlated with soil bulk density. Changes in these soil physical factors by amendment with the cotton gin trash were related to the increased disease levels observed in these soils. In our experiments, measurements of soil physical and chemical factors were done with cores removed from the field. However, disease assays were done in the greenhouse in soil that was composited, so bulk density measurements were probably lower across all treatments in the greenhouse.

The third question addressed was whether changes in soil physical, chemical, and biological parameters were suppressive to pathogen dispersal and associated disease. Some researchers have suggested that a higher level of EA, sum of cation, CEC, BS, P, K, Mg, Mn, Zn, and humic matter will aid plant growth and increase resistance of plants to disease (Schoeneweiss 1975). However, our results indicate that disease spread to the greatest extent in soils amended with cotton gin trash even though these soils had high levels of K, Ca, Mg, EA, and CEC. Other factors including soil physical factors such as soil water content, probably played a more important role than chemical factors in disease development in this pathosystem.

We found that although the incorporation of the fertility amendments was based on a standardized calculation of nitrogen (approximately 112 kg ha^{-1}) in each treatment, with 6 years of soil fertility amendments, soil extractable nitrogen and net nitrogen mineralization were highest in soil amended with cotton gin trash, followed by soils amended with poultry manure, synthetic fertilizer and rye-vetch green manure (Tu et al. 2005). In addition, greatest microbial biomass N and C were found in soils amended with cotton gin trash. Nitrogen can be a limiting factor for plant resistance or susceptibility to plant pathogens (Schoeneweiss 1975). Net mineralizable N levels were positively correlated with disease in our study. Higher mineralizable N levels may have led to enhanced root growth that could have increased host susceptibility to disease in soils with cotton gin trash amendments. However, we did not quantify root growth to confirm this observation. Alternatively, higher mineralizable N levels may have had a direct impact on pathogen populations in soils. However, further experimentation would be needed to determine the actual mechanism by which N levels enhanced disease.

Phytophthora blight on bell pepper is a polycyclic disease and multiple cycles of inoculum production and dispersal occur during epidemic development (Ristaino and Gumpertz 2000). Disease onset occurred earlier in soil amended with cotton gin trash and this could have been a factor for the rapid production of secondary inoculum during subsequent soil saturation periods. The pathogen spread to the other end of the flat in soil amended with cotton gin trash much faster than in soils with synthetic fertilizer, poultry manure, or the rye-vetch green manure.

In the pot assay, there was significantly less disease in soils amended with an incorporated rye-vetch green manure. We incubated the pathogen in soils for 2 weeks before planting pepper, which allowed the pathogen more time to interact with soil microbial communities and chemical factors, than in the flat assays that were planted and inoculated at the same time. This may have affected the level of suppressiveness of the soils to disease. We previously obtained suppression of disease spread in the field with stubble from a rye-vetch cover crop (Ristaino and Gumpertz 2000).

Soil physical factors can influence water flow and pathogen dispersal. The soil type we used in our experiment was an Orangeburg sandy loam soil from the coastal plain region of North Carolina. Zoospores released from sporangia can move rapidly in these soils to infect roots and crowns of plants. Zoospore movement in soils can be affected by soil texture and porosity (Ristaino 1991; Ristaino et al. 1993; Sujkowski et al. 2000). Disease will progress more rapidly if inoculum movement occurs through the soil to roots than via root growth to inoculum (Ristaino et al. 1994). Higher levels of soil porosity in soils amended with cotton gin trash or rye-vetch green manure and the subsequent degree of water-filled pores in soil may have affected zoospore movement in the flats.

We characterized the soil microbial biomass and microbial activity in the soils (Tu et al. 2005). Soil respiration and microbial biomass C and N were significantly different among soils with different amendments, and the greatest microbial biomass C and N were found in the plots amended with cotton gin trash, followed by poultry manure, synthetic fertilizer and rye-vetch green manure. Soils amended with cotton gin trash also had higher levels of thermophillic organisms including Actinomycete species, which are commonly used as biological control agents. However, we found that neither microbial activity nor population levels of thermophiles were correlated with disease incidence.

Changes in soil fertility amendments and tillage practices can have significant impacts on the temporal and spatial components of epidemic development of *P. capsici*. Some soil amendments such as cotton gin trash or incorporation of surface-applied straw mulches can significantly enhance the development of Phytophthora blight due to increased porosity, water content, humic matter and extractable N levels in soils, while rye-vetch green manures may be suppressive to disease.

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