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Soil receptivity and host–pathogen dynamics in soils naturally infested with *Fusarium oxysporum* f. sp. *cubense*, the cause of Panama disease in bananas

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Abstract. Disease severity associated with the pathogen *Fusarium oxysporum* is generally thought to be proportional to the population of fungal propagules in the soil. However, results from studies using naturally infested soil are contradictory, implicating host predisposition to disease. In this study, soil was amended with chicken manure to investigate the interdependence between the activity and invasiveness of the pathogen, and the incidence of Panama disease in susceptible banana plantlets. Two soil types naturally infested with either race 1 or race 4 of the pathogen, and cultivars Lady finger and Grande Naine, were used. Pathogen activity was measured by burying root tip segments for 5 days, then calculating the frequency of isolation of *Fusarium* from the segments. Pathogen invasion was measured by transplanting banana plantlets into trays of amended and unamended soil for 4 weeks, then calculating the frequency of recovery of *Fusarium* from each pseudostem. Amending both soil types with chicken manure enhanced both pathogen invasion and disease incidence. However, pathogen activity was not correlated with either parameter. We postulate that the addition of chicken manure is predisposing banana plantlets to Panama disease, by reducing the efficacy of the host wound response.

Additional keywords: bioassay, predisposition to disease.

Introduction

Researchers generally accept that the soil-borne fungal pathogen *Fusarium oxysporum* Schlecht. preferentially invades root tips (Bloomberg 1979*a*). Disease severity is also assumed to be directly proportional to the pathogen population present. If this is the case, then each pathogen propagule must be equally capable of infection, and invasion after infection must be discrete. Dose–response relationships have been achieved with the addition of inoculum to sterilised soil, or when soil-less container media have been used (Mace and Veech 1971; Alon *et al.* 1974; Pera and Calvert 1989; Ben-Yephet *et al*. 1994). However, in the absence of disinfection treatments, variations in soil type can substantially alter the disease severity associated with a given pathogen dose (Smith and Snyder 1971; Oyarzun *et al.* 1994).

The differential effect of soil type on the severity of disease associated with a given inoculum is described as soil receptivity. Soil receptivity is determined by comparing the severity of disease in susceptible plants when inoculum is added to sterilised soil, with disease severity in the same unsterilised soil type (Greenberger *et al.* 1987; Oyarzun *et al.* 1994). Conducive soils are those exhibiting an increase in disease severity, and suppressive soils exhibit a comparative decrease in severity. Studies on composts and soils suppressive to Fusarium diseases have implicated the activity of antagonistic microbes in reducing the survival of the pathogen (Scher and Baker 1980; Greenberger *et al.* 1987; Pera and Calvert 1989). These results support the hypothesis that disease severity is directly proportional to the pathogen population present.

Typically, dose–response studies involve the addition of artificially grown inocula into the test soil, using dilution plate counts at the end of the experiment to quantify pathogen survival (Elmer and Lacy 1987; Brake *et al.* 1995). However, the quantification of viable propagules is only a measure of pathogen survival. Pathogen survival may not

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necessarily be related to either pathogen activity in the soil, or to the extent of pathogenic invasion of the host. Field observations indicate that it is possible to have high specific pathogen populations detectable in naturally infested soil, in the absence of a correspondingly high disease incidence in susceptible hosts (Abawi and Lorbeer 1971). Moreover, resistance to Fusarium wilt in susceptible plants grown in naturally infested field soils has been improved when the nutrition of the host plants has been altered (Stoddard 1947). These results suggest that the receptivity of a soil to a specific disease may also depend on the ability of the host to resist invasion, after infection. Further support for this hypothesis is the evidence that the field resistance of bananas to *Fusarium oxysporum* f. sp. *cubense* can be broken down when plants experience adverse environmental conditions (Pegg *et al.* 1996).

In the dose-response studies cited above, the actual number of infection sites and the rate of tissue invasion after infection were not measured. However, in studies where these parameters were measured, neither inoculum density nor infection was correlated with disease severity (Ashworth *et al*. 1979; Bloomberg 1979*b*). In these studies, disease severity was most highly correlated with the rate of invasion of host tissue after infection. Field-resistant cultivars tolerated invasion to a greater extent than did susceptible cultivars. Therefore the physiological proneness of the host must be considered when investigating dose–response relationships in naturally infested soil. In this study, our aim was to develop a glasshouse bioassay to distinguish between the activity of *Fusarium oxysporum* f. sp. *cubense* (*Foc*) in naturally infested soil, and the extent of invasion in the stem tissue of susceptible banana plantlets.

Panama disease has devastated banana plantations in many countries throughout the world (Stover 1986). The selection of field-resistant cultivars has been the only successful strategy for managing this disease (Pegg *et al.* 1996). Comparisons of the invasion process in intact roots washed free of soil indicate that both resistant and susceptible cultivars are infected (Beckman *et al.* 1962). Observations from Queensland growers indicate that applying chicken manure to susceptible varieties enhances disease severity. We compared the effect of chicken manure on disease severity, as a function of the activity of the pathogen in the soil and of the pathogenic invasion of the pseudostems of tissue-cultured banana plantlets. Field soils known to be infested with either race 1 or race 4 (Pegg *et al*. 1996) were collected from banana plantations exhibiting Panama disease symptoms in south-eastern Queensland.

Materials and methods

Soil preparation

Field soil was collected to a depth of up to 20 cm from under the canopy of mature banana plants showing wilting symptoms characteristic of Panama disease. A soil type previously tested as being naturally infested with race 4 was collected from under cv. Cavendish plants at a breeding trial site at Wamuran (27°3′S, 152°22′E) in south-eastern Queensland. A soil type previously tested as being naturally infested with race 1 was collected from under cv. Lady finger plants from 2 properties at Currumbin (28°15′S, 153°26′E), also in south-eastern Queensland. The soils were stored in the field state in 55-L plastic bins under ambient temperature conditions. Before use the soils were coarsely sieved (1-cm^2 grid) to remove coarse plant debris and to crumble larger soil aggregates.

Chicken manure was collected at 1-m depth from a deep litter poultry shed (litter had accumulated over a 6-month period). Treatments of both race 1 and race 4 soil types were amended at a ratio of 9:1 (v:v) field soil and aged chicken manure. Soil analyses of NO_3-N and NH_4-N were done at the end of each experiment on soil samples extracted with 2 M KCl (Catchpole and Weier 1980), and total N was estimated by Kjeldahl digestion of ground material (<2 mm, Dalal *et al.* 1984). Amended and unamended sieved soil was placed on geotextile over a 2-cm-deep bed of washed sand, in plastic trays 45 cm wide by 31 cm long by 25 cm deep (44 by 70 by 26 cm for race 1 experiments). Capillary watering was achieved by maintaining a permanent reservoir of water within the sand, refilling the 2 inverted wine bottles per tray as required. Sterile gravel was placed over the surface to improve capillary rise to the soil surface. Race 4 soil trays were placed in 2 waterbaths maintained at 27°C for the duration of each experiment. Race 1 soil trays were placed in a glasshouse with temperatures maintained between 27 and 30°C. All soil treatments were equilibrated under the capillary watering regime for 14 days before starting each bioassay. Weeds germinating during this time were removed by hand.

Foc *soil activity bioassays*

Two 2-cm root tip lengths were cut from the first 4 cm of actively growing roots of cv. Williams banana plantlets grown in soil-less container media. Sterilised steel quilting pins were inserted into each root tip for ease of location after burial in the soil treatments. In each tray, 10 excised root tips were buried to a depth of 5 cm placed in a grid pattern mid-way between the banana transplants. Experiments using race 4 (Wamuran) soil were conducted during February 1995 and experiments using race 1 (Currumbin) soil during March 1996.

Burial of the excised root tips was coincident with the transplanting of banana plantlets for the *Foc* invasion bioassay. Three trays of soil amended with chicken manure and 3 unamended trays were placed in an interspersed pattern in the 2 waterbaths. After 5 days of burial the excised root tips were recovered from the soil, washed and surface-sterilised in 3% sodium hypochlorite, and cut into 10 pieces prior to plating to minimise the saprophytic overgrowth of putative *Foc* colonies. The 10 segments of each original root tip were plated onto $\frac{1}{6}$ strength potato dextrose agar (PDA) amended with 0.5 g/L of streptomycin. Putative *Foc* isolates were identified on the basis of colony morphology and the pigmentation of mycelia. One isolate from each root tip colonised by *Foc* was subcultured onto minimal media and identified using the Vegetative Compatability Grouping technique (VCG, Moore *et al.* 1993). VCG reference mutants 0120, 0124, 0125, and 0129 were tested against *Foc* strains isolated from both the Wamuran and Currumbin soil experiments. In addition, all race 4 isolates colonising the excised root segments in the Wamuran soil type were tested for volatile odour production (Moore *et al*. 1991). The activity of *Foc* was calculated as the proportion of the 10 buried root segments per tray, colonised by the pathogen.

Foc *plantlet invasion bioassays*

Six-week-old tissue-cultured plantlets of the susceptible cultivars Grande Naine (susceptible to race 4) and Lady finger (susceptible to race 1) were provided by staff of the Qld Department of Primary Industries Maroochy Research Station. The plantlets were deflasked

into 10-cm- diameter pots filled with soil-less container media, and grown on for a further 4 weeks prior to transplanting. Ten plantlets were transplanted in a grid pattern into each of the 3 chicken manure amended and the 3 unamended race 4 soil trays. Using the same methods, 10 plantlets were transplanted into the larger race 1 soil trays. After a further 4 weeks, all plantlets were recovered from the trays, and roots were washed free of soil. All pseudostems were surface-sterilised in 3% sodium hypochlorite, cut into 10 segments, and plated onto the PDA-streptomycin amended agar. One *Foc* isolate recovered from each invaded pseudostem was identified using the VCG technique (Moore *et al*. 1993). Each *Foc* race 4 isolate was also tested for volatile odour production (Moore *et al*. 1991). The invasiveness of *Foc* was calculated as the frequency of the total of 10 banana plantlets per tray, from which *Foc* was recovered from the pseudostem tissue.

Statistical analysis of the data

In both the Wamuran race 4 and the Currumbin race 1 experiments the effect of chicken manure on both the activity of *Foc* in the soil and the invasion of banana pseudostems by *Foc* was statistically compared using a log-linear model. Data were entered binomially, using the Genmod procedure of the SAS computer package (Version 6.10), specifying the logit link function. An analysis of deviance approximated by the chi-square distribution tested for effects attributable to the position of the trays (× 2 waterbaths for race 4, × 2 benches for race 1), comparisons of the 3 trays used per treatment, and the addition of chicken manure. Changes in the activity of *Foc* in the soil associated with the addition of chicken manure were compared with changes in pseudostem invasion using a proportional odds model. Results were presented as the log of the odds ratio plus and minus the log of the 95% confidence interval estimates, using the unamended soil results as the zero base-line.

Results

Plant growth and disease symptom severity.

During the 2-week equilibration period, weed seeds of *Amaranthus* sp. germinated in both the Wamuran and Currumbin soils. Seeds of *Paspalum* sp. also germinated in the Wamuran race 4 soil trays. The growth rate of weed seedlings in the chicken manure amended soils was more vigorous than that in unamended soils. The growth stimulation reflects the increase in total nitrogen from 0.17 and 0.18 mg/kg in unamended soil to 0.31 and 0.28 mg/kg in the amended Wamuran and Currumbin soils, respectively (Table 1). Several root systems of *Paspalum* and *Amaranthus* growing in the Wamuran soil were washed, surface-sterilised, and plated onto the PDA-streptomycin media to test their suitability as hosts for *Foc*. Both weed species were colonised by volatile odour producing race 4 isolates conforming to the 0120 VCG.

Disease symptoms in the banana plantlets commenced with a localised bleaching on <50% of the leaves, progressing to total leaf wilting of >50% of the leaves. After 4 weeks growth in both the Wamuran and Currumbin soils, the addition of chicken manure markedly increased the severity of foliar symptoms (Table 1). In the Wamuran soil in the absence of chicken manure, 5 out of the total of 30 plantlets had disease symptoms, whereas all of the plantlets in the amended treatment had symptoms. Similarly, in the Currumbin soil, 9 out of the total of 30 plantlets in the unamended control showed symptoms, whilst all plantlets in the amended treatment had symptoms.

Activity of Foc *in soils amended with chicken manure*

The frequency of colonisation of the excised root tips by *Foc* (activity) was very high in control and treated trays for both soil types (Table 1). The results of the analysis of deviance indicate that positional effects relating to the placement of the trays in the waterbath (Wamuran soil) or placement on the glasshouse benches (Currumbin soil) did not significantly alter *Foc* activity ($\chi^2 < 0.01$ with $P = 0.95$, and $\chi^2 < 0.01$ with $P = 0.98$, respectively). Similarly, there was no

Table 1. Severity of foliar disease symptoms, pathogen activity in the soil, and invasion of the pseudostems of 4-week-old transplanted banana plantlets grown in soils naturally infested with *Fusarium oxysporum cubense* with and without the addition of aged chicken manure

Wamuran soil was infested with race 4, and the cultivar Grande Naine was the susceptible host. Currumbin soil was infested with race 1, and the cultivar Lady finger was the host. Results for the analysis of deviance comparing amended treatments with the unamended control are given

	Total N in soil (%)	NH_4-N and NO_3- N (mg/kg)	Plantlets with disease symptoms (%)[A]	*Foc* activity (% recovery)[B]	*Foc* invasion (% recovery)[C]
			Wamuran		
Unamended	0.17	3.6, 116.7	16.7	86.7	24.0
With chicken manure	0.31	413.1, 321.6	100	95.3 n.s.	78.7***
			Currumbin		
Unamended	0.18	3.4, 25.6	30.0	89.0	19.7
With chicken manure	0.28	511.2, 281.6	100	94.0 n.s.	61.3***

*** $P < 0.001$; n.s., not significant at $P = 0.05$.
[A]Of 30 plantlets. [B]From 30 root tips. [C]From 30 pseudostens.

evidence of deviation from the expected activity frequencies in the 3 tray replicates used in control and chicken-manure treatments (χ^2 = 2.15 with P = 0.34 for Wamuran, and χ^2 = 0.13 with P = 0.94 for Currumbin). Unexpectedly, the activity of *Foc* in both amended soil types was not significantly different to the activity in the respective unamended soils at the 0.05 level (χ^2 = 2.39 with P = 0.12 for Wamuran, and χ^2 = 2.15 with P = 0.14 for Currumbin).

All of the *Foc* isolates from colonised root tips buried in the Wamuran soil produced volatile odours, and all were compatible with the 0120 VCG, characterised as race 4 strains (Bentley *et al.*1998). Similarly, all of the *Foc* isolates from colonised root tips buried in the Currumbin soil were compatible with the 0125 VCG, characterised as race 1. No saprophytic strains of *Fo* were recovered from either the excised root tips, or the weed roots, or the pseudostems of banana plantlets tested in this study.

Invasion of banana pseudostems by Foc *in soils amended with chicken manure*

All *Foc* isolates recovered from the pseudostems of Grande Naine plantlets grown in the Wamuran soil were volatile odour producers and conformed to the 0120 VCG. All pseudostem isolations of *Foc* from Lady finger plantlets grown in the Currumbin soil conformed to the 0125 VCG. There was no evidence of deviation from the expected frequency of recovery of *Foc* from the pseudostem tissue of banana plantlets (invasion), associated with either the water-baths or benches (χ^2 = 1.19 with P = 0.28 for Wamuran soil, χ^2 = 0.02 with P = 0.88 for Currumbin soil). Likewise, frequency distributions in the 3 tray control and treatment replicates did not significantly differ from those expected (χ^2 = 1.51 with P = 0.47, and χ^2 = 1.71 with P = 0.43, respectively).

The invasion of pseudostems by race 4 and race 1 pathogens was substantially increased in the treatments amended with chicken manure (Table 1). The frequency of recovery from banana pseudostems in unamended Wamuran soil was 24%, increasing to 79% in amended treatments (χ^2 = 152.63 with P < 0.0001). Similarly, the increase in invasion of pseudostem tissue in the Currumbin soil was from 20% to 61% (χ^2 = 98.87 with P < 0.0001).

Our results confirm that the addition of chicken manure to soils naturally infested with *Foc* renders the soil more conducive to Panama disease. However, when expressed as the log of the odds ratio, the increase in *Foc* invasion is disproportionately greater than the increase in *Foc* activity (Fig. 1). Invasion of pseudostems in the amended Wamuran soil was 14 times greater ($e^{2.63}$) than in unamended soil, whereas the colonisation of excised root tips (*Foc* activity) was not significantly different. Similarly, in Currumbin soil the increase in pseudostem invasion was 7 times greater ($e^{1.92}$) that in unamended soil, whereas the activity of *Foc* was no different. This disproportionate increase in the extent of invasion suggests that in the Panama disease pathosystem, disease severity is related to the ability of the host to resist invasion after infection. Disease severity is not proportional to the activity of the pathogen in the soil.

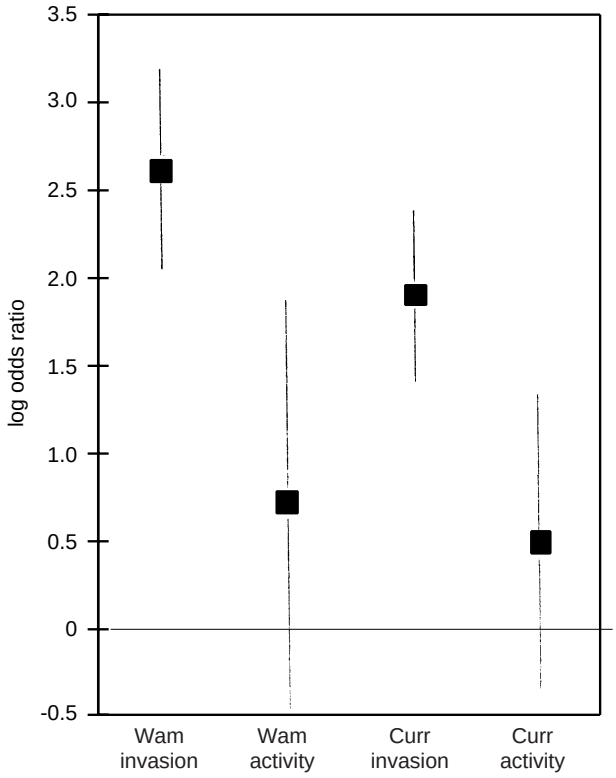

Fig 1. The log of the odds ratio for *Foc* activity in soil amended with chicken manure and the invasion of susceptible banana plantlet pseudostems relative to the unamended soil control (represented as the zero base-line). Grande Naine was the cultivar used in the race 4 soil collected from Wamuran (Wam) and Lady finger the cultivar used in the race 1 soil collected from Currumbin (Curr). Squares indicate the log of the odds ratio, with vertical lines plus and minus the log of the 95% confidence interval estimates. Vertical lines overlapping the base-line are not significantly different from the control.

Discussion

Response of Fusarium oxysporum *f. sp.* cubense *to the addition of chicken manure*

In both the Wamuran and Currumbin soil types there was no evidence of the activity of saprophytic strains of *Fo* to confound the interpretation of host–pathogen interactions. The enhanced growth of weeds within the 2-week equilibration period in the chicken manure amended treatments was expected to increase the activity of *Foc,* given that both the *Amaranthus* and *Paspalum* species were alternative hosts. Moreover the growth of *Foc* is favoured by the addition of nitrate (Hendrix and Toussoun 1964). By using well aged chicken manure, root burning associated with high levels of ammonium was avoided, and the conversion of ammonium

to nitrate was favoured (Huber and Watson 1974). However, neither of these factors contributed to any statistically significant increase in the activity of either race of the fungus in either soil type.

Accordingly, the highly significant increase in disease severity cannot be attributed to the activity (inoculum potential) of the fungus in the soil. Amir and Alabouvette (1993) and Abawi and Lorbeer (1971) also found no correlation between the inoculum potential of pathogenic strains of *Fo* and the conduciveness of different soil types to wilt diseases. Therefore disease severity is determined by the effect of the soil environment on the proneness of the plantlets to invasion, after infection. Comparative studies on the colonisation of cultivars differing in their susceptibility to *Fo* wilt show that resistant species respond more rapidly and effectively to pathogenic invasion (Beckman *et al*. 1962; Baayen and Elgersma 1985). Vascular gelation and the formation of tyloses successfully restricted invasion after infection, to a low level in the resistant varieties. The cultivars used in this study were susceptible to Panama disease. Therefore we postulate that the addition of chicken manure predisposed the banana plantlets to disease, by reducing the efficacy of the host wound response.

Nitrogen form and disease severity

Traditionally the addition of sulfate of ammonia was recommended to increase the maturation rate (time to shooting) of bananas (Simmonds 1959). However, Rishbeth (1957) found that high rates of application enhanced Panama disease. In a more detailed study, varying application rates of urea nitrogen, Butler was unable to repeat Rishbeth's results (Stover 1962). In our study the application of aged chicken manure predominantly enhanced the organic N content of the soil, with lesser increases in both the ammonium and nitrate nitrogen pools (Table 1). However, for both soil types the proportional increase was greatest for the ammonium nitrogen pool.

Depending on the composition and maturity of composts, high levels of ammonium and salts can inhibit plant growth. In our study the use of aged chicken manure (Mahimairaja *et al.* 1994) and the equilibration period of 14 days prior to transplanting the banana plantlets (O'Brien and Barker 1996) should have been sufficient to minimise such problems. Moreover the growth stimulation associated with applications of sulfate of ammonia (Simmonds 1959) suggests that bananas are better adapted for ammonium rather than nitrate utilisation. Ammonium is more rapidly assimilated by plants, and the enhanced rate of amino acid synthesis may deplete circulating soluble carbohydrate concentrations. Ammonium is also known to stimulate root and leaf exudation (Huber and Watson 1974). The depletion of circulating soluble carbohydrate compounds, by inference, must have an impact on the ability of a plant to mobilise a defense reaction, as the energy reserves immediately available have been reduced. Sun and Su (1984) added ammonium sulfate to 8-week-old plantlets in a soil-less medium, and were able to reproduce resistant and susceptible field responses to Panama disease after inoculation with *Foc* races 1 and 4.

More research is required to demonstrate conclusively that the ammonium component of chicken manure amendments is responsible for predisposing banana plantlets to disease. However, our results indicate that chicken manure amendments provide a simple and reproducible method for predisposing banana plantlets grown in naturally infested soil to Panama disease. Studies attempting to identify soil factors associated with variations in soil receptivity to Panama disease have concluded that many factors are involved (Rishbeth 1957; Stover 1962; Stotzky and Torrence Martin 1963). Such interactions have confounded the selection of cultivars with improved disease resistance, due to the difficulty in reproducing appropriate levels of disease severity. Our results indicate that the addition of chicken manure to naturally infested soils may provide a reproducible screening technique to select cultivars with improved resistance to Panama disease.

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